

# **RECOVERY OF RANGELANDS**

**The functioning of soil seed banks in a semi-arid  
African savanna**

**Tessema Zewdu Kelkay**

## **Thesis committee**

### **Thesis supervisor**

Prof. dr. H.H.T. Prins  
Professor of Resource Ecology  
Wageningen University

### **Thesis co-supervisors**

Dr. W.F. de Boer  
Associate Professor at the Resource Ecology Group  
Wageningen University

Dr. R.M.T. Baars  
Team leader development studies  
Van Hall Larenstein University of Applied Sciences  
Wageningen University and Research (WUR)

### **Other members**

Prof. dr. F.J.J.M. Bongers  
Wageningen University

Dr. E.M. Veenendaal  
Wageningen University

Prof. dr. M.G. Rietkerk  
Utrecht University

Prof. dr. S. Deckers  
University of Leuven  
Belgium

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## **The functioning of soil seed banks in a semi-arid African savanna**

**Tessema Zewdu Kelkay**

### **Thesis**

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Tessema Zewdu Kelkay

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**To**

*My late father, Zewdu Kelkay, and my late mother, Anguach Zenebe who  
passed away before seeing my success*



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Rangelands in Africa provide important forage resources for herbivores; particularly perennial grasses provide grazing for domestic and wild herbivores. However, semi-arid African rangelands experience severe vegetation and soil degradation due to heavy grazing, causing negative impacts on the ecosystems, livestock production and livelihoods of the people. Semi-arid African rangelands can be described by a state-and-transition models, often with three stable states, the first one being a state with ample herbaceous cover, perennial grasses and scattered trees, the second one as a state with a poor cover of annual grasses, absence of perennial grasses, and the third state with a high proportion of bare soil and/or often bush encroached. This thesis aims to fill important information gaps concerning soil seed banks that play in the recovery and possible restoration of degraded semi-arid African rangelands with particular emphasis on Ethiopia. This was done through investigating the mechanisms of how heavy grazing affects the soil seeds bank dynamics so as to understand stable states and transition processes of aboveground vegetation. In this thesis, aboveground vegetation and soil seed bank dynamics were studied under heavy and light grazing pressures in a field and experimental conditions. Results show that heavy grazing resulted in the disappearance of perennial grasses, a reduction in herbaceous species diversity and their plant abundance, standing biomass and basal cover, as well as a decrease in the soil nutrient conditions. The soil seed banks was correlated to differences in grazing pressure, with a greater seedling density under light grazing compared with heavy grazing. Immediately after seed dispersal, the seedling density increased over the first first three months until the eight months of soil sampling, and decreased thereafter. Under light grazing, perennial grass species dominated, whereas annual species were abundant at the heavily grazed sites, indicating that perennial grasses, with good fodder value, are replaced by annual species in the soil seed banks due to heavy grazing. With increasing soil depth, the seedling density and its species richness declined. Moreover, the seeds of perennial grasses were less abundant in the soil seed banks under heavy grazing. The similarity in species composition between the soil seed banks and aboveground vegetation was low under heavy grazing. Results also show that annual grasses had a lower germination and mortality, and higher viability, leading to a longevity of 62% over the 120 days burial in the soil, which was high compared to the 28% for perennials. Moreover, most perennial grasses germinate rapidly

after initial seed dispersal at the first rains early in the year, whereas annual grasses show a linear germination pattern over time, indicating that perennial grasses have different survival strategy in semi-arid Africa. As a result, annual species are expected to dominate the soil seed banks, whereas most perennial grass species do not form persistent soil seed banks. The mean mortality from the seedling stage to adult plants in grass species was 65%, and the seed-to-seedling stage was found the most critical transitional stage for grass survival on these rangelands, suggesting that exclusion from grazing and trampling in the early germination stage is important to facilitate the transition from seedling to established plants. Depletion of perennial grass seeds in the soil due to heavy grazing coupled with high seedling mortality leads to a strong decrease in perennial grasses both in the soil seed banks, as well as in the aboveground vegetation. I found that the positive relationship between plant cover and differences in soil seed bank dynamics, i.e., seed density, seed germination rate and longevity, trigger the transition from perennial grasses to annuals and from annual plant cover to bare soil under heavy grazing. I hypothesize that the restoration of perennial grasses from the soil seed banks in heavily grazed areas in semi-arid African rangelands cannot be successful without an extraneous source of perennial grass seeds and without protecting the young plant's regrowth from trampling and grazing. Therefore, the persistence of species and maintenance of biodiversity in semi-arid rangelands depends mainly on the recruitment of seedlings from annual species, and on vegetative reproduction of perennial grasses and woody species. These findings have important implications for the management, conservation and restoration of semi-arid African rangelands.

**Keywords:** Africa; Aboveground vegetation; Ethiopia; Pastoral system; Rangeland; Restoration; Soil seed bank; Savanna; Semi-arid ecosystem; Vegetation and soil degradation



# 1

## General introduction



**Tessema Zewdu Kelkay**

## **Background**

Savannas occupy approximately 20% of the land surface of the earth (Mistry, 2000; Sankaran et al., 2005), including extensive areas of sub-Saharan Africa, South America and northern Australia (Scott et al., 2010). They support a large proportion of the world's human population and a majority of its rangeland and livestock, together with many wildlife species (Scholes and Archer, 1997; Sankaran et al., 2004). Savannas are found in a transitional zone between forest regions and the desert, characterized by seasonal availability of rainfall. They are found in tropical or subtropical ecosystems (Scholes and Archer, 1997; Simioni et al., 2003), dominated by grasses and a discontinuous to some extent very open woody layer (Frost et al., 1986; Scholes and Archer, 1997).

Savannas have been considered to be stable ecosystems around one or more steady states or points of equilibrium (Illius and Swift, 1988; Illius and O'Conner, 1999), but they are highly dynamic over temporal and spatial scales, and vary with changes in rainfall, soil nutrients, fire and herbivory (Rietkerk and van de Koppel, 1997; van de Koppel et al., 1997; Briske et al., 2003). Tree-grass interactions have been regarded as fundamentally unstable systems in savannas (House et al., 2003; Sankaran et al., 2004). The models to explain and understand the dynamics of tree-grass ecosystems are still in their infancy stages and the mechanisms how trees and grasses interact in savannas are still under debate (Scholes and Archer, 1997; House et al., 2003; Sankaran et al., 2005).

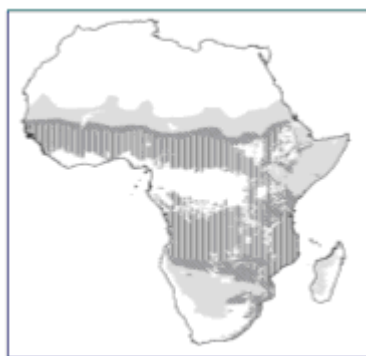
## **Typical features of semi-arid savannas**

Semi-arid savannas can be described by a state-and-transition model (Rietkerk et al., 1996; Mayer and Rietkerk, 2004). In semi-arid savannas, three extreme states are often described, the first one being a state with ample herbaceous cover, perennial grasses and scattered trees (Scholes and Archer, 1997; Simioni et al., 2003), the second one as a state with a poor cover of annual grasses and absence of perennial grasses, and the third state with a high proportion of bare soil and/or often bush encroached (Rietkerk et al., 1996; Roques et al., 2001). For instance, van Langevelde et al. (2003), studying the interactions of fire and herbivory, suggested that an increase in the level of grazing leads to a reduced fuel load, which leads to less intense fires and, thus, to less damage on trees and, consequently, results in an increase in woody vegetation. The system then switches from a state with trees and grasses to a state with solely trees (Rutherford et al., 2006). Browsers may enhance the effect of fire on trees, because they reduce the woody biomass, thus indirectly stimulating grass growth, and this consequently increases the fuel load, which results in more intense fires and further decline of

woody biomass, and it shifted from a state with solely trees to a state with trees and grasses (Rutherford et al., 2006). The consumption of grasses by grazers can lead to a reduction in fuel biomass available for burning, and in the absence of fire, shrubs are able to establish during wet years and these shrubs can suppress grass cover (van Langevelde et al., 2003).

### **The economic significance of African savannas**

In Africa, savannas cover 50% of the land surface (Rutherford et al., 2006). They extend from north of South Africa and Swaziland to southern Mozambique in the east and from the central Namibia in the West to the central Angola, and across to the Congo Basin and extend further into eastern Africa (Rutherford et al., 2006). In East Africa, savannas extend from Kenya into southern Somalia and to the South-eastern and western Ethiopia. From here, it extends West between the Sahel to the North and South-West Africa until the coast of Senegal (Scholes and Walker, 1993; Rutherford et al., 2006; Fig. 1.1).



**Fig. 1.1.** The distribution of savannas in Africa; Striped areas represent woodland savannas and gray-shaded areas are grassland savannas (Modified from Sankaran et al., 2005).

The semi-arid African savannas are occupied by the earth's richest and most spectacular large mammal fauna, and this fauna was even higher in the distant past (Cumming, 1982; Sinclair, 1983). These large animals influence the vegetation on which they feed and assumed to shape the savanna structure (Cumming, 1982; Sinclair, 1983). The African savannas include more ungulate species than any other continent (Du Toit, 2003). Moreover, savannas in Africa are the most important ecosystems for raising herbivores (Prins, 1988). They have been used for rangeland resources (Pratt and Gwynne, 1977), as grazing lands for livestock, and millions of humans depend to varying degrees as pastoral production systems (Skarpe, 1991a). These rangelands have magnificent landscapes that provide vital ecosystem service such as home to vast wildlife populations and domestic herbivores and yield valuable

livestock products (Desta and Coppock, 2004; Coppock et al., 2011). Rangelands are defined as indigenous vegetation used for grazing and/or browsing by both domestic and wild herbivores (Pratt and Gwynne, 1977). The arid and semi-arid zones of sub-Saharan Africa account for 55% of the continent's area and hold 57% of the total biomass of domestic ruminants (Sandford, 1995; Rutherford et al., 2006). Livestock products from these regions constitute between 14 - 25% of the total agricultural production of the continent (Scoones and Graham, 1994; Hagmann and Speranza, 2010). Herds of different livestock species are an effective way of satisfying human needs on extensive rangelands in semi-arid African savannas (Richardson et al., 2010). For instance, the semi-arid East African rangelands account 86% of the total area, and accommodate all of the small ruminants, 73% of the cattle and 45% of the camels (Kassahun et al., 2008a). Similarly, the semi-arid areas in Ethiopia are used as rangelands, which cover about 62% of the total land area of the country (Tessema and Oustalet, 2007; Kassahun et al., 2008a).

Semi-arid rangelands in East Africa are known for their traditional pastoral livestock production systems (Prins, 1989; Abule et al., 2005a). Livestock not only constitutes the main livelihood of the pastoralists (Harris, 2010; Ho and Azadi, 2010), but also represents the main component of the gross domestic product (GDP) of the economy in East Africa (Kassahun et al., 2008a). However, the pastoral production system is a significant but declining economic sector in most African countries (Prins, 1992; Coppock et al., 2011), and rangeland-based life-styles, their associated industries and the rangeland environment are under threat due to rangeland degradation (Gemedo et al., 2006; Harris, 2010; Ho and Azadi, 2010). Rangeland degradation is caused due to population growth, deforestation, continuous heavy grazing and climate changes (Dodd, 1994; Harris, 2010). Rangeland degradation is defined as a decrease in plant species diversity, plant height, vegetation cover, and plant productivity (Han et al., 2008; Ho and Azadi, 2010). This degradation causes a reduction in total vegetation cover and palatable plant species, an increase in undesirable and unpalatable plants, as well as a depletion of soil quality (Gemedo et al., 2006; Mekuria et al., 2007). This can also affect plant regeneration capacities (Abule et al., 2005b; Tessema et al., 2011a) and constrain restoration of denuded rangelands (Gemedo et al., 2006; Angassa and Oba, 2010). Furthermore, rangeland degradation has become a serious challenge, bearing negative impacts on the pastoral ecosystems, livestock production and livelihoods thereof (Vetter, 2005; Kassahun et al., 2008a). The focus of this thesis in general is to assess the impact of sustained livestock grazing on communal rangelands in semi-arid savanna systems, most specifically on Ethiopia and the restoration potentials of these degraded rangelands from the soil seed banks.

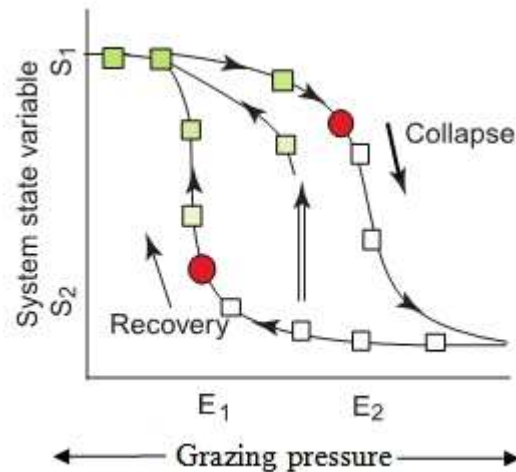
### **Impact of grazing on rangeland degradation in semi-arid Africa**

Rangelands provide the major feed resources in the form of grazing for domestic and wild herbivores (Prins, 1988, 1989). With increasing global warming and increasing number of people, the sustainable utilization of arid and semi-arid savannas becomes more and more important (Zimmermann et al., 2010). The management of rangelands plays an important role in the mitigation of rising atmospheric carbon dioxide concentrations, as the soils and vegetation are large stores of soil carbon that serves as a carbon storage (carbon sink), a process called carbon sequestration (Derner and Shuman, 2007). Globally, there are more than 120 million pastoralists who are custodians of more than 5000 million ha of rangelands, which store up to 30% of the world's soil carbon (Tennigkeit and Wilkes, 2008). More importantly, the available estimates suggest that improving rangeland management has a biophysical potential of sequestering 1300 - 2000 MtCO<sub>2</sub> worldwide up to 2030 (Tennigkeit and Wilkes, 2008), indicating that rangelands play an important role in reducing greenhouse gases released into the atmosphere and as good sources of biomass for fuel by substituting fossil fuels.

In semi-arid savannas, rangeland resources such as plant species diversity, plant abundance, species composition, and aboveground standing biomass are determined by a combination of factors like grazing intensity, fire frequency, and availability of moisture or nutrients (Scheffer et al., 2001; Suding et al., 2004). In this thesis, I focused only impacts of grazing on communal rangelands, because herbivory beyond a certain threshold point causes a nonlinear decline in the biomass of herbaceous and browse vegetation that is not simply reversible (Rietkerk et al., 1996; Didham et al. 2005). Several studies (Westoby et al., 1989; Abule et al., 2005b) reported the rapid disappearance of perennial grass community and their subsequent replacement by annual herbs due to heavy grazing. Moreover, there have been dramatic declines in perennial grass cover and substantial increases in woody or shrub density in many rangeland ecosystems around the world (Van Auken, 2000; Roques et al., 2001) due to intensive herbivory by domestic livestock (Valone et al., 2001; Mayer and Rietkerk, 2004).

It is believed that degraded semi-arid grazing systems can be greatly modified by changing the grazing pressure. The herbaceous layer, more specifically, perennial grasses, can persist if grazing pressure is low but if grazing pressure increases, the herbaceous vegetation leads to the disappearance of perennial grasses and replacement by annual herbs, and finally the vegetation would collapse to a degraded system (Fig. 1.2). Once the herbaceous vegetation has collapsed, it will not recover easily or return to the grassland state. In this situation, the vegetation often requires a prolonged reduction in grazing pressure so that the

grass vegetation can recover through time or there should be a large persistent seed banks in the soil for the recovery of aboveground vegetation, more specifically grass species after their collapse. Therefore, the grass species may re-colonize the area through seeds in the soil seed banks imported by wind, water, or animals since the area is rested from grazing that causes plant mortality and soil compaction, and these grass species, often with good fodder value, eventually establish, stabilize the soil, and contribute to the vegetation recovery as well as for possible restoration of degraded semi-arid rangelands in savanna ecosystems.



**Fig. 1.2.** Effect of grazing on system state variables such as plant species composition, species diversity, plant abundance, plant cover, or biomass in a semi-arid savanna ecosystem (Modified from Suding et al., 2004);  $E_1$  and  $E_2$  represent low and high grazing pressures, and  $S_1$  and  $S_2$  represent high and low system state variables, respectively.

### The role of soil seed banks in vegetation restoration

Knowledge of the dynamics of soil seed banks provide clues about the potential of a plant community to restore after disturbances (Leck et al., 1989; Scott et al., 2010). All viable seeds including both dormant as well as ready to germinate seeds present on or in the soil or associated litter constitutes the soil seed banks (Baker, 1989; Leck et al., 1989; Simpson et al., 1989). Soil seed banks have spatial and temporal dimensions and display both vertical and horizontal distributions that reflect seed dispersal mechanisms and subsequent movement of seeds in the soil (Rice, 1989; Page et al., 2006). The pool of long-lived seeds in the soil accumulated over time ensures the continuous re-colonization of plant species on a site after disturbances (O'Connor and Pickett, 1992; Scott et al., 2010). Therefore, understanding of the population dynamics of viable seeds buried in the soil has practical significance in the restoration of degraded vegetation in semi-arid African rangelands (de Villiers et al., 2003; Snyman, 2004; Dreber, 2011; Dreber and Elser, 2011).

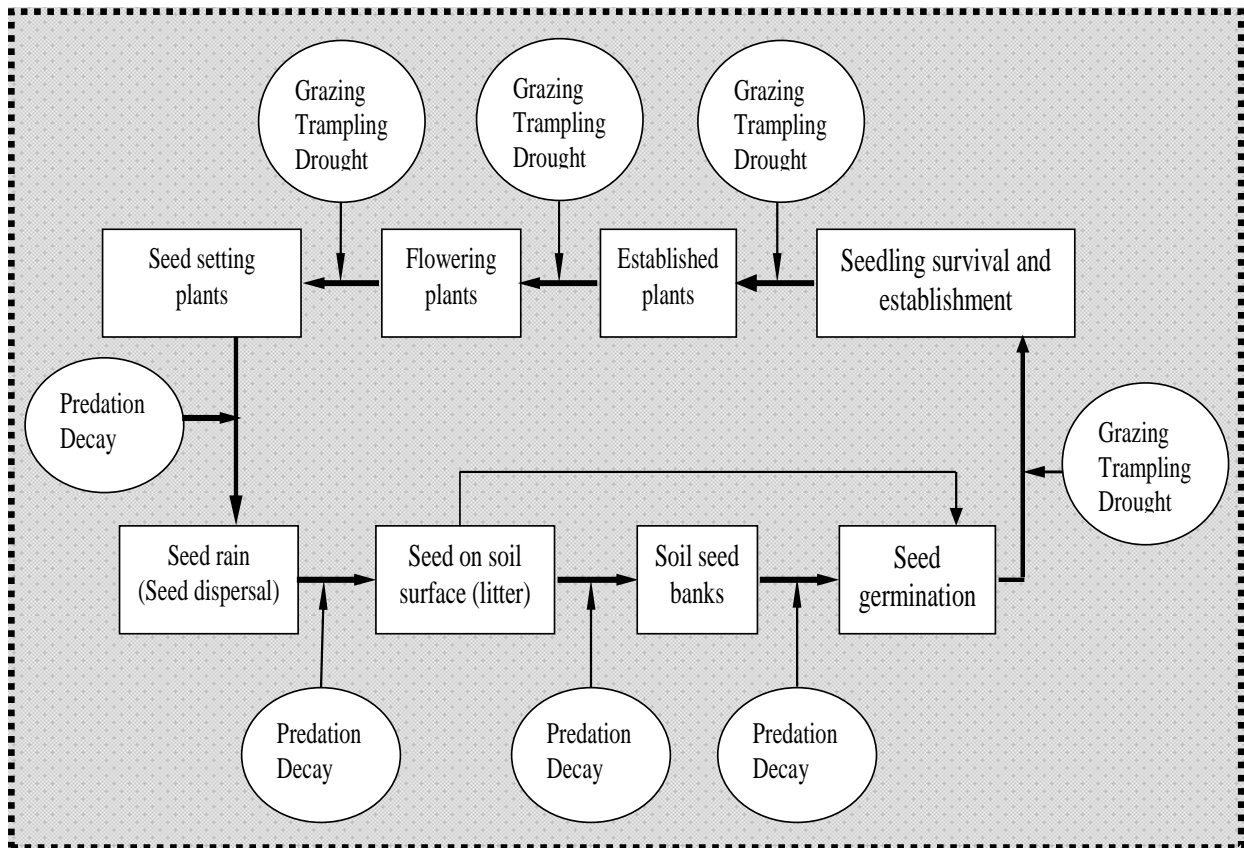
Some studies conducted elsewhere suggest that the return of perennial grasses and other species that disappear under extensive grazing can be facilitated by the soil seed banks and stimulate vegetation recovery in degraded ecosystems (Baker, 1989; Leck et al., 1989). This is because of the fact that soil seed bank serves as a reserve to return to the original aboveground vegetation conditions. Therefore, the soil seed bank forms a pool of propagules for the regeneration of the native vegetation after disturbance, and stimulating the recovery of aboveground vegetation (Thompson and Grime 1979; Leck et al., 1989; Scott et al., 2010). Hence, regeneration from the soil seed banks has long been considered an important pathway for the restoration of degraded ecosystems (Garwood, 1989; Thompson et al., 1989).

In this PhD thesis, I hypothesize that the availability of seeds in the soil seed banks could: (i) “kick start” the recovery of the vegetation, and (ii) accelerate the transition from a degraded state to vegetation with a perennial grass cover in semi-arid savanna grazing systems. Understanding the importance and mechanisms behind the restoration of degraded semi-arid savanna ecosystems and the role soil seed banks play in the sustainability of savannas is a prerequisite for proper management of these systems. Therefore, knowledge of the soil seed bank dynamics can improve our understanding of important limiting factors or processes that occur within the community. Hence, the resilience of these systems depends to a large extent on the role of the soil seed banks. The persistence of seeds in the soil seed banks is determined by seed rain, dispersal, predation, longevity, and factors controlling germination and recruitment (O’Connor, 1991; Leck et al., 1989; Simpson et al., 1989; Fig. 1.3). Soil seed banks may be either transient, with seeds that germinate within a year of initial dispersal, or persistent, with seeds that remain in the soil for more than one year, which serves as a reserve of genetic potential and gene pool accumulated over time (Simpson et al., 1989; Bekker et al., 1998).

However, there are still contrasting views on the possible role of soil seed banks in the restoration of ecosystems dominated by grasslands (Kassahun et al., 2009; Valkó et al., 2011). Several studies emphasize that soil seed banks form an important source of re-colonization (Garwood, 1989; Snyman, 2004), particularly when seed dispersal is limited (Valkó et al., 2011). Other investigations have, however, found that target species, (i.e., perennial grasses) often lack persistent seed banks and the similarity between the grassland vegetation and soil seed banks in semi-arid savannas is limited under the influence of grazing (de Viller et al., 2003; Hopfensperger, 2007; Scott et al., 2010). This dissimilarity could be due to low seed output into the soil seed banks by direct removal of flowers and seeds as a result of continuous heavy grazing (O’Connor and Pickett, 1992; O’Connor, 1994; Hoshino et



al., 2009), or depletion of seeds in the soil as a result of germination and mortality, or differences in longevity and germination of seeds between species in the soil seed banks (Pons, 1991; Baskin and Baskin, 2004; Snyman, 2004). Therefore, understanding the similarity of species composition between the soil seed banks and aboveground vegetation at various spatial and temporal scales can provide insight into whether the soil seed bank is driving aboveground vegetation composition, or the aboveground vegetation is driving the soil seed bank composition (Henderson et al. 1988; de Villers et al., 2003; Hopfensperger, 2007).



**Fig. 1.3.** General model of soil seed banks and aboveground vegetation dynamics in a semi-arid savanna grazing system (modified from Simpson et al., 1989; O'Connor, 1991).

Vegetation studies in semi-arid savanna communal grazing systems of the world in general and in semi-arid African rangelands in particular are mostly restricted to the aboveground vegetation (de Villers et al., 2003; Abule et al., 2005b; Solomon et al., 2006; Kassahun et al., 2008b), and information is lacking about the role that soil seed banks could play in the restoration of degraded vegetation under influence of grazing. For instance, from the review paper of Hopfensperger (2007; 108 reviewed papers from 1945-2006) and other studies (Solomon et al., 2006; Dreber, 2011), I concluded that apart from the presence of



some information on soil seed banks in forests and woodlands in South and North America, and grasslands from Europe, Australia and South Africa, knowledge about the factors contributing towards vegetation recovery and their associated recovery mechanisms through the soil seed banks is lacking. According to Kassahun et al. (2009), there is no adequate evidence to prove that severely degraded rangelands in Ethiopia maintain adequate soil seed banks that would improve its condition through restoration from the soil seed banks. However, information on species composition in the soil seed banks, as well as its similarity with the aboveground vegetation are to a very large extent lacking in semi-arid African rangelands (Dreber, 2011; Tessema et al., 2011a), indicating that there is a shortage of soil seed bank records, especially for perennial grass species, with good fodder value, for domestic and wild herbivores. Ultimately, lack of information about these grass species in databases of semi-arid savanna rangelands may hamper understanding of the role that soil seed banks could play in the restoration of grass species in particular and aboveground vegetation in general.

Until we understand the relative importance of the determining factors for the restoration of aboveground vegetation through soil seed banks, we cannot adequately predict the vegetation dynamics of semi-arid savanna grazing systems, and hence we will have little to add to current knowledge and approaches to the restoration of degraded semi-arid savanna ecosystems. However, if we are able to understand the mechanisms that can trigger the recovery of degraded ecosystems and the role that the soil seed banks could play in the aboveground vegetation dynamics, we can improve our knowledge and ability to predict the potential for vegetation restoration in degraded ecosystems. This PhD thesis aims to contribute new insight to the dynamic interactions between aboveground vegetation and soil seed banks thereof, which may contribute to the restoration and conservation of semi-arid African rangelands. Moreover, this PhD thesis provides information to researchers, development workers and policy makers for designing proper technologies and policies for sustainable management of communal rangelands with the involvement and participation of pastoral communities living in semi-arid Ethiopian savannas in particular and in Africa in general.

### **Study objectives and hypotheses**

The main objective of this thesis is to contribute to a better understanding of aboveground vegetation dynamics by investigating the role that soil seed bank dynamics play in the

restoration of degraded semi-arid savanna grazing systems in Africa. More specifically this thesis addresses:

- (i) Changes in vegetation structure, soil nutrients and herbaceous biomass in response to grazing,
- (ii) Species composition, seedling density and species diversity of the soil seed banks under the influence of grazing, and the similarity between the soil seed banks and aboveground vegetation,
- (iii) Survival of grass plant populations and temporal variations in soil seed bank dynamics under light and heavy grazing pressures, and
- (iv) Seasonal patterns of longevity and germination success of grass species in a laboratory and in a field experiment in a semi-arid savanna system.

Based on the above objectives, the thesis tested the following hypotheses:

- (i) Heavy grazing reduces the species diversity and changes the species composition both in the aboveground vegetation and soil seed banks in semi-arid savannas,
- (ii) The seeds available in the soil seed banks promote the restoration of vegetation and accelerate the transition from a degraded state to a vegetation with a perennial grass cover,
- (iii) Species composition in soil seed banks are more similar than species composition in the aboveground vegetation as a result of grazing, and
- (iv) Seed germination and longevity of plant species influence the restoration potential of aboveground vegetation in semi-arid savannas.

### **Focus and thesis outline**

In this thesis, I focus on the role that soil seed banks plays in the potential restoration of degraded semi-arid African communal rangelands, through investigating the mechanisms how grazing affects both the aboveground vegetation and availability of viable seeds (seedling density), species composition and species diversity, functional groups in the soil seeds bank over time, as well as the germination ecology of grass species, in a typical semi-arid African savanna grazing systems, with particular emphasis on Ethiopia. To address the research objectives and to test the hypotheses, the thesis is organized into 8 chapters (Fig. 1.4).

Chapter 2 describes the aboveground vegetation, particularly the changes in vegetation structure of herbaceous and woody species, soil nutrients and herbaceous biomass in response

to grazing. Understanding the responses of vegetation to different grazing intensities is crucial to facilitate the management of these semi-arid African rangelands for both biological conservation and sustainable use (Abule et al., 2005b; Hoshino et al., 2009). The interplay between grazing impacts and vegetation (Bilotta et al., 2007; Moussa et al., 2009), and especially the impacts of grazing on soil nutrients (Han et al., 2008), thereby affecting the relative abundance of different plant functional groups, and plant species richness is poorly understood in a semi-arid African savannas.

Chapter 3 indicates how differences in grazing pressure influence the soil seed bank dynamics in communal rangeland, as well as the similarity in species composition between the soil seed banks and aboveground vegetation in semi-arid African savannas, and the role that soil seed bank could play in the restoration of degraded vegetation after heavy grazing.

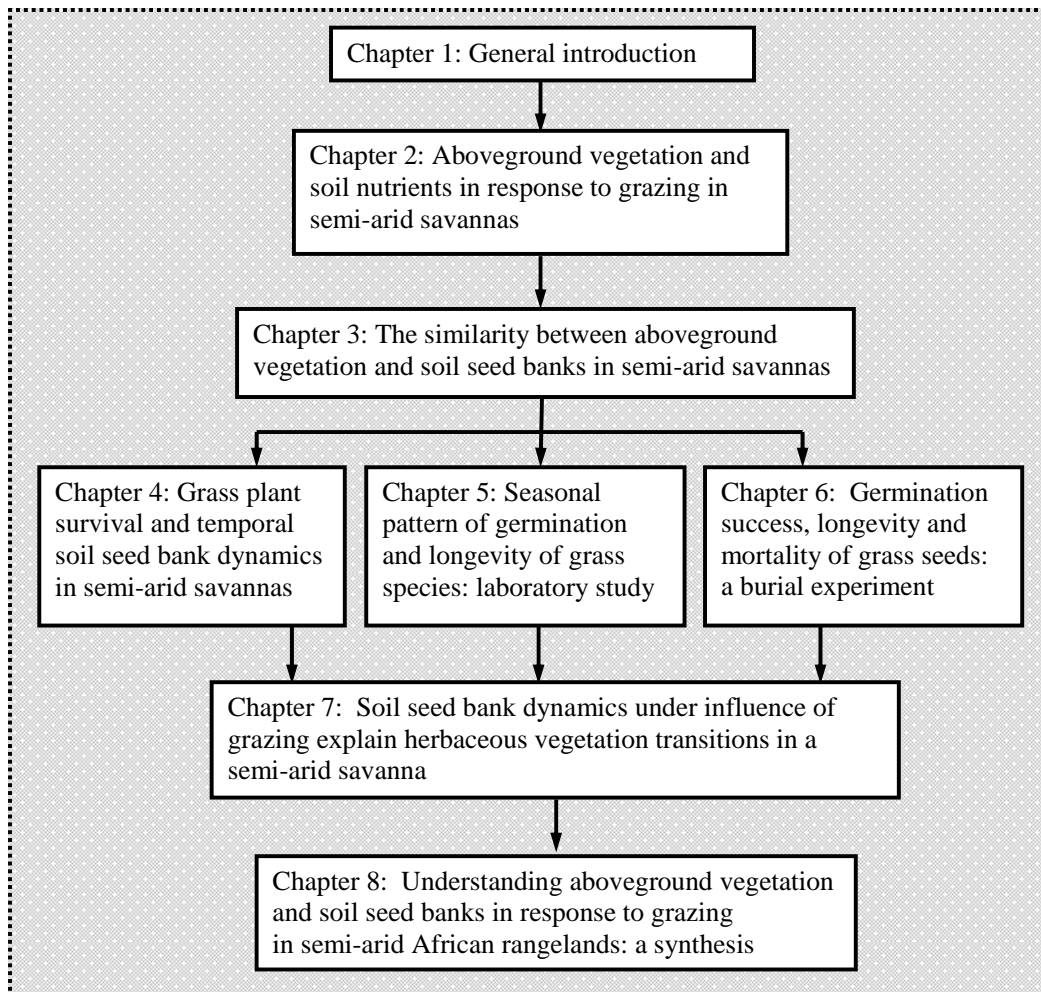
The ability of grasses to survive under the influence of grazing can be understood mechanistically through examination of the life cycle processes (O'Connor, 1994; Snyman, 2004) such as seed germination, seedling establishment, or maturation and mortality of standing populations (Veenendaal et al., 1996a; Scott et al., 2010). Therefore, Chapter 4 addresses the temporal variations in soil seed bank dynamics under low and heavy grazing pressures and the changes in grass plant populations in semi-arid African savannas.

The recovery potential of grass species in semi-arid African rangelands after sustained heavy grazing depends mainly on the longevity (O'Connor and Pickett, 1992; O'Connor, 1996) and survival of seeds buried in the soil after seed dispersal (Pake and Venable, 1996). In Chapters 5 and 6, I assess the longevity, germination success and mortality of seeds of major annual and perennial grass species commonly found both under light and heavy grazing under laboratory and field conditions, respectively.

Chapter 7 focuses on how differences in grazing pressure and soil seed bank dynamics trigger the transitions of semi-arid savanna grazing systems. The recovery processes of degraded semi-arid African grazing systems and the transition from one stable state to another could be controlled by two important factors, the intensity of grazing and availability of seeds in the soil seed banks. Here in this chapter, the availability of seeds in the soil seed banks together with seed germination rates and longevity triggers the transition of degraded semi-arid African savannas, from a bare soil state to an assemblage dominated by annual and/or perennial grass states under decreasing grazing pressure.

Finally, Chapter 8 synthesizes the main findings of the thesis in the light of the available literatures and indicates the implications of the findings of the thesis for

conservation, utilization and management, and restoration of semi-arid African rangelands from ecological, economical and societal perspectives.



**Fig. 1.4.** Schematic outline of the PhD thesis that illustrates the different chapters

### Description of the study areas

The research for this PhD thesis was conducted in two semi-arid locations: Abernosa Cattle Breeding Ranch (7°47'N, 38°40'E, 1660 to 1740 m above sea level) and Awash National Park (9°20'N, 40°20'E, 960 to 1050 m above sea level) (Fig. 1.5). The distance between these two locations is about 220 km, both located in the Ethiopian Rift Valley, typical for many semi-arid African savannas (Tessema et al., 2011a). The soils of Abernosa Cattle Breeding Ranch and Awash National Park are largely derived from recent volcanic rocks (Itana, 2005). The soil types of the actual experimental areas in Abernosa Cattle Breeding Ranch were sand (42.4%), silt (31.5%) and clay (26.1%), whereas the study sites in Awash National Park contained sand (47.4%), silt (31.6%) and clay (21%) (Tessema et al., 2011a). The two locations were purposely selected because both areas are rangelands occupied by pastoralists

and it was possible to contrast a site with heavy grazing and a site with light grazing at both locations in semi-arid savanna systems of Ethiopia (Mekuria et al., 1999; Abule et al., 2005b).

The Awash National Park was established in 1966, which covers about 756 km<sup>2</sup> and is located 225 km east of Addis Ababa, the capital of Ethiopia. The mean annual rainfall (1989-2008: Tessema et al., 2011a, b; Fig. 1.6) of Awash National Park was 512 mm, ranging between 277 to 653 mm, and is highly variable among the years (coefficient of variation CV = 103%). Its main rainy season is from July to September with a second short rainy season from February to April. The long dry period is from October to January and the short dry period is from May to June. The mean daily minimum and maximum temperatures are 18°C and 34°C, respectively (Tessema et al., 2011a, b). The number of rainy days per month is the highest in August (15 days). The vegetation of the Awash National Park was described as an *Acacia* shrub land and open grassland (Abule et al., 2005b).

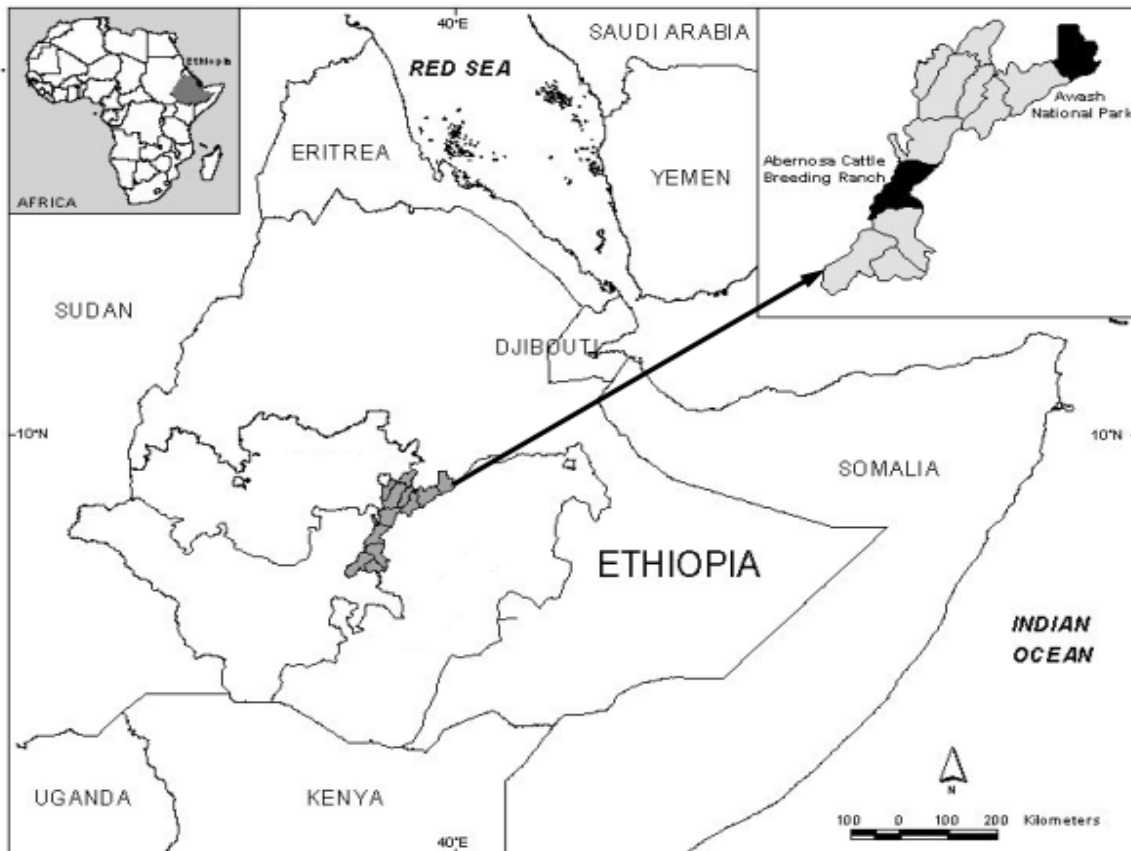
The Abernosa Cattle Breeding Ranch covers about 23 km<sup>2</sup>, and is located 175 km south of Addis Ababa, the capital of Ethiopia. Abernosa Cattle Breeding Ranch has a bimodal rainfall; the short rain is from March-April, with a short dry spell in May and June. The main rainy season is from July to October and the long dry period is from November to February. The average annual rainfall of Abernosa Cattle Breeding Ranch was 734 mm (346-959 mm; CV = 116%; Tessema et al., 2011a, b; Fig. 1.6). The mean minimum and maximum temperatures are 14°C and 28°C, respectively. The ranch was established about 40 years ago, to conserve the genetic variation of Borana cattle and for distributing breeding bulls and heifers to the surrounding communities through crossbreeding with Holstein Friesian and Jersey cattle (Mekuria et al., 1999; Tessema et al., 2011a). The ranch was established by fencing the woodland, and paddocks were established for rotational grazing. 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*, *Acacia seyal* and *Balanites aegyptiaca*). The area around the ranch is not fenced and grazing impact was very high due to high livestock densities there (Mekuria et al., 1999; Tessema et al., 2011a).

Light and heavy grazing sampling sites were systematically identified inside and outside the Awash National Park and Abernosa Cattle Breeding Ranch, based on the history and intensity of livestock grazing according to previous studies (Mekuria et al., 1999; Abule et al., 2005b) and visual field observations prior to this study. Four sampling sites in each

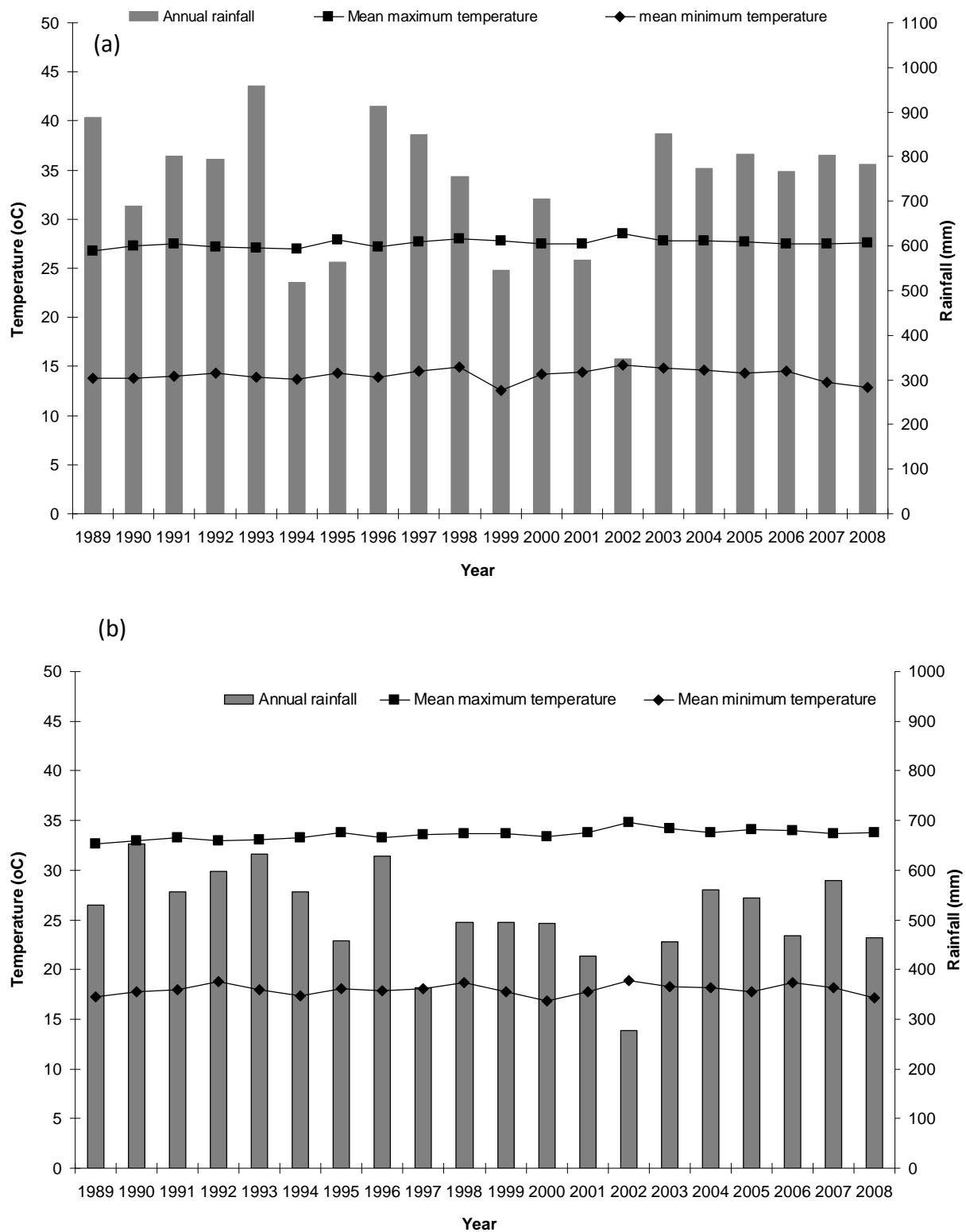
light and heavy grazing area in each location were selected, using a stratified sampling procedure (Tessema et al., 2011a).

In Awash National Park, the light grazing sites are usually grazed by few wild herbivores (e.g., East African or Fringe-eared Oryx (*Oryx beisa*), Soemmerring's Gazelle (*Nanger soemmerringii*), Dik-dik (*Madoqua kirkii*), and a Lesser kudu (*Tragelaphus imberbis*) and Greater kudu (*Tragelaphus strepsiceros*)) and only intermittently by livestock; hence the vegetation cover and the composition is in good condition every year. The heavy grazed sites are open grasslands, 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., 2005b).

In Abernosa Cattle Breeding Ranch, 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 and the basal cover is dense. The heavy grazing sites outside the ranch are grazed throughout the year and are now dominated by short annual grass species, with a high percentage of bare ground (Mekuria et al., 1999; Tessema et al., 2011a).



**Fig. 1.5.** 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. 1.6.** Twenty years (1989–2008) total annual rainfall (mm) and mean annual maximum and minimum temperatures at Abernosa Cattle Breeding Ranch (a) and Awash National Park (b) in semi-arid savanna grazing systems of Ethiopia.





# 2

Changes in soil nutrients, vegetation structure and herbaceous biomass in response to grazing in a semi-arid savanna of Ethiopia



Z K. Tessema, W.F. de Boer, R.M.T. Baars and H.H.T. Prins

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### **Abstract**

The effect of grazing was studied on vegetation structure, herbaceous biomass, basal and bare ground covers, together with soil nutrient concentrations in two locations in an Ethiopian semi-arid savanna. The lightly grazed sites had significantly higher herbaceous diversity, total abundance, basal cover and aboveground biomass, and a lower percentage of bare ground compared with the heavy grazed sites. Grazing pressure had no effect on the density and number of woody species as well as on the proportion of encroaching woody species. The light grazing sites had higher organic carbon, phosphorus and exchangeable bases, and therefore a higher pH and higher electrical conductance, indicating an improved soil nutrient status compared with heavy grazing sites, mainly attributed to the higher basal cover and standing biomass at light grazed sites, and the export of nutrients through grazing and dung collection from the heavily grazed sites. There were significantly higher soil nutrients, species diversity, aboveground biomass and basal cover in the light grazing sites compared with heavy grazing sites. We concluded that changes in herbaceous vegetation, standing biomass and soil compositions are caused by interactions between grazing, soil and vegetation, and these interactions determine the transitions of semi-arid savannas.

**Keywords:** Grazing pressure; Perennial grasses; Plant abundance; Soil composition; Species richness; Woody species

## **Introduction**

Savannas, characterized by the coexistence of trees and herbaceous vegetations (van Langevelde et al., 2003), occupy a fifth of the earth's land surface and support a large portion of the world's human population and most of its livestock and wild herbivores (Sankaran et al., 2005). The semi-arid savannas have been described as stable ecosystems around one or more steady states (Rietkerk et al., 1996), but they are highly dynamic, and transitions from one state to the next often occur under influence of disturbances, such as through grazing or bush fires (van de Koppel and Prins, 1998). Semi-arid savanna grazing systems can therefore be described by state-and-transition models (Rietkerk et al., 1996). Two extreme states are often described, the first one being a state with ample herbaceous cover, perennial grasses and scattered trees (Scholes and Archer, 1997; Simioni et al., 2003), the second one as a state with a poor cover of annual grasses, absence of perennial grasses, a high proportion of bare soil and/or often bush encroached (Richter et al., 2001; Roques et al., 2001). Moreover, there are feedbacks within these stable states that perpetuate or maintain stability (Rietkerk et al., 1996). The vegetation structure is influenced by the soil composition (Augustine, 2003), under influence of the grazing and fire regimes (Moussa et al., 2009). However, the processes leading the vegetation from one state to the next are still poorly understood, especially the role of the soil nutrients in relation to the vegetation, and how grazing influences this interaction.

Heavy grazing leads to excessive defoliation of herbaceous vegetation, reducing standing biomass, basal cover and plant species diversity, often triggered by a decline in net primary productivity (NPP), as the intensity of grazing increases (Bilotta et al., 2007). The decline in NPP under heavy grazing is attributed to a reduction of plant material available for photosynthesis. Moreover, heavy grazing alters the herbaceous vegetation composition through an increase in the abundance of annual species with a decline in perennials (Hoshino et al., 2009). Smith (1979) reported that heavy grazing reduces the growth rate and reproductive potential of perennial grasses, and influences the competitive relationships among the different species, so that the heavily grazed perennial grass species lose competitive power over the lightly grazed ones, and subsequently, unpalatable and grazing tolerant annual species become dominant in heavily grazed patches. At heavy grazing pressures, grazing intolerant species disappear because they are highly nutritious and eaten before seed setting, or species that cannot tolerate physical damage die and these species are subsequently replaced by less palatable species.

In African savannas, intensive grazing has therefore frequently resulted in species turnover, reducing the overall palatability of the sward, and decreasing the plant species diversity (Sarmiento, 1992). An increase in the level of grazing also reduces the fuel load, which makes fires less intense and thus less damaging to trees and, consequently, results in an increase in woody vegetation (van Langevelde et al., 2003). Moreover, heavy grazing has a negative impact on the grass layer, reducing the water and nutrient uptake by the grass layer, thus making more resources available for woody growth, and this may result in an encroachment of shrubs (Skarpe, 1991b). Grasses typically out-compete trees in open savannas by growing fast and intercepting moisture from the upper soil layers, thereby preventing trees from gaining access to precipitation in the lower soil layers where their roots are mostly found. When heavy grazing occurs, grasses are removed and soil moisture then becomes available to the trees, because they are more deeply rooted, allowing them to grow, recruit and expand (Scholes and Archer, 1997; Richter et al., 2001).

As heavy grazing and trampling by large herbivores reduces the vegetation cover and standing biomass (Skarpe, 1991a; Bilotta et al., 2007), bare soil patches develop, increasing the chances for soil surface erosion, and this leads to physical and chemical changes in soil properties (Skarpe, 1991b). Through trampling, consumption, and excreta deposition, large herbivores alter soil nutrient availability for plants, changing the soil nutrient cycling rates and redistribution of soil nutrients (Bardgett and Wardle, 2003). The nutrient content of soils on heavily grazed grasslands generally decreases through export of nutrients, especially that of phosphorus (Lavado et al., 1996; Jewell et al., 2007; Moe and Wegge, 2008), although nutrients accumulate at kraal areas (i.e., an enclosure for confining livestock during night in grazing areas) long after they have been used for kraaling (van der Waal et al., 2009). Grazing also affects the carbon (C) and nitrogen (N) accumulations in the soil (Piñeiro et al., 2006) through modifying the C and N cycles (Han et al., 2008).

Understanding the responses of vegetation to different grazing intensities is crucial to facilitate the management of these arid and semi-arid savannas for both biological conservation and sustainable use (Hoshino et al., 2009). Grazing is also considered essential to maintain the structure, functionality and diversity of plant communities. To achieve an optimal sustainable use of savannas, we need to understand the dynamic interactions between herbivores, vegetation and soils (Skarpe, 1991b). Augustine (2003) suggested that future studies should incorporate not only the direct effects of grazing on vegetation, but especially the effects of grazing on vegetation via the changes in soil nutrients that are directly caused by grazing (e.g., plant removal and damage) and indirectly by the impact of grazing on

vegetation (e.g., removal of nutrients from the system by grazing and trampling). Grasses dominate the herbaceous vegetation in arid and semi-arid African rangelands, but these rangelands are often degraded due to heavy grazing by pastoral communities (Abule et al., 2005b; Angassa and Oba, 2007). However, we poorly understand the interplay between grazing impacts and vegetation and soil properties (Bilotta et al., 2007; Moussa et al., 2009), and especially the impacts of grazing on soil nutrients (Han et al., 2008), thereby affecting the relative abundance of different plant functional groups, and plant species richness. We therefore set out to study the effect of heavy and light grazing on aboveground vegetation and soil in an experimental setup in a semi-arid savanna in Ethiopia. Based on the above reasoning, we tested the following hypotheses: heavy grazing (i) results in a decrease in fertility status of the soil, (ii) reduces the herbaceous species diversity and their plant abundance, (iii) results in a shift from grass species with a perennial life history to grass species with an annual life history, (iv) reduces basal cover and standing biomass while increases the proportion of bare ground, and (v) increases the proportion of bush encroachment.

## **Materials and methods**

### **Description of the study area**

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

The ANP was established in 1966, covers about 756 km<sup>2</sup> and is located 225 km east of Addis Ababa. The mean annual rainfall (1989-2008: Tessema et al., 2011b) of ANP was 512 mm, ranging between 277-653 mm, and was highly variable among the years (coefficient of variation CV = 103%). Its main rainy season is from July-September with a second short rainy season from February-April. The mean daily minimum and maximum temperatures are 18°C and 34°C, respectively (Tessema et al., 2011b). The number of rainy days per month is the highest in August (15 days). The vegetation of the ANP was described as an *Acacia* shrub land and open grassland (Abule et al., 2005b).

The ACBR covers about 23 km<sup>2</sup>, and is located 175 km south of Addis Ababa. ACBR has a bimodal rainfall; the short rain is from March-April, with a short dry spell in May and June. The main rainy season is from July to October and the long dry period is from November to February. The average annual rainfall of ACBR was 734 mm (346-959mm; CV = 116%; Tessema et al., 2011b). The mean minimum and maximum temperatures are 14°C and 28°C, respectively. The ranch was established about 40 years ago, for the genetic conservation of Borana cattle and for distributing breeding bulls and heifers to the surrounding communities through crossbreeding with Holstein Friesian and Jersey cattle (Mekuria et al., 1999). The ranch was established by fencing the woodland, and paddocks were established for rotational grazing. 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*, *Acacia seyal* and *Balanites aegyptiaca*), the area around the ranch is not fenced and grazing impact was very high due to high livestock densities there (Mekuria et al., 1999).

### **Selection of sampling sites**

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 (Mekuria et al., 1999; Abule et al., 2005b) and visual field observations prior to this study. Four sampling sites in each light and heavy grazing area in each location were selected, using a stratified sampling procedure. In ANP, the light grazing sites are usually grazed by few wild herbivores (e.g., East African Oryx (*Oryx beisa*), Soemmerring's Gazelle (*Nanger soemmerringii*), Dik-dik (*Madoqua kirkii*), and a Lesser kudu (*Tragelaphus imberbis*) and Greater kudu (*Tragelaphus strepsiceros*)) and only intermittently by livestock; hence the vegetation cover and the composition is in good condition every year. The heavy grazed sites are open grasslands, 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., 2005b). 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 and the basal cover is dense. The heavy grazing sites outside the ranch are grazed throughout the year and are now dominated by short annual grass species, with a high percentage of bare ground (Mekuria et al., 1999).

### **Soil sampling and analysis**

Ten soil samples in each site at a depth of 0-10 cm, yielding a total of 160 soil samples (2 locations x 2 grazing intensities x 4 sample sites x 10 soil samples). Each sample was collected in a 1 m x 1 m quadrat. The soil samples at each site were pooled to form one composite soil sample per sampling site, yielding a total of 16 soil samples (2 locations x 2 grazing intensities x 4 sample sites). The composite soil samples were divided into three equal parts, out of which one was randomly chosen and stored in plastic bags, labelled, sealed and transported to the soil laboratory of Haramaya University in Ethiopia for physical and chemical analysis. The pH and texture of the soil were determined in a 1:2.5 soil water ratio suspensions using the Bouyoucos hydrometer method (Bouyoucos, 1962), while electrical conductivity (EC) was determined using the sodium saturation ratio (Van Reeuwijk, 1992). The percentage organic carbon (OC) was determined according to the Walkley and Black (1934) method, and total N using the Kjeldahl procedure (Jackson, 1970). Available phosphorus (P), exchangeable potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na) were analyzed according to Olsen et al. (1954). Cation exchangeable capacity (CEC) was analyzed using the method of NRC (1996).

### **Sampling of herbaceous and woody vegetations**

For all the sampling sites, the herbaceous species composition (at species level) and their abundance were assessed using a 1 m x 1 m quadrat during the flowering stages of most herbaceous species in September and October 2008. Twenty quadrats were randomly taken in each sampling site under light and heavy grazing pressures, totalling 320 quadrats (2 locations x 2 grazing pressures x 4 sampling sites x 20 quadrats). The species were classified into grasses (annual or perennial), herbaceous legumes and forbs within each quadrat to determine the contribution of each group within the quadrat, according to ILCA (1990). After determining the species composition and plant functional groups in each quadrat, individual plants were counted to determine the abundance of each species. The percentages of basal cover and bare ground were recorded using visual estimation in each quadrat. Dry matter (DM) above ground biomass of the herbaceous layer was determined by harvesting the whole fresh biomass within each quadrat, and oven-drying at 70°C for 48 h and weighing.

The woody species composition (comprising all trees and shrubs >1m height) and their density were recorded in a sample area of 100 m x 100 m at each site under heavy and light grazing conditions in both locations. Three of these 1 ha plots were assessed per site, yielding a total of 48 ha (2 locations x 2 grazing pressures x 4 sampling sites x 3 quadrats).

All species were listed, recorded and identified based on their morphological, structural and floristic characteristics, and pooled by grazing treatment at each sampling site. For those species that were difficult to identify in the field, herbarium specimens were collected, and transported to the Herbarium of Haramaya University of Ethiopia for further identification. Plant nomenclature follows Cufodontis (1953-1972), Fromann and Persson (1974), and Philips (1995).

### **Data analysis**

Ordination of sampling sites under light and heavy grazing conditions in both locations was done by multivariate techniques, using Canoco (ter Braak, 1997) to determine the similarity in herbaceous and woody species using the mean species composition per site. We conducted a Detrended Correspondence Analysis (DCA) of the abundance data of herbaceous and woody species as well as soil parameters to calculate the length of gradients on the 1<sup>st</sup> ordination axis. The result of the DCA analyses revealed that the length of gradients on the 1<sup>st</sup> ordination axis for herbaceous species was unimodal ( $>4$ ), but was linear ( $<3$ ) for both the woody species and the soil parameters. Therefore, the ordination of herbaceous species was done using a Correspondence Analysis (CA), while the ordination of the woody species and the soil parameters was done by a Principal Component Analysis (PCA). Moreover, the correlations of soil parameters with the herbaceous species were done using a Canonical Correspondence Analysis (CCA).

The hypotheses were tested with a General Linear Model (GLM) using SPSS software, in a randomized complete block design, with location as a random block and grazing pressure as a fixed effect. The density and proportion of encroaching woody species was compared between high and low grazing pressures and locations, using the classification of encroaching species from previous studies (Abule et al., 2007; Angassa and Oba, 2007). Averages were calculated per sampling site to avoid pseudo-replication, as sampling sites were assumed to be independent. Proportional data were arcsine transformed to meet the assumption of normality and homogeneous variances prior to carrying out the GLM. Because of the higher elevation and annual rainfall, we expected to have higher vegetation biomass and species richness at ACSR.

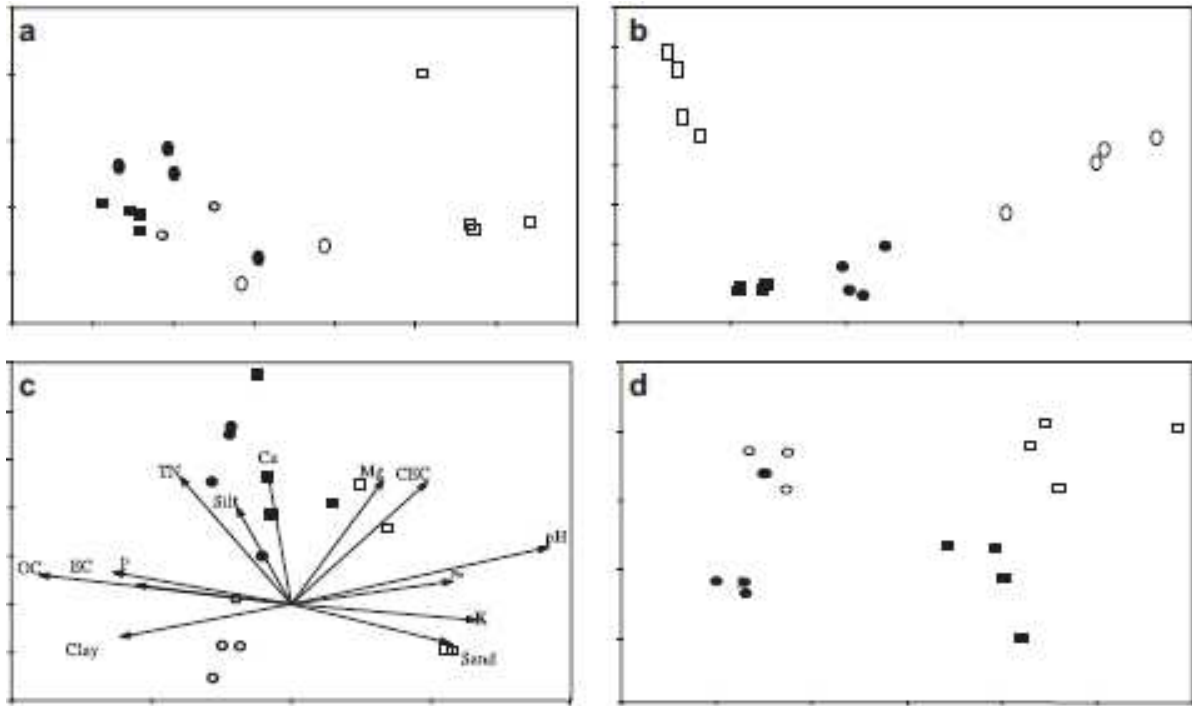


## Results

### Soil parameters

The largest fraction of the soil was sand, but the soil texture was influenced by grazing pressure in both locations (Table 2.1). The heavy grazing sites had a higher sand content than the lightly grazed sites, with the highest sand content of 49% in ANP. The lowest sand content of 33% was recorded under light grazing also in the ANP. The clay content varied considerably, and the lowest (21.0%) and the highest (34.4%) clay contents were recorded in the ANP under heavy and light grazing, respectively, whereas the silt content of the ACBR was almost similar for both grazing pressures. However, neither grazing pressure nor location had a significant effect on clay content.

The PCA ordination result showed a clear separation of the 16 sites for the soil parameters, as the light grazing sites are separately clustered from the heavy grazing sites in each location (Fig. 2.1a). The first and second axis explained together 88% of the total variation. Neither grazing pressure nor location had a significant effect on total N content in our study. ACBR sites had a higher P content than those in the ANP, and the P content was higher under light grazing at ACBR compared with ANP. The Mg contents were also highest in the light grazing site at ANP. The soils in ANP were higher in exchangeable bases compared with ACBR. In a similar fashion, the CEC was higher in the ANP, and higher under light grazing, following the trend of exchangeable bases. The EC was not affected by location or grazing pressure. The grazing pressure did not significantly affect soil pH, although the soil pH was slightly higher in ANP ( $>8$ ) compared with ACBR ( $<7$ ), indicating that the ANP soils were more alkaline, and pH was slightly, but not significantly, lower under heavy grazing. The OC content was highest at the ACBR, both under light and heavy grazing, with mean values of 11 and 10%, respectively, but OC content was not affected by grazing.



**Fig. 2.1.** Ordination diagram of 16 sampling sites for soil parameters (1a), herbaceous species (1b), sampling sites x soil parameters (1c), and woody species (1d) within two grazing pressures (heavily grazed sites = filled symbols; lightly grazed sites = open symbols) at two locations, the Abernosa Cattle Breeding Ranch, (ACBR = circles), and the Awash National Park (ANP = squares) by Correspondance Analysis (CA), Canonical Correspondance Analysis (CCA) and Principal Component Analysis (PCA), respectively in a semi-arid savanna in Ethiopia. Ca = calcium; CEC = cation exchange capacity; EC = electrical conductance; Mg = magnesium; K = potassium; Na = sodium; N = nitrogen; OC = organic carbon; P = phosphorus.

## Herbaceous vegetation

### *Species composition and functional groups*

Out of all herbaceous species identified, the number of grass species, herbaceous legumes and forbs were 46 (65%), 6 (9%) and 18 (26%), respectively. In total, we recorded 26 annual and 20 perennial grass species (Appendix Table 2.1). The ordination result showed a clear separation of the 16 sites for the herbaceous species, as the light grazing sites are separately clustered from the heavy grazing sites in each location (Fig. 2.1b). The first and the second ordination axis explained cumulatively 68% of the total variance extracted by the CA. The result of the sampling site x soil parameter using CCA showed higher relationships with herbaceous species on the first and second ordination axes with a correlation coefficient of

0.998 and 0.987, respectively. The first and second ordination axis explained 40% of the total variance. **Fig. 2.1.** Ordination diagram of 16 sampling sites for soil parameters (1a), herbaceous species (1b), sampling sites x soil parameters (1c), and woody species (1d) within two grazing pressures (heavily grazed sites = filled symbols; lightly grazed sites = open symbols) at two locations, the Abernosa Cattle Breeding Ranch, (ACBR = circles), and the Awash National Park (ANP = squares) by Correspondence Analysis (CA), Canonical Correspondence Analysis (CCA) and Principal Component Analysis (PCA), respectively in a semi-arid savanna in Ethiopia. Ca = calcium; CEC = cation exchange capacity; EC = electrical conductance; Mg = magnesium; K = potassium; Na = sodium; N = nitrogen; OC = organic carbon; P = phosphorus.

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*Species diversity and abundance*

ACBR had significantly more herbaceous species compared with ANP, and light grazing had a higher total abundance of herbaceous species compared with the heavy grazed sites in both locations (Table 2.3). The relative decreases in herbaceous species richness under the heavy grazing (from 8.1 species to 6.3 in ACBR, and from 4.5 species to 3.6 in ANP), was by far smaller than the decrease in abundance of herbaceous species (from 559 to 197 plants/m<sup>2</sup> in ACBR, and from 444 to 36 plants/m<sup>2</sup> in ANP).

**Bare ground, basal cover, and standing biomass**

Location and grazing pressure had a highly significant effect on the percentages of bare ground and basal cover for herbaceous species. The percentages of bare ground were lower for light grazing sites compared with heavy grazing sites (Fig. 2.2a;  $F_{1,1}=287.360$ ,  $P<0.001$ ). Similarly, the percentage basal cover of herbaceous species was larger on lightly grazed sites (Fig. 2.2b;  $F_{1,1}=302.879$ ,  $P<0.001$ ). Light grazing sites also had a higher standing biomass of herbaceous species compared with the heavy grazing sites in both locations (Fig. 2.2c;  $F_{1,1}=218.855$ ,  $P<0.001$ ). There was even no measurable herbaceous biomass left in the ANP heavy grazed sites at the end of the dry season, due to heavy grazing.



**Table 2.1.** Influence of light (LG) and heavy grazing (HG) conditions on physical and chemical soil properties at two locations, the Abernosa Cattle Breeding Ranch (ACBR) and Awash National Park (ANP), in a semi-arid savanna Ethiopia (n=160), with statistical results of the mixed GLM (*F*, *P* values).

Soil parameter	ACBR		ANP		Location (Loc)		GP		Loc x GP	
	LG	HG	LG	HG	<i>F</i> (df = 1, 1)	<i>P</i>	<i>F</i> (df =1,1)	<i>P</i>	<i>F</i> (df =1,12)	<i>P</i>
	Mean ± 95% CI									
Sand (%)	43.8±4.35	44.1±2.45	33.0±2.03	48.9±1.52	0.144	0.769	1.078	0.488	31.009	<0.001
Silt (%)	37.0±2.31	34.6±3.13	38.2±3.90	33.5±1.94	0.000	0.986	9.804	0.197	0.594	0.456
Clay (%)	23.4±3.24	26.1±1.67	34.4±3.94	21.0±0.70	0.140	0.772	0.443	0.626	35.190	<0.001
pH	6.74±0.34	6.4±0.34	8.2±0.13	8.0±0.34	205.67	0.044	4.534	0.280	0.506	0.490
EC (mmhos/Cm)	0.17±0.04	0.16±0.04	0.15±0.01	0.12±0.02	4.457	0.282	3.568	0.310	0.603	0.452
CEC (Meq/100g soil)	16.5±1.70	14.5±1.24	26.2±3.04	19.2±2.16	8.175	0.214	3.261	0.322	5.467	0.037
Total N (%)	2.1±0.44	1.9±0.21	2.3±0.21	1.7±0.10	0.001	0.979	3.869	0.299	1.951	1.188
P (mg/Kg Soil)	10.9±1.70	9.0±1.47	5.8±0.25	7.4±0.65	3.574	0.310	0.007	0.948	9.188	0.010
Ca (Cmol+)/Kg soil)	35.0±9.18	26.6±8.60	47.8±8.53	25.8±2.68	0.770	0.542	4.920	0.270	3.160	0.100
Mg (Cmol+)/Kg soil)	28.4±4.30	24.0±2.95	40.0±1.24	28.9±2.75	5.888	0.249	5.231	0.262	5.064	0.044
K (Cmol+)/Kg Soil)	2.1±0.78	2.2±0.17	3.2±0.18	2.7±0.34	7.893	0.218	0.523	0.602	1.691	0.218
Na (Cmol+)/Kg soil)	0.53±0.05	0.30±0.02	1.5±0.76	0.84±0.26	13.506	0.169	4.676	0.276	0.451	0.514
OC (%)	3.4±0.61	3.0±0.42	1.8±0.98	1.6±0.75	323.42	0.035	12.937	0.173	0.188	0.673

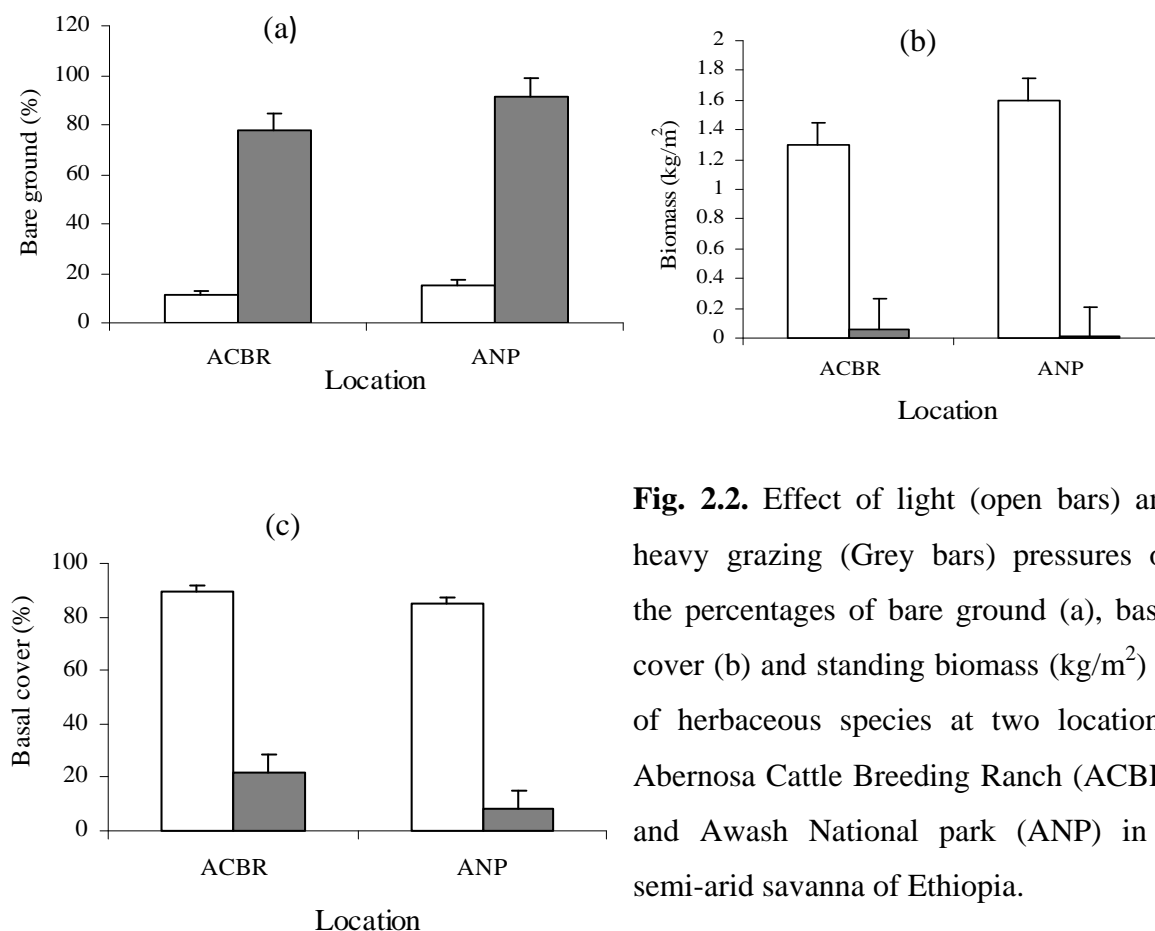
Ca = calcium; CEC = cation exchange capacity; EC = electrical conductance; Mg = magnesium; K = potassium; Na = sodium; N = nitrogen; OC = organic carbon; P = phosphorus.

**Table 2.2.** Effect of light and heavy grazing on the cover of the different functional groups of herbaceous species at two locations in semi-arid savanna ecosystems (N = 320), together with the results (F, P values ) from the mixed GLM, testing for effects of location and grazing pressure on cover.

	Proportion of functional groups (%)					Herbac eous legume	Forbs
	Total grass (TG)	Annual grass (AG) AG from the TG	AG from total species	Perennial grass (PG) PG from the TG	PG from the total species		
Mean ± 95% CI							
Abernosa Cattle Breeding Ranch							
light grazing	85.3 ±4.4	52.2±3.0	44.5±2.8	47.8±3.0	40.8±3.40	8.2±2.5	6.6±1.9
heavy grazing	90.4± 2.6	70.1±3.3	63.1±3.6	29.9±3.2	27.0±3.05	6.2±3.4	3.4±0.6
Awash National Park							
light grazing	85.7±9.8	27.8±6.0	23.7±5.3	72.2±6.0	62.3±6.49	9.1±2.9	12.5±4.9
heavy grazing	95.7±7.4	69.1±8.5	68.2±8.1	30.9±8.2	27.5±7.48	1.5±0.4	8.0±2.2
Location (loc)							
<i>F</i> (df = 1, 1)	1.861	1.042	0.377	1.042	1.032	3.549	23.042
<i>P</i>	0.403	0.493	0.650	0.493	0.495	0.311	0.131
Grazing pressure (GP)							
<i>F</i> (df: = 1, 1)	5.457	6.068	5.706	6.069	5.600	3.303	268.700
<i>P</i>	0.257	0.245	0.252	0.245	0.255	0.320	0.039
Loc x GP							
<i>F</i> (df: = 1, 12)	1.090	6.637	9.287	6.637	5.128	0.641	0.011
<i>P</i>	0.317	0.024	0.010	0.024	0.043	0.439	0.917

**Table 2.3.** Effect of light and heavy grazing on species richness (number of species) and total abundance of all species for herbaceous (N/m<sup>2</sup>) (N = 320) and woody species (n/ha) (N = 48) at two locations (Abernosa Cattle Breeding Ranch and Awash National Park) in a semi-arid savanna in Ethiopia, with statistical results of the mixed GLM (F, P values).

	Herbaceous species		Woody species	
	species richness	total abundance	species richness	Total abundance
Mean $\pm$ 95% CI				
Abernosa Cattle Breeding Ranch				
light grazing	8.1 $\pm$ 0.31	559.1 $\pm$ 163.90	5.9 $\pm$ 2.22	534.5 $\pm$ 78.97
heavy grazing	6.3 $\pm$ 0.22	196.6 $\pm$ 85.10	2.9 $\pm$ 0.83	225.0 $\pm$ 36.45
Awash National Park				
light grazing	4.5 $\pm$ 1.01	444.1 $\pm$ 137.47	7.5 $\pm$ 2.74	384.8 $\pm$ 56.35
heavy grazing	3.6 $\pm$ 0.36	36.3 $\pm$ 11.46	5.7 $\pm$ 1.51	592.5 $\pm$ 90.15
Location (Loc)				
F (df = 1, 1)	48.415	28.937	13.109	0.148
P	0.091	0.117	0.172	0.766
Grazing pressure (GP)				
F (df = 1, 1)	7.801	238.213	15.725	0.009
P	0.219	0.041	0.157	0.940
Loc x GP				
F (df: = 1, 12)	2.527	0.190	0.379	1.707
P	0.138	0.671	0.549	0.216



**Fig. 2.2.** Effect of light (open bars) and heavy grazing (Grey bars) pressures on the percentages of bare ground (a), basal cover (b) and standing biomass (kg/m<sup>2</sup>) (c) of herbaceous species at two locations, Abernosa Cattle Breeding Ranch (ACBR) and Awash National park (ANP) in a semi-arid savanna of Ethiopia.

### Woody vegetation

The ordination result by PCA also clearly distinguished the 16 sampling sites with response to heavily and lightly grazed areas and in terms of locations (Fig. 2.1d). Out of the total variance extracted by PCA, the first and the second ordination axis together explained 90% of the total variation. Location had an effect on the woody species richness, with a larger number of woody species in ANP, whereas neither grazing pressure nor location had a significant effect on the total abundance of woody species (Table 2.3). Neither grazing pressure nor location had a significant effect on the number of woody plant species compared with lightly grazed sites (Table 2.3). We compared the density and proportion of encroaching woody species (i.e., *Dicrostachys cinerea*, *Acacia mellifera*, *A. senegal*, *A. nubica*, *Pithecellobium dulce* and *Solanum somalensis*) with the non-encroaching woody species in the study areas (Appendix Table 2). The result showed that neither grazing pressure nor location had any significant effect on the density of encroaching and non-encroaching woody species. However, heavy grazing had a higher ( $P < 0.014$ ) proportions of encroacher woody species at ANP than ACBR, whereas ACBR had a higher proportions on non-encroaching woody species. However, the

proportions of encroaching and non-encroaching woody species were not affected grazing pressure (Table 2.4).

**Table 2.4.** Effect of light and heavy grazing on woody species encroachment (n = 48) at two locations (Abernosa Cattle Breeding Ranch and Awash National Park) in a semi-arid savanna in Ethiopia, together with the results of a mixed GLM (F, P values), testing for difference in location and grazing pressure on species richness and relative abundance.

	number of Encroacher	number of non- encroacher	encroacher (%)	Non-encroacher (%)
Mean ± 95% CI				
Abernosa Cattle Breeding Ranch				
light grazing	122.8±48.1	411.8±54.1	26.3±9.2	73.7±9.2
heavy grazing	5.5±1.1	219.5±28.6	3.5±0.9	96.4±3.6
Awash National Park				
light grazing	135.5±10.0	249.3±63.5	36.4±6.9	63.6±6.8
heavy grazing	400.8±60.1	191.8±94.1	46.8±8.9	53.2±8.9
Location (loc)				
F (df = 1, 1)	1.138	1.993	2.576	2.576
P	0.479	0.392	0.355	0.355
Grazing pressure (GP)				
F (df: = 1, 1)	0.150	3.435	0.139	0.139
P	0.765	0.315	0.773	0.773
Loc x GP				
F (df: = 1, 12)	1.488	0.694	8.196	8.196
P	0.246	0.421	0.014	0.014

## Discussion

### Effect of grazing on soil nutrients

The soil sand content was higher under heavy grazing sites both in the ANP and ACBR. Moreover, grazing pressure had also an effect on the silt content. The higher sand content is probably caused by increasing run off and soil erosion, triggered by the higher percentage of bare ground and low basal cover, as well as low standing biomass of the herbaceous vegetation. Grazing affects the flux of nutrients in grazing lands through trampling, consumption, excreta deposition and redistribution and export (Lavado et al., 1996). The increased concentrations of total N under light grazing is probably due to the availability of organic material, higher standing biomass, and the export of nutrients through grazing at the heavy grazing sites. Similarly, a high concentration of exchangeable bases like Ca, K, Na and Mg was observed under light grazing. Hence, the CEC and pH were higher under light



grazing, following the trend of exchangeable bases. The EC was not significantly affected by location and grazing pressure, but also showed an increasing trend at light grazing.

According to Lavado et al. (1996), the difference in OC and total N of heavily and lightly grazed sites is mainly related to differences in the soil structure, with a well developed litter layer, a higher standing biomass and basal cover. Moreover, the higher N content in the lightly grazed sites might reflect the higher biological activities of soil micro-organisms, and this higher microbial activity might increase the N and C soil contents (Lavado et al., 1996; Han et al., 2008). Glaser et al. (2001) reported the influence of manure on soil nutrient status under heavy grazing conditions in a semi-arid region of northern Tanzania. The result of this latter study revealed that the nutrient status of the soil was improved as the grazing intensity reduced from heavy to light grazing conditions. The lower soil nutrient contents in the present study under the heavily grazed sites could be explained by the higher sand and lower clay contents since the continuous trampling by grazing animals will lead the blowing away of clay particles during the dry season, and their washing away during the wet season. Moreover, the lower soil nutrient content in the heavy grazing sites might be associated with the lack of animal excreta, which is probably amplified by the continuous removal of manure by the communities for fuel and other purposes (field observation).

### **Effect of grazing on herbaceous species**

As expected, lightly grazed sites had a higher herbaceous species richness compared with heavy grazed sites both in ACBR and ANP. Furthermore, the lightly grazed sites were dominated with grasses and herbaceous legumes of a perennial growth habit, while the heavy grazed sites were dominated by annuals. This is in agreement with our hypotheses that heavy grazing reduces herbaceous species diversity and results in a shift from grass species with a perennial life history to grass species with an annual life history. Moreover, the number of grass species found in the lightly grazed sites was higher than in the heavily grazed sites, and most of them were perennials. Heavy grazing reduces the growth rate and reproductive potential of perennial grasses and in so doing, influences the competitive relationships among the different species (Smith, 1979; Bilotta et al., 2007), so that heavily grazed perennial grass species lose competitive power compared with the lightly grazed ones, and subsequently unpalatable and grazing tolerant annual species become dominant in heavily grazed patches. Palatable perennial grass species are replaced by annual species, weeds and woody plants associated with increasing grazing pressure (Milton et al., 1994).

In African savannas, Sarmiento (1992) reported that, intensive livestock grazing has frequently resulted in a large species turn-over, with a reduction in palatability of the sward under heavy grazing. Also in South America, the dominant grasses are often unpalatable and grazing resistant, and are usually confined to disturbed, grazed habitats (Sarmiento, 1992). The mechanism is described by previous studies (Dyksterhuis, 1949; Smith, 1979) as an interaction between grazing and competition within the plant community. In this situation, grazing intolerant species disappear (e.g., *Panicum coloratum*, *Chloris gayana*, *Cenchrus ciliaris*, *Brachiaria comata*) because they are highly nutritious and eaten before seed setting or other species that can tolerate heavy grazing and physical damage (e.g., *Cynodon dactylon*, *Pennisetum candestenum*, *Sporobolus pyramidalis*) survive and subsequently replace highly grazed palatable species in the area. For instance, the presence of *A. adscenionsis*, *T. berteronianus*, *D. aegyptium* and *D. ternata* were reported to increase under heavy grazing in east African savannas (Abule et al., 2005b).

According to Skarpe (1991a), a reduction in basal cover and total standing biomass was observed in east African savannas due to intensive communal grazing. Similarly, Todd and Hoffman (1999) reported a reduction of perennial grass cover on the communal rangelands in Namaqualand, South Africa, of almost 20% in comparison with the commercial rangelands. The annual grass cover on the communal rangelands was, however, more than 11% higher than that of the commercial rangelands, indicating that the loss in perennial grass cover has been at least partially compensated for by an increase in annual cover. According to Todd and Hoffman (1999), in arid and semi-arid regions, heavy grazing is associated with a reduction in basal cover and standing biomass, and an increase in bare ground cover. In the present study, we observed that heavy grazing has lead to excessive defoliation of herbaceous vegetation (particularly annual and perennial grasses), and has a serious implication on herbaceous species diversity and their abundance as well as on aboveground standing biomass and percentage of basal cover in a semi-arid savanna of Ethiopia.

Annual rainfall was higher at ACBR, and we also found, as expected, a higher basal cover there, a lower proportion of bare ground, higher herbaceous species richness and abundance. However, the woody species richness was lower in ACBR, which can be explained by a difference in use history of the woody species.

### **Effect of grazing on woody vegetation**

Grazing pressure had a significant effect on the number of woody species in the present study. Similarly, location had an effect on the density of encroaching and non-encroaching woody

species. However, the proportion of encroaching and non-encroaching woody species was not influenced by grazing pressure. The increase in density of woody plants beyond a critical density suppresses herbaceous growth and its production in semiarid ecosystems (Richter et al., 2001). The threshold to distinguish between encroached and non-encroached conditions was set at 2400 woody plants ha<sup>-1</sup> by Roques et al. (2001). However, in our study the density of woody plants was far below this threshold for the encroached condition (Appendix Table 2.2). According to Mekuria et al. (1999), uncontrolled removal of trees and shrubs for fuel and various other purposes severely reduced the number of species and their density adjacent to the ACBR, and this in turn affected the regeneration capacity of woody species at heavy grazing sites by exposing the land to erosion and reducing seedling tree growth.

### **The interaction of grazing, vegetation and soil**

Heavy grazing in the present study resulted in the disappearance of perennial grass species and their replacement with annuals as well as in a reduction of species richness, plant abundance, standing biomass, basal cover, and a decrease in soil nutrient concentrations, compared with light grazing. Bilotta et al. (2007) has reported the reduction of herbaceous vegetation and soil nutrient concentrations as a consequence of defoliation and soil compaction due to heavy grazing, since herbivores consume aboveground biomass and in doing so, they reduce the amount of litter that falls to the soil surface (Singers and Schoenecker, 2003) and hence, the decomposition rate in the soil is reduced. According to Milton et al. (1994), excessive plant defoliation by grazing damages plant tissues, and compaction reduces plant species diversity and the percentage cover of the herbaceous vegetation. This would lead to a decline in plant abundance, standing biomass, and eventually produce bare patches where the soil surface is exposed to water and wind erosion, causing soil structural deformation and loss of soil nutrients. Similarly, the soil structural alteration caused by grazing animals also depends on the availability of the vegetation cover and standing biomass (Bilotta et al., 2007)

Under the prevailing conditions at our study sites, the higher soil nutrient contents under light grazing conditions are mainly attributed to the larger basal cover and the larger amounts of standing biomass. Higher soil C has been reported in lightly grazed sites compared with heavy grazed ones in Mongolia (Reeder and Schuman, 2002), due to an increase in aboveground plant litter, and an increase in annual forbs and grasses that enhance soil OM formation and accumulation (Han et al., 2008). Reeder and Schuman (2002) also found that grazing affects the redistribution of C within the plant-soil system as a result of changes in

plant species composition that may be affected by the interaction of soil and plant community composition under the influence of grazing practices. Herbivores may move net N from one habitat to another, and particularly in Africa, cattle and other wild herbivores rest under tree canopies for shade or in bomas at night (van der Waal et al., 2009), and, as a result, more faeces and urine are deposited under trees and in these pens than in open areas. The island of fertility pattern under shrub canopies is also perpetuated by the shrubs themselves, as a result of litter fall. The spatial heterogeneous grazing and resting increases the spatial heterogeneity in soil nutrient content (Augustine, 2003; Moe and Wegge, 2008). For instance, in east African rangelands, for cattle grazing an area of 20-25 km<sup>2</sup> boma<sup>-1</sup>, an estimated 0.24-0.30 g N m<sup>2</sup> year<sup>-1</sup> is removed (Augustine, 2003) due to heavy grazing, causing a gradual decline in the productivity of the grasslands (Jewell et al., 2007). Moreover, grazing could also affect the movement of N in the soil-plant-animal system as only a small portion of ingested N is retained by the livestock with the majority returning to the land in the form of faeces and urine, thereby decreasing the soil fertility, and increasing the spatial heterogeneity in N mineralization rates and N availability (Rossignol et al., 2006). Similarly, Moussa et al. (2009) also reported severe soil degradation in communal grazing areas in South Africa, due to interruption of nutrient cycles and loss of plant species and decrease in plant productivity, because of intensive grazing.

## **Conclusions**

We concluded that a reduction in soil quality parameters was observed as a direct effect of heavy grazing in a semi-arid savanna of Ethiopia and this consequently affected the growth, diversity, abundance, aboveground standing biomass and basal cover of herbaceous species. In addition, these semi-arid savannas seem to confirm the existence of two stable states and transitions described by other studies under the influence of grazing. One state was typical for sites with a low grazing pressure, characterized by ample herbaceous cover (basal cover), perennial grasses with scattered trees and good soil conditions. The second states can be found at sites with heavy grazing, with poor annual grasses, absence of perennial grasses, and a high proportion of bare soil with high soil pavements and pedestals. With an increase in pressure on land resources, the traditional transhumance disappeared, and herd mobility reduced, and as a result, pastoralists have been invading the game reserve and cattle ranch during the dry season and during droughts. If the current grazing practices continue, it seems likely that the ANP and the ACBR, which still have relatively good vegetation and soil conditions, become degraded within a short time. The rehabilitation of such a degraded state is unlikely to be achieved

spontaneously with simple reduction of the heavy grazing pressure because these areas may develop feedback loops that inhibit rehabilitation due to changes in vegetation structure and composition, and changes in soil properties associated with heavy grazing.

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**Appendix Table 2.1.** List of herbaceous species with their average abundance (N/m<sup>2</sup>), life forms (LF) and functional groups (FG) under light (LG) and heavy grazing (HG) conditions at two locations in a semi-arid savanna in Ethiopia (N = 320)

Species	Abundance (n/m <sup>2</sup> )					
	Abernosa Cattle Breeding Ranch		Awash National Park			
	HG	LG	HG	LG	LF	FG
<i>Achyranthus aspera</i>	-	4.0	-	-	A	F
<i>Amaranthus caudatus</i>	1.0	-	-	1.0	A	F
<i>Andropogon kelleri</i>	-	-	-	59.5	P	G
<i>Aristida adoensis</i>	30.8	86.1	11.0	42.3	A	G
<i>Aristida adscensionis</i>	-	113.4	-	-	A	G
<i>Belpharis ciliaris</i>	-	10.0	-	11.7	P	G
<i>Bidens pilosa</i>	-	2.4	-	6.5	A	F
<i>Bothriochloa radicans</i>	-	-	-	142.3	P	G
<i>Cenchrus ciliaris</i>	8.5	58.4	12.7	-	P	G
<i>Cenchrus setigerus</i>	-	12.0	10.6	-	P	G
<i>Chloris gayana</i>	-	46.3	-	-	P	G
<i>Chloris radiata</i>	17.4	116.2	-	-	P	G
<i>Chrysopogon plumulosus</i>	-	-	8.5	245.7	P	G
<i>Crotalaria albicaulis</i>	-	4.4	-	-	P	L
<i>Cynodon dactylon</i>	12.4	-	22.0	35.0	P	G
<i>Cyperus distens</i>	-	23.5	-	-	A	F
<i>Dactyloctenium aegyptium</i>	65.0	106.4	21.8	57.3	A	G
<i>Desmodium sericeus</i>	-	6.6	-	-	P	L
<i>Digitaria diagnolisis</i>	-	29.5	-	-	A	G
<i>Digitaria ternata</i>	-	96.6	-	-	A	G
<i>Digitaria velutina</i>	34.4	104.1	-	-	A	G
<i>Eleusine indica</i>	-	209.0	-	-	A	G
<i>Enneapogon cenchroides</i>	-	-	-	5.0	P	G
<i>Enteropogon macrostachyus</i>	-	-	-	39.6	P	G
<i>Epomoea cardofana</i>	1.0	-	-	-	A	F
<i>Eragrostis abyssinica</i>	37.2	59.4	-	-	A	G
<i>Eragrostis cilianensis</i>	10.5	7.0	6.8	17.0	A	G
<i>Eragrostis papposa</i>	24.2	48.3	8.1	65.3	A	G
<i>Eragrostis racemosa</i>	28.5	-	6.0	-	A	G
<i>Eriochloa nubica</i>	7.5	31.5	8.8	-	A	G
<i>Erucastrum arabicum</i>	1.0	4.0	-	-	A	F
<i>Galinsoga perviflora</i>	-	73.0	-	-	A	F
<i>Harpachne schimpri</i>	8.0	17.5	-	-	A	G
<i>Heteropogon contortus</i>	7.0	39.4	-	-	P	G
<i>Hibiscus aponeurus</i>	-	6.0	-	-	A	F
<i>Hyparrhenia hirta</i>	-	42.2	-	84.0	P	G
<i>Hyparrhenia rufa</i>	-	158.6	-	2.0	P	G
<i>Indigofera spicata</i>	2.0	12.7	1.0	5.0	P	L

Appendix Table 2.1. continued ...

<i>Indigofera vicioides</i>	-	4.3	-	-	P	L
<i>Ischaemum brachyatherum</i>	-	-	-	204.6	P	G
<i>Leucas microphyllia</i>	2.2	19.2	-	6.5	A	F
<i>Linthonia nutans</i>	-	-	-	47.3	P	G
<i>Macrotyloma axillare</i>	-	-	-	2.0	P	L
<i>Microchloa indica</i>	8.5	18.0	-	-	A	G
<i>Nicandra physalodes</i>	-	1.0	-	-	A	F
<i>Ocimum basilicum</i>	-	-	-	8.0	A	F
<i>Panicum atrosanguinium</i>	3.0	98.5	7.3	53.2	A	G
<i>Panicum coloratum</i>	2.0	48.3	-	117.4	P	G
<i>Panicum maximum</i>	-	8.0	-	-	P	G
<i>Parthenium hystereresis</i>	-	-	-	2.0	A	F
<i>Ruellia patula</i>	-	23.0	-	-	A	F
<i>Sehima nervosa</i>	-	55.0	-	-	P	G
<i>Setaria acromeleana</i>	-	15.0	-	-	A	G
<i>Setaria incrossata</i>	-	19.7	-	54.0	A	G
<i>Setaria pumila</i>	6.8	77.1	2.5	55.2	A	G
<i>Snowdenia polystachia</i>	-	196.0	-	-	A	G
<i>Solanum incanum</i>	-	3.7	-	1.6	A	F
<i>Solanum nigrum</i>	-	5.0	-	-	A	F
<i>Solanum somalensis</i>	-	-	2.0	-	P	F
<i>Sorghum verticilliforum</i>	-	-	-	126.8	A	G
<i>Sporobolus ioclodus</i>	-	-	7.5	-	P	G
<i>Sporobolus pyramidalis</i>	18.4	110.3	4.8	27.8	P	G
<i>Tagetes minuta</i>	-	8.2	-	-	A	F
<i>Tephrosia subtriflora</i>	-	2.1	-	4.5	P	L
<i>Tetrapogon cenchrifomis</i>	-	-	-	14.0	P	G
<i>Tetrapogon tenellus</i>	-	65.0	7.3	32.0	P	G
<i>Tragus berteronianus</i>	75.0	28.4	-	-	A	G
<i>Tragus racemosus</i>	68.1	6.0	7.9	16.0	A	G
<i>Tribulus ternatus</i>	6.0	-	-	-	A	F
Total number of species	26	51	17	33	-	-
No. of grass species	20	33	15	24	-	-
No. of annual grasses	14	20	8	14	-	-
No. of perennial grasses	6	13	7	10	-	-
Total no. herbaceous legumes	1	6	1	3	-	-
Forb total	5	12	1	6	-	-

\* A = annuals; P = perennials; \*\* F = forbs; G = grasses; L = herbaceous legumes; LF = Life form; FG = Functional group

**Appendix Table 2.2.** List of woody species with their average abundance (N/ha) under light (LG) and heavy grazing (HG) conditions at two locations (Abernosa Cattle Breeding Ranch and Awash National Park) in a semi-arid savanna in Ethiopia.

Species	Abernosa Cattle Breeding Ranch		Awash National Park	
	HG	LG	HG	LG
<i>Acacia brevispica</i>	-	-	-	7.5
<i>Acacia mellifera</i>	-	-	26.5	1.75
<i>Acacia nubica</i>	-	-	115	15.6
<i>Acacia senegal</i>	-	-	56.3	8.6
<i>Acacia seyal</i>	9.3	17.9	-	2.3
<i>Acacia sieberiana</i>	4.5	52.0	-	-
<i>Acacia tortilis</i>	57.2	73.3	30.3	17.2
<i>Asparagus asiaticus</i>	-	1.7	-	-
<i>Balanites aegyptiaca</i>	8.0	9.6	15.4	27.8
<i>Barbeya oleoides</i>	-	2.5	-	-
<i>Commiphora africana</i>	-	4.0	7.0	4.3
<i>Dicrostachys cinerea</i>	16.7	43.6	18.0	45.4
<i>Ehratia cymosa</i>	-	2.0	-	-
<i>Erythrina burana</i>	-	4.5	-	-
<i>Grewa bicolor</i>	-	1.5	-	-
<i>Grewa erythraea</i>	-	-	24.6	8.2
<i>Grewa villosa</i>	-	-	5.8	7.7
<i>Gutenbergia cordifolia</i>	-	-	-	25.2
<i>Hypoestes triflora</i>	-	-	2.0	11.0
<i>Opuntia ficus-indica</i>	-	4.0	-	-
<i>Pithecellobium dulce</i>	-	-	2.7	3.75
<i>Polyscias fulva</i>	-	2.5	-	-
<i>Solanum somalensis</i>	-	-	-	2.0
<i>Terminalia brownie</i>	-	2.0	-	-
<i>Vernonia cinerascens</i>	-	-	-	6.0
<i>Ximenia Americana</i>	-	1.0	-	-
<i>Ziziphus spina-christi</i>	-	2.0	-	-
Total number species	4.0	16.0	10.0	16.0
Number of species from the total (%)	14.8	59.3	27.0	59.3



# 3

Influence of grazing on soil seed banks determines the restoration potential of aboveground vegetation in a semi-arid savanna of Ethiopia



Z.K. Tessema, W.F. de Boer, R.M.T. Baars and H.H.T. Prins

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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. However, species richness in the seed bank was 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.

**Keywords:** Functional group; Grass species; Grazing pressure; Savannas restoration; Seed banks; Vegetation degradation

## Introduction

A continuous grass layer with a discontinuous layer of trees and shrubs are typical features of semi-arid savannas (Van de Koppel and 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 and Lazzaro, 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). Grazing is often regarded as the most important factor responsible for large structural changes in savanna ecosystems. Increasing the grazing pressure beyond a certain threshold, often leads to irreversible effects. At high grazing pressures, the perennial grasses disappear and are replaced by annual herbs, which could trigger a vegetation collapse; once the herbaceous vegetation collapses, it is extremely difficult to return to the grassland state, even if the grazing pressure is greatly reduced (Rietkerk et al., 1996; Van de Koppel et al., 1997). However, the return of species that disappeared from the aboveground vegetation under extensive, or “heavy” grazing can be facilitated by the soil seed banks (Baker, 1989; Leck et al., 1989; de Villiers et al., 2003), as the soil seed bank forms a pool of propagules for the regeneration of the native vegetation after disturbance, stimulating recovery of the vegetation (Thompson and Grime, 1979; Leck et al., 1989). 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 a vegetation with a perennial grass cover.

Similarities between the soil seed banks and aboveground vegetation have been reported by previous studies (Leck and Gravelline, 1979; Henderson et al., 1988; Levassor et al., 1991), although several studies show poor similarities of species composition between the soil seed banks and the aboveground vegetation (Bakker and Berendse, 1999; de Villiers et al., 2003; Lemenih and Teketay, 2006; Solomon et al., 2006). This dissimilarity is characterized by more perennial grasses and woody plants in the aboveground vegetation (Abule et al., 2005b; 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 and Baskin, 2004; Scott et al., 2010, Tessema et al., 2011b), caused by either embryonic dormancy or impermeable seed coat 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. Moreover, soil depth has an influence on the density of seeds and

number of species in the soil seed bank, as the majority of seeds and species in the soil seed bank are found in the upper soil layer, but density gradually decreases with increasing soil depth (O'Connor and Pickett, 1992; Wassie and Teketay, 2006). 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 and Graham, 1983), under influence of grazing (Bilotta et al., 2007; 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 (de Villiers et al., 2003; Solomon et al., 2006; Hopfensperger, 2007; Kassahun et al., 2008b). Indeed, knowledge about the factors and mechanisms that contribute to the recovery of vegetation, and information on the species composition in the 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: (i) 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 (ii) 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<sup>2</sup> 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 277-653 mm, and was highly variable among years (coefficient of variation CV = 103%). Its main rainy season is from July-September, with a short rainy

season from February-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., 2005a).

The ACBR covers about 23 km<sup>2</sup>, 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-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 years ago by fencing the woodland and paddocks were established for rotational grazing.

The vegetation is open Acacia woodland dominated with grasses (Mekuria 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 (Mekuria et al., 1999; Abule et al., 2005b; 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<sup>2</sup> 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, totalling 320 (2 locations x 2 grazing pressures x 4 sampling sites x 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 >1m height) and their density were recorded in a sample area of 100 m x 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 (2 locations x 2 grazing pressures x 4 sampling sites x 3 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 soil samples, 1-m<sup>2</sup>, were collected in each sampling site at two soil depths (0-5 and 5-10 cm), yielding a total of 640 samples in both locations (2 locations x 2 grazing pressures x 4 sample sites x 20 subsamples x 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 (2 locations x 2 grazing pressures x 4 sample sites x 2 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 non-viable seeds (Poiani and 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<sup>2</sup>) were used per composite soil sample per soil depth, totalling 160 pots. The pots were placed at random in the greenhouse at Haramaya University of Ethiopia, with no artificial light supplied. The greenhouse temperature was 19-22°C during the day and 10-12°C during the 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 after 1 week, 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 months (November 2008 - April 2009), since the number of emerging seedlings, particularly grasses and forbs declined considerably after 6 months. 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):  $\sum \sum d_{ij} P_i P_j$ , where  $d_{ij}$  and  $P_i P_j$  represents the dissimilarity and the relative abundance between species  $i$  and  $j$ , respectively (Ricotta and Szeidl, 2006; Ricotta and 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.

## **Results**

### **Number of emerged seedlings**

The lightly grazed sites had a higher number of emerged seedlings (2061 seeds/m<sup>2</sup>) in the soil seed bank compared with the heavily grazed sites (1302 seeds/m<sup>2</sup>). There were also site-specific differences, as the number of emerged seedlings at ACBR was higher than those at ANP (2807 and 557 seeds/m<sup>2</sup>, respectively; Table 3.1). As expected, the upper soil layer had more emerged seedlings compared with the deeper soil layer in both locations (Table 3.1). 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 x soil depth; Table 3.1). The full model explained together 87% 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 one Acacia species germinated (Appendix Table 3.1). The number of species at ACBR and ANP was similar (59 and 58 species, respectively). Ten grass species (5 perennial and 5 annuals) were found only in the lightly grazed sites and were totally absent from the heavily grazed sites. However, only one unique perennial grass species (*Belpharis ciliaris*) was found at the heavily grazed sites, and these sites were dominated by annual forbs.

The average number of emerged species (species richness) in the soil seed bank was higher at ACBR (Table 3.1) than at ANP with a mean of 6.8 and 3.1 species/m<sup>2</sup>, respectively (Table 3.1). More species emerged from the upper soil layer than the deeper soil layer (8 and 3.8 species/m<sup>2</sup>, respectively; Table 3.1).

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 3.3).





**Table 3.1.** 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 GLM (F, P,  $R^2_{\text{adjusted}}$ ).

	Number of species (n/m <sup>2</sup> )	Seed density (n/m <sup>2</sup> )
Mean ± 95% CL		
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±15.9
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 x GP		
F (df = 1, 24)	2.41	5.001
P	0.13	0.040
LOC x SD		
F (df = 1, 24)	0.27	6.871
P	0.61	0.020
GP x SD		
F (df = 1, 24)	0.09	9.492
P	0.62	0.011
LOC x GP x SD		
F (df = 1, 24)	0.01	0.030
P	0.967	0.875
$R^2_{\text{adjusted}}$	0.66	0.874

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 (Appendix Fig. 3.1a and 3.1b). 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 (Appendix Fig. 3.1a). 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 (Appendix Fig. 3.1b).

### 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 3.2). 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 3.2). The upper soil layers produced more seedlings of annual grasses, perennial grasses, herbaceous legumes and annual forbs compared with the lower soil layers (Table 3.2).

**Table 3.2.** Effect of light and heavy grazing on number of emerging seedlings ( $n/m^2$ ) for the different functional group from the soil seed bank samples at two locations in a semi-arid savanna of Ethiopia, together with results ( $F$ ,  $P$ ,  $R^2_{\text{adjusted}}$ ) of the GLM that tested for differences in location, grazing pressure, and soil depth and their interactions.

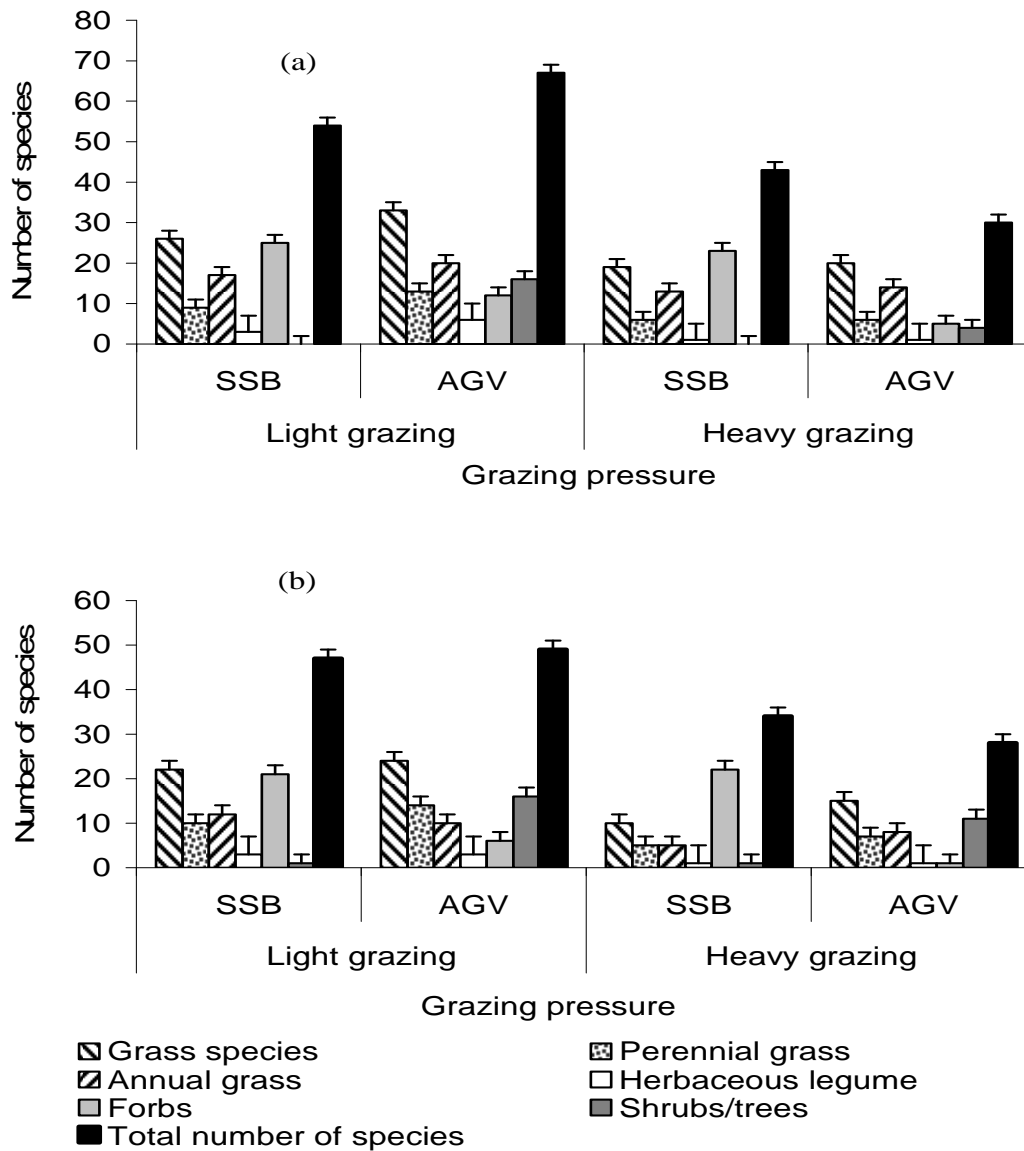
	Functional group (Mean $\pm$ 95% CI)				
	Annual grass	Perennial grass	Total grass	Herbaceous legume	Annual forbs
Abernosa Cattle Breeding Ranch					
Light grazing					
5 cm	1458.4 $\pm$ 87.2	1172.5 $\pm$ 61.9	2630.8 $\pm$ 111.8	169.0 $\pm$ 31.4	1491.8 $\pm$ 77.2
10 cm	796.1 $\pm$ 87.8	626.5 $\pm$ 61.9	1422.6 $\pm$ 111.8	60.7 $\pm$ 31.4	632.1 $\pm$ 77.2
Heavy grazing					
5 cm	911.8 $\pm$ 87.8	413.9 $\pm$ 61.9	1325.7 $\pm$ 111.8	27.7 $\pm$ 31.4	809.1 $\pm$ 77.2
10 cm	300.5 $\pm$ 87.8	293.1 $\pm$ 61.9	593.6 $\pm$ 111.8	26.6 $\pm$ 31.4	529.4 $\pm$ 77.2
Awash National Park					
Light grazing					
5 cm	408.1 $\pm$ 87.8	748.7 $\pm$ 61.9	1156.8 $\pm$ 111.8	84.3 $\pm$ 31.4	268.4 $\pm$ 77.2
10 cm	132.1 $\pm$ 87.8	95.1 $\pm$ 61.9	224.3 $\pm$ 111.8	11.1 $\pm$ 3.6	108.1 $\pm$ 31.4
Heavy grazing					
5 cm	103.8 $\pm$ 7.6	55.0 $\pm$ 22.3	125.9 $\pm$ 65.7	6.7 $\pm$ 1.5	124.6 $\pm$ 9.8
10 cm	5.8 $\pm$ 2.1	27.4 $\pm$ 4.7	60.8 $\pm$ 10.5	3.1 $\pm$ 1.5	41.6 $\pm$ 6.2
Location (LOC)					
$F$ (df = 1, 4)	129.484	81.350	194.224	4.041	178.727

Table 3.2. continued...

<i>P</i>	<0.001	<0.001	<0.001	0.046	<0.001
Grazing Pressure (GP)					
<i>F</i> (df = 1, 24)	35.404	111.981	110.904	8.634	20.778
<i>P</i>	<0.001	<0.001	<0.001	0.004	<0.001
Soil Depth					
<i>F</i> (df = 1, 24)	44.284	54.470	86.398	4.387	40.075
<i>P</i>	<0.001	<0.001	<0.001	0.038	<0.001
LOC x GP					
<i>F</i> (df = 1, 24)	6.102	3.561	8.842	1.019	6.936
<i>P</i>	0.015	0.061	0.003	0.314	0.009
LOC x SD					
<i>F</i> (df = 1, 24)	13.213	0.054	8.897	0.133	16.847
<i>P</i>	0.357	0.816	0.003	0.716	<0.001
GP x SD					
<i>F</i> (df = 1, 24)	0.854	39.909	18.069	3.949	9.052
<i>P</i>	0.357	<0.001	<0.001	0.049	0.003
LOC x GP x SD					
<i>F</i> (df = 1, 24)	0.263	2.136	1.532	0.176	5.301
<i>P</i>	0.609	0.146	0.218	0.673	0.023
<i>R</i> <sup>2</sup> <sub>adjusted</sub>	0.585	0.643	0.726	0.088	0.630

### 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 (Fig. 3.1a and 3.1b). However, the total number of germinated species in the soil seed bank was 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 (Fig. 3.1a and 3.1b). 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 (Fig. 3.1a and 3.1b). 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.



**Fig. 3.1.** 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.

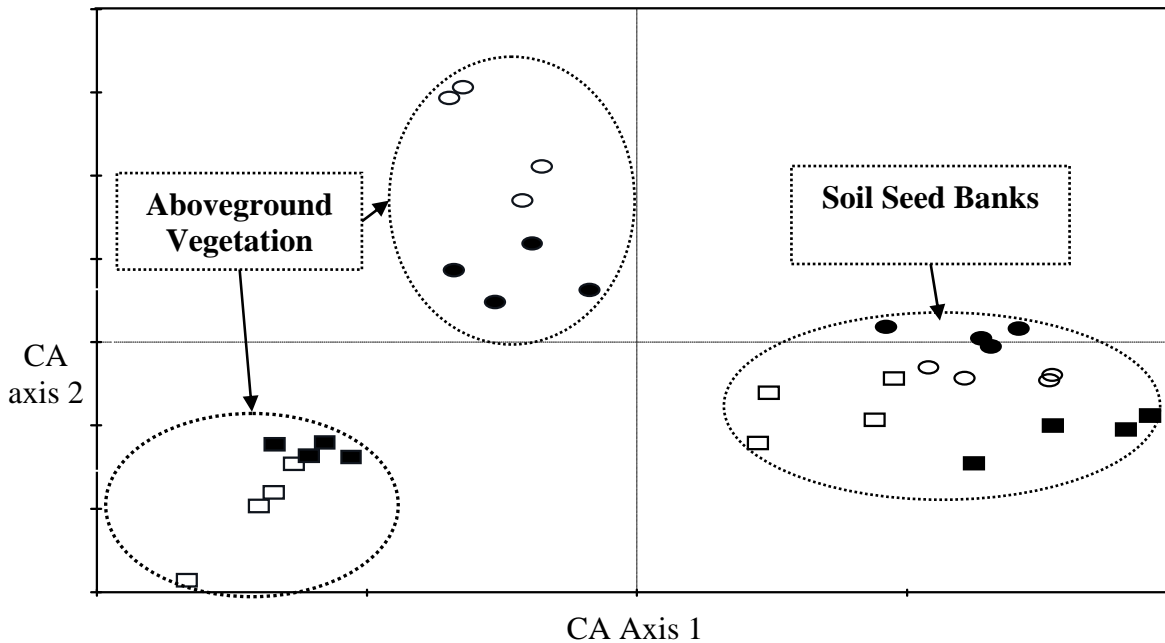
The lightly grazed sites had a higher ( $F_{2,979} = 4.10$ ;  $P < 0.02$ ;  $R^2 = 0.68$ ) Jaccard's coefficient of similarity than the heavily grazed sites both in the soil seed bank and aboveground vegetation (Table 3.3). The mean similarity in species composition of the aboveground vegetation was 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 3.3). The mean similarity coefficient between the soil seed bank and aboveground vegetation was relatively low (0.13; Table 3.3), 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 3.3).

**Table 3.3.** Mean Rao's quadratic diversity index (Q) and mean Jaccard's coefficient of similarity (N = 160) for species composition, comparing the soil seed banks (SSB) and aboveground vegetation (AGV) 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.

			SSB				AGV		
			ACBR		ANP		ACBR	ANP	
Q			LG	HG	LG	HG	LG	HG	LG
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

The CA ordination separated the soil seed bank and aboveground vegetation composition along the first ordination axis (Fig. 3.2). 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.



**Fig. 3.2.** Ordination diagram of the 16 sampling sites for the soil seed bank species and aboveground vegetation under two grazing pressure (filled symbols = heavily grazed sites and open symbols = lightly grazed sites) at two locations (circles = Abernosa Cattle Breeding Ranch and squares = Awash National Park) by a Correspondance Analysis (CA) in a semi-arid savanna of Ethiopia.

## 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 (Veenendaal et al., 1996a; Tessema et al., 2011a), leading to smaller seed banks. 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.

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 and Teketay, 2006; Solomon et al., 2006), which is in agreement with our findings. Moreover, that woody species do not accumulate seeds in the soil seed bank suggests that their regeneration from seeds would be prevented by the removal of mature individuals in the aboveground vegetation (Wassie and 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). However, the number of seeds emerged in the soil seed banks depends on the characteristics of the study sites (Meissner and Facelli, 1999; Kinloch and 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 variations in seed density might be associated with changes in soil structure due to heavy grazing (Hopkins and Graham, 1983). According to Skoglund (1992) recruitment from the seed bank is restricted to periods with favourable conditions of soil parameters controlling seed germination. The presence of bare soil and the sand content tend to increase under heavily grazing (Abule et al., 2005b; 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 the heavily grazed sites, indicating that grazing has reduced the species diversity not only in the aboveground vegetation but also in the soil seed banks as a result that has been obtained in Australia and South Africa (Snyman, 2004; Kinloch and Friedel, 2005). The number of species and species composition on heavily grazed areas often do not revert to that of lightly grazed areas after good rainfall, indicating that the species composition on the heavily grazed areas has undergone persistent changes (Abule et al., 2005b; 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 the soil seed banks.

### **Functional group**

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 competitive pressure and seed production of the perennial grass component, thereby allowing annual forbs to reproduce, increasing their seed contribution to the soil seed banks (Solomon et al., 2006). Annual species are more abundant in soil seed bank compared with perennial species owing to their high productive output (Sternberg et al., 2003; Scott et al., 2010) because perennial grasses often propagate vegetatively (O'Connor, 1994, 1996).

### **Similarity between the soil 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 and Teketay, 2006), Church forests (Wassie and Teketay, 2006) and in Acacia woodlands (Mekuria et al., 1999). Previous studies (Thompson and 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 and Berendse, 1999). Others, however, report much higher similarity (Leck and Gravelline, 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).



## **Conclusions**

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 differences 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 concluded 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 good fodder value in semi-arid savannas.

## **Acknowledgements**

The authors would like to thank Nuffic for funding this research, the Haramaya University of Ethiopia for providing greenhouse and transport facilities during the research, and Mr. Mekonen and Mr. Abera for allowing us to collect soil samples in the ACBR and ANP, respectively. We extend our gratitude to the editors of *Biotropica* and anonymous reviewers for their valuable comments on the manuscript.



**Appendix Table 3.1.** List of species in the soil seed banks (SSB, germinated seedlings (n/m<sup>2</sup>)) and aboveground vegetation (AGV, relative abundance (n/m<sup>2</sup>)) with their life forms (LF) and functional groups (FG) under light and heavy grazing conditions at two locations in semi-arid savannas of Ethiopia

Species	Abernosa Cattle Breeding Ranch				Awash National Park				LF	FG
	Heavy grazing		Light grazing		Heavy grazing		Light grazing			
	SSB	AGV	SSB	AGV	SSB	AGV	SSB	AGV		
<i>Abutilon figarianum</i>	-	-	-	-	-	-	15.2	-	A	F
<i>Acacia senegal</i>	-	-	-	-	15.2	56.3	15.2	8.6	P	SH
<i>Acalypha indica</i>	-	-	-	-	15.2	-	-	-	A	F
<i>Acanthospermum hispidum</i>	20.2	-	15.2	-	-	-	-	-	A	F
<i>Achyranthes aspera</i>	-	-	15.2	-	15.2	-	-	-	A	F
<i>Alchemilla abyssinica</i>	15.2	-	15.2	-	15.2	-	30.4	-	A	F
<i>Alchemilla rothii</i>	15.2	-	109.3	-	91.1	-	45.5	-	A	F
<i>Amaranthus caudatus</i>	30.4	1.0	30.4	-	30.4	-	-	1.0	A	F
<i>Amaranthus dubius</i>	20.2	-	15.2	-	22.8	-	15.2	-	A	F
<i>Andropogon kelleri</i>	-	-	-	-	-	-	-	59.5	P	G
<i>Aristida adoensis</i>	136.6	30.8	145.9	86.1	121.4	11.0	183.6	42.3	A	G
<i>Aristida adscensionis</i>	-	-	102.4	113.4	-	-	333.9	-	A	G
<i>Asterolinum adoense</i>	117.2	-	62.0	-	-	-	151.8	-	A	F
<i>Belpharis ciliaris</i>	15.2	-	-	10.0	-	-	-	11.7	P	G
<i>Bidens pilosa</i>	15.2	-	22.8	2.4	-	-	-	6.5	A	F
<i>Bothriochloa radicans</i>	-	-	-	-	-	-	136.7	142.3	P	G
<i>Brachiaria comata</i>	-	-	45.5	-	-	-	546.3	-	P	G
<i>Brachiaria eruciformis</i>	-	-	243.0	-	-	-	-	-	P	G
<i>Cenchrus ciliaris</i>	-	8.5	58.4	58.5	12.7	12.5	-	-	P	G
<i>Cenchrus setigerus</i>	-	-	-	12.0	-	10.6	-	-	P	G
<i>Chenopodium album</i>	237.7	-	182.1	-	37.9	-	30.4	-	A	F
<i>Chenopodium murale</i>	173.7	-	75.9	-	30.4	-	-	-	A	F
<i>Chloris gayana</i>	129.0	-	249.7	46.3	235.2	-	60.7	-	P	G
<i>Chloris radiata</i>	783.7	17.4	2092.6	116.2	37.9	-	68.3	-	P	G
<i>Chrysopogon plumulosus</i>	121.4	-	379.4	-	75.9	8.5	637.9	245.7	P	G
<i>Commelina benghalensis</i>	15.2	-	-	-	15.2	-	15.2	-	A	F
<i>Chrysopogon aucheri</i>	-	-	15.2	-	-	-	318.7	-	P	G
<i>Conyza bonariensis</i>	15.2	-	15.2	-	15.2	-	15.2	-	A	F
<i>Corchorus oliotrius</i>	-	-	-	-	-	-	15.2	-	A	F
<i>Corchorus trilocularis</i>	-	-	-	-	-	-	15.2	-	A	F

Appendix Table 3.1. continued....

<i>Crotalaria albicaulis</i>	15.2	-	15.2	4.4	15.2	-	15.2	-	P	L
<i>Cynodon dactylon</i>	113.8	12.4	246.1	-	-	22.0	283.3	35.0	P	G
<i>Cyperus distans</i>	-	23.5	-	-	-	-	-	-	A	F
<i>Cyperus rotundus</i>	-	-	-	-	83.5	-	-	-	A	F
<i>Dactyloctenium aegypticum</i>	205.6	65.0	460.4	106.4	-	21.8	2640.4	57.3	A	G
<i>Dactyloctenium scindicum</i>	106.3	-	91.1	-	-	-	-	-	A	G
<i>Desmodium sericeus</i>	-	6.6	-	-	-	-	-	-	P	L
<i>Digitaria abyssinica</i>	293.2	-	561.5	-	-	-	189.7	-	A	G
<i>Digitaria diagnolisis</i>	-	66.7	-	59.4	-	-	-	-	A	G
<i>Digitaria ternata</i>	195.4	-	249.3	96.6	-	-	-	-	A	G
<i>Digitaria velutina</i>	91.1	34.4	121.4	104.1	-	-	-	-	A	G
<i>Echinochloa colonum</i>	-	-	-	-	91.1	-	417.3	-	P	G
<i>Eleusine indica</i>	-	-	166.9	209.0	-	-	-	-	A	G
<i>Eleusine jaegeri</i>	182.1	-	295.9	-	-	-	45.5	-	A	G
<i>Enneapogon cenchriodes</i>	-	-	-	-	-	-	-	5.0	P	G
<i>Enteropogon macrostachyus</i>	-	-	-	-	-	-	-	39.6	P	G
<i>Eragrostis aspera</i>	625.8	-	977.7	-	15.2	-	108.1	-	A	G
<i>Eragrostis cilianensis</i>	60.7	10.5	177.0	7.0	-	6.8	-	17.0	A	G
<i>Eragrostis papposa</i>	313.6	24.2	335.2	48.3	333.9	8.1	432.5	65.3	A	G
<i>Erica arborea</i>	-	-	-	-	15.2	-	-	-	A	F
<i>Eriochloa nubica</i>	-	7.5	121.4	31.5	-	8.8	-	-	A	G
<i>Erucastrum arabicum</i>	19.0	1.0	20.2	4.0	-	-	15.2	-	A	F
<i>Euphorbia hirta</i>	60.7	-	45.5	-	37.9	-	60.7	-	A	F
<i>Galinsoga parviflora</i>	34.7	-	60.7	73.0	20.2	-	30.4	-	A	F
<i>Harpachne schimpri</i>	65.8	8.0	68.3	17.5	-	-	-	-	A	G
<i>Heteropogon contortus</i>	-	7.0	-	39.4	-	-	-	-	P	G
<i>Hibiscus aponerus</i>	-	6.0	-	-	-	-	-	-	A	F
<i>Hibiscus calyphyllus</i>	-	-	-	-	15.2	-	15.2	-	A	F
<i>Hibiscus micranthus</i>	-	-	35.4	-	-	-	-	-	A	F
<i>Hyparrhenia hirta</i>	-	-	-	42.2	-	-	-	84.0	P	G
<i>Hyparrhenia rufa</i>	-	-	-	158.6	-	-	-	2.0	P	G
<i>Hypoestes forskalii</i>	-	-	53.1	-	-	-	-	-	A	F
<i>Indigofera coerulea</i>	-	-	15.2	-	-	-	-	-	P	L
<i>Indigofera spicata</i>	-	2.0	15.2	12.7	-	1.0	26.6	5.0	P	L
<i>Indigofera vicioides</i>	-	-	-	4.3	-	-	-	-	P	L

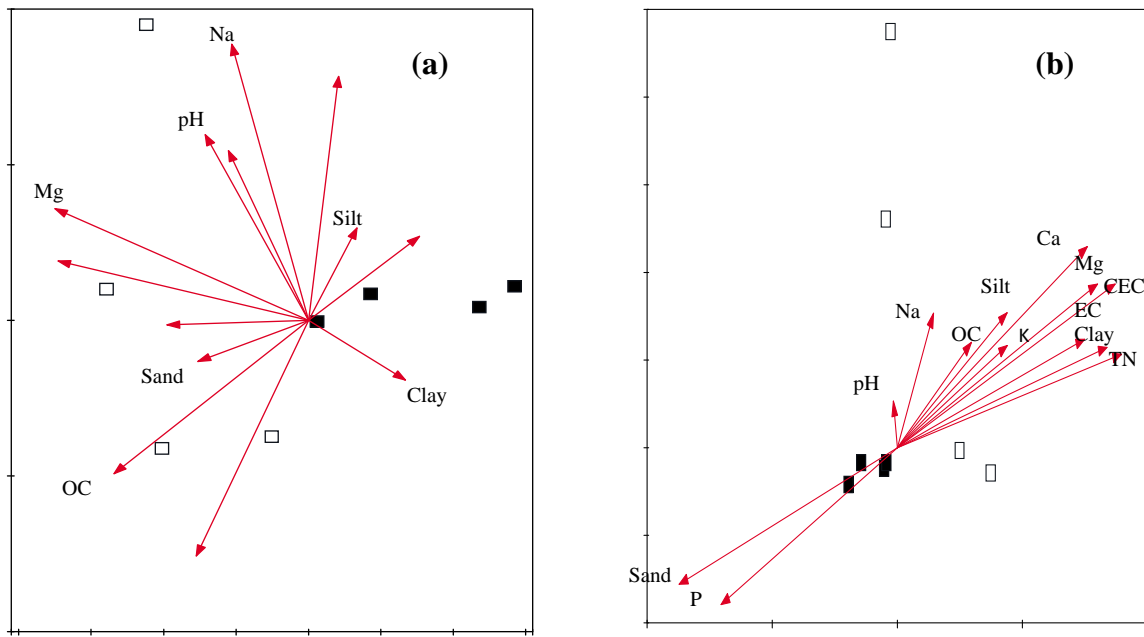
Appendix Table 3.1. continued....

<i>Ipomoea cordofana</i>	16.6	1.0	15.2	-	-	-	15.2	-	A	F
<i>Ipomoea ochracea</i>	-	-	15.2	-	-	-	-	-	A	F
<i>Ischaemum brachyatherum</i>	-	-	-	-	-	-	-	204.6	P	G
<i>Leucas microphylla</i>	15.2	2.2	-	18.0	15.2	-	15.2	6.5	A	F
<i>Linthonia nutans</i>	-	-	-	-	-	-	45.5	47.3	P	G
<i>Macrotyloma axillare</i>	-	-	-	-	-	-	-	2.0	P	L
<i>Microchloa indica</i>	-	8.5	-	18.0	-	-	-	-	A	G
<i>Nicandra physaloides</i>	18.2	-	15.2	1.0	-	-	-	-	A	F
<i>Ocimum basilicum</i>	-	-	-	-	15.2	-	30.4	8.0	A	F
<i>Ocimum verticillifolium</i>	-	-	-	-	136.6	-	-	-	A	F
<i>Orobanche ramose</i>	15.2	-	-	-	-	-	-	-	A	F
<i>Otostegia tomentosa</i>	15.2	-	22.8	-	15.2	-	-	-	A	F
<i>Oxalis latifolia</i>	-	-	15.2	-	22.8	-	-	-	A	F
<i>Panicum atrosanguinum</i>	75.9	3.0	106.2	98.5	45.5	7.3	-	53.2	A	G
<i>Panicum coloratum</i>	91.1	2.0	96.1	48.3	-	-	58.2	117.4	P	G
<i>Panicum maximum</i>	-	-	-	8.0	-	-	-	-	P	G
<i>Parthenium hysterisis</i>	-	-	-	-	-	-	-	2.0	A	F
<i>Ruellia patula</i>	-	-	-	23.0	-	-	-	-	A	F
<i>Sehima nervosa</i>	-	-	-	55.0	-	-	-	-	P	G
<i>Setaria acromeleana</i>	-	-	-	15.0	-	-	45.5	-	A	G
<i>Setaria incrossata</i>	-	-	-	19.7	-	-	-	54.0	A	G
<i>Setaria pumila</i>	-	6.8	-	77.1	-	2.5	197.3	55.2	A	G
<i>Snowdenia polystachia</i>	-	-	-	196.0	-	-	-	-	A	G
<i>Solanum incanum</i>	-	-	-	3.7	-	-	22.8	1.6	A	F
<i>Solanum nigrum</i>	62.7	-	20.2	5.0	15.2	-	20.2	-	A	F
<i>Solanum somalensis</i>	-	-	15.2	-	-	2.0	60.7	-	P	F
<i>Sonchus oleraceus</i>	18.2	-	41.7	-	38.8	-	19.5	-	A	F
<i>Sorghum verticillifolium</i>	-	-	-	-	-	-	-	126.0	A	G
<i>Sporobolu ioclades</i>	-	-	-	-	-	7.5	-	-	P	G
<i>Sporobolus pyramidalis</i>	-	18.4	-	110.3	-	4.8	229.0	27.8	P	G
<i>Tagetes minuta</i>	-	-	15.2	8.2	-	-	-	-	A	F
<i>Tephrosia pentaphylla</i>	-	-	-	-	-	-	15.2	-	P	L
<i>Tephrosia subtriflora</i>	-	-	-	2.1	-	-	-	4.2	P	L
<i>Tetrapogon cenchroides</i>	-	-	-	-	-	-	-	14.0	P	G
<i>Tetrapogon tenellus</i>	-	-	-	65.0	-	7.3	-	32.0	P	G

Appendix Table 3.1. continued....

<i>Tragus berteronianus</i>	88.9	75.0	53.1	28.4	46.6	-	68.3	-	A	G
<i>Tragus racemosus</i>	60.7	68.1	106.2	6.0	-	7.9	30.4	16.0	A	G
<i>Tribulus ternatus</i>	-	6.0	-	-	-	-	-	-	A	F
<i>Tribulus terrestris</i>	15.2	-	-	-	-	-	-	-	A	F
<hr/>										
Number of species										
Grass species	19	20	26	33	10	15	22	24	-	-
Perennial grass	6	6	9	13	5	7	10	14	-	-
Annual grass	13	14	17	20	5	8	12	10	-	-
Herbaceous legume	1	1	3	6	1	1	3	3	-	-
Forbs	23	5	25	12	22	1	21	6	-	-
Shrubs/trees	0	4	0	16	1	11	1	16	-	-
Total number of species	43	30	54	67	34	28	47	49	-	-
<hr/>										
Percentage of species										
Grass species	44.2	66.7	48.2	49.3	29.4	53.6	46.8	49.0	-	-
Perennial grass	14.0	20.0	16.7	19.4	14.7	25.0	21.3	28.6	-	-
Annual grass	30.2	46.7	31.5	29.9	14.7	28.6	25.5	21.3	-	-
Herbaceous legume	2.3	3.3	5.6	9.0	2.9	3.6	6.4	6.1	-	-
Forbs	53.5	16.7	46.3	17.9	64.7	3.6	44.7	12.3	-	-
Shrubs/trees	0.0	13.3	0	23.9	2.9	39.3	2.1	32.7	-	-
Total percentage of species	100	100	100	100	100	100	100	100	-	-

A = annuals; P = perennials; F = forbs; G = grasses; L = herbaceous legumes; SH = shrubs



**Appendix Fig. 3.1.** Ordination diagram of the sampling sites  $\times$  soil parameters under two grazing pressures (filled symbols = heavily grazed sites and open symbols = Lightly grazed sites) at Abernosa Cattle Breeding Ranch (a) and Awash National Park (b) by a Canonical Correspondence Analysis (CCA) in a semi-arid savanna of Ethiopia. Ca = calcium; CEC = cation exchange capacity; EC = electrical conductance; Mg = magnesium; K = potassium; Na = sodium; N = nitrogen; OC = organic carbon; P = phosphorus.



# 4

Grass plant survival and temporal soil seed bank dynamics under contrasting grazing regimes in a semi-arid savanna



Z.K. Tessema, W.F. de Boer, R.M.T. Baars and H.H.T. Prins (submitted)

### **Abstract**

Successful plant recruitment is a function of seed availability, germination, and seedling survival. We studied the number of viable seeds, species richness and functional groups in the soil seed banks under light and heavy grazing over time, as well as the mortality of grass populations in a semi-arid Ethiopian savanna. A total of 103 species (15 perennial and 29 annual grasses, 6 legumes, 52 forbs and 1 woody species) emerged from all soil samples over the nine months sampling period. Lightly grazed sites had a higher seedling density compared with heavily grazed sites. Seedling density increased over the first three months of soil sampling and decreased thereafter. Perennial grass species 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 banks through grazing. The mean mortality from the seedling stage to adult plants was 65%, which might be due to moisture stress and poor soil conditions as a result of heavy grazing. The seed-to-seedling stage was the most critical transitional stage for grass survival, suggesting exclusion from grazing in the early germination stage and/or supply of water to facilitate the transition from seedling-to-established plants in semi-arid savannas. In conclusion, depletion of perennial grass seeds in the soil due to heavy grazing coupled with high seedling mortality can disappear perennial grasses in the soil seed banks, triggering to local extinction of perennial grasses in the aboveground vegetation in semi-arid savannas.

**Keywords:** Grass population; Growth stage; Functional group; Seedling density; Species richness; Vegetation restoration



## **Introduction**

The disappearance of good fodder grasses are serious challenges in arid and semi-arid savannas as a result of continuous heavy grazing (Valone and Sauter, 2004; Tessema et al., 2011a). The structure and composition of savanna vegetation is highly resilient to disturbances, as most grasses establish by the expansion and subsequent fragmentation of vegetative parts (Prins, 1988; O'Connor, 1994), or establish from the soil seed banks (Snyman, 2004). These seeds survive in the soil seed bank bridge the gap between seed production and seed germination (Williams et al., 2005; Scott et al., 2010).

Heavy grazing reduces seed production of grass species by affecting the allocation of resources for reproduction and by direct removal of flowers and seeds (O'Connor and Pickett, 1992). Thus, perennial grass species that are palatable to herbivores (Prins, 1988), and especially those with a low seed output, as well as short seed longevity might disappear in the system due to heavy grazing (O'Connor, 1994). 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, many perennial grass species have a high germination and a low dormancy, which do not favour the formation of a persistent soil seed bank (Mott, 1978; McIvor and Howden, 2000). Therefore, sustained heavy grazing could trigger the disappearance of perennial grass species both in the aboveground vegetation (O'Connor, 1994; Tessema et al., 2011a) and in the soil seed banks (Kinloch and Friedel, 2005). Plant species persisting under heavy grazing are usually unpalatable species, or species with short life history, such as short-lived tufts or species with a high output of small, long lived and well dispersed seeds (O'Connor, 1994).

Successful plant recruitment is a function of seed availability, seed germination, seedling establishment, plant growth, flowering, and seed setting (Baskin and Baskin, 2004). The re-colonization of grass species depends primarily on the survival of an established population (O'Connor, 1994) that can provide new seeds into the soil seed bank (Snyman, 2004; Scott et al., 2010). The ability of grasses to survive under the influence of grazing can be understood mechanistically through examination of the life cycle processes (O'Connor, 1994; Snyman, 2004) such as seed germination, seedling establishment, or maturation and mortality of standing populations (Veenendaal et al., 1996b; Scott et al., 2010).

Studies into the temporal dynamics of soil seed banks (Dreber and Esler, 2011) and survival of grass plants (O'Connor, 1994; Zimmermann et al., 2010) help to understand and facilitate the conservation, management, and restoration of grass species in semi-arid savannas (Snyman, 2004). However, knowledge on temporal soil seed bank dynamics under

contrasting grazing regimes as well as the mortality of grasses at various growth stages is either minimal or lacking in semi-arid African savannas. In this research, we addressed the following questions: (i) how do seedling density and species richness vary in soil seed banks under light and heavy grazing regimes over time? (ii) are effects of grazing regimes in soil seed banks similar across functional groups (i.e., grasses, herbaceous legumes and forbs) over time?, and (iii) which growth stage is most critical to the survival of grass plants in semi-arid savannas?

## Materials and methods

### 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 m above sea level) and Awash National Park (ANP: 9°20'N, 40°20'E, 960-1050 m above sea level), both located in the Ethiopian Rift Valley. The locations are typical for many semi-arid savannas. The mean annual rainfall (1989-2008: Tessema et al., 2011a) of ANP was 512 mm, and rainfall in 2009 was 413 mm. The main rainy season is 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., 2011a). 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., 2011a) and the rainfall in 2009 was 705 mm. The mean minimum and maximum temperatures were 14°C and 28°C, respectively.

### Selection of sampling sites

Light and heavy grazing sites were systematically selected inside and outside the ANP (Abule et al., 2005b) and ACBR (Mekuria et al., 1999) based on the history and intensity of livestock grazing using a stratified sampling procedure (Tessema et al., 2011a). In ANP, the light grazing sites were grazed by few wild herbivores, e.g., East African Oryx (*Oryx beisa*), Soemmerring's Gazelle (*Nanger soemmerringii*), Dik-dik (*Madoqua kirkii*), Lesser kudu (*Tragelaphus imberbis*) and Greater kudu (*Tragelaphus strepsiceros*), and only intermittently by livestock. 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 (Tessema et al., 2011a). 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 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., 2011a).

### **Procedures of soil seed bank studies**

The soil seed bank study covered nine months, during which soil samples were collected seven times such as in October, November and December 2008 (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 sampling over a nine month period was to determine germination patterns of seeds in the soil over time as a result of breaking dormancy, particularly for older, dormant seeds found in the 5-10 cm soil layer. Soil samples were collected in 4 sampling sites, with a size of 10 m x 10 m (100-m<sup>2</sup>), which were located in four different paddocks to be independent. Each sampling site was further subdivided into 17 subsamples (0.5 m x 0.5 m quadrats), which was sampled at the center, horizontal, vertical and diagonal directions (Fig. 4.1), at two soil depths (0-5 and 5-10 cm), yielding a total of 544 subsamples (2 locations x 2 grazing pressures x 4 sampling sites x 17 quadrats x 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 8 (2 locations x 2 grazing pressures x 2 soil depths) composite soil samples was divided into 3 equal parts, out of which one was randomly chosen for the seed bank study.

The seedling emergence method was used to estimate the seedling density and species composition of composite soil samples (Roberts, 1981). The emergence method is more appropriate than actual identification of seeds (Gross, 1990; Page et al., 2006) because it determines the relative abundance of viable seeds that can germinate, and excludes 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<sup>2</sup>) were used per composite soil sample, totaling 40 pots. 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

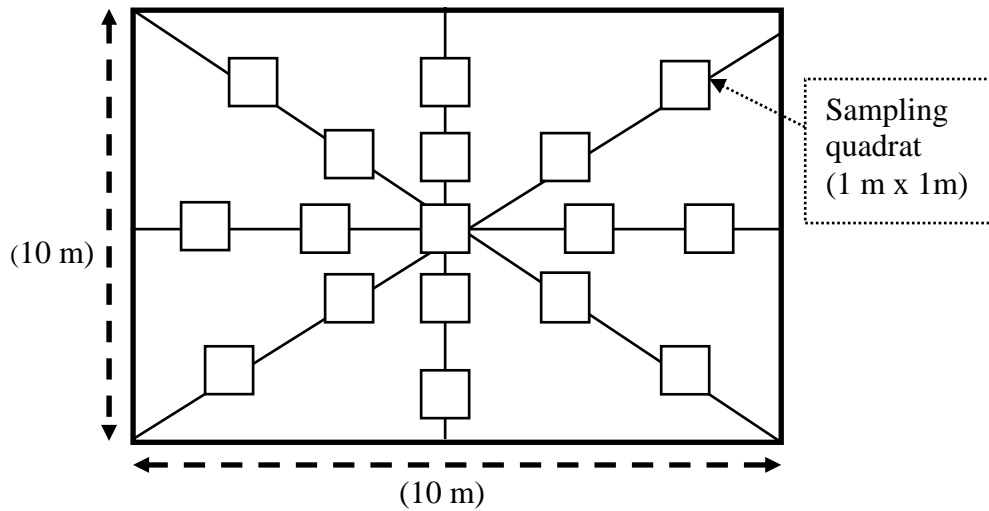
the experiment. Seedlings started to emerge within one week, and those seedlings that were readily identifiable counted, recorded and discarded. Those difficult to identify at the seedling stage were first counted, but maintained in the pots until identified. The first soil sample incubation (for October samples) started on the first day of November 2008, and the soil sample incubation was repeated for each month consecutively, for a period of six months since the number of seedlings, particularly grasses and forbs, considerably declined after 6 months (Page et al., 2006). Plant nomenclature follows Cufodontis (1953-1972), Fromann and Persson (1974), and Philips (1995).

### **Grass plant population in different growth stages**

A 50 m x 100 m heavily grazed site was fenced both at ACBR and ANP for monitoring the number of seedlings (NSL), number of established plants (NEP), number of flowering plants (NFP) and number of seed setting plants (NSP) of the grass species, so grazing by large herbivores was excluded. Only bunch (tufted) grasses were recorded, excluding grass species propagated by rhizomes and/or stolons because bunchgrasses are more dependent upon seed production than rhizomatous or stoloniferous grasses for survival. Within the fenced area in each location, we used a 10 m x 10 m (100-m<sup>2</sup>) sampling site similar to the soil seed bank sampling in 17 quadrats (1-m<sup>2</sup>) at the center, and at the horizontal, vertical and diagonal axes, to record NSL, NEP, NFP and NSP of grass species, yielding a total of 34 subsamples (2 locations x 17 sample quadrats). 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 mortality stage that is largely responsible for the observed changes in a plant population (Sibly and Smith, 1998; Zimmermann et al., 2010).

### **Data analyses**

The number of viable seeds (seedling density), number of species (species richness), species composition and functional groups (grasses, herbaceous legumes, forbs and woody species) were recorded. A Generalized Linear Model (GLM) fitted with Poisson distribution as Log-link function was applied to test for differences in number of germinated seeds, species richness and functional groups in the soil seed banks, using PASW (version 17), with location, grazing pressure, months, soil depth and their interactions as independent factors. The Tukey's HSD multiple comparisons were used to test for significant differences among the means.



**Fig. 4.1.** Diagram illustrating quadrat position in a 10 m x 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

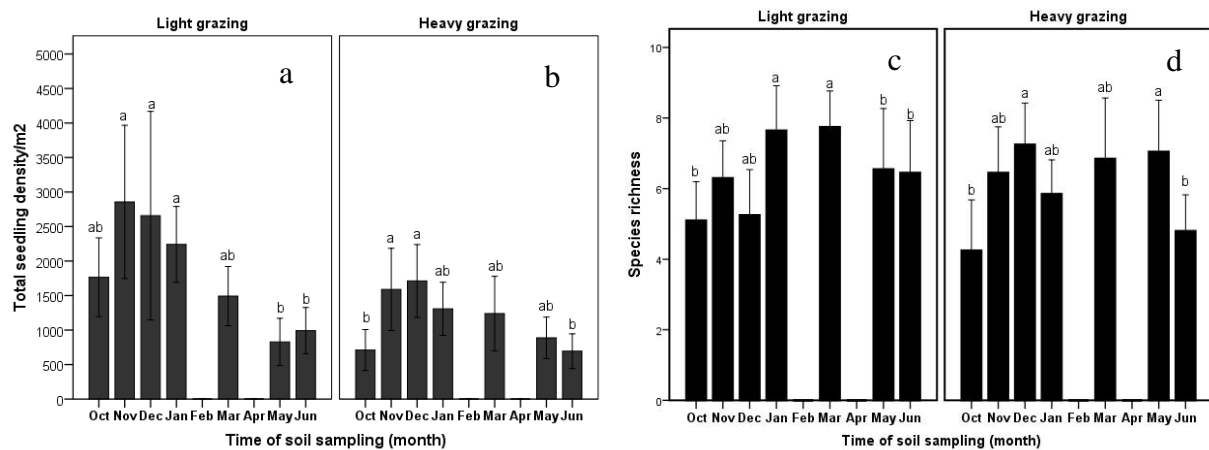
The key stages in our study included the number of germinated seeds in the soil seed banks (SSB), NSL, NEP, NFP, and NSP of the grass species. The key stages between the soil seed banks and aboveground vegetation involve four transitions, indicated as: SSB-►NSL-►NEP-►NFP-►NSP. A Generalized Linear Model (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 key ( $k$ ) 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  $k_{\text{total}} = k_1 + k_2 + k_3 + k_4$  (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):  $k_1 = \log (\text{SSB}/\text{NSL})$ ;  $k_2 = \log (\text{NSL}/\text{NEP})$ ;  $k_3 = \log (\text{NEP}/\text{NFP})$ ;  $k_4 = \log (\text{NFP}/\text{NSP})$ , with  $K_{\text{total}} = \log (\text{SSB}/\text{NSP})$ . 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.

## Results

### Total seedling density in the soil seed banks

The lightly grazed sites had a higher total seedling density (1849 seeds/m<sup>2</sup>) from the soil seed bank samples compared with the heavily grazed sites (1164 seeds/m<sup>2</sup>), with on average greater at ACBR (2045 seeds/m<sup>2</sup>) than at ANP (968 seeds/m<sup>2</sup>; Table 4.1). The top soil layer had a higher seedling density (2244 seeds/m<sup>2</sup>) compared with the deeper soil layer (769 seeds/m<sup>2</sup>). The light grazing sites had greater number of total seedling density than the heavy grazing sites both at ACBR and ANP (Table 4.1).

The months of soil sampling had a significant ( $F_{6,270} = 6.758$ ,  $P < 0.010$ ;  $R^2_{\text{adjusted}} = 0.540$ ) effect on total seedling density from the soil seed banks. The total seedling density increased over the first three months until May, and decreased thereafter (Fig. 4.2a and 4.2b). The light and heavy grazing sites showed a similar trend over time, except that the total seedling density was higher under the light grazing than the heavily grazing sites (Fig. 2).



**Fig. 4.2.** Total seedling density (n/m<sup>2</sup>, a and b) and species richness (n/pot, c and d) from the seed banks under light and heavy grazing sites over time (months) in a semi-arid Ethiopian savanna (N = 544).

**Table 4.1.** Species richness, total seedling density and seedling density over the different functional groups (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 ( $F$ ,  $P$ ,  $R^2_{adjusted}$ ;  $N = 544$ ).

	Species richness (n/m <sup>2</sup> )	Seedling density (Mean ± 95% CI)					Total seedling density
		Functional groups (n/m <sup>2</sup> )					
		Annual grasses	Perennial grasses	Total grass	Herbaceous legumes	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	5.3±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±5.1	417.2±71.3	1165.6±148.3
10 cm	3.9±0.4	82.2±46.1	84.0±68.1	166.2±145.3	18.4±5.1	138.0±71.3	322.6±139.6
Location (LOC)							
<i>F</i> (df = 1,270)	19.871	54.188	38.481	57.422	4.144	44.665	77.937
<i>P</i>	<0.001	<0.001	<0.001	<0.001	0.043	<0.001	<0.001
Grazing pressure (GP)							
<i>F</i> (df = 1,270)	1.727	14.532	30.792	25.195	26.644	0.581	30.458
<i>P</i>	0.190	<0.001	<0.001	<0.001	<0.001	0.446	<0.001
Soil depth (SD)							
<i>F</i> (df = 1,270)	119.923	77.790	77.283	94.402	31.705	54.303	141.033
<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Time							

Table 4.1. continued...

<i>F</i> (df = 6,270)	28.413	7.280	7.608	5.179	9.099	3.228	6.758
<i>P</i>	<0.001	0.007	0.006	0.024	0.003	0.033	0.010
LOC x GP							
<i>F</i> (df = 1,270)	0.080	3.738	11.006	7.737	7.176	0.001	4.517
<i>P</i>	0.777	0.054	0.001	0.006	0.008	0.984	0.034
LOC x SD							
<i>F</i> (df = 1,270)	0.017	6.324	6.163	7.550	2.258	0.022	3.873
<i>P</i>	0.898	0.013	0.014	0.006	0.134	0.882	0.050
GP x SD							
<i>F</i> (df = 1,270)	0.054	5.623	12.119	9.835	13.119	6.591	17.247
<i>P</i>	0.817	0.018	0.001	0.002	<0.001	0.011	<0.001
LOC x GP x SD							
<i>F</i> (df = 1,270)	0.192	1.085	1.901	1.709	3.553	0.777	1.053
<i>P</i>	0.662	0.298	0.169	0.192	0.061	0.379	0.306
<i>R</i> <sup>2</sup> adjusted	0.368	0.397	0.453	0.467	0.247	0.271	0.536



### **Species richness and species composition in the soil seed banks**

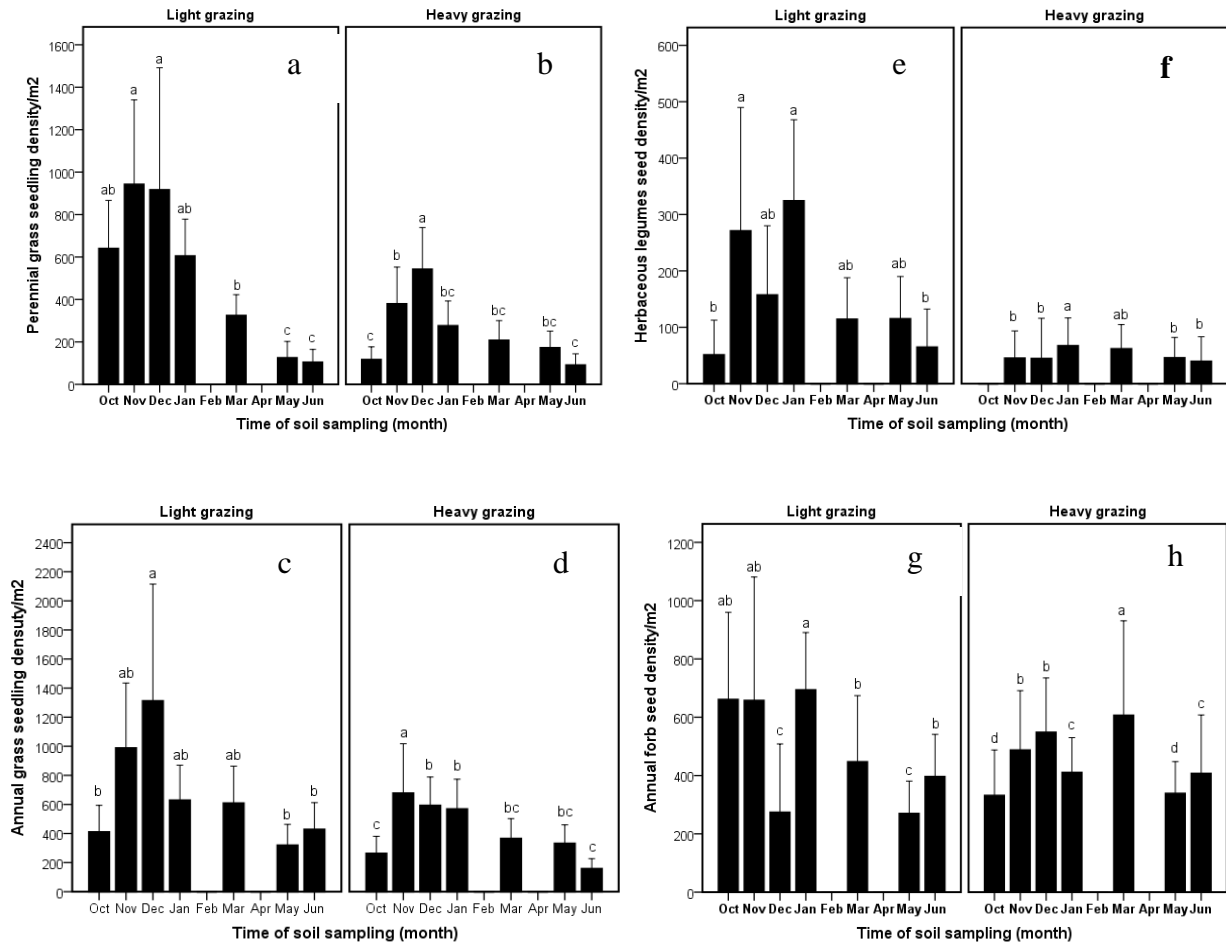
A total of 103 plant species emerged from all soil samples throughout the 9 months soil seed bank study (Appendix Table 4.1 and 4.2). The number of species emerged from the soils of ACBR and ANP was 82 and 87 species, respectively (Appendix Table 4.1). The total number of species emerged at the light 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 Table 4.1).

The number of species was higher at ACBR (6.9 species/pot) than ANP (5.7 species/m<sup>2</sup>; Table 4.1). Similarly, the upper soil layer had more number of species (7.8 species/m<sup>2</sup>) than the deeper soil layer (4.8 species/m<sup>2</sup>). Time (months) had a significant effect on the number of species in the seed banks (Fig. 4.2c and 4.2d), as the number of species in the seed banks was higher in January and March under light grazing (Fig. 4.2c).

### **Soil seed banks according to functional groups**

The seedling density for annual and perennial grasses, herbaceous legumes and annual forbs in the seed banks were higher at ACBR than at ANP (Table 4.1). The light grazing sites had higher seedlings for annual and perennial grasses, and herbaceous legumes compared with the heavily grazed sites in both locations (Table 4.1). The top soil layer had more emerged seedlings for annual and perennial grasses, herbaceous legumes and annual forbs than deep soil layer (Table 4.1).

The number of annual and perennial grass seedlings increased until the 3 months (December) of the soil sampling, and decreased thereafter, both under light (Fig. 4.3a and 4.3b) and heavy grazing (Fig. 4.3c and 4.3d). The number of perennial grass seedlings was low, and was even lower than that of annual forbs under heavy grazing. The seedling density of herbaceous legumes almost increased until 4 months (January) of soil sampling and decreased thereafter for both grazing regimes (Fig. 4.3e and 4.3f), except that of December under light grazing. Annual forbs did not show a distinct pattern of seedling density under both grazing regimes over time (Fig. 4.3g and 4.3h) as those of grass species, which might be due to differences in dormancy characteristics within their group.

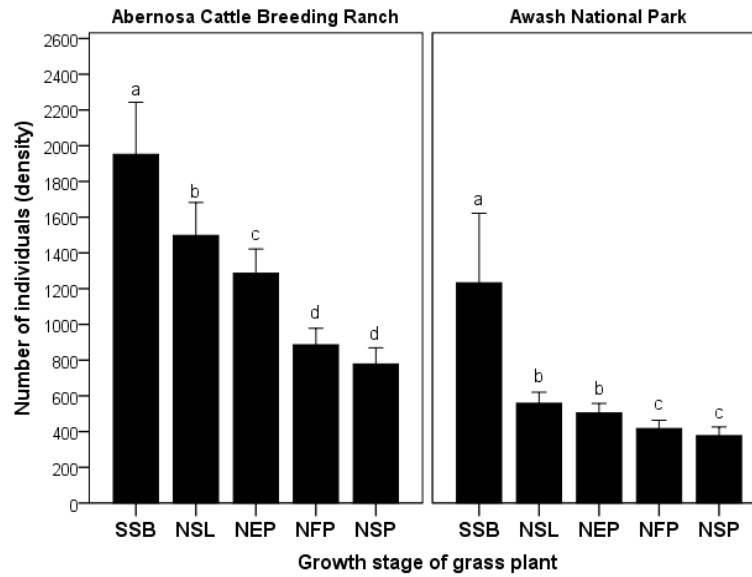


**Fig. 4.3.** Seedling density ( $N/m^2$ ) for different functional groups of herbaceous species recovered from the soil seed banks: perennial grasses (a and b), annual grasses (c and d), herbaceous legumes (e and f) and annual forbs (g and h) under light and heavy grazing sites over time (months) in a semi-arid savanna in Ethiopia ( $N = 544$ ).

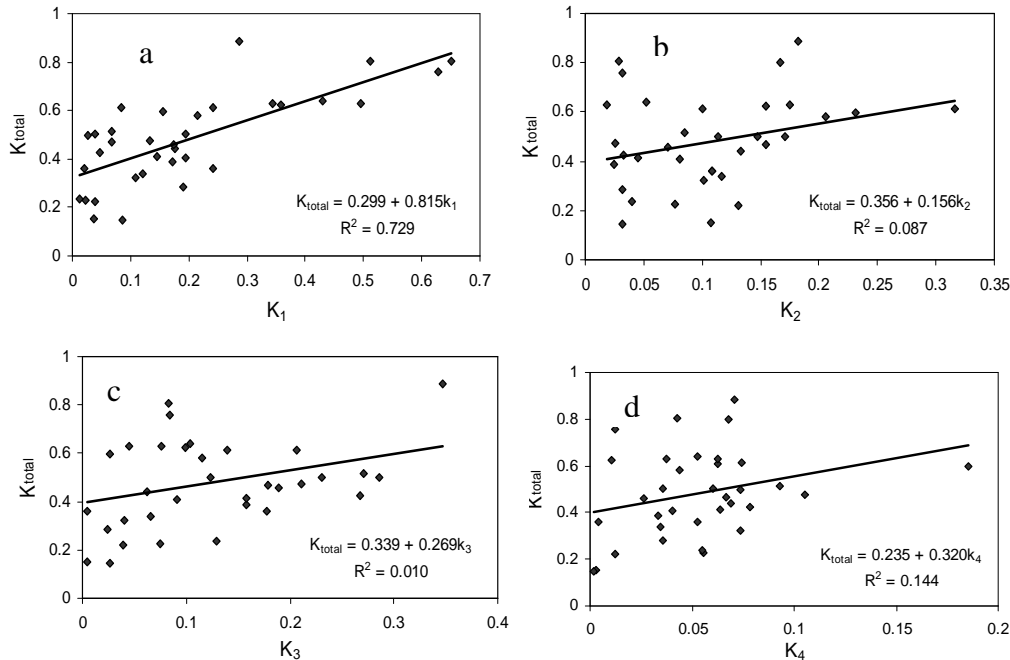
#### Changes in grass populations at various growth stages

Location had a highly significant ( $F_{1,160}=155.301$ ,  $P<0.001$ ,  $R^2_{adjusted}=0.671$ ) effect on the number of individuals over the different growth stages, with higher values at ACBR than ANP (Fig. 4.4). The total mortality rates, recorded from the seedling stage until the plants reached the seed setting stage, were 60% and 69% at ACBR and ANP, respectively (Fig. 4.4). In addition, the growth stage from seeds to seedlings ( $k_1$ ) could best explain the variation in total mortality ( $K_{total}$ ) compared with other growth stages ( $F_{1,32}=86.177$ ,  $P<0.001$ ,  $R^2_{adjusted}=0.729$ ; Fig. 4.5a). Moreover, the seed-to-seedling transition had a higher slope, close to unity (0.815), larger than the other growth stages, indicating that this stage is the critical transitional stage in the life cycle of these species. The transitions from established plants to flowering

and from flowering to seed setting stages had lower slopes ( $<0.269$ ), so these stages are less important for the overall plant mortality.



**Fig. 4.4.** The survival of grass plants at various stages (SSB = number of seeds in the seed banks, NSL = number 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 = 34).



**Fig. 4.5.** The contribution of each growth stage ( $k_1 = \log$  (number of seeds in the soil 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 mortality of grass plants ( $K_{total} = k_1 + k_2 + k_3 + k_4$ ) in a semi-arid savanna of Ethiopia (N = 34).

## **Discussion**

### **Response of soil seed banks to grazing regimes over time**

Soil seed banks of a semi-arid Ethiopian savanna varied with grazing regime, with greater seedling density at the light grazing than at the heavy grazing sites. Similarly, the structure of soil seed banks in the plant communities (Kinucan and Smeins, 1992; Dreber and Esler, 2011) are shaped by severity of grazing over extended periods (Kinloch and Friedel, 2005; Solomon et al., 2006). The greater seedling densities in the light grazing sites may be due to the higher seed rain in lightly grazed than heavily grazed sites. However, Dreber and Esler (2011) and Snyman (2004) reported that continuous heavy grazing increased seedling 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 many small-seeded annual species in the seed banks (Solomon et al., 2006; Scott et al., 2010).

In our study, the total seedling density increased over the first 3 months until December, and decreased thereafter. Williams et al. (2005) reported that temporal variation in germinable seeds in seed banks is a common feature of savanna vegetation. According to Scott et al. (2010), the density of germinable seeds in the seed banks was much higher in early dry season compared with the late dry season in northern Australia, similar to our findings. The higher seedling 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 seed banks might be associated with the germination of seeds immediately after seed dispersal, seed predation and mortality over time (Veenendaal et al., 1996a; Onaindia and Amezaga, 2000).

The temporal variations in the soil seed banks of semi-arid ecosystems could be due to depletion of seeds in the soil after initial seed dispersal (Scott et al., 2010), and/or due to differences in longevity and germination of seeds of species in the seed banks (Baskin and Baskin, 2004). Moreover, the optimum time for seed germination in semi-arid savannas is as early in the growing season as possible to secure resources such as nutrients and water for growth and reproduction (Rathcke and Lacey, 1985; Prins, 1988).

### **Effect of grazing regimes on species richness in soil seed banks over time**

The lightly grazed sites had a higher number of species richness in the seed banks compared with heavily grazed sites in a semi-arid Ethiopian savanna. According to Snyman (2004), species richness in the seed bank declined with rangeland degradation in South Africa, which

is similar to our finding. However, number of species emerged from the 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) variability between soil sampling sites may be the cause of variation in species richness. The higher number of species in soil seed bank at the degraded condition may be related to heavy grazing that could provide opportunities for more annual species to recolonize bare patches (Landsberg et al., 2002).

#### **Soil seed bank response according to functional groups over time**

Under the light grazing, perennial grass species dominated, while the heavily grazed sites were dominated by annual forbs in our study. This indicates that perennial grass species 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 seed banks since they tolerate heavy grazing and trampling through various adaptive mechanisms, such as their small seeds may 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).

#### **Changes in grass populations according to growth stage**

According to Scott et al. (2010) the resilience of grass plant populations in relation to grazing can be examined through an examination of life-cycle processes. We found a mortality rate of 60% and 69% (mean: 65%), from the seedling stage until the grass plants reached the seed setting at ACBR and ANP, respectively. This result is in line with Lauenroth and Adler (2008) who reported mortality rates of 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. According to O'Connor (1994), mortality of seedlings and established populations is high in semi-arid savannas in general compared with temperate ecosystems.

The growth stage from seeds to seedlings ( $k_1$ ) explained best the variation in total mortality ( $K_{total}$ ) of grass plants compared with the establishment, flowering and seed setting stages in our study. This indicates that seedling stage is the critical transitional stage in the growth stages of 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 water stress and an increased competition during drought times. Snyman (2004) defined successful seedling recruitment as a seedling that survives at least one growing season or up to flowering and seed setting. However, seedling establishment and subsequent survival of grass species are strongly

affected by temporal variation in rainfall in semi-arid African savannas (Veenendaal et al., 1996a). 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., 1996a). For instance, a minimum amount of 15-25 mm rainfall is reported to trigger a cohort of seedlings of grass species in semi-arid savannas (Andrew and Mott, 1983) and followed by long dry spell causes high seedling mortality in grass species. Thus, exclusion from grazing and trampling 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 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 with appropriate stocking rate, especially later in the growing season, could still be used to exploit these grasslands.

Our results confirmed that high grass mortality rates are possible in semi-arid savannas due to biotic and abiotic factors. For instance, grass plant mortality is dependent upon the intensity of grazing (Zimmermann et al., 2010), as a consequence of subdivision and fragmentation related to the intensity and frequency of grazing (O'Connor, 1994; Oliva et al., 2005). Moreover, heavy grazing reduces stored energy reserves, leading to a reduced resilience of grass seedlings or newly grown tufts (Zimmermann et al., 2010). This leads to a conclusion that perennial grass, with a lower seed producing ability, may become locally extinct, as a result of sustained heavy grazing coupled with long periods of drought in semi-arid African savannas (O'Connor and Pickett, 1992; O'Connor, 1994). Therefore, seedling survival and subsequent establishment are critical processes determining the successful recovery, growth and long-term persistence of grass populations under influence of heavy grazing in semi-arid savannas.

## **Conclusions**

In our study, the light grazing sites had more emerged seedling densities in the soil seed banks than the heavy grazing sites. Similarly, the lightly grazed sites were characterized by long-lived, perennials, whereas the heavily grazed sites by short-lived, forb species. The mean mortality rate from the seedling stage until the grass plants reached the seed setting stage was of 65%. We concluded that the depletion of seeds in the soil over time as a result of heavy grazing coupled with high seedling mortality considerably decrease the abundance of perennial grasses in soil seed banks in semi-arid savannas. Therefore, exclusion from grazing

in the early germination (re-growth) 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 savannas.

### **Acknowledgments**

We would like to thank Nuffic for the financial support of this research and the Haramaya University of Ethiopia for providing transport and greenhouse facilities during the research.



**Appendix Table 4.1.** List of species and mean number of emerged seedlings (n/m<sup>2</sup>) in the soil seed banks under light (LG) and heavy grazing (HG) conditions at Abernosa Cattle Breeding Ranch (ACBR) and Awash National Park (ANP) in semi-arid savannas of Ethiopia (N = 544).

Species	ACBR		ANP		Mean	Life form	Functional group
	HG	LG	HG	LG			
<i>Abutilon figarianum</i>	0	0	0	15.2	15.2	A	F
<i>Acacia senegal</i>	0	15.2	15.2	0	15.2	P	W
<i>Acalypha fruticosa</i>	0	0	0	22.8	22.8	A	F
<i>Acanthospermum hispidum</i>	15.2	15.2	0	0	15.2	A	F
<i>Achyranthes aspera</i>	0	15.2	19.0	0	18.2	A	F
<i>Aeschynomene schimperi</i>	23.6	30.4	148.0	30.4	41.4	P	HL
<i>Ageratum conyzoides</i>	15.2	0	0	15.2	15.2	A	F
<i>Alchemilla abyssinica</i>	60.7	42.5	15.2	50.6	47.9	A	F
<i>Alchemilla rothii</i>	0	80.9	36.4	30.4	58.2	A	F
<i>Amaranthus caudatus</i>	27.8	0	15.2	0	26.0	A	F
<i>Amaranthus dubius</i>	40.0	30.4	102.2	136.6	74.0	A	F
<i>Anagallis arvensis</i>	49.3	15.2	15.2	17.7	30.4	A	F
<i>Aristida adoensis</i>	209.0	610.6	203.8	149.0	377.1	A	G
<i>Aristida adscensionis</i>	301.0	750.3	295.9	172.0	536.1	A	G
<i>Asterolinum adoense</i>	495.0	84.7	273.2	299.2	352.4	A	F
<i>Asterolinum stellatum</i>	683.0	0	0	0	682.9	A	F
<i>Bidens pilosa</i>	30.4	62.9	0	0	60.7	A	F
<i>Bothriochloa radicans</i>	0	0	0	121.4	121.4	P	G
<i>Brachiaria comata</i>	0	0	0	652.5	652.5	P	G
<i>Cenchrus ciliaris</i>	0	45.5	0	0	45.5	P	G
<i>Chenopodium album</i>	126.0	75.9	161.9	45.5	130.9	A	F
<i>Chenopodium murale</i>	105.0	91.1	155.1	30.4	128.8	A	F
<i>Chloris gayana</i>	200.0	482.9	121.4	77.8	332.4	P	G
<i>Chloris radiata</i>	408.0	1158	165.8	285.3	723.9	P	G
<i>Chrysopogon aucheri</i>	167.0	0	218.0	757.1	527.7	P	G
<i>Chrysopogon plumulosus</i>	156.0	106.2	153.9	694.0	530.2	P	G
<i>Commelina benghalensis</i>	30.4	0	91.1	91.1	70.8	A	F
<i>Conyza bonariensis</i>	60.7	22.8	15.2	15.2	29.1	A	F
<i>Corchorus olitorius</i>	0	0	0	19.5	19.5	A	F
<i>Corchorus trilocularis</i>	0	0	0	15.2	15.2	A	F
<i>Crotalaria albicaulis</i>	15.2	15.2	20.3	18.2	18.2	P	HL
<i>Crotalaria pallida</i>	15.2	15.2	0	26.6	20.3	P	HL
<i>Cynodon dactylon</i>	225.0	75.9	226.1	0	217.5	P	G
<i>Cyperus distans</i>	0	0	30.4	45.5	34.2	A	F
<i>Cyperus obtusiflorus</i>	0	0	15.2	0	15.2	A	F
<i>Cyperus rotundus</i>	15.2	45.5	37.9	37.9	35.7	A	F
<i>Dactyloctenium aegypticum</i>	264.0	368.0	189.7	235.2	315.0	A	G
<i>Digitaria abyssinica</i>	45.5	91.1	258.0	186.5	183.2	A	G
<i>Digitaria ternata</i>	142.0	98.7	141.6	197.3	139.1	A	G
<i>Digitaria velutina</i>	97.1	117.6	80.0	0	91.8	A	G
<i>Echinochloa colonum</i>	0	0	182.1	75.9	129.0	A	G
<i>Eleusine indica</i>	96.1	227.6	0	166.9	136.6	A	G



Appendix Table 4.1 continued...

<i>Eleusine jaegeri</i>	0	60.7	0	75.9	70.8	P	G
<i>Eleusine multiflora</i>	60.7	0	0	0	60.7	A	G
<i>Enteropogon macrostachyus</i>	0	0	129.0	0	129.0	P	G
<i>Epomoea alba</i>	17.3	15.2	0	15.2	16.6	A	F
<i>Eragrostis abyssinica</i>	0	0	136.6	15.2	75.9	A	G
<i>Eragrostis aethiopica</i>	0	0	0	60.7	60.7	A	G
<i>Eragrostis cilianensis</i>	30.4	60.7	22.8	561.5	121.4	A	G
<i>Eragrostis ciliaris</i>	60.7	60.7	0	0	60.7	A	G
<i>Eragrostis aspera</i>	428.0	276.4	291.4	96.1	326.1	A	G
<i>Eragrostis tenuifolia</i>	406.0	60.7	232.7	251.3	334.7	P	G
<i>Eragrostis papposa</i>	126.0	561.5	395.5	238.4	305.3	A	G
<i>Eragrostis superba</i>	375.0	75.9	205.6	115.4	240.4	A	G
<i>Eragrostis racemosa</i>	0	0	318.7	0	318.7	A	G
<i>Eriochloa nubica</i>	156.0	45.5	65.8	115.7	101.7	A	G
<i>Erucastrum arabicum</i>	15.2	46.91	0	21.7	34.0	A	F
<i>Euphorbia hirta</i>	46.6	21.7	43.1	22.8	39.8	A	F
<i>Flaveria trinervia</i>	0	45.5	0	0	45.5	A	F
<i>Galinsoga parviflora</i>	147.0	33.1	25.3	22.8	72.3	A	F
<i>Guizotia scabra</i>	0	26.6	0	0	26.6	A	F
<i>Guizotia schimperi</i>	0	15.2	0	0	15.2	A	F
<i>Harpachne schimperi</i>	156.0	37.9	0	15.2	101.9	A	G
<i>Heliotropium cinerascens</i>	15.2	22.8	15.2	15.2	17.4	A	F
<i>Hibiscus aponerus</i>	0	0	15.2	0	15.2	A	F
<i>Hibiscus micranthus</i>	15.2	45.5	15.2	0	30.4	A	F
<i>Hyparrhenia hirta</i>	0	402.2	0	0	402.2	P	G
<i>Hyparrhenia rufa</i>	0	225.1	0	0	225.1	P	G
<i>Hypoestes forskalii</i>	69.1	114.4	0	0	95.9	A	F
<i>Indigofera spicata</i>	53.1	36.4	48.3	32.3	41.5	P	HL
<i>Ipomoea cordofana</i>	0	45.5	0	15.2	30.4	A	F
<i>Ipomoea fulvicaulis</i>	0	0	15.2	15.2	15.2	A	F
<i>Leucas martinicensis</i>	30.4	29.0	19.5	43.0	29.8	A	F
<i>Leucas microphylla</i>	15.2	40.5	0	133.6	75.9	A	F
<i>Linthonia nutans</i>	0	0	280.8	0	280.8	P	G
<i>Mollugo cerviana</i>	15.2	0	68.3	0	57.7	A	F
<i>Neonotonia wightii</i>	0	0	0	22.8	22.8	A	HL
<i>Nicandra physaloides</i>	15.2	15.2	0	0	15.2	A	F
<i>Nicotiana tabacum</i>	30.4	0	0	0	30.4	A	F
<i>Ocimum basilicum</i>	0	0	33.4	25.3	29.0	A	F
<i>Oplismenus compositus</i>	30.4	70.8	60.7	0	63.2	A	F
<i>Oxalis latifolia</i>	0	15.2	15.2	0	15.2	A	F
<i>Panicum atrosanguineum</i>	60.7	55.7	53.6	543.2	271.1	A	G
<i>Panicum coloratum</i>	106.0	75.9	136.6	45.5	87.3	P	G
<i>Setaria pumila</i>	0	101.9	0	0	101.9	A	G
<i>Setaria sphacelata</i>	0	15.2	0	68.3	60.7	A	G
<i>Snowdenia polystachya</i>	45.5	144.9	0	0	136.6	A	G
<i>Solanum incanum</i>	15.2	53.1	15.2	22.8	53.1	A	F
<i>Solanum indicum</i>	0	0	0	15.2	15.2	A	F
<i>Solanum nigrum</i>	26.0	28.7	45.5	30.4	30.4	A	F
<i>Solanum somalensis</i>	0	15.2	15.2	0	15.2	P	F

Appendix Table 4.1 continued...

<i>Sonchus oleraceus</i>	63.4	52.7	32.2	47.4	48.7	A	F
<i>Sporobolus pyramidalis</i>	212	75.9	45.5	30.4	91.1	P	G
<i>Tagetes minuta</i>	0	15.2	0	15.2	15.2	A	F
<i>Tephrosia pentaphylla</i>	45.5	15.2	15.2	40.8	35.3	A	HL
<i>Tetrapogon cenchrififormis</i>	0	0	723.4	60.7	557.7	A	G
<i>Tetrapogon tenellus</i>	75.9	0	178.3	83.5	129.0	P	G
<i>Tragus berteronianus</i>	335.0	269.4	152.5	184.1	207.8	A	G
<i>Tragus racemosus</i>	733.0	155.6	271.5	108.4	331.6	A	G
<i>Tribulus terrestris</i>	56.9	0	0	0	56.9	A	F
<i>Urochloa panicoides</i>	60.7	0	0	60.7	60.7	A	G
<i>Verbesina encelioides</i>	0	0	15.2	15.2	15.2	A	F
<i>Xanthium spinosum</i>	15.2	0	0	0	15.2	A	F
Number of species						-	-
Grass species	29	33	29	32	44	-	-
Perennial grass	8	11	10	8	15	-	-
Annual grass	21	22	19	24	29	-	-
Herbaceous legume	5	5	4	6	6	-	-
Forbs	32	31	30	32	52	-	-
Shrubs/trees	0	1	1	0	1	-	-
Total number of species	66	70	64	70	103	-	-
Percentage of species						-	-
Grass species	43.9	47.1	45.3	45.7	42.7	-	-
Perennial grass	12.1	15.7	15.6	11.4	14.6	-	-
Annual grass	31.8	31.4	29.7	34.3	28.1	-	-
Herbaceous legume	7.6	7.2	6.3	8.6	5.8	-	-
Forbs	48.5	44.3	46.9	45.7	50.5	-	-
Shrubs/trees	0.0	1.4	1.6	0.0	1.0	-	-
Total percentage of species	100.0	100.0	100.0	100.0	100.0	-	-

A = annual; P = perennial; F = forbs; G = grass; HL = herbaceous legumes; W = woody species

**Appendix Table 4.2.** List of species and mean number of emerged seedlings (n/m<sup>2</sup>) in the soil seed banks in semi-arid savanna grazing system of Ethiopia from October 2008 - June 2009 (N = 544).

Species	Time of soil sampling (months)							Mean	LF	FG
	October	November	December	January	March	May	June			
<i>Abutilon figarianum</i>	15.2	0	0	0	0	0	0	15.2	A	F
<i>Acacia senegal</i>	0	15.2	0	15.2	0	0	0	15.2	P	W
<i>Acalypha fruticosa</i>	0	15.2	0	0	30.4	0	0	22.8	A	F
<i>Acanthospermum hispidum</i>	0	15.2	0	0	0	0	15.2	15.2	A	F
<i>Achyranthes aspera</i>	15.2	15.2	15.2	0	0	15.2	30.4	18.2	A	F
<i>Aeschynomene schimperi</i>	0	103.7	15.2	43.0	15.2	34.9	26.0	41.4	P	HL
<i>Ageratum conyzoides</i>	0	15.2	0	0	0	15.2	0	15.2	A	F
<i>Alchemilla abyssinica</i>	15.2	15.2	0	62.4	0	0	0	47.9	A	F
<i>Alchemilla rothii</i>	98.7	38.0	0	0	0	0	0	58.2	A	F
<i>Amaranthus caudatus</i>	0	0	0	0	34.2	15.2	15.2	26.0	A	F
<i>Amaranthus dubius</i>	20.2	22.8	82.4	0	30.4	194.3	71.6	74.0	A	F
<i>Anagallis arvensis</i>	0	31.7	25.3	0	0	15.2	40.5	30.4	A	F
<i>Aristida adoensis</i>	179.1	770.2	374.7	215	423.3	42.5	53.12	377.1	A	G
<i>Aristida adscensionis</i>	75.9	684.5	722.9	296.0	564.6	0	0	536.1	A	G
<i>Asterolinum adoense</i>	83.5	52.3	394.6	159.4	391.0	571.6	662.2	352.4	A	F
<i>Asterolinum stellatum</i>	0	0	0	0	0	682.9	0	682.9	A	F
<i>Bidens pilosa</i>	22.8	0	0	0	15.2	48.1	93.6	60.7	A	F
<i>Bothriochloa radicans</i>	166.9	0	182.1	0	0	0	15.2	121.4	P	G
<i>Brachiaria comata</i>	770.1	0	182.1	0	0	0	0	652.5	P	G
<i>Cenchrus ciliaris</i>	0	0	0	45.5	0	0	0	45.5	P	G
<i>Chenopodium album</i>	230.7	25.3	58.2	0	78.9	37.9	364.2	130.9	A	F
<i>Chenopodium murale</i>	83.5	45.6	39.5	0	121.4	173.8	153.9	128.8	A	F
<i>Chloris gayana</i>	320.4	658.0	203.1	402.2	200.2	101.2	0	332.4	P	G
<i>Chloris radiata</i>	1432	691.4	1220	663.8	495.5	232.4	330.1	723.9	P	G
<i>Chrysopogon aucheri</i>	0	1035.8	470.5	796.1	135.2	91.1	0	527.7	P	G
<i>Chrysopogon plumulosus</i>	917.0	415.3	464.4	722.2	65.8	106.2	0	530.2	P	G
<i>Commelina benghalensis</i>	0	0	0	91.1	30.4	0	0	70.8	A	F

Appendix Table 4.2. continued...

<i>Conyza bonariensis</i>	15.2	15.2	0	43.0	0	0	0	29.1	A	F
<i>Corchorus olitorius</i>	15.2	15.2	15.18	0	25.3	0	15.2	19.5	A	F
<i>Corchorus trilocularis</i>	15.2	0	0	0	0	0	15.2	15.2	A	F
<i>Crotalaria albicaulis</i>	15.2	15.2	30.4	22.8	15.2	0	0	18.2	P	HL
<i>Crotalaria pallida</i>	0	0	15.2	0	0	20.3	22.8	20.3	P	HL
<i>Cynodon dactylon</i>	204.0	245.0	136.6	227.7	0	0	0	217.5	P	G
<i>Cyperus distans</i>	0	0	40.5	0	0	0	15.2	34.2	A	F
<i>Cyperus obtusiflorus</i>	0	0	0	0	15.2	0	0	15.2	A	F
<i>Cyperus rotundus</i>	0	0	26.6	81.0	22.8	30.4	25.3	35.7	A	F
<i>Dactyloctenium aegypticum</i>	268.5	454.4	399.9	347.2	326.7	136.6	158.5	315.0	A	G
<i>Digitaria abyssinica</i>	106.2	151.8	0	121.4	371.8	0	30.4	183.2	A	G
<i>Digitaria ternata</i>	176.0	0	182.1	121.4	113.8	86.0	0	139.1	A	G
<i>Digitaria velutina</i>	91.1	151.8	182.1	113.8	136.6	67.2	57.7	91.8	A	G
<i>Echinochloa colonum</i>	80.9	0	177.1	0	0	0	0	129.0	P	G
<i>Eleusine indica</i>	0	0	0	0	0	136.6	0	136.6	A	G
<i>Eleusine jaegeri</i>	0	106.2	53.1	0	0	0	0	70.8	A	G
<i>Eleusine multiflora</i>	0	0	0	0	60.7	0	0	60.7	A	G
<i>Enteropogon macrostachyus</i>	0	129.0	0	0	0	0	0	129.0	P	G
<i>Epomoea alba</i>	16.7	0	0	0	0	0	15.2	16.6	A	F
<i>Eragrostis abyssinica</i>	0	0	0	0	75.9	0	0	75.9	A	G
<i>Eragrostis aethiopica</i>	0	0	60.7	0	0	0	0	60.7	A	G
<i>Eragrostis cilianensis</i>	0	561.5	45.5	0	0	0	25.3	121.4	A	G
<i>Eragrostis ciliaris</i>	491.1	661.7	493.2	302.5	74.0	100.2	151.8	326.1	A	G
<i>Eragrostis aspera</i>	318.7	513.8	126.5	371.1	125.2	60.7	75.9	334.7	A	G
<i>Eragrostis tenuifolia</i>	364.2	138.8	604.0	256.3	323.1	106.2	75.9	305.3	P	G
<i>Eragrostis papposa</i>	0	0	624.4	0	0	188.0	122.3	240.4	P	G
<i>Eragrostis superba</i>	0	318.7	0	0	0	0	0	318.7	A	G
<i>Eragrostis racemosa</i>	0	0	0	0	0	0	60.7	60.71	A	G
<i>Eriochloa nubica</i>	0	212.5	166.9	0	121.4	95.6	68.3	101.7	A	G
<i>Erucastrum arabicum</i>	15.2	0	0	0	0	19.7	54.0	34.0	A	F
<i>Euphorbia hirta</i>	15.2	25.3	63.2	19	32.3	46.8	51.6	39.8	A	F

Appendix Table 4.2. continued...

<i>Flaveria trinervia</i>	0	0	0	0	45.5	0	0	45.5	A	F
<i>Galinsoga parviflora</i>	35.4	0	0	15.2	108.4	15.2	15.2	72.3	A	F
<i>Guizotia scabra</i>	0	0	0	0	26.6	0	0	26.6	A	F
<i>Guizotia schimperi</i>	0	0	0	0	15.2	0	0	15.2	A	F
<i>Harpachne schimperi</i>	0	0	379.4	68.3	15.2	45.5	0	101.9	A	G
<i>Heliotropium cinerascens</i>	0	15.2	0	19.0	0	15.2	0	17.4	A	F
<i>Hibiscus aponerus</i>	0	0	15.2	0	0	0	0	15.2	A	F
<i>Hibiscus micranthus</i>	45.5	0	0	0	0	15.2	15.2	30.4	A	F
<i>Hyparrhenia hirta</i>	0	0	0	402.2	0	0	0	402.2	P	G
<i>Hyparrhenia rufa</i>	0	0	0	903.0	60.7	103.2	79.7	225.1	P	G
<i>Hypoestes forskalii</i>	0	30.4	221.6	63.8	66.8	0	64.5	95.9	A	F
<i>Indigofera spicata</i>	15.2	36.1	34.2	48.6	81.0	15.2	0	41.5	P	HL
<i>Ipomoea cordofana</i>	0	0	0	45.5	0	0	15.2	30.6	A	F
<i>Ipomoea fulvicaulis</i>	0	0	15.2	0	0	15.2	0	15.2	A	F
<i>Leucas martinicensis</i>	0	0	20.3	0	0	23.5	38.6	29.8	A	F
<i>Leucas microphylla</i>	15.2	0	0	0	0	63.8	156.8	75.9	A	F
<i>Linthonia nutans</i>	0	227.7	333.9	0	0	0	0	280.8	P	G
<i>Mollugo cerviana</i>	0	0	0	106.2	0	45.5	0	57.7	A	F
<i>Neonotonia wightii</i>	0	15.2	0	30.4	15.2	0	0	22.8	P	HL
<i>Nicandra physaloides</i>	0	0	0	15.2	15.2	15.2	0	15.2	A	F
<i>Nicotiana tabacum</i>	0	30.4	0	0	0	0	0	30.4	A	F
<i>Ocimum basilicum</i>	15.2	30.4	38.0	26.6	34.2	25.3	15.2	29.0	A	F
<i>Oplismenus compositus</i>	0	0	60.7	15.2	68.3	0	0	63.2	A	F
<i>Oxalis latifolia</i>	15.2	0	0	0	0	0	0	15.2	A	F
<i>Panicum atrosanguineum</i>	0	0	121.4	0	91.1	208.5	350.5	271.1	A	G
<i>Panicum coloratum</i>	50.6	0	75.9	242.8	0	75.9	0	87.3	P	G
<i>Setaria pumila</i>	0	96.1	0	0	0	30.4	35.4	60.7	A	G
<i>Setaria sphacelata</i>	0	0	0	0	0	94.9	111.3	101.9	A	G
<i>Snowdenia polystachya</i>	0	0	145.7	0	0	156.8	110.0	136.6	A	G
<i>Solanum incanum</i>	22.8	15.2	0	0	15.2	15.2	53.1	53.2	A	F
<i>Solanum indicum</i>	0	0	0	0	0	15.2	0	15.2	A	F

Appendix Table 4.2. continued...

<i>Solanum nigrum</i>	30.4	15.2	15.2	0	42.5	24.3	30.4	30.4	A	F
<i>Solanum somalensis</i>	0	0	0	15.2	0	15.2	0	15.2	P	F
<i>Sonchus oleraceus</i>	30.4	29.2	15.2	79.2	24.9	15.2	35.4	48.7	A	F
<i>Sporobolus pyramidalis</i>	30.4	212.5	60.7	0	0	0	0	91.1	P	G
<i>Tagetes minuta</i>	15.2	0	0	15.2	15.2	0	0	15.2	A	F
<i>Tephrosia pentaphylla</i>	15.2	24.3	41.7	25.3	58.0	27.3	21.3	35.3	P	HL
<i>Tetrapogon cenchrifolius</i>	0	0	557.7	0	0	0	0	557.7	P	G
<i>Tetrapogon tenellus</i>	0	75.9	189.7	0	83.5	30.4	0	129.0	P	G
<i>Tragus berteronianus</i>	53.1	655.1	341.5	121.4	38.0	150.7	177.8	207.8	A	G
<i>Tragus racemosus</i>	151.7	603.7	223.5	0	151.8	0	0	331.6	A	G
<i>Tribulus terrestris</i>	0	0	56.9	0	0	0	0	56.9	A	F
<i>Urochloa panicoides</i>	0	0	0	0	60.7	60.7	0	60.7	A	G
<i>Verbesina encelioides</i>	0	0	15.2	0	0	15.2	15.2	15.2	A	F
<i>Xanthium spinosum</i>	0	0	0	15.2	0	0	0	15.2	A	F
Number of species										
Grass species	20	24	31	20	23	24	19	44		
Perennial grasses	9	9	17	9	6	8	4	18	-	-
Annual grasses	11	15	14	11	17	16	15	26	-	-
Herbaceous legumes	3	5	5	5	5	4	3	6	-	-
Forbs	24	21	20	18	24	28	27	52	-	-
Woody species	0	1	0	1	0	0	0	1	-	-
Total number of species	47	51	56	44	52	56	49	103	-	-
Percentage of species									-	-
Grass species	42.6	47.1	55.4	45.5	44.2	42.9	38.8	42.7	-	-
Perennial grass	19.1	17.7	30.4	20.5	11.5	14.3	8.2	17.5	-	-
Annual grass	23.4	29.4	25.0	25.0	32.7	28.6	30.6	25.2	-	-
Herbaceous legumes	6.4	9.8	8.9	11.4	9.6	7.1	6.1	5.8	-	-
Forbs	51.1	41.2	35.7	40.9	46.2	50.0	55.1	50.5	-	-
Woody species	0	2.0	0	2.3	0	0	0	1.0	-	-
Total species (%)	100	100	100	100	100	100	100	100	-	-

A = annual; P = perennial; F = forbs; G = grass; HL = herbaceous legumes; W = woody species; LF – Life form; FG = Functional group

# 5

Seasonal patterns of germination and longevity in grass species in  
a semi-arid African savanna: Implications for restoration

Z.K. Tessema, W.F. de Boer, R.M.T. Baars and H.H.T. Prins (submitted)

## **Abstract**

Plant regeneration from seeds is an essential feature of the life cycle of most grass species, enabling vegetation recovery in degraded ecosystems. Therefore, the viability and germination success of grass species collected in semi-arid savannas of Ethiopia were studied. We tested whether the differences in species composition between the aboveground vegetation and soil seed banks could be explained by differences in germination between annual and perennial grass species. Fully matured seeds of 16 grass species (4 annuals and 12 perennials) were collected between October and November 2008. The viability and germination tests for all species were repeated six times with an interval of 2 months in one year, from January to December 2009. The mean viability of annual and perennial grass species was 34% (range: 16-78%) and 51% (30-90%), respectively. Similarly, the mean germination of annual and perennial grass species was 5.5% (0-9.8%) and 32% (9.8-75%), respectively. For grass species with a mean germination of at least 20%, germination was positively related to the differences in the relative species composition between the aboveground vegetation and soil seed banks. Our study confirmed that differences in germination between annual and perennial grass species partly explained the variation in species composition between the aboveground vegetation and the soil seed banks in semi-arid savannas. We concluded that perennial grass species had a high germination, indicating that they might not form persistent seeds in the soil seed banks, and can rapidly disappear after germination, especially under influence of grazing, erratic rainfall events, or prolonged dry periods, which are typical features of the semi-arid African savannas.

**Keywords:** Annual grasses; Ethiopia; Grazing; Perennial grass; Seed dormancy; Soil seed banks; Land degradation



## **Introduction**

In tropical savannas, grasses comprise the dominant herbaceous vegetation (van de Koppel and Prins, 1998). However, grazing (Angassa and Oba, 2010; Tessema et al., 2011a), the dominant form of land use practice in African semi-arid rangelands (Solomon et al. 2006; Angassa and Oba, 2010), often leads to degradation of the grass cover. This causes serious challenges and can have negative impacts on the ecosystems, livestock production and livelihoods of the pastoral communities (Vetter, 2005; Harris, 2010). This degradation is characterized by a reduction in total vegetation cover and cover of palatable plant species, a change in species composition, as well as by a reduction in soil quality (Tefera et al., 2010; Tessema et al., 2011a).

However, some studies suggested that the return of perennial grasses, and other species that disappeared under intensive grazing, can be facilitated by the soil seed bank and trigger the vegetation recovery (Garwood, 1989; Thompson et al., 1989). Hence, the soil seed bank serves as a reserve to return to the original vegetation conditions, and regeneration from the soil seed banks has therefore been considered an important pathway for restoration of degraded vegetations (Garwood, 1989; Thompson et al., 1989). However, most seed bank studies show that there is a limited similarity between the grassland vegetation and soil seed banks (Bakker and Berendse, 1999; de Villers et al., 2003; Solomon et al., 2006). This dissimilarity is characterized by more perennial grasses in the standing vegetations (Kassahun et al., 2009; Tessema et al. 2011a), and more annual forbs in the soil seed banks (Solomon et al., 2006; Hopfensperger, 2007; Tessema et al., 2011b, d). This dissimilarity could be due to differences in seed germination and longevity between annual and perennial grasses (Baskin and Baskin, 2004; Scott et al., 2010).

Plant regeneration from seeds is an essential feature of the life cycle of most grass species, enabling vegetation recovery in degraded ecosystems (El-Keblawy and Al-Rawai, 2005; Guan et al., 2009). Successful plant recruitment is a function of seed availability, seed germination, and seedling survival (Baskin and Baskin, 2004). Once the seeds reach the soil surface, the seeds may be dormant for some time, after which the germination starts. During these stages the seeds are exposed to predation, microbial degradation or burial, depending on species and environmental conditions (Fenner and Thompson, 2005). If seeds do not germinate immediately, and escape predation and microbial degradation after dispersal, they usually enter the soil and become part of the soil seed bank (Wassie and Teketay, 2006). However, various studies (Solomon et al., 2006; Kassahun et al., 2009; Tessema et al., 2011b, d) showed that grass seeds in the soil seed banks could not able to “kick-start” the vegetation

recovery and accelerate the transition from a degraded vegetation state to vegetation with a perennial grass cover and good fodder value in semi-arid African savannas. Similarly, semi-arid rangelands did not recover from heavy livestock grazing, even after many years of grazing enclosures (Page and Beeton, 2000; Vetter, 2005). This might be associated with the depletion of soil seed banks (Scott et al., 2010; Tessema et al., 2011b, d), or differences in germination and longevity of seeds between plant species (Baskin and Baskin, 2004).

Soil seed bank forming species have seeds with an environmental adaptive strategy that delays germination until specific conditions of the environment are met (Teketay and Granström, 1995). How long these seeds can remain buried in the soil while maintaining viability depends on the type of species and climatic factors after initial dispersal (Garwood, 1989; Fenner and Thompson, 2005). The optimum time for seed germination in strongly seasonal climates (i.e., arid and semi-arid savannas) is as early in the growing season as possible. This is to secure resources such as nutrients and water for growth and reproduction, but not so early that survival is unlikely (Rathcke and Lacey, 1985; Prins, 1988). Seed dormancy is one of the main strategies ensuring suitable timing of germination with respect to favourable climatic conditions (Fenner and Thompson, 2005; Wesche et al., 2006). The accumulation of seeds in the soil is favoured by dormancy, caused by the presence of embryo dormancy, an impermeable seed coat or both (Baskin and Baskin, 2004). The seeds of most grass 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 (Mott 1978; McIvor and Howden, 2000). Despite a loss of dormancy during the dry season, germination is usually prevented by a lack of moisture (Scott et al., 2010), after which, in response to the first rainfall events of the wet season, seeds germinate in a series of cohorts until no viable seed remain in the soil (Andrew and Mott, 1983; Prins, 1988; Veenendaal et al., 1996a).

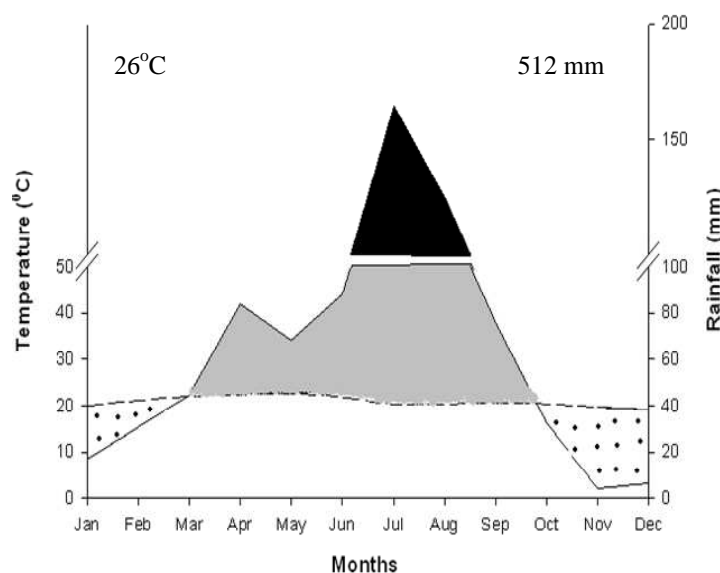
Understanding the dormancy and seed germination of grass species is vital to facilitate rehabilitation of degraded areas (Baskin and Baskin, 2004). Therefore, we studied the viability and germination of annual and perennial grass species collected in semi-arid savanna of Ethiopia to understand whether the higher seed abundance of annual grasses and the lower seed abundance of perennial grasses in the soil seed banks (Tessema et al., 2011a, b) could be related to differences in germination between annual and perennial grass species. Therefore, the general objective of the study was to assess the differences in viability and germination rates between annual and perennial grass species over time. Hence, we tested the following hypotheses: (i) perennial grass species have different germination strategy than annuals,

characterized by a high germination and a low dormancy, so that they do not form persistent seeds in the soil seed bank and thereafter disappear rapidly, (ii) annual grass species have a low germination and high dormancy, so that they form persistent seeds in the soil seed banks, and (iii) the variation in grass species composition between aboveground vegetation and soil seed banks in semi-arid savannas could be explained by the difference in survival of seeds in the soil between annual and perennial grass species.

## Materials and methods

### Study areas

The seeds for our study were collected at lightly grazed sites at Awash National Park (9°20'N, 40°20'E, 960-1050 m above sea level), located in the Ethiopian Rift Valley, Ethiopia, typical of semi-arid savannas grazing areas. The mean annual rainfall (1989-2008: Tessema et al., 2011a) of Awash National Park was 512 mm (277-653 mm) and was highly variable among years (coefficient of variation CV = 103%). It has a bimodal rainfall; the main rainy season is from July-October with a short rainy season from February-April. The long dry period is from November-January and the short dry spell is in May and June. The mean daily minimum and maximum temperatures were 18°C and 34°C, respectively (Tessema et al., 2011a). Figure 5.1 shows the dry and wet periods in relation to mean monthly rainfall and temperature (1989 – 2008) at Awash National Park.



**Fig. 5.1.** Climate diagram of the study site: Awash National Park in a semi-arid savanna grazing system of Ethiopia. Dotted lines refer to average monthly temperature and solid lines to rainfall. For both climate variables monthly averages for the years 1989-2008 are presented.

### Procedures of seed collection and germination

Fully mature seeds of 16 grass species were collected at opportunistically after fruiting/seeding of most grass species between the end of October and November 2008. The seeds were collected by cutting the heads of mature seed setting plants using a sickle until enough seeds (full caryopsis) of each species were collected. It should be noted that the term “seed” used in this study is synonym to dispersal unit/caryopsis. The grass species used for this experiment included both annual (N = 4) and perennial grass (N = 12) species found in the lightly grazed areas. We selected these species based on their higher abundance ( $m^{-2}$ ) under the light grazing sites and lower abundance under the heavy grazing sites in the study site (Tessema et al. 2011a, c), as well as based on availability of enough quality seeds for the study. For further details, the description of the light and heavy grazing sites at Awash National Park is reported in Tessema et al. (2011a, b). Annual grass species included in this study were *Dactyloctenium aegyptium* (L.) Willd., *Panicum atrosanguineum* (A.) Rich., *Eragrostis papposa* (Roem. & Schult.) Steud. and *Sorghum verticilliflorum* (Steud.) Stapf, and perennial grass species were *Chloris gayana* Kunth, *Andropogon kelleri* Hack., *Chrysopogon plumulosus* Hochst, *Heteropogon contortus* (L.), *Hyparrhenia hirta* (L.) Stapf., *Hyparrhenia rufa* (Nees) Stapf, *Panicum coloratum* (L.), *Sporobolus pyramidalis* (P.) Beauv., and *Tetrapogon tenellus* (Koen. ex Roxb.) Chiov., *Bothriochloa radicans* (Lehm.) A. Camus, *Cenchrus ciliaris* (L.) and *Linthonia nutans*.

Prior to the viability and germination studies, the seeds were checked whether they were intact seeds (filled seeds), or physically damaged, or attacked by insects or other organisms. After cleaning and checking, only intact (filled seeds) seeds were stored in paper bag individually for each species in a laboratory until the viability and germination studies. The laboratory temperature was ranged between 22-25°C during the day and 10-15°C during the night, which is assumed to be optimum for germination of grass species collected in semi-arid areas of Africa (Veenendaal, 1991). Seeds were not scarified prior to the viability and germination experiments, except that the viability of *Sorghum verticilliflorum* seeds was assessed with scarification since we observed a hard seed coat during a pilot study.

The seed germination test for all species was repeated six times with an interval of 2 months in one year, from January to December 2009 at Haramaya University in Ethiopia. For each species, 600 seeds (full caryopses) were used for the germination study, and 100 seeds of each species, replicated four times, with 25 seeds were used for each germination interval. The seeds were sown on a double layer of filter paper, which was kept moist with distilled

water in Petri dishes (9 cm diameter). The 16 grass species were placed randomly in a row replicated four times on a bench in a laboratory for a period of 28 days (El-Keblaw and Al-Rawai, 2005). The germinated seeds were counted, recorded and removed every two days until the end of the germination time (28 days) (El-Keblaw and Al-Rawai, 2005).

Similarly, for each species, 600 seeds (full caryopses) were used for the viability study, and 100 seeds of each species, replicated four times, with 25 seeds were used to test the seed viability, using a tetrazolium solution (10 gm tetrazolium mixed with one litre of distilled water; Peters, 2000) in Petri dishes, also repeated 6 times with an interval of 2 months for one year, similar to the germination test. Full caryopsis or seeds were considered viable, when the embryo part was coloured brightly red and the endosperm light pink to brightly red stained after immersing in a tetrazolium solution overnight. Counting of the seeds as well as the viability and germination status of the caryopsis or seeds was done under a microscope in a laboratory at Haramaya University in Ethiopia.

### **Data collection and analyses**

The seed germination (G) and the viability (V) for each grass species were calculated as  $G_i (\%) = (\sum n_i / N_i) \times 100$ , and  $V_i (\%) = (v_i / V_i) \times 100$ , where  $\sum n_i$  is the cumulative number of seeds germinated per month,  $N_i$  is the total number of seeds sown for the germination test,  $V_i$  is the total number of seeds sown for the viability test and  $v_i$  is the number of seeds with red stained embryo at the end of the tetrazolium test. To test for differences in germination (%) and viability (%), a two-way analysis of variance (ANOVA) was carried using a General Linear Model (GLM) in PASW (v.17), with species and time (months) as fixed effects. Comparison between annual grasses ( $n = 4$ ) versus perennial grasses in terms of their germination and viability was done using GLM. The viability and germination percentage data were arcsine transformed to meet the assumptions of normality and homogeneous variances prior to carrying out the GLM.

To investigate the differences in germination between annual and perennial species, a Kaplan-Meier survival analysis and a log rank test were used over the 28 days in each of the six germination periods (Kleinbaum and Klein, 2005). Moreover, regression analysis was carried out to investigate whether the difference in species composition between the aboveground vegetation and soil seed banks could be explained by the differences in germination between annual and perennial grass species (Table 5.1). The detail procedures for

the aboveground vegetation and soil seed bank composition are described in Chapter 2 (Tessema et al., 2011a) and Chapter 3 and 4 (Tessema et al., 2011b, d), respectively.

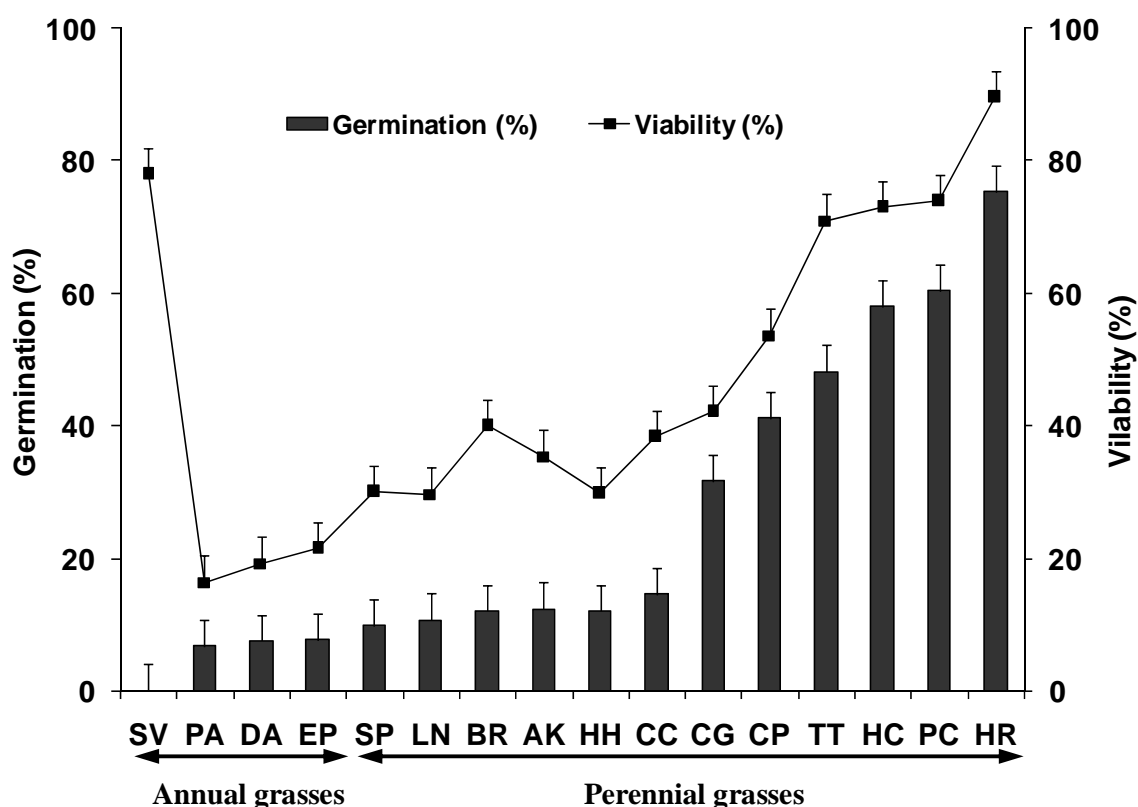
**Table 5.1.** Species composition (abundance  $m^{-2}$ ) of annual and perennial grasses both in the soil seed bank and aboveground vegetation, and their difference between aboveground vegetation and soil seed bank under light (LG) and heavy grazing (HG) in semi-arid savannas of Ethiopia. Data on soil seed banks and aboveground vegetation are obtained from previous studies (Tessema et al., 2011a, b).

Species	Soil seed banks		Aboveground vegetation		Differences between aboveground vegetation and soil seed banks		Germination (%)
	HG	LG	HG	LG	HG	LG	
<i>Andropogon kelleri</i>	0	0	0	1.72	0	1.72	11.7
<i>Bothriochloa radicans</i>	0	1.5	0	4.12	0	2.62	7.8
<i>Cenchrus ciliaris</i>	0	0.8	2.31	1.69	2.31	0.89	12.5
<i>Chloris gayana</i>	2.64	3.1	0	1.34	-2.64	-1.76	31.7
<i>Chrysopogon plumulosus</i>	3.7	6.8	1.91	7.11	-1.79	0.31	41.2
<i>Dactyloctenium aegyptium</i>	3.3	5.7	10.9	2.89	7.60	-2.81	7.5
<i>Eragrostis papposa</i>	5.5	3.6	3.59	1.53	-1.91	-2.07	7.7
<i>Heteropogon contortus</i>	0	0	1.60	1.14	1.60	1.14	59.8
<i>Hyparrhenia hirta</i>	0	0	0	2.02	0	2.02	12.0
<i>Hyparrhenia rufa</i>	0	0	0	4.50	0	4.50	80.2
<i>Linthonia nutans</i>	0	0.5	0	1.40	0	0.90	9.2
<i>Panicum atrosanguinium</i>	1.1	1.2	1.41	2.1	0.31	0.90	6.7
<i>Panicum coloratum</i>	1.5	0.8	0.45	2.96	-1.05	2.16	52.0
<i>Sorghum verticilliflorum</i>	0	0	0	3.7	0	3.70	0
<i>Sporobolus pyramidalis</i>	0	2.5	3.4	2.7	3.4	0.20	9.2
<i>Tetrapogon tenellus</i>	0	0	1.7	1.4	1.7	1.4	49.5

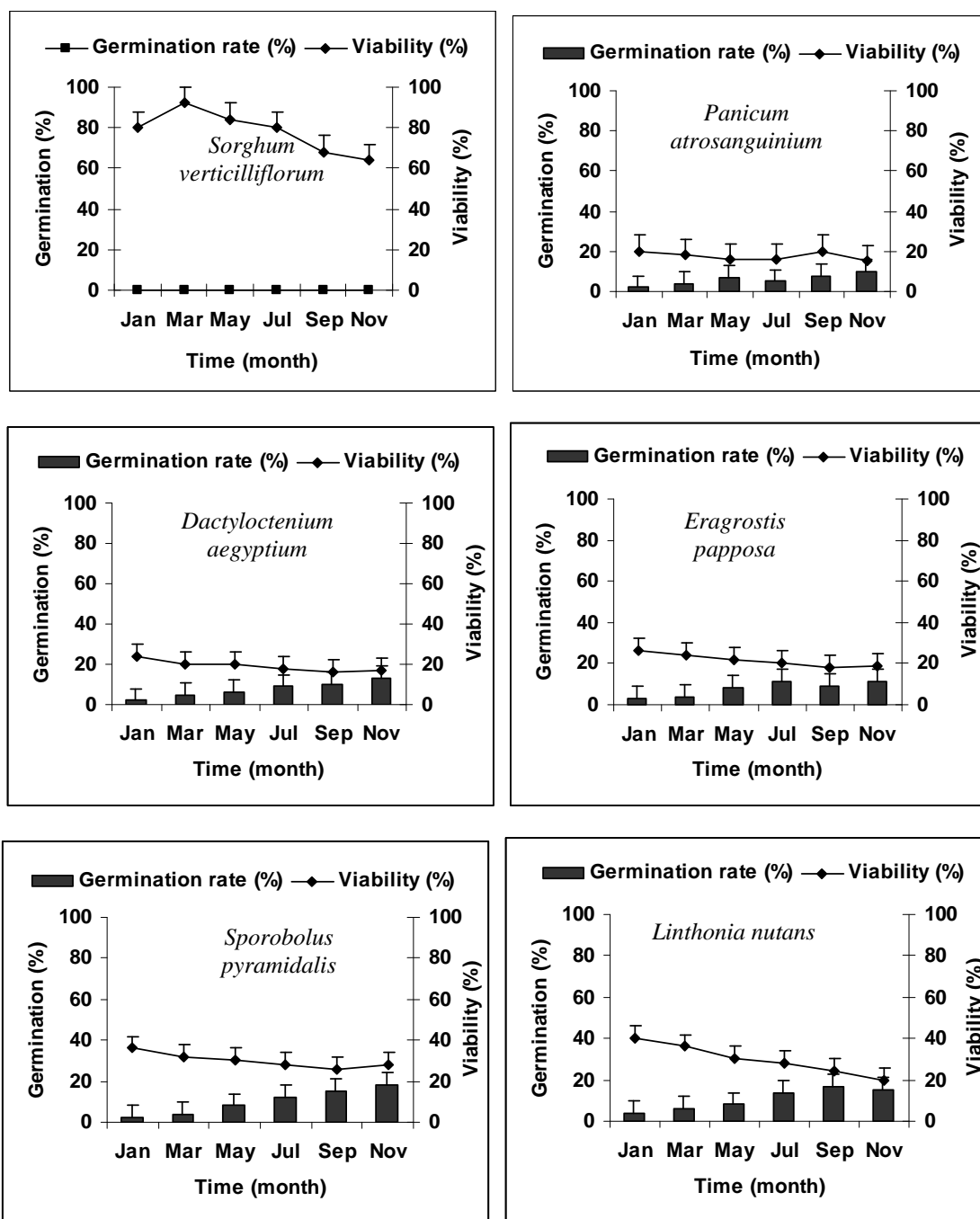
## Results

Grass species differed significantly in seed viability ( $F_{15,75} = 47.072$ ,  $P < 0.001$ ), with nearly half of the perennial grass species tending to have a higher viability than 3 of the 4 annual grass species (Fig. 5.2). At species level, the viability of grass species ranged from 16% (*Panicum atrosanguinium*) to 90% (*Hyparrhenia rufa*; Fig. 5.3). Among the annual grass, *Sorghum verticilliflorum* had a higher viability (mean: 78%, range: 64%-92%) over the entire test period compared with other annuals. The mean viability of annual and perennial grass were 34 (range: 16.3-78%) and 51% (range: 30-90%), respectively. The seed viability of most perennial grass species generally declined over time, whereas the seed viability of annual grass species relatively remained stable until the end of the 12 month study period ( $F_{5,75} = 10.079$ ,  $P < 0.001$ ).

Six of the 12 perennial grass species had a higher germination percentages than annual grass species ( $F_{15,75} = 88.891$ ,  $P < 0.001$ ; Fig. 5.2). The mean germination success (%) of perennial grass species ranged from 9.8% (*Sporobolus pyramidalis*) to 75% (*Hyparrhenia rufa*), whereas for annuals this value ranged from 0% (*Sorghum verticilliflorum*) to only 8% (*Eragrostis papposa*; Fig. 5.3). Among the perennial grass species, such as *Chloris gayana*, *Chrysopogon plumulosus*, *Tetrapogon tenellus*, *Panicum coloratum*, *Heteropogon contortus* and *Hyparrhenia rufa* had a higher germination than all annual grass species. Except *Sorghum verticilliflorum*, the germination of annual grass species showed an increasing trend until the end of the germination study, whereas the germination of most perennial grasses increased for a certain period after the onset of the study and decreased thereafter ( $F_{5,75} = 8.641$ ,  $P < 0.001$ ).



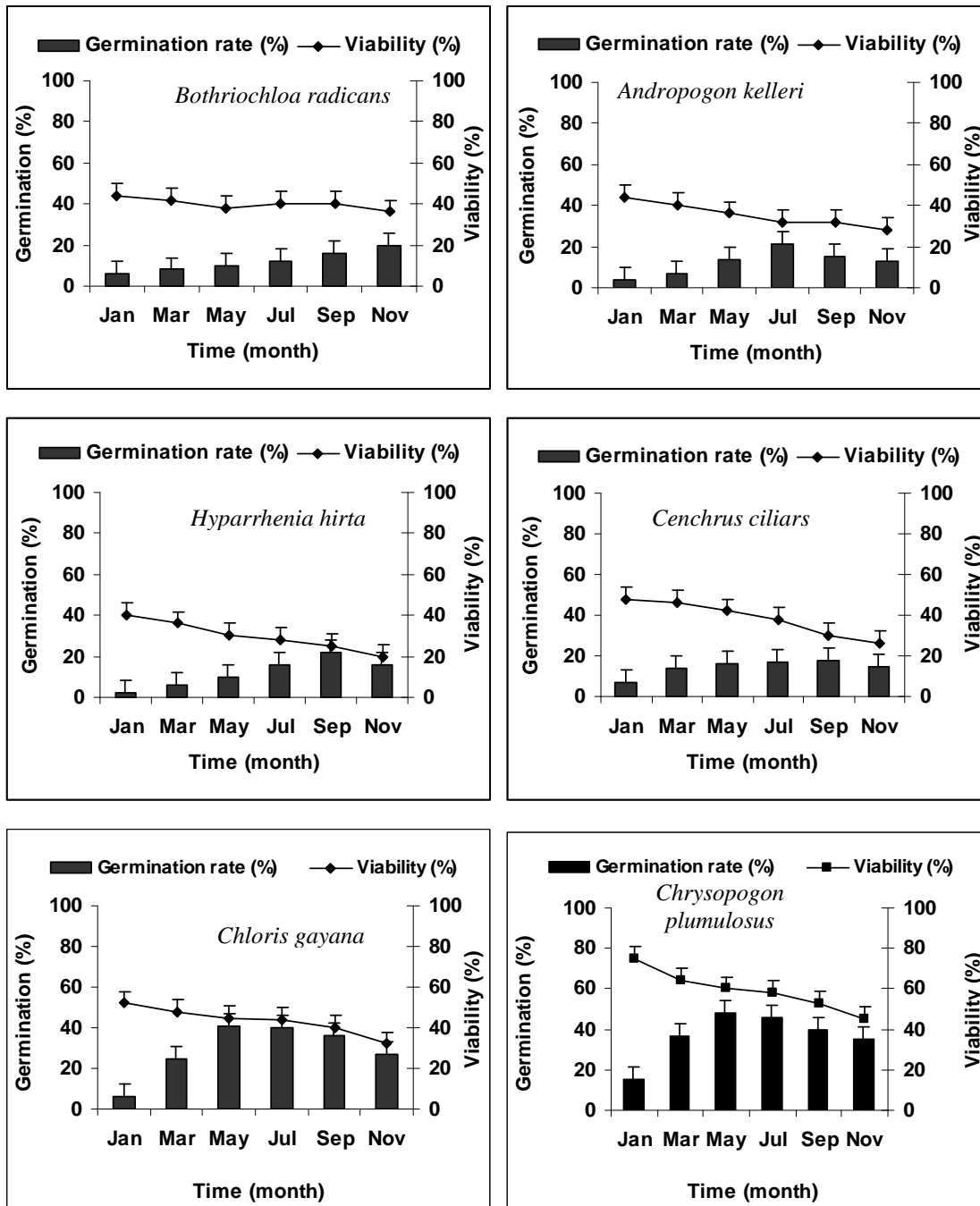
**Fig. 5.2.** Mean ( $\pm 95\%$  CI) viability and germination rates (%) of annual grass species (SV = *Sorghum verticilliflorum*; PA = *Panicum atrosanguineum*; DA = *Dactyloctenium aegyptium*; EP = *Eragrostis papposa*) and perennial grass species (BR = *Bothriochloa radicans*; LN = *Linthonia nutans*; SP = *Sporobolus pyramidalis*; AK = *Andropogon kelleri*; HH = *Hyparrhenia hirta*; CC = *Cenchrus ciliaris*; CG = *Chloris gayana*; CP = *Chrysopogon plumulosus*; TT = *Tetrapogon tenellus*; HC = *Heteropogon contortus*; PC = *Panicum coloratum*; HR = *Hyparrhenia rufa*), collected in a semi-arid savanna grazing systems of Ethiopia.

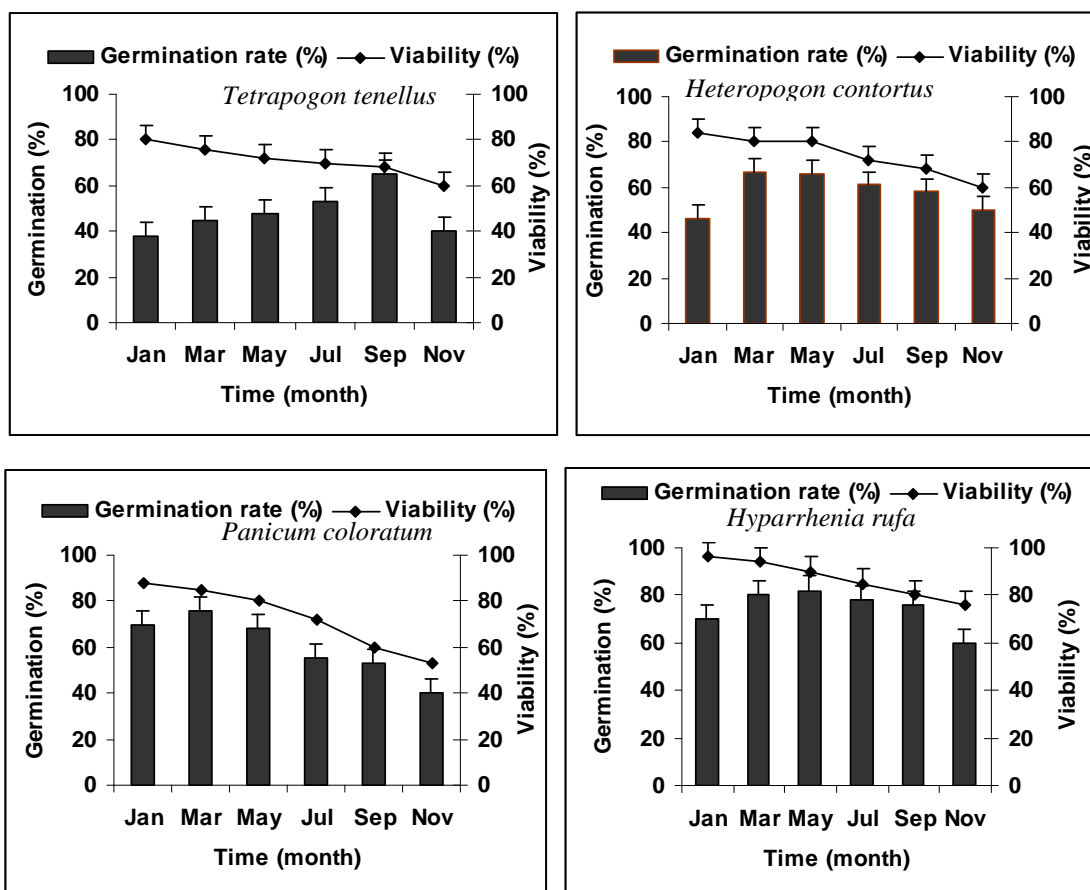


**Fig. 5.3.** Mean viability and germination rates (%;  $\pm 95\%$  CI) over time (from January 2009–December 2009; with an interval of 2 months) of annual grass species (SV = *Sorghum verticilliflorum*; PA = *Panicum atrosanguineum*; DA = *Dactyloctenium aegyptium*; and EP = *Eragrostis papposa*) and perennial grass species (SP = *Sporobolus pyramidalis*; LN = *Linthonia nutans*; BR = *Bothriochloa radicans*; AK = *Andropogon kelleri*; HH = *Hyparrhenia hirta*; CC = *Cenchrus ciliaris*; CG = *Chloris gayana*; CP = *Chrysopogon plumulosus*; TT = *Tetrapogon tenellus*; HC = *Heteropogon contortus*; PC = *Penicum coloratum* and HR = *Hyparrhenia rufa*).



Fig. 5.3. continued...

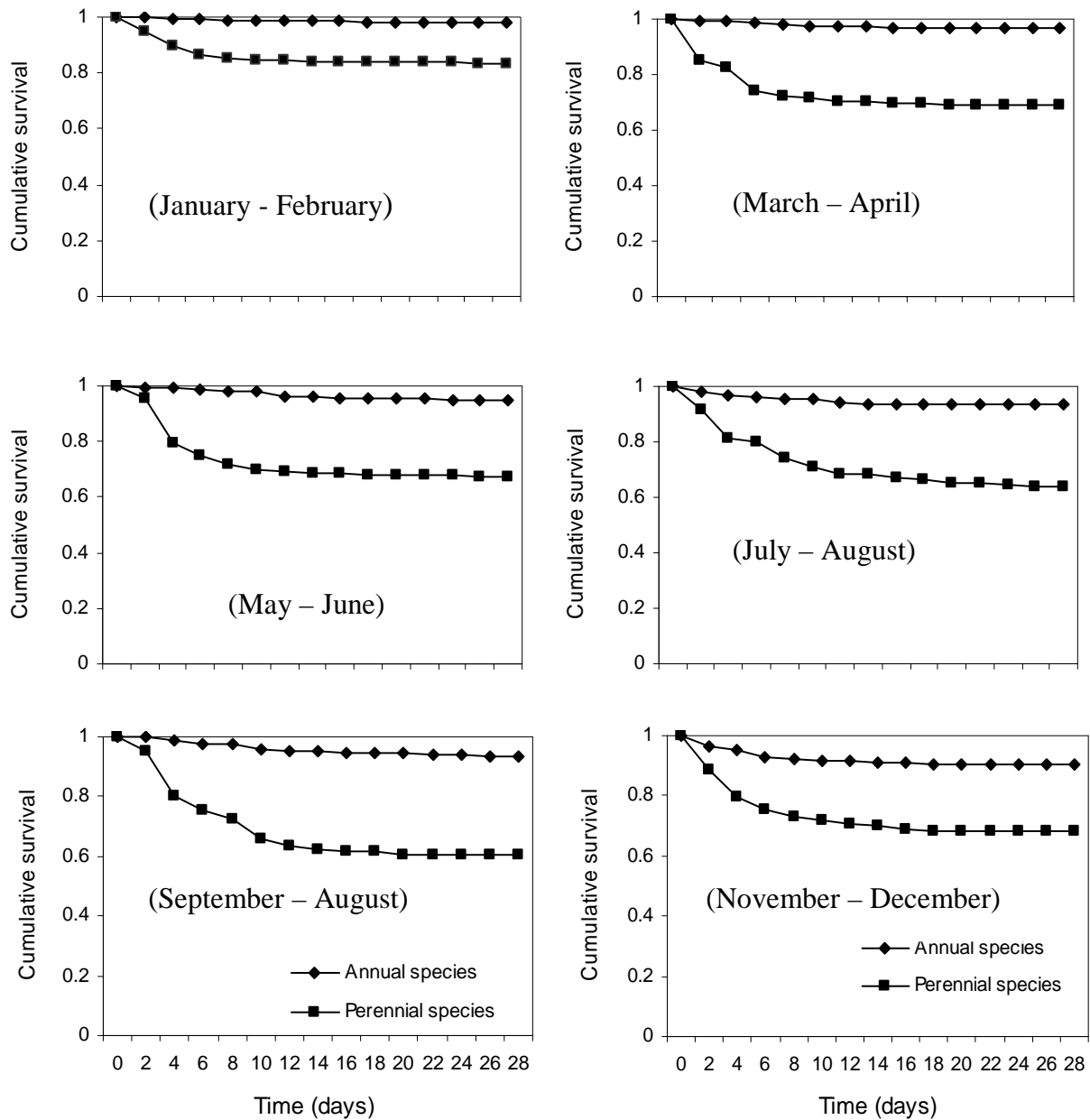




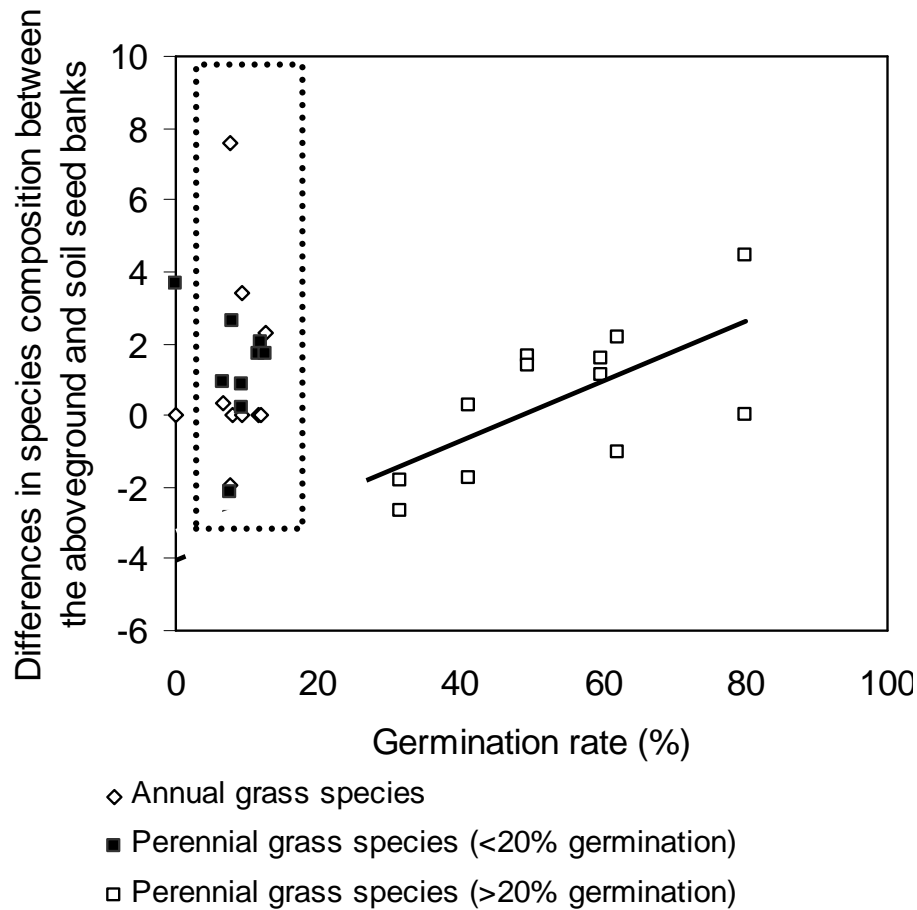
Regarding the cumulative survival of the individual seeds over the 28 days period, annual grass species showed a linear increase in germination over time, whereas germination of perennial grass species was rapid at the first days of the trial, but slowed down thereafter (Fig. 5.4). This indicates that annual grass species have an increase in cumulative seed survival, whereas perennial grass species have a general decrease in cumulative seed survival due to their higher germination compared with annuals. Moreover, large differences in germination success were observed between annual and perennial species, especially in the period from May – June (Log rank test,  $X^2 = 116.5$ ,  $df = 1$ ,  $P < 0.001$ ) and from September – October (Log rank test,  $X^2 = 141.0$ ,  $df = 1$ ,  $P < 0.001$ ), with a higher germination success for perennials. Also, annuals increase slightly each time period.

Our result confirmed that differences in germination percentages between annual and perennial grass species partly explained the variations in difference in species compositions between the aboveground vegetation and soil seed banks. A low germination percentage of grass species, which is less than 20%, could not explain the differences in relative species composition between aboveground vegetation and soil seed banks in semi-arid Ethiopian savannas (Fig. 5.5). However, for grass species with a mean germination percentages of at

least 20% were, as expected, positively related to the differences in the relative species composition between the aboveground vegetation and soil seed banks ( $R^2 = 0.458$ ,  $F_{1,11} = 8.445$ ,  $P = 0.016$ ; Fig. 5.5). This indicates that the lower the germination of the grass species, and hence the higher the dormancy, the lower the relative contribution of the species in the aboveground vegetation compared to the soil seed banks.



**Fig. 5.4.** Cumulative germination (survival of seeds) for annual and perennial grass species collected in semi-arid savanna grazing systems of Ethiopia over the 28 days germination trial carried out at six different periods from January 2009 - December 2009, with an interval of 2 months.



**Fig. 5.5.** Differences in germination (%) between annual and perennial grass species explain the differences in relative species composition between the soil seed banks and aboveground vegetation in a semi-arid savanna of Ethiopia.

## Discussion

There were wide ranges in seed viability and germination rates of grass species over time. Thus, grass species with different dormancy and germination characteristics coexist. In general, annual grass species had a lower germination rate, which could be explained either by a longer seed dormancy characteristics, and is potentially associated with a lower production of viable seeds from the mother plants (Veenendaal et al., 1996b). The accumulation of seeds of annual species in the soil seed bank might be increased due to the presence of dormancy or an impermeable seed coat (Mott, 1978; Fenner and Thompson, 2005). According to some studies (Veenendaal et al., 1996a), dormancy is selected for most annual species to avoid local extinction because these species are typically found in areas characterized by long dry seasons and unreliable rainfall periods, such as in African semi-arid savannas (Vleeshouwers et al., 1995).

The germination rates of annual grass species were low but increased towards the end of the study, indicating that annual grass species may possess dormancy characteristics, in which the germination is blocked (Eira and Caldas, 2000). For instance, the annual grass *Sorghum verticilliflorum* had a higher viability but did not germinate at all due to a hard seed coat (observed in this study), indicating some kinds of seed treatment prior to germination (i.e., physical scarification of the seed coat). According to Mott (1978), seed dormancy is a temporary delay of seeds to germinate under particular environmental conditions, but possible to germinate later by applying different dormancy breaking strategies. Hence, the annual grasses, *Dactyloctenium aegyptium* and *Eragrostis papposa*, are good colonizers of bare areas under heavy grazing in Ethiopian savannas (Angassa and Oba, 2010; Tessema et al., 2011a), in degraded areas (Yayneshet et al., 2009), and in other tropical areas (McIvor and Howden, 2000; Tefera et al., 2010), which might be due to their long dormancy, or they are better dispersers into disturbed areas as many annual grasses are well known to be. These allow annual grasses to form persistent soil seed banks and germinate when a suitable window arises (Solomon et al., 2006; Tessema et al., 2011b).

The germination of half of the perennial grass species in this study increased until 5 months, peaked at 10 months, and decreased thereafter at 12 months. However, the germination of half the perennial grass species were intermediate between annuals and other perennials, which are typically found both under the light and heavy grazed areas (Tessema et al., 2011a, b). According to Mott (1978) and McIvor and Howden (2000) the seeds of most perennial grass species are dormant following seed dispersal at the end of the growing season, but overcome their dormancy during the late dry season due to high soil temperatures. Most of the perennial grass species such as *Chrysopogon plumulosus*, *Tetrapogon tenellus*, *Panicum coloratum*, *Heteropogon contortus* and *Hyparrhenia rufa* showed higher germination immediately at the beginning of the germination experiment, from January to June, indicating that these species could germinate with the onset of the short rains that usually occur from February-April, but also that these seedlings could die due to short dry spells, which occur from May-June. As a result, perennial grass species with good fodder values are expected to lose most of their seeds in the soil (O'Connor and Pickett, 1992; O'Connor, 1994; Scott et al., 2010) and the possibility that these seeds germinate during the favourable period, the long rainy season from July-September, decreases (McIvor and Howden, 2000; Baskin and Baskin, 2004). Moreover, perennial grass such as *Chrysopogon plumulosus*, *Panicum coloratum* and *Hyparrhenia rufa*, which had high germination rates, are typically found under light grazing conditions in Ethiopia (Abule et al., 2005b; Tessema et

al., 2011a, c). Similarly, McIvor and Howden (2000) reported that *Heteropogon contortus*, *Chloris gayana* and *Chrysopogon* sp. had a low dormancy during the dry and wet seasons in seasonally dry tropical areas of Australia.

A number of perennial grasses are dormant at seed maturity but they start to break their dormancy during the long dry season, especially when approaching the wet season (Mott, 1978). Despite the loss of dormancy in the dry season, germination of perennial grasses is usually prevented by a lack of moisture (Scott et al., 2010), which is a characteristic of semi-arid savannas, and seed germinate in a series of cohorts until no viable seed remain in the soil (Andrew and Mott, 1983; Veenendaal et al., 1996a). Hence, long term dormancy of most perennial grass seeds (O'Connor and Everson 1998; Gardener et al., 2001) and persistent seed banks of these perennials are not common in tropical savannas (Scott et al., 2010; Tessema et al., 2011b). Also our results suggest that perennial grass species may not contribute much to the formation of persistent seed banks in semi-arid savannas of Africa due to their higher germination rates and low dormancy characteristics.

In our study, annual grass species had a lower germination, and longer dormancy periods before germination. As a result of longer dormancy, annual grasses and other plants with an annual life history usually dominate the heavily grazed areas, whereas the lightly grazed areas are dominated by most perennial grass species with a higher germination and a lower dormancy (Tessema et al. 2011f, g). Therefore, with increasing grazing pressure, perennial grass species, often with good fodder value, are replaced by annual species in the soil seed banks (Wassie and Teketay 2006; Tessema et al. 2011b). This is relevant for livestock production systems, to maintain the diversity of perennial grasses on their grazing lands, as annual grasses often have a lower forage value for herbivores (Prins, 1988, 1996; Prins and Beekman, 1989).

In general, based on the germination success and time of germination, the grass species in our study could be categorized into 4 groups:

- Group I- the annual grass *Sorghum verticilliflorum* with no germination during the entire study period;
- Group II- annual grass species with a low germination (<8%), germinating most often in the long rainy seasons, such as *Panicum atrosanguineum*, *Dactyloctenium aegyptium* and *Eragrostis papposa*;
- Group III- perennial grass species with intermediate germination (>9-20%), germinating partly in the short rainy season, but mostly in the long rainy

seasons, such as *Sporobolus pyramidalis*, *Linthonia nutans*, *Bothriochloa radicans*, *Hyparrhenia hirta*, *Andropogon kelleri*, *Cenchrus ciliaris* and;

- Group IV- perennial grass species with high germination (30-75%), which break their dormancy in the long dry season and germinate generally in the short rainy seasons. As a result their seedlings are expected to die during short dry periods, and ultimately disappear in the aboveground vegetation over time. These include *Chloris gayana*, *Chrysopgon plumulosus*, *Tetrapogon tenellus*, *Heteropogon contortus*, *Panicum coloratum* and *Hyparrhenia rufa*.

The African semi-arid savanna grazing systems are characterized by large temporal and spatial variation in rainfall (Prins and Loth, 1988; Tilahun, 2006). Moreover, there are often two dry spells in semi-arid savannas of Ethiopia, the long dry season (November-January), and the short dry season (May-June), and two rainy seasons in between (Tilahun, 2006). Most perennial grass species are expected to break their dormancy immediately after seed dispersal during the long dry season, and start germination in the short rainy season, which would drastically affect the survival of these perennials. According to Veenendaal et al., (1996a) seedling emergence and subsequent survival of perennial grass species may be strongly influenced by the timing and variation in rainfall. A minimum amount of 15-25 mm rainfall has been reported to trigger widespread germination of grass species in arid and semi-arid grasslands (Andrew and Mott, 1983; Prins, 1988; Elberse and Breman, 1990). However, a single rainfall event, especially if early in the dry season, may be followed by a dry spell, increasing the mortality of perennial grass seedlings.

## Conclusions

Most perennial grasses germinated rapidly after initial seed dispersal and declined thereafter, whereas annual grass species showed a more linear increase in germination rate over time, indicating that perennial and annual grass species have different germination strategies. Moreover, the wide variation in germination between annual and perennial grass species revealed that there could be large differences in establishment of grass seedlings after small rainfall events. This rapid germination of most perennials may particularly increase the likelihood for their establishment in semi-arid African savannas. The implication in this study is that the seedlings are mostly eaten because of high grazing or die due to trampling or frequent drought or erratic rainfall. Therefore, removal of perennial grass species from the rangeland community in semi-arid African savannas for more than 1 or 2 years by heavy

grazing is likely to exhaust the seeds available for re-establishment in the soil seed banks, triggering permanent changes to these communities, unless the species are able to re-colonize from elsewhere or are deliberately re-introduced. We concluded that differences in germination rates between annual and perennial grass species partly explain the variation in species composition between the aboveground vegetation and the soil seed banks.

### **Acknowledgment**

We would like to acknowledge Nuffic for funding this research, the Haramaya University of Ethiopia for providing laboratory facilities, and Mr. Abiyou Debasso for his assistance during the laboratory studies.



# 6

Why perennial grass species disappear and annual grass species become abundant in soil seed banks of semi-arid savannas



Z.K. Tessema, W.F. de Boer, R.M.T. Baars and H.H.T. Prins (submitted)

### **Abstract**

Buried seeds can play a pivotal role in the restoration of degraded ecosystems, where plant species have disappeared from the established vegetation but survive in the soil seed banks. Therefore, we studied the fate of grass seeds buried in the soil within mesh bags over time, from June to October, 2009 in a semi-arid Ethiopian savanna. There were significant differences in germination, viability and mortality of seeds among grass species. Perennial grasses lost their longevity due to higher germination (46%) and mortality (28%), whereas annual grasses had a lower germination (24%) and mortality (14%) while buried in the soil. Moreover, perennial grass seeds had a lower germination rate at the beginning of the burial time, peaked at the middle of the study period and declined thereafter, whereas annual grass showed an increasing trend in germination until the end of the study. The seed viability of perennial grasses was higher at the beginning of the burial experiment, but rapidly declined thereafter, whereas annual grass species maintained their seed viability at the beginning and remained stable over time. The proportion of dead seeds in all grass species increased with increasing burial time. Due to the lower germination, higher viability, and lower mortality rates, annual grasses had a survival of 62 percent over time, considerably larger than the 28 percent for perennial grasses. We concluded that perennial grasses rapidly disappear in the soil, whereas annual grasses form persistent soil seed banks in semi-arid savannas.

**Keywords:** Dormancy; Ethiopia; Germination success; Seed survival; Seed viability; Soil seed bank; Vegetation recovery

## **Introduction**

In tropical and sub-tropical savannas and grasslands, annual and perennial grasses are crucial for an ecosystem's functioning, through supporting herbivores and preventing soil erosion (Zimmermann et al., 2010). However, many arid and semi-arid savannas now face different forms of soil and vegetation degradation (Snyman, 1998), often triggered by high grazing pressures (Rietkerk et al., 1996; Tessema et al., 2011a), affecting the survival of wildlife and livestock (Briske et al., 2003, Kassahun et al., 2008b). Very heavy grazing might result in a decline of rangeland productivity, a loss of biodiversity, and an increase in soil erosion (Illius and O'Connor, 1999; Harris 2010). The disappearance of good fodder grasses is a serious challenge in semi-arid African savannas (O'Connor, 1994; Angassa and Oba, 2010).

According to some studies conducted elsewhere the recovery of plant species that disappeared under heavy grazing could be facilitated by the presence of soil seed bank and trigger the vegetation recovery (Snyman, 2004; Hopfensberger, 2007) since the soil seed bank serves as a reserve to return to the original vegetation conditions (Bekker et al., 1998). However, grass seeds available in the soil seed banks in semi-arid African savannas were confirmed unable to “kick-start” the vegetation recovery and accelerate the transition from degraded vegetation condition to vegetation with a perennial grass cover (Solomon et al. 2006; Kassahun et al., 2009; Tessema et al., 2011b, d). Similarly, Page and Beeton (2000) and Vetter (2005) reported that semi-arid rangelands did not recover from heavy livestock grazing even after many years of grazing exclosures. This might be due to the depletion of seeds in the soil as a result of germination and mortality, and/or differences in longevity and germination of seeds between species in soil seed banks (Pons, 1991; Baskin and Baskin, 2004; Snyman, 2004).

Plant recruitment through germination from the soil seed bank (Dreber and Esler, 2011; Tessema et al., 2011b) and subsequent development (O'Connor, 1994, 1996) can lead to the establishment of new individuals for restoration of degraded grazing systems (Fay and Schultz, 2009; Zimmermann et al., 2010). Seed germination and seedling survival are however highly sensitive to environmental variability, and require favourable soil conditions (Fay and Schultz, 2009). Under natural conditions seeds and seedlings routinely experience periods of alternating wet and dry conditions, with consequently large impacts on seed stock and vegetation dynamics (Prins, 1988; Fay and Schultz, 2009).

Seed longevity in soil seed banks is an important determinant of plant community dynamics, and a wide range of seed germination strategies exist, with clear differences

between plant functional groups (Prins and Loth, 1988; Baskin and Baskin, 2004). Seeds do not always germinate under a given set of conditions (Brown, 1992), and dormancy and the speed at which seeds germinate differ among species, change over time, and are dependent on local conditions (Baskin and Baskin, 2004). More specifically, soil seed bank forming species have seeds with an environmental adaptive strategy that delays germination until specific environmental conditions are met (Teketay and Granström, 1995). The composition of the soil seed bank depends on the longevity of the seeds of each species under local conditions (Bakker et al., 1996). According to Bekker et al. (1998) and Luzuriaga et al. (2005), seed burial experiments showed that seeds of many pioneer species in tropical areas maintained their viability for long periods (Shaukat and Siddiqui, 2004) in the soil seed banks, under the influence of several factors that control their germination and longevity (Masin et al., 2006; Page and Harrington, 2009). For instance, moisture conditions immediately prior to germination play a dominant role in regulating seed germination in arid and semi-arid systems (Prins, 1988; Veenendaal et al., 1996a). How long seeds can remain buried in the soil while maintaining viable depends on the species (Masin et al., 2009), and on the climatic factors after initial dispersal (Williams et al., 2005; Fay and Schultz, 2009).

Buried seeds can play a pivotal role in the conservation, management and restoration of degraded ecosystems, where plant species that have disappeared from the established vegetation possibly survive in the soil seed banks (Luzuriaga et al., 2005; Hopfensberger, 2007). The recovery potential of grass species in semi-arid savanna after sustained heavy grazing is believed to depend mainly on the longevity of seeds buried in the soil ((O'Connor, 1996; Pake and Venable, 1996). Hence, seed persistence in soils can influence population persistence of the aboveground vegetation (Reed et al., 2002, Saatkamp et al., 2009). Knowledge on the fate of seeds is therefore crucial for understanding the abundance and distribution of plant communities (Pake and Venable, 1996), and ultimately, community composition and diversity (Clark and Wilson, 2003). Survival of seeds in soil seed banks is therefore highly important to ensure persistence of local plant populations (Pake and Venable, 1996; Thompson et al., 2003), and for restoration of degraded ecosystems (Williams et al., 2005; Hopfensberger, 2007; Saatkamp et al., 2009).

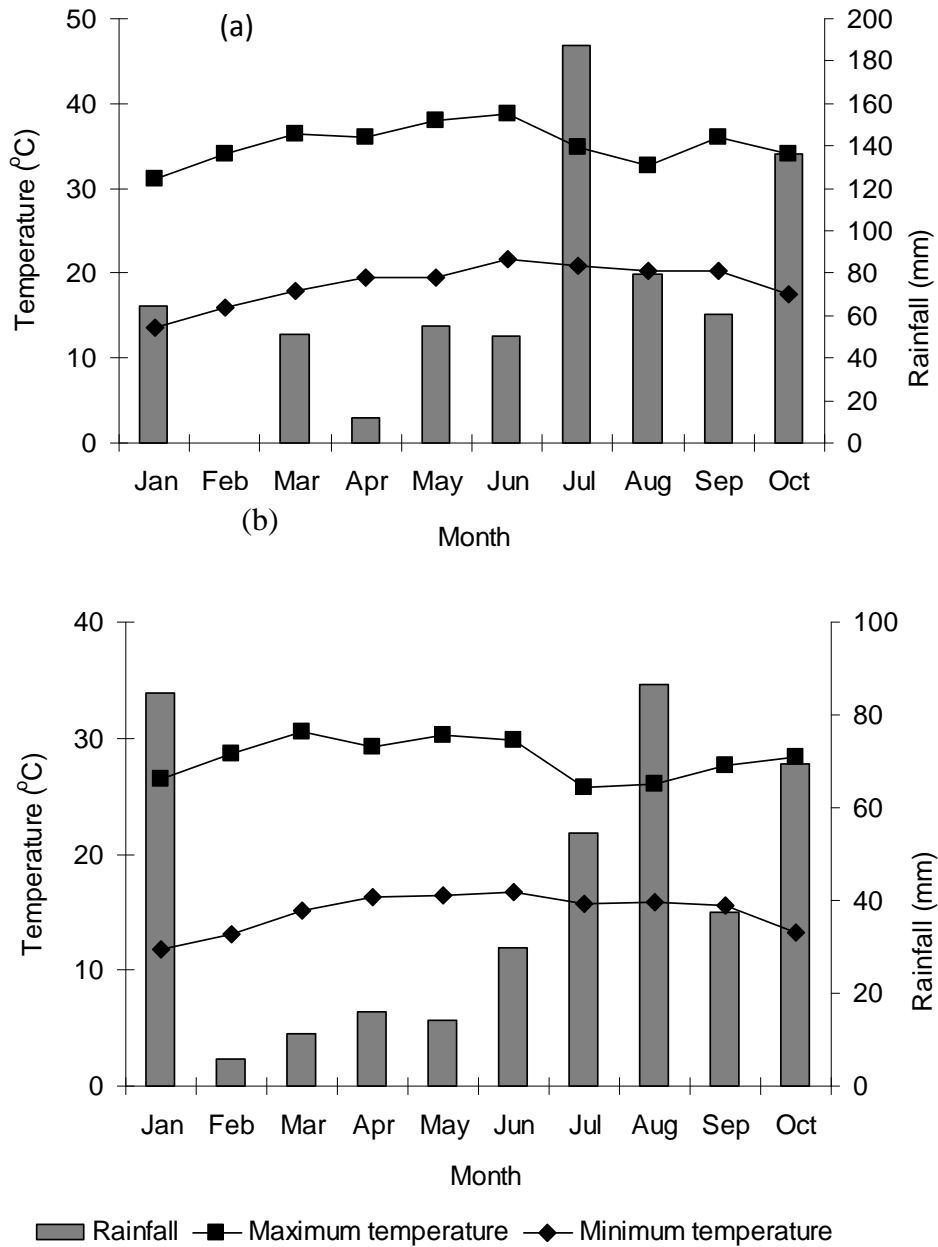
The seed bag burial method is used to monitor the longevity and dormancy of seeds in the soil, and this method is frequently used when very small seeds are being studied (Van Mourik et al., 2005). Information on germination success and longevity of grass seeds buried in soil, as well as knowledge on the underlying processes controlling the fates of these seeds

in semi-arid savannas is limited. The objective of this study was therefore to quantify the fates of grass seeds buried in the soil over time in semi-arid savannas. We addressed the hypothesis that the seeds of annual grasses have lower germination and mortality rates than perennial grasses while buried in the soil, so that they maintain their longevity longer in the soil. If these differences between annual and perennial grasses exist, we predict that perennial grasses form less persistent seed banks in the soil in semi-arid savannas than annual grasses.

## **Materials and methods**

### **Location of the study**

The study was conducted in two semi-arid locations: the Abernosa Cattle Breeding Ranch (7°47'N, 38°40'E, 1660-1740 m asl) and Awash National Park (9°20'N, 40°20'E, 960-1050 m asl). The distance between these two locations is about 220 km, both located in the Ethiopian Rift Valley, typical for many semi-arid African savannas (Tessema et al., 2011a). The mean annual rainfall of Awash National Park was 512 mm (1989-2008: Tessema *et al.* 2011a, b), and was highly variable among years, with a main rainy season from July to October and a short rainy season from February to April. The mean daily minimum and maximum temperatures were 18°C and 34°C, respectively (Tessema et al., 2011a, b). The Abernosa Cattle Breeding Ranch has a bimodal rainfall; the short rains fall between February to April, followed by a short dry spell in May and June, the main rainy season from July to October, and a long dry period between November and January. The average annual rainfall of Abernosa Cattle Breeding Ranch was 734 mm, with mean minimum and maximum temperatures of 14°C and 28°C, respectively (Tessema et al., 2011a, b). The monthly rainfall and the mean monthly minimum and maximum temperature at Abernosa Cattle Breeding Ranch and Awash National Park during the study are relevant for the interpretation of the seed experiment and are presented in Fig. 6.1. The soil types of the actual experimental areas in Abernosa Cattle Breeding Ranch were sand (42.4%), silt (31.5%) and clay (26.1%), and the study site in Awash National Park contained sand (47.4%), silt (31.6%) and clay (21%) (Tessema et al., 2011a).



**Fig. 6.1.** Monthly rainfall (mm) and mean monthly minimum and maximum temperatures (°C) at Abernosa Cattle Breeding Ranch (a) and Awash National Park (b) in semi-arid savannas of Ethiopia, during the study (2009)

#### Grass species tested, and seed collection, cleaning and storage

Three annual grass species (*Dactyloctenium aegyptium* (L.) Willd, *Panicum atosanguineum* (A.) Rich. and *Sorghum verticilliflorum* (Steud.) Stapf) and seven perennial grass species (*Chloris gayana* Kunth, *Chrysopogon plumulosus* Hochst, *Heteropogon contortus* (L.), *Hyparrhenia rufa* (Nees) Stapf, *Panicum coloratum* (L.), *Sporobolus pyramidalis* (P.) Beauv

and *Tetrapogon tenellus* (Koen. ex Roxb.) Chiov) were investigated for longevity of their seeds buried in the soil. We selected these species based on their higher abundance per m<sup>2</sup> on light grazing sites and lower abundance on heavy grazing sites in the study site (Tessema et al., 2011a), as well as on the availability of sufficient seeds for the burial experiment.

For each species, mature seeds were collected directly from several individuals among the mother plants by cutting their inflorescences, which contained mature light brown to dark brown seeds in the field at the light grazing sites during November and December 2008. After cutting, the inflorescences were rubbed gently between the thumb and forefinger several times to obtain seeds with full caryopsis of each species. It should be noted that the term “seed” is used as synonym for caryopsis in this study. The seeds of each species were sieved several times and mixed well together and stored under dry conditions in paper bags at a room temperature until the burial experiment. Only intact seeds (full caryopsis) were selected for the burial study using three criteria: (i) a seed should not have visible signs of damage from insects or pathogens, (ii) the seed that was easily damaged by the pressure applied to it between two fingers was considered dead, and (iii) the seed was considered viable when the embryo stained red after immersing the seed in the tetrazolium solution (10 gm tetrazolium chloride mixed with one litre of distilled water) (ISTA 1999; Peters 2000) in a Petri-dish overnight. For each species, 800 viable seeds were randomly selected from those harvested and were further divided into 32 bags with 25 seeds, enclosed in a 10 x 15 cm nylon mesh bags (mesh size: 250 µm) for the burial experiment both at Awash National Park and Abernosa Cattle Breeding Ranch.

### **Procedures of seed burial experiment**

A 50 x 100 m heavily grazed site was fenced both at the Abernosa Cattle Breeding Ranch and at the Awash National Park until the end of the burial experiment to exclude both large domestic livestock and wild herbivores. The sites represent typical semi-arid degraded rangelands in Ethiopia as a result of continuous heavy grazing. A representative experimental plot of 32 x 30 m was selected within the fenced area, and divided into 4 blocks of 32 x 6 m, which were 2 m apart from each other (Fig. 6.2). The seed bags were buried at the end of June 2009 before the beginning of the wet season when the soil was dry, and bags were exhumed every month for 4 months until the end of the wet season (October 2009).

The seed burial experiment was set up as a randomized block design comprising 4 blocks (4 replications), and each block consisted of 4 subplots, one for each exhumation times

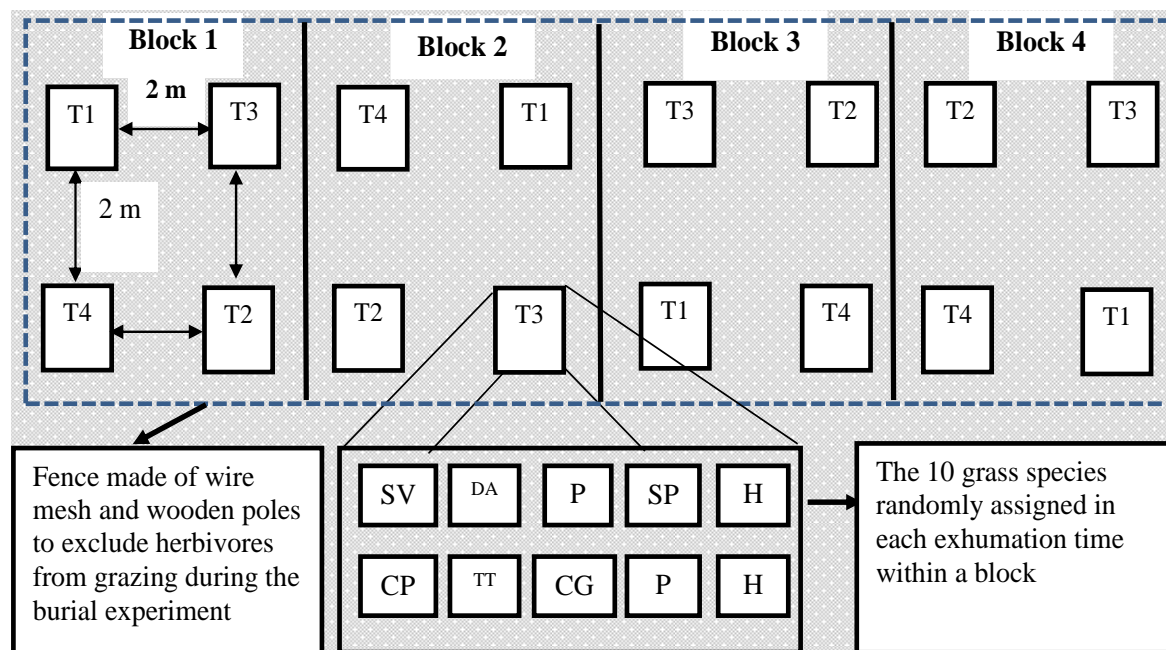
(T1 = end of July; T2 = end of August; T3 = end of September and T4 = end of October; Fig. 2). All seed bags were buried at random locations within a subplot. The seed bags of each grass species were buried at a depth of 5 cm, and 0.5 m apart from each other (Teketay & Granstörn 1997). The bags were inserted into the soil by lifting the top 5 cm soil layer, and carefully covered by immediately putting the lifted soil layer back again over the seed bags. Hence, the bag was taken as the unit of measurement.

The first exhumation was done at the end of July (T1), and the seed bags containing all species in a subplot were recovered, and this was repeated every month until the end of the experiment. After exhumation, the outside of the seed bags was cleaned of any soil and other materials. The bags were then opened, and the seeds were placed on filter paper in a Petri-dish (9 cm diameter) to examine their contents. The 25 seeds in each bag was counted under a microscope and the recovered seeds were classified as germinated, viable (intact), or dead. A seed was considered germinated when a living or dead seedling was attached to the seed. We used 3 methods to check the seed viability after exhumation: (i) the seeds with intact internal content were considered viable after pressing the seeds with a needle to find if the embryo was firm (Ter Heerdt *et al.* 1996), followed by (ii) the seed that was easily damaged by the pressure applied to it between two fingers was considered dead, and (iii) the tetrazolium method (see above). The mortality of seeds was calculated as the difference between the number of seeds buried in the soil and the sum of the remaining viable (intact) and germinated seeds after seed exhumation (Clark & Wilson 2003). The seed counting and viability tests were carried out at the seed laboratory of the Haramaya University of Ethiopia.

### **Data analyses**

To test for differences in the fate of seeds, we used three response variables, *i.e.*, (i) the percentage of seeds that germinated; (ii) remained viable or intact; and (iii) the mortality percentages. Analyses of variance were carried out using General Linear Models (GLM) in PASW (version 17), with location, grass species and time (months) as fixed effects and percentages of germinated, viable and dead seeds as response variables. We repeated the GLM analysis to test for differences in percentages of germinated, viable, and dead seeds between the two life forms (annual versus perennial grass species). The percentage data were arcsine transformed to meet the requirements of normality and homogeneous variances prior to carrying out the GLM.





**Fig. 6.2.** Randomization of the the 10 grass species over 4 blocks and 4 subplots (exhumation time: T1-T4) during the burial experiment in a semi-arid savanna of Ethiopia from end of June – end of October 2009 (SV = *Sorghum verticilliflorum*; DA = *Dactyloctenium aegyptium*; PA = *Panicum atrosanguineum*; CG = *Chloris gayana*; CP = *Chrysopogon plumulosus*; HC = *Heteropogon contortus*; HR = *Hyparrhenia rufa*; PC = *Panicum coloratum*; SP = *Sporobolus pyramidalis* and TT = *Tetrapogon tenellus*).

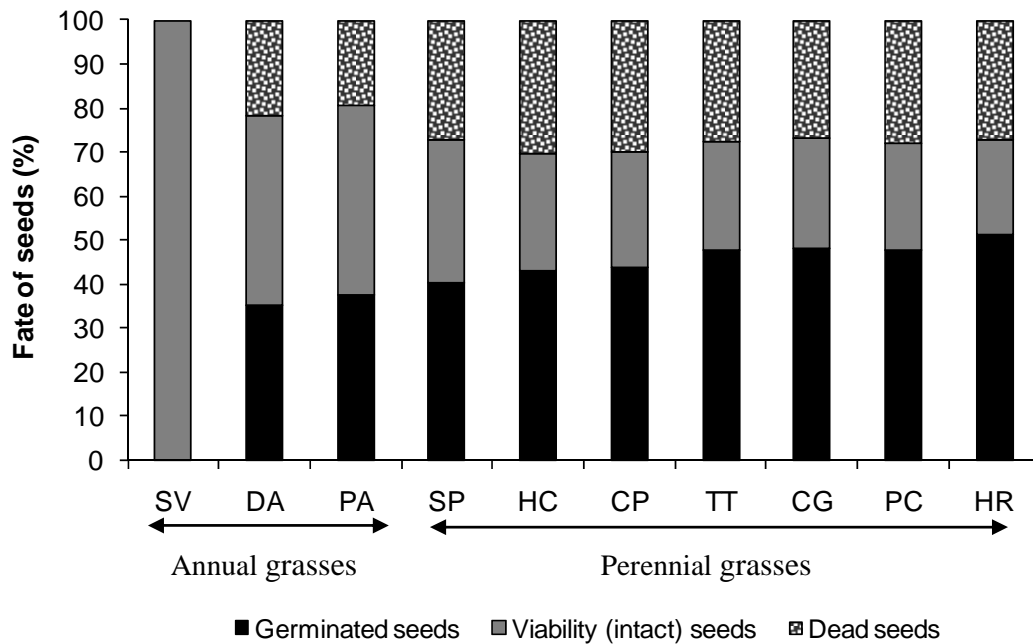
## Results

### Germination success

Grass species varied significantly in seed germination percent ( $F_{9,240} = 233.670$ ,  $P < 0.001$ ,  $R^2 = 0.89$ ). At species level, the seed germination rate ranged from 0 percent for *Sorghum verticilliflorum* to 51 percent for *Hyparrhenia rufa* (Fig. 6.3). The interaction of grass species x exhumation time was also affected germination percentage ( $F_{27,240} = 7.804$ ,  $P < 0.001$ ). Hence, *Chloris gayana*, *Hyparrhenia rufa*, *Panicum coloratum* and *Heteropogon contortus* had higher germination percent than other species with respectively 60, 59, 55, and 52 percent especially at the end of August compared to other exhumation times (Fig. 6.4). Moreover, the seeds of annual grass species had on average a lower germination percentage (24%;  $F_{1,304} = 222.514$ ,  $P < 0.001$ ) compared with perennial grasses (46%; Fig. 6.5). However, the germination percentage of annual grass seeds showed an increasing trend until the end of the

burial time (Fig. 6.5), whereas the perennial grass seeds had a lower germination percentage at the first exhumation time (July), peaked at the end of August and declined thereafter (Fig. 6.5).

For all species, germination percentage differed over the four exhumation times ( $F_{3,240} = 63.420$ ,  $P < 0.001$ ). Location had a significant effect on the germination percent of grass seeds ( $F_{1,240} = 13.283$ ,  $P < 0.001$ ), as Abernosa Cattle Breeding Ranch had a higher germination success compared to Awash National Park.



**Fig. 6.3.** Fate of grass seeds buried (mean percentage) in the soil in semi-arid savannas of Ethiopia (SV = *Sorghum verticilliflorum*; DA = *Dactyloctenium aegyptium*; PA = *Panicum atrosanguineum*; SP = *Sporobolus pyramidalis*; HC = *Heteropogon contortus*; CP = *Chrysopogon plumulosus*; TT = *Tetrapogon tenellus*; CG = *Chloris gayana*; PC = *Panicum coloratum* and HR = *Hypparrhenia rufa*).

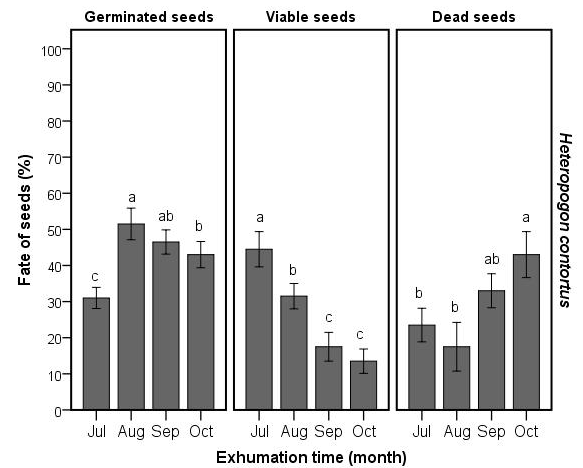
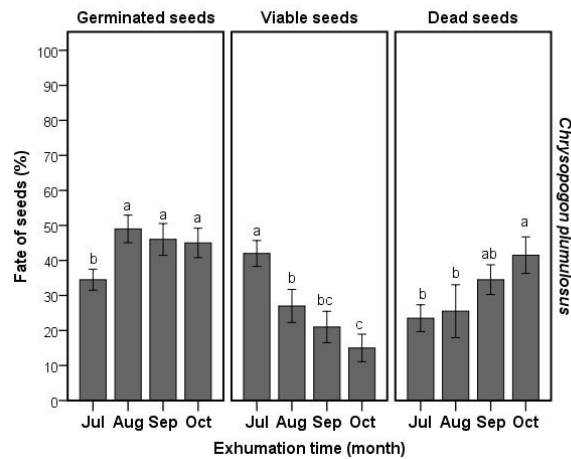
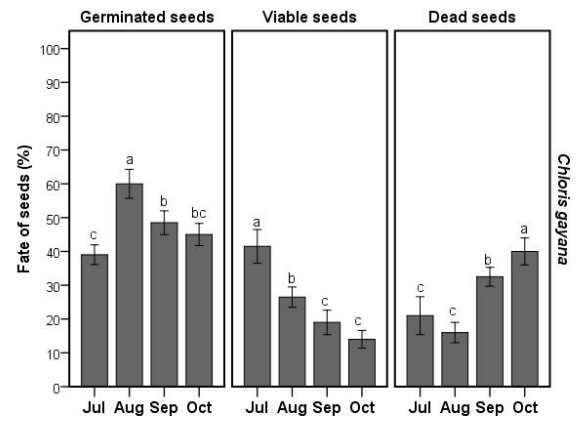
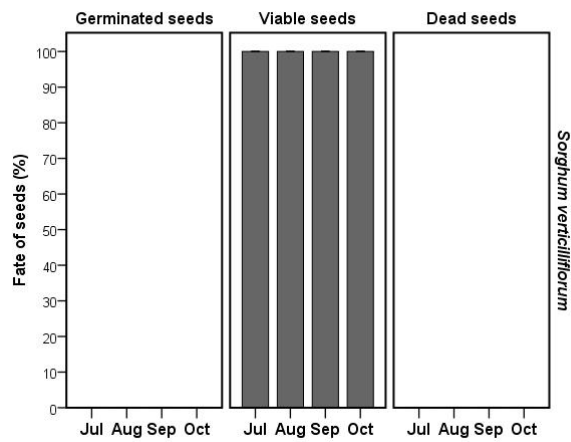
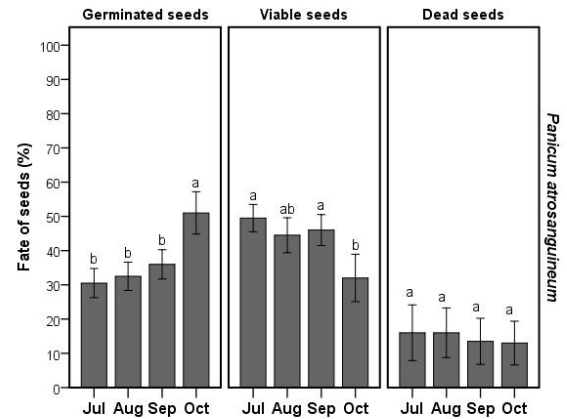
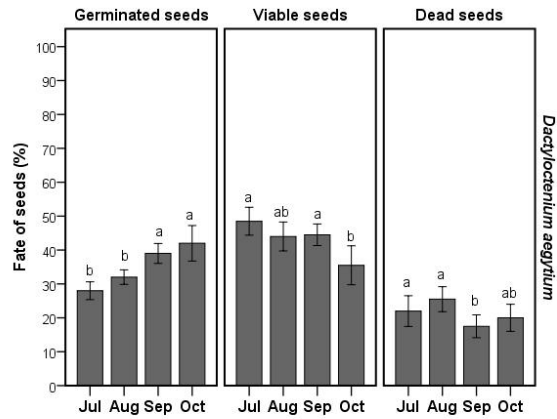
### Seed viability

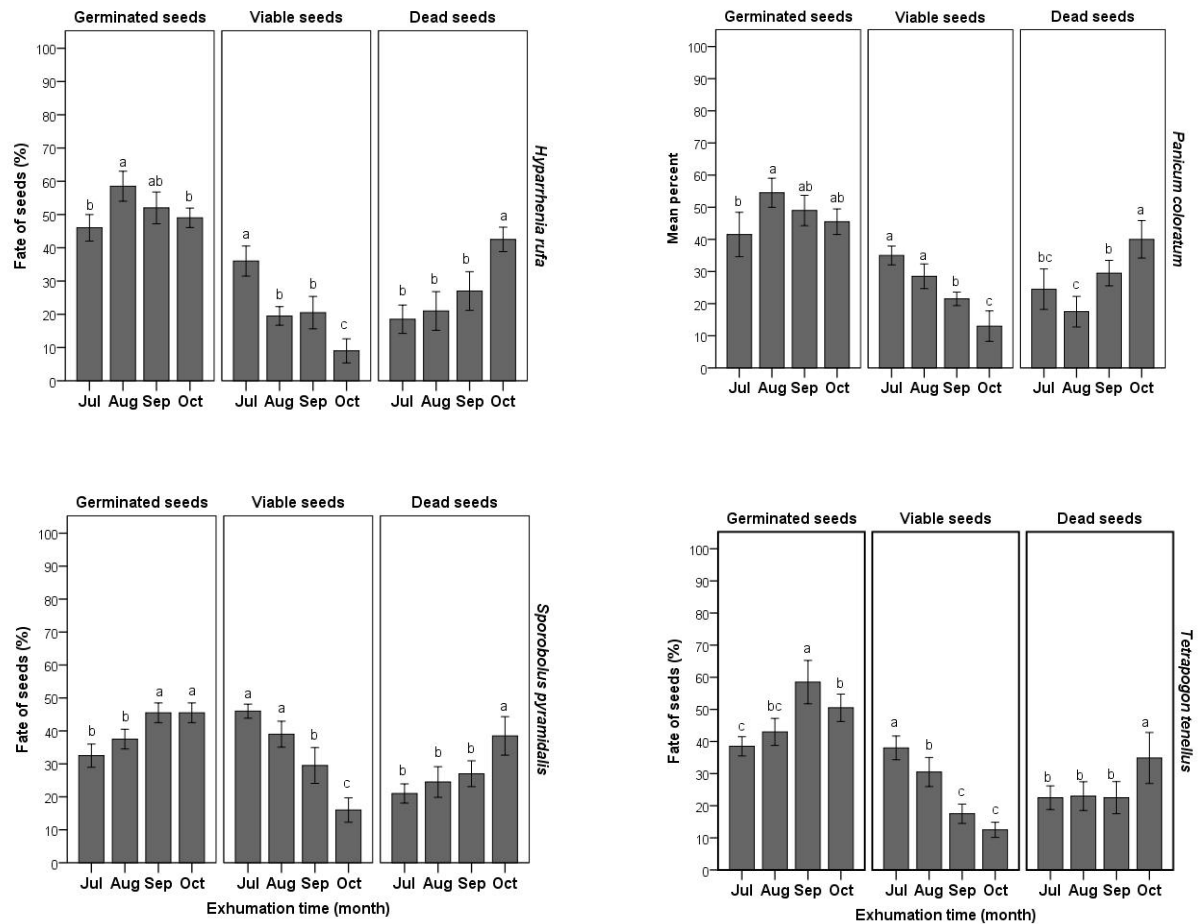
There were significant differences in seed viability among the study species ( $F_{9,240} = 688.129$ ,  $P < 0.001$ ,  $R^2 = 0.96$ ). The grass species *Sorghum verticilliflorum* had maintained its seed viability (100%), followed by *Dactyloctenium aegyptium* (43.1%) and *Panicum atrosanguineum* (43%; Fig. 6.3). However, *Hypparrhenia rufa* had the lowest seed viability (21%) in the burial experiment. In general, all grass species had higher seed viability at the first exhumation time (July), but this decreased gradually over time until the end of the burial

experiment ( $F_{27,240} = 7.733$ ,  $P < 0.001$ ; Fig. 6.4), except for the grass species *Sorghum verticilliflorum*. Annual grass seeds had a higher seed viability (62%) compared to perennial grass species (26%) ( $F_{1,304} = 327.230$ ,  $P < 0.001$ ;  $R^2 = 0.56$ ). Seed viability of perennial grass species was higher at the beginning (July) of the burial experiment but rapidly declined thereafter (Fig. 6.5), whereas the seed viability of annual grass species remained almost stable until the end of the burial experiment (Fig. 6.5). Seed viability was not dependent on the study locations ( $F_{1,240} = 0.017$ ,  $P = 0.90$ ).

### Seed mortality

There were significant differences in the mortality rate of seeds between grass species ( $F_{9,240} = 83.171$ ,  $P < 0.001$ ,  $R^2 = 0.80$ ). The mortality over a period of 120 days, was ranged between 0 percent for *Sorghum verticilliflorum* to 30 percent for *Heteropogon contortus* (Fig. 6.3). The proportion of dead seeds in grass species increased as the burial time increased, from July to the end of October (Fig. 6.4). As with germination percentages, perennial grass seeds had higher mortality (%) compared with annual grass seeds ( $F_{1,304} = 196.876$ ,  $P < 0.001$ ;  $R^2 = 57$ ; Fig. 6.5). Moreover, the mortality rates of perennial grass seeds increased over time throughout the burial experiment, whereas the mortality rates of annual grass seeds remained stable over time. Location had a significant effect on the mortality of grass seeds ( $F_{1,240} = 13.463$ ,  $P < 0.001$ ), as Awash National Park had a slightly higher grass seed mortality than Abernosa Cattle Breeding Ranch.





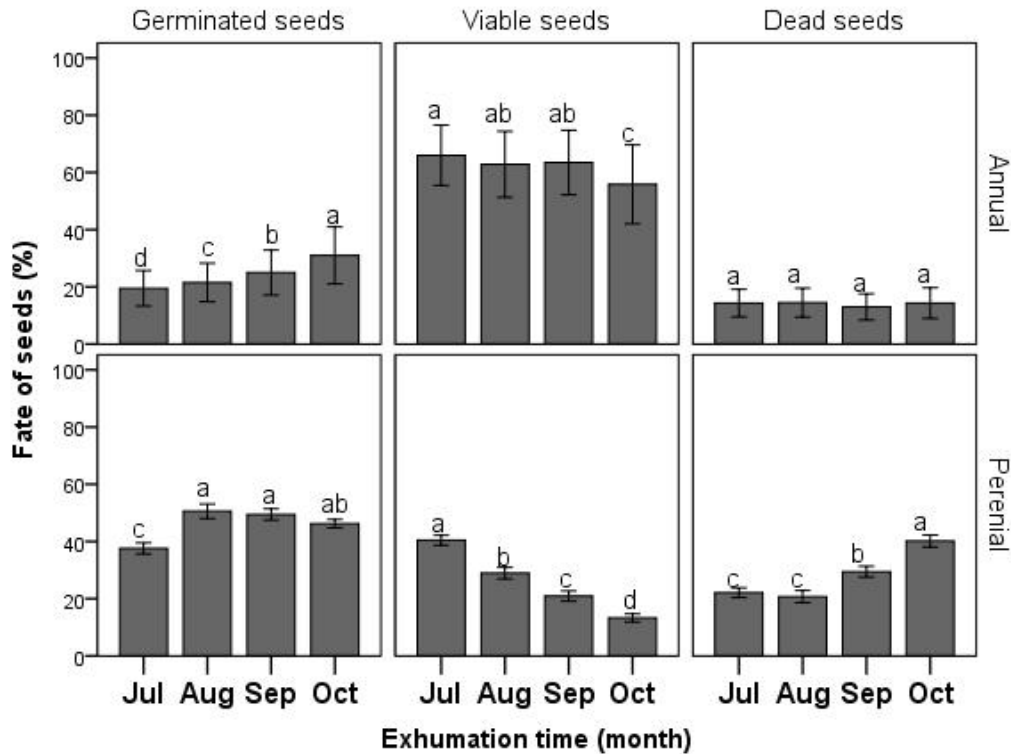
**Fig. 6.4.** Germination, viability and mortality rates ( $\% \pm 95\%$  CI) of grass seeds while buried in the soil and exhumed over time (months) in a semi-arid Ethiopian savanna.

## Discussion

### Seed germination

Differences in germination patterns of buried seeds can be explained by the individual plant species' traits that differ among the functional types (Prins, 1988; Masin et al., 2006). In our study, grass species varied significantly in germination rates when buried in the soil over time, as the seeds of annual grasses had lower germination rates compared with perennial grass species. A wide range in germination rates between annual and perennial grass species was also reported in earlier studies (Tessema et al., 2011e). These differences in germination rates between annual and perennial grass species could reflect the different adaptations to environmental variability (Prins, 1988; Perez-Fernandez et al., 2000; Fay and Schultz, 2009), the different survival strategies under unfavourable conditions. Pons (1991) indicated that

when seeds become buried in the soil after dispersal, germination may be delayed until more favourable times for establishment of seedlings occur.



**Fig 6.5.** Differences in fate (mean percentage of seeds that germinated, remained viable or were dead  $\pm$  95% CI) of seeds buried in the soil between annual and perennial grass species exhumed at monthly intervals in semi-arid savannas of Ethiopia

Accordingly, mechanisms that delay germination are often found among short-lived species from habitats with a high frequency of disturbances (e.g., fire, grazing, drought), enabling them to form persistent seed banks, whereas long-lived species lack these capabilities (Pons, 1991; Gutterman, 2000). This might be because perennial grasses invest more in vegetative structures for reproduction as survival mechanism than seed production compared with annual grasses (Veenendaal et al., 1996b). According to some studies (Vleeshouwers et al., 1995, Veenendaal et al., 1996a), dormancy is selected in most annual species, which are abundant in semi-arid ecosystems characterized by long dry seasons and unreliable rainfall periods (Veenendaal et al., 1996b; Tilahun et al., 2006). So, unfavourable temperature and moisture conditions in combination with primary dormancy are factors that delay germination after seed dispersal (Baskin and Baskin, 2004; Page and Harrington, 2009).

Yet, perennial grass species do not form persistent seed banks because their seeds have an innate dormancy that lasts for only few months, and have a limited intrinsic capacity for survival in the soil when in a state of induced or enforced dormancy (O'Connor, 1991). Therefore, the size of the soil seed banks of perennial grasslands is determined primarily by the annual input of seed from the established perennial vegetation.

In our seed burial study, germination rate of grass seeds buried in the soil subsequently increased over time, which is an indicator of breaking of dormancy. According to Rathcke and Lacey (1985) and Prins (1988), the optimum time for seed germination (and vegetative resprouting) in arid and semi-arid savannas is as early as possible in the growing season, to monopolize the scarce moisture and nutrient resources for growth and reproduction, which is in agreement with the strategy adopted by the perennials in our study. However, annual grass species typically have a longer dormancy period, which allows them to stay longer in the soil until environmental conditions are met for germination, as dormancy (Baskin and Baskin, 2004) is their main strategy that ensures these species germinate under favourable conditions (Fenner and Thompson, 2005; Wesche et al., 2006). According to our study and Tessema et al. (2011e), most perennial grass species, such as *Chrysopogon pulmosus*, *Tetrapogon tenellus*, *Panicum coloratum* and *Hyparrhenia rufa* had higher germination rates immediately after seed dispersal. A common feature of most perennial grasses is producing low number of seeds that are poorly dispersed with an innate dormancy characteristics that does not persist long (O'Connor, 1991), indicating that it is an adaptation that ensures a perennial grass seed to germinate at the first onset of any small rainfall event. However, annual grasses like *Dactyloctenium aegyptium* and *Eragrostis papposa* are good colonizers of bare areas under heavy grazing (Angassa and Oba, 2010; Tessema et al., 2011a). This indicates that annual and perennial grass species have different germination and survival strategies in semi-arid savannas.

There is a general tendency for annual species with smaller seeds to persist longer in the soil than perennials with larger seeds (Peco et al., 2003; Thompson et al., 2003). The longer the residence time of seeds in the soil, the less precise is the mechanism for timing of germination (Pons, 1991). The size and shape of seeds are considered to be important to determine seed bank behaviour (Thompson et al., 1993; Bekker et al., 1998). Large seeds and seeds with a large surface/volume ratio, such as perennial grasses are less likely to be incorporated into the soil because they have a lower chance of finding their way down cracks for burial (Bekker et al., 1998). Grass species with awns become readily anchored and

germinated quickly at the soil surface (Peart 1984) instead of developing a soil seed bank as the seeds of grasses without appendage tend to do so (Williams and Huijmans 1994). This indicates that small, compact seeds escape from processes that prevent penetration into the soil (i.e., germination, predation and secondary dispersal), and thus tend to live longer (Bekker *et al.* 1998). Hence, soil seed banks in semi-arid savannas are dominated by annual grass species and other plants with annual life history characteristics (O'Connor and Pickett, 1992; Solomon *et al.*, 2006; Kassahun *et al.*, 2009b). Long term dormancy of perennial grass seeds and a persistent soil seed bank of these perennials are uncommon in most tropical savannas (O'Connor 1991; O'Connor and Everson, 1998; Gardner *et al.*, 2001). Hence, our results showed that perennial grass species are expected to lose most of their seeds in the soil as a result of high germination rates and short longevity, and may not contribute to the formation of persistent seed banks, whereas annual grass species are more abundant in the soil seed banks of semi-arid African savannas due to their higher longevity characteristics.

### **Seed viability**

Maintaining seed viability in soils for longer determines the ability of seeds to form persistent soil seed banks and the restoration potential of degraded systems (Bekker *et al.*, 1998). In our study, there were significant differences between grass species in seed viability dynamics. The annual grass species, *Sorghum verticilliflorum* maintained seed viability (100%) at the end of the burial experiment, which is probably due to the presence of a hard seed coat. Mohamed-Yasseen *et al.* (1994) suggested that longer viability might be due to a hard seed coat, and for instance, removing the seed hull from sorghum reduces viability. In general, species had higher seed viability at the beginning of the burial experiment but this decreased gradually over time, indicating that grass seeds continuously break their dormancy in the soil as the burial time increases. At the first and second exhumation dates (July and August), which correspond to the months with the highest rainfall, more germinated seeds were recorded in the nylon bags, indicating that seeds lose their viability when soil moisture conditions increase. Annual grass seeds had a higher seed viability compared to perennial grass species. In our study, annual grass species maintained 62 percent of their longevity as a result of their dormancy, whereas perennial grass species only maintained 28 percent of their longevity as a result of high germination characteristics.



### **Seed mortality**

After dispersal, seed can germinate and establish as seedlings, remain dormant and persist as seeds, or die (Clark and Wilson, 2003), and it is the balance between these processes that determine the turnover rate of soil seed banks (Bakker et al., 1996; Snyman, 2004). On average, our grass seeds lost about 24 percent of their longevity when buried in the soil over time as a result of mortality. Similar to the germination rate, perennial grass seeds had higher mortality rates compared with annual grass seeds, although the proportion of dead seeds in all grass species increased with increasing burial time.

In our study, the grass species of the semi-arid savannas that have been investigated showed a large variation in germination and survival rates. Moreover, there were also large differences in germination, longevity and mortality rates between the functional groups (i.e., annual and perennial). Annual grasses had lower germination, higher viability, and lower mortality rates, and therefore maintained 62 percent of their longevity compared to perennial grasses, which only maintained 28 percent of their longevity. As a result of their longer longevity and lower mortality rates while buried in the soil, coupled with good seed producing and successful seed deposition capacities, as well as the ability to complete their life cycle rapidly in one growing season, annual species are expected to dominate soil seed banks in semi-arid savannas. Due to high seed germination and mortality rates, as well as a low seed production potential, most perennial grass species might disappear and become locally extinct in these soil seed banks. Veenendaal et al. (1996b) indicated that the persistence of species and the maintenance of biodiversity in semi-arid savanna grasslands depend on the annual recruitment of seedlings from annual grasses, and on the vegetative reproduction of perennial grasses. As a result, annual grasses may be successful in disturbed habitats because of their large seed production efforts and adaptation to open micro-sites (Veenendaal et al., 1996b). However, perennial grass species also have an alternative survival strategy, such as the development and expansion of vegetative parts (i.e., tillers, rhizomes, and/or stolons) (O'Connor and Picket, 1992). This allows perennial grasses to survive in the aboveground vegetation under unfavourable conditions, such as under the influence of high grazing pressures, drought, or fire. Consequently, perennials are at a loss if, for instance under the influence of heavy grazing, the aboveground vegetation has been removed. The colonization strategy from the soil seed bank is not adapted to bridge long periods of unfavourable conditions, rapidly leading to vegetation dominated by annuals.

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# 7

Soil seed bank dynamics under the influence of grazing explain herbaceous vegetation transitions in a semi-arid savanna



Z.K. Tessema, F. Van Langevelde, W.F. de Boer and H.H.T. Prins

## **Abstract**

Knowledge on vegetation dynamics plays an important role in management of rangelands. Models show the existence of alternate states and transitions in these rangelands. In this paper, we hypothesize that the availability of seeds in the soil seed bank as function of plant cover can trigger transitions between three states: from perennial to annual grasses and from annual grasses to bare soil with increasing grazing pressure. To explore this hypothesis, we developed a model to describe herbaceous vegetation dynamics using grazing, seed availability in the soil, seed germination rate and longevity as possible mechanisms. When grazing is low, a high cover of perennial grasses and a large soil seed bank of these grasses are present, whereas with increasing grazing, vegetation cover and soil seed bank size decline. We found that the positive relationship between plant cover and differences in soil seed bank dynamics, i.e., seed germination rate and longevity, trigger the transition from perennial grasses to annuals and from annual plant cover to bare soil under heavy grazing. This positive feedback is an alternative explanation for sudden vegetation changes in dry areas, other than the positive relationship between plant cover and infiltration of rain into the soil. In contrast to this latter positive feedback, our model can also explain changes in vegetation from perennials to annuals and vice versa. Our model contributes to understanding of the vegetation dynamics of semi-arid savannas for management and restoration.

**Keywords:** Alternate stable states; Annual grass; Bare soil; Germination; Grazing; Longevity; Perennial grass; State-and-transition; Vegetation dynamics

## **Introduction**

Semi-arid savannas have been described as ecosystems with more than one state and transitions from one state to another, often occurring under influence of disturbances such as grazing or fires (Rietkerk et al., 1996; Van Langevelde et al., 2003). Semi-arid savannas can therefore be described by state-and-transition models (Westoby et al., 1989; Rietkerk et al., 1996). A bush encroached state, dominated by shrubs and trees with a low cover of grasses, has been reported frequently and is considered as a serious threat for livestock and biodiversity (Richter et al., 2001; Roques et al., 2001; Ward, 2005). One of the mechanisms that could lead to bush encroachment is the interaction between herbivory and grazing (Van Langevelde et al., 2003). In the herbaceous layer, two states have been documented: a state with ample herbaceous cover, mainly perennial grasses, and scattered trees (Scholes and Archer, 1997; Simioni et al., 2003), and a state with a low cover of annual grasses, absence of perennial grasses, and a high proportion of bare soil (Rietkerk et al., 2002). Tessema et al. (2011a) studied these two states under the influence of grazing for semi-arid savannas in Ethiopia: the state with herbaceous cover was found in sites with low grazing pressure, whereas the second state with bare ground was found in sites with heavy grazing.

The replacement of perennial grasses in semi-arid grazing systems due to increasing grazing pressure (Noy-Meir et al., 1975; van de Koppel et al., 1997), leads to the transitions of semi-arid grazing systems (Westoby et al., 1989; Rietkerk et al., 1996). Previous models showed the transitions of semi-arid grazing systems between effective rainfall and grazing intensity (Rietkerk et al., 1996) and water infiltration or nutrient retention in the soil and plant density as possible mechanisms (Rietkerk and van de Koppel, 1997). A reduction of aboveground biomass due to heavy grazing leads to a reduction of the infiltration of rain in the soil in bare patches that results in lower soil water availability, and consequently reduced plant growth, leading to the transitions of semi-arid grazing systems (Rietkerk and van de Koppel, 1997; Rietkerk et al., 2002). However, previous models do not indicate the combination of annuals and perennials with bare soil but they only recognized the occurrence of vegetation states consisting of densely vegetated patches alternating with bare areas (van de Koppel et al., 1997). However, the infiltration of rainfall in the soil is increased by the presence of perennials, but annuals hardly increase infiltration in the soil (Rietkerk et al., 2000), so that infiltration may not be a good mechanism to explain the transitions in annuals. Moreover, previous models in semi-arid grazing systems do not show the source of recovery in perennial grasses after they have totally disappeared from the system. However, we believe

that the route to recovery of semi-arid grazing systems is not via infiltration but from seeds in the soil.

In semi-arid African savannas, it has been found that intensive grazing has indeed resulted in a rapid species turn-over (Abule et al., 2005; Tessema et al., 2011a), reducing the forage availability and forage quality to sheep and cattle (Prins, 1989; Sarmiento, 1992). However, the soil seed bank can serve as a buffer mechanism, as, e.g., perennial grasses after their disappearance can re-colonize bare areas from their buried seed (Leck et al., 1989; de Villiers et al., 2003; Scott et al., 2010). Besides differences in seed production, factors like seed longevity and seed germination may contribute to the transition from one state to another in semi-arid savannas (O'Connor, 1991; Pons, 1991; Sternberg et al., 2003). There are wide ranges in seed viability and germination rates in grass species over time (McIvor and Howden, 2000; Tessema et al., 2011d), as annual grass species have a lower germination rate than perennials. In contrast, most perennial grasses germinate rapidly after initial seed dispersal at the first rains early in the year (Rathcke and Lacey, 1985; Veenendaal et al., 1996a; Tessema et al., 2011e), so that perennials can quickly disappear from the system if seedlings are heavily damaged due to grazing and/or trampling. Therefore, the recovery processes of degraded semi-arid savannas and the transition from one state to another are controlled by two important factors, the intensity of grazing (Noy-Meir et al., 1975; Westoby et al., 1989; Rietkerk and Van de Koppel, 1997) and the seed availability in the soil seed bank (Leck et al., 1989; de Villiers et al., 2003). Here, we hypothesize that the emergence of seedlings from seeds in the soil bank as function of grazing mediated plant cover and differences in longevity and germination rate can trigger the transitions between three stable states: from perennial to annual grasses and from annual grasses to bare soil. To explore this hypothesis, we developed a model to describe the herbaceous vegetation transitions in semi-arid savannas using grazing, seed availability in the soil seed bank, and seed germination rate and longevity as possible mechanisms for these transitions.

### **Modelling interaction between seed bank and vegetation**

We use plant cover in our model because annual grasses grow only with decreasing in cover of perennial grasses, and plant cover is better to detect a bare ground state than biomass. First, we model the relationship between the soil seed bank of one grass species and the cover of this grass species, as a proxy for plant abundance. The rate of change of the plant cover ( $P$  as

fraction per  $m^2$ ) is determined by the recruitment of the plants, the natural losses and the losses due to herbivory:

$$\frac{dP}{dt} = \text{recruit}P - \text{loss}P - \text{grazing}P \quad (1)$$

The perennial grass are recruited from seeds in the soil ( $S_p$  in  $m^{-2}$ ), which is dependent upon the availability of resource ( $R$ , assuming here rainfall in  $mm\ t^{-1}$ ). The seeds determine the recovery of tufted perennial grasses, which are commonly found in semi-arid savanna grazing systems (O'Connor and Pickett, 1992), so that we did not include vegetative recruitment in our models. As plant available moisture is limited, we assume a linear relationship between water availability and plant recruitment. We define plant recruitment (in  $t^{-1}$ ) therefore as:

$$\text{recruit}P = R c_p g_p S_p P(1 - P) \quad (2)$$

where  $c_p$  is the rate of increase of plant cover due to germination of the seeds in the soil bank (in  $m^2$ ) and  $g_p$  is the germination rate of the seeds in the soil seed bank per unit of water availability (in  $mm^{-1}$ ). The natural loss rate is defined as:

$$\text{loss}P = l_p P \quad (3)$$

where  $l_p$  is the decrease of plant cover, for example due to death (in  $t^{-1}$ ). The effect of herbivory is modelled as:

$$\text{grazing}P = b_p h P \quad (4)$$

where  $b_p$  is the decrease of plant cover due to herbivory (in  $m^2\ g^{-1}\ t^{-1}$ ) and  $h$  the herbivore density (in  $g\ m^{-2}$ ).

The rate of change of the soil seed bank size (in  $m^{-2}\ t^{-1}$ ) is determined by the increase of the number of seeds in the soil, the losses of the seeds and the germination of seeds, described as:

$$\frac{dS_p}{dt} = \text{increase}S_p - \text{loss}S_p - \text{germ}S_p \quad (5)$$

The increase of seeds in the soil seed bank is determined by the plant cover, and we assume that there is always a certain small amount of seeds in the seed bank due to dispersal from external sources ( $s_{p0}$  in  $m^{-2}$ ), regardless of the present plant cover. The production of seeds saturates with increasing plant cover (Veenendaal et al., 1996b). We modelled this production as:

$$\text{increase}S_p = s_{pm} \frac{P + k_p s_{p0}}{P + k_p} \quad (6)$$

where  $s_{pm}$  is the maximum number of seeds produced when plant cover is maximal (in  $m^{-2}$ ), and  $k_p$  is the plant cover where the rate of seed production is half of its maximum (half saturation constant, as fraction). The loss rate of seeds in the soil is defined as:

$$lossS_p = l_{sp} S_p \quad (7)$$

where  $l_{sp}$  is the specific loss rate of seeds (in  $t^{-1}$ ). This loss rate determines longevity of seeds: low values of  $l_{sp}$  mean high longevity. The rate of germination is:

$$germS_p = g_p R S_p \quad (8)$$

Similar formulations can be used for annual grasses (A) and the seeds from annual grasses ( $S_A$ ). We only added a competition term: annuals and perennials compete for water, and we assume that this competition is asymmetric as perennial grasses can outcompete annual grasses by reducing light availability (Veenendaal et al., 1996b). Then the rate of increase of annual grass cover decreases when the cover of perennial grasses increases as:

$$c_a = \frac{c_{am} k_l}{P + k_l} \quad (9)$$

where  $c_{am}$  is the maximal increase in annual grass cover when light is not limiting and  $k_l$  is the plant cover where the light availability for annual grasses is half of  $c_{am}$ .

Due to the smaller impact of herbivory on annual grasses because of their lower palatability and their seed bank dynamics, e.g., more seeds produced and lower germination than seeds from perennial grasses (O'Connor and Pickett, 1992; Veenendaal et al., 1996b), annual grasses can occur at herbivore densities where perennial grasses are grazed down. The model of perennial plant cover, annual plant cover, seeds of perennial plants in the soil and seeds of annual plants in the soil then becomes:

$$\frac{dP}{dt} = P(R c_p g_p S_p (1 - P) - l_p - b_p h) \quad (10)$$

$$\frac{dA}{dt} = A \left( R \frac{c_{am} k_l}{P + k_l} g_a S_a (1 - P - A) - l_a - b_a h \right) \quad (11)$$

$$\frac{dS_p}{dt} = s_{pm} \frac{P + k_p s_{p0}}{P + k_p} - l_{sp} S_p - g_p R S_p \quad (12)$$

$$\frac{dS_a}{dt} = s_{am} \frac{A + k_a s_{a0}}{A + k_a} - l_{sa} S_a - g_a R S_a \quad (13)$$



We analysed the model by first focusing on the effect of herbivory, the germination rate of the seed, and seed mortality on the cover of perennial grass and the seed bank of perennial grasses. We then included the cover of annual grass and the soil seed banks of annual grasses. We only model the change of plant cover and seed availability in the soil with time scales of one year. The used symbols, their units, interpretation, values and sources are given in Table 1.

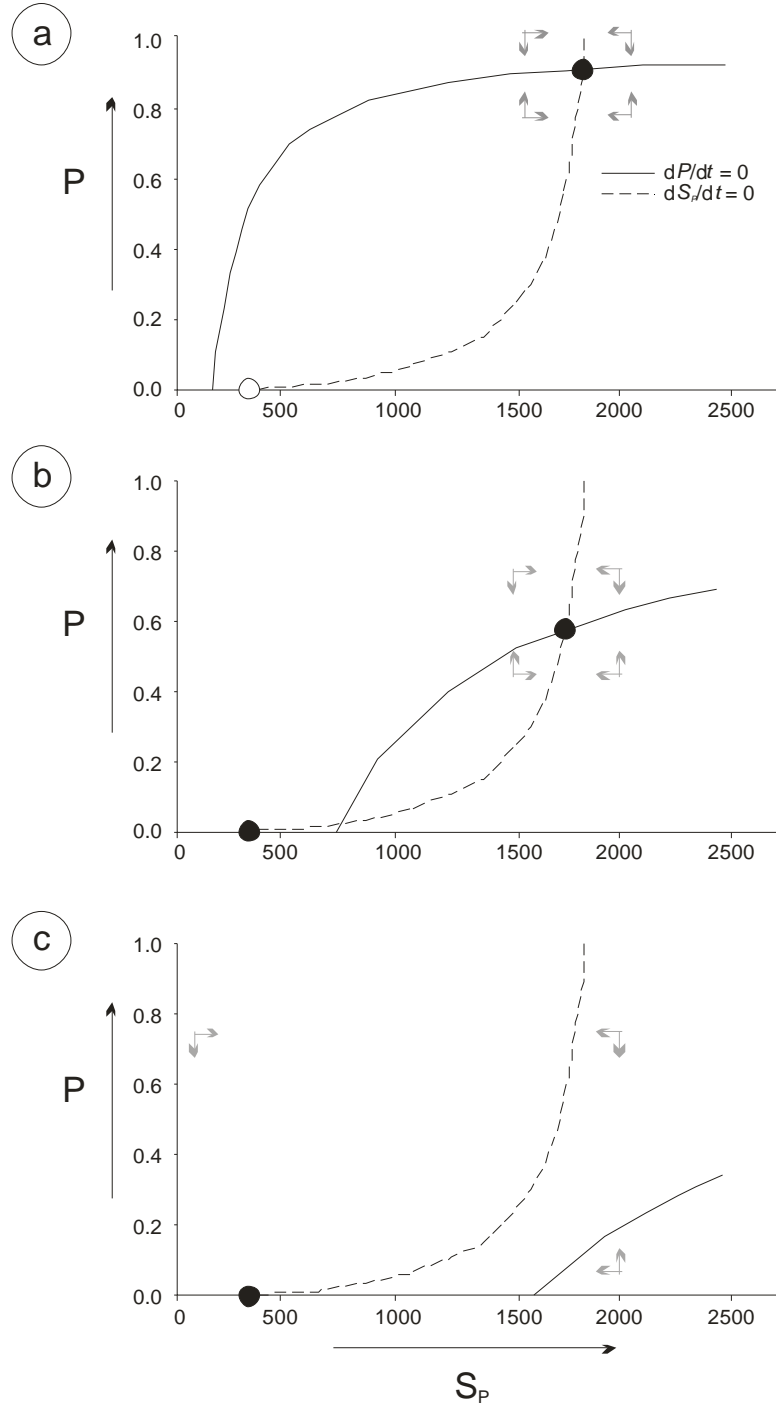
## Results

### Perennial grass cover and the seed bank of perennial grass

One way of analyzing the dynamics of the cover – soil seed bank dynamics of perennial grasses is by plotting the zero-isoclines of the perennial grass cover and the size of the soil seed bank in a phase plane (Fig. 7.1). The soil seed bank zero-isocline is the line joining combinations of soil seed bank size and cover of perennial grasses where there is no change in soil seed bank size ( $dS_p/dt = 0$ ). With increasing cover of perennial grasses, the size of the soil seed bank increases. The zero-isocline of the cover of perennial grasses is the line showing combinations of soil seed bank size and cover of perennial grasses where there is no change in the cover of perennial grasses ( $dP/dt = 0$ ).

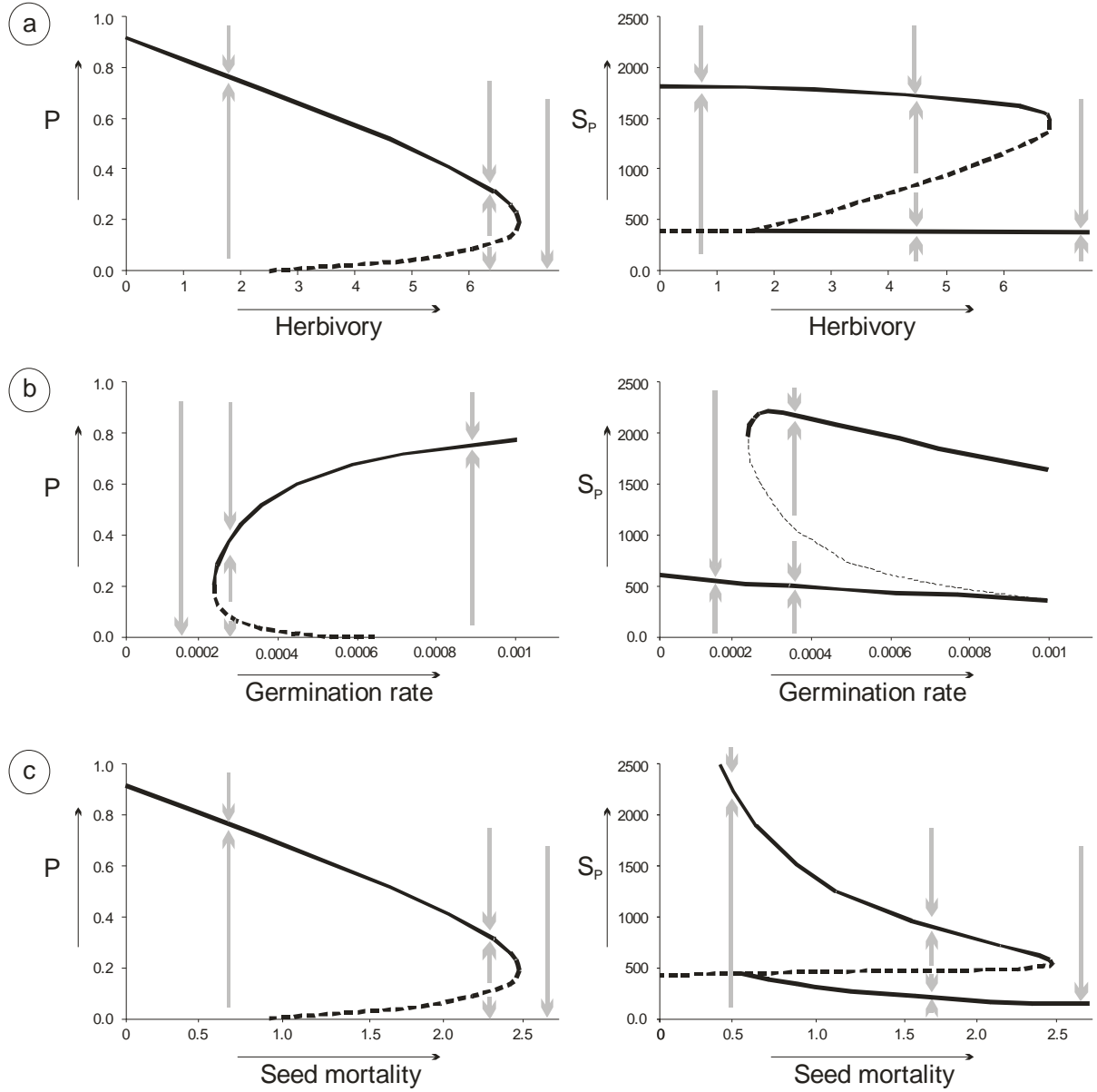
When herbivory is absent (Fig. 7.1a), a high cover of perennial grasses and a large seed bank in the soil is present. This cover and soil seed bank size decreases with increasing herbivory. When the point where the zero-isocline of the soil seed bank meets the  $S_p$ -axis (Fig. 7.1b) is at the left hand side of the point where the zero-isocline of the grass cover meets this axis, a different stable state occurs: a small soil seed bank size in the absence of perennial grasses. Under this herbivore pressure, there are two stable states: one with both a soil seed bank and a cover of perennial grasses, and one with only a small soil seed bank size in the soil and no perennial grasses. The stable state with both a soil seed bank and a cover of perennial grasses disappears when herbivore pressure increases (Fig. 7.1c). This figure suggests that there is a threshold in herbivore pressure below which there is a stable state with a sufficiently large soil seed bank size and cover of perennial grasses, and above which there is a stable state with only a small seed bank in the soil. When both perennial grasses and a soil seed bank can be found, apparently sufficient seeds are produced to maintain the cover of perennial grasses, whereas a low cover of perennial grasses under high herbivore pressure might not be able to produce sufficient seeds to maintain the grass cover. Consequently, perennial grasses

disappear and the soil seed bank is only supplied by dispersing seeds ( $s_{p0}$ ) from external sources.



**Fig. 7.1.** The zero-isoclines for the cover of perennial grass  $P$  (solid line,  $dP/dt = 0$ ) and the soil seed bank of perennial grass  $S_p$  (broken line,  $dS_p/dt = 0$ ) drawn in a phase plane for fixed values of herbivory. The vectors (arrows) indicate the direction of change. Solid circles indicate a stable equilibrium, and open circles indicate an unstable equilibrium. (a) no herbivores  $h = 0$ , (b),  $h = 4$ , and (c)  $h = 10$ . Parameter values are:  $R=500$ ,  $c_p=0.01$ ,  $c_{am}=0.001$ ,  $l_p=0.6$ ,  $k_p=0.1$ ,  $s_{p0}=0.2$ ,  $s_{pm}=2200$ ,  $b_a=0.4$ ,  $k_1=1$ ,  $g_p=0.8 \cdot 10^{-3}$ ,  $l_{sp}=0.7$ .

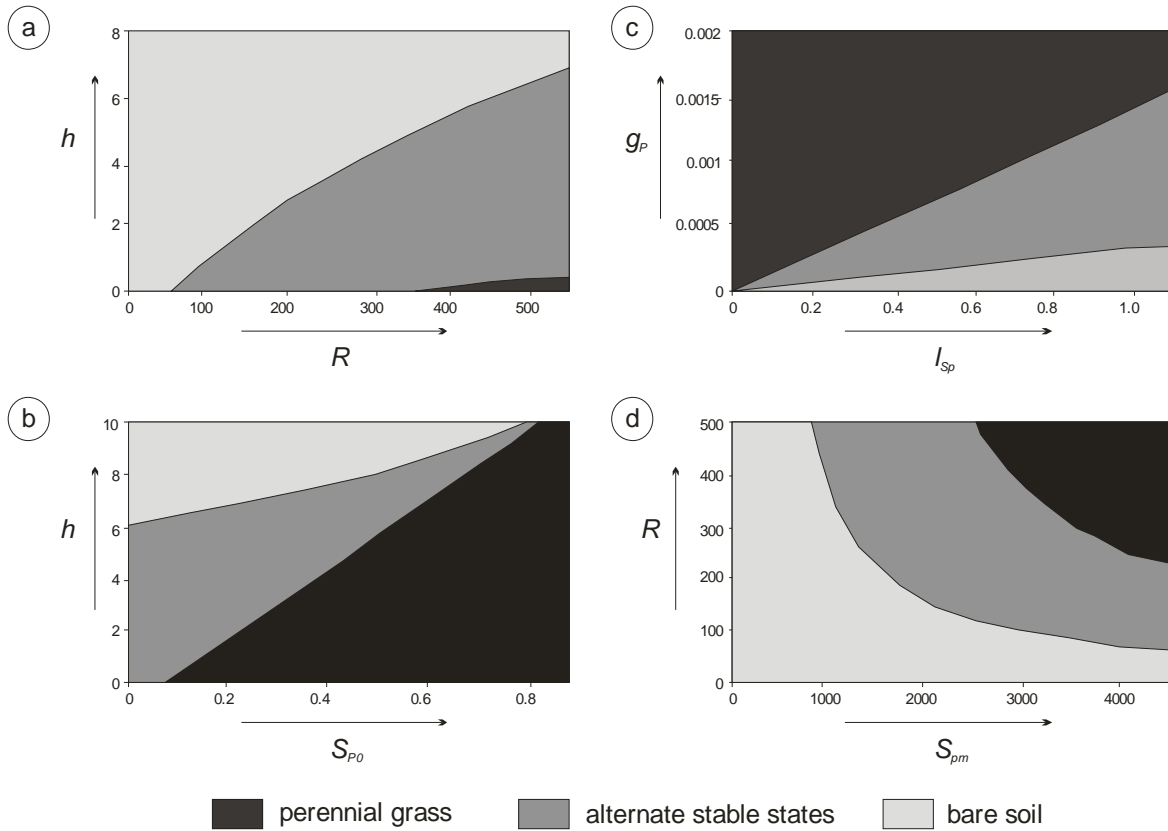
The equilibrium cover of perennial grasses and the equilibrium size of the seed bank decreases with increasing herbivore pressure (Fig. 7.2a), with decreasing germination rate (Fig. 7.2b) and with increasing seed mortality (Fig. 7.2c). The solid lines give the stable equilibria for the cover and the seed bank of perennial grasses, whereas the dashed lines refer to the unstable equilibria. Perennial grass cover and soil seed bank size are related: decreasing cover of perennial grasses lowers the seed production, whereas a small seed bank can only support a low perennial cover. This figure shows that discontinuous changes in the cover and the soil seed bank of perennial grasses occur at distinct levels of herbivore pressure, germination rate and seed mortality. Discontinuous changes in the cover and the soil seed bank of perennial grasses due to changes in, for example, herbivory may be irreversible to a certain extent. For example, events such as droughts may carry the grass cover below a break point value leading to a collapse of the perennial grasses and a subsequent decrease in the size of the soil seed bank. Under certain values for herbivore pressure, there are two stable states: one with both a seed bank and perennial grasses, and one with only a small seed bank without perennial grasses (see also Fig. 7.1). These discontinuous changes imply that when perennial grasses collapse, a gradual decrease in herbivore density could lead to the recovery of perennial grasses. However, herbivore density should be brought back to very low levels to allow perennial grasses to invade the area again, using the seeds that occur in the seed bank due to dispersal. The existence of different pathways of the perennial grasses due to increasing or decreasing herbivore pressure is called hysteresis.



**Fig. 7.2.** Effect of (a) herbivory  $h$ , (b) germination rate of the seeds in the soil bank  $g_p$ , and (c) seed mortality  $l_{sp}$  on the cover of perennial grass  $P$  and the soil seed bank of perennial grass  $S_p$ . Solid lines give the stable equilibria, and dashed lines give the unstable equilibria. Arrows indicate the direction of development of the state variables. Parameter values (see Table 7.1) are:  $R=500$ ,  $c_p=0.01$ ,  $c_{am}=0.001$ ,  $l_p=0.6$ ,  $k_p=0.1$ ,  $s_{p0}=0.2$ ,  $s_{pm}=2200$ ,  $b_a=0.4$ ,  $k_1=1$ , (a)  $g_p=0.8 \cdot 10^{-3}$ ,  $l_{sp}=0.7$ , (b)  $h=0.5$ ,  $l_{sp}=0.7$ , and (c)  $h=0.5$ ,  $g_p=0.8 \cdot 10^{-3}$ .

The effects of water availability in the soil ( $R$ ), herbivory pressure ( $h$ ), germination rate of the seeds in the soil bank ( $g_p$ ), seed mortality ( $l_{sp}$ ), increase in the soil seed bank due to dispersing seeds ( $s_{p0}$ ), and the maximum number of seeds produced when plant cover is maximal ( $s_{pm}$ ) on the transitions between the states are shown in Fig. 7.3. These diagrams

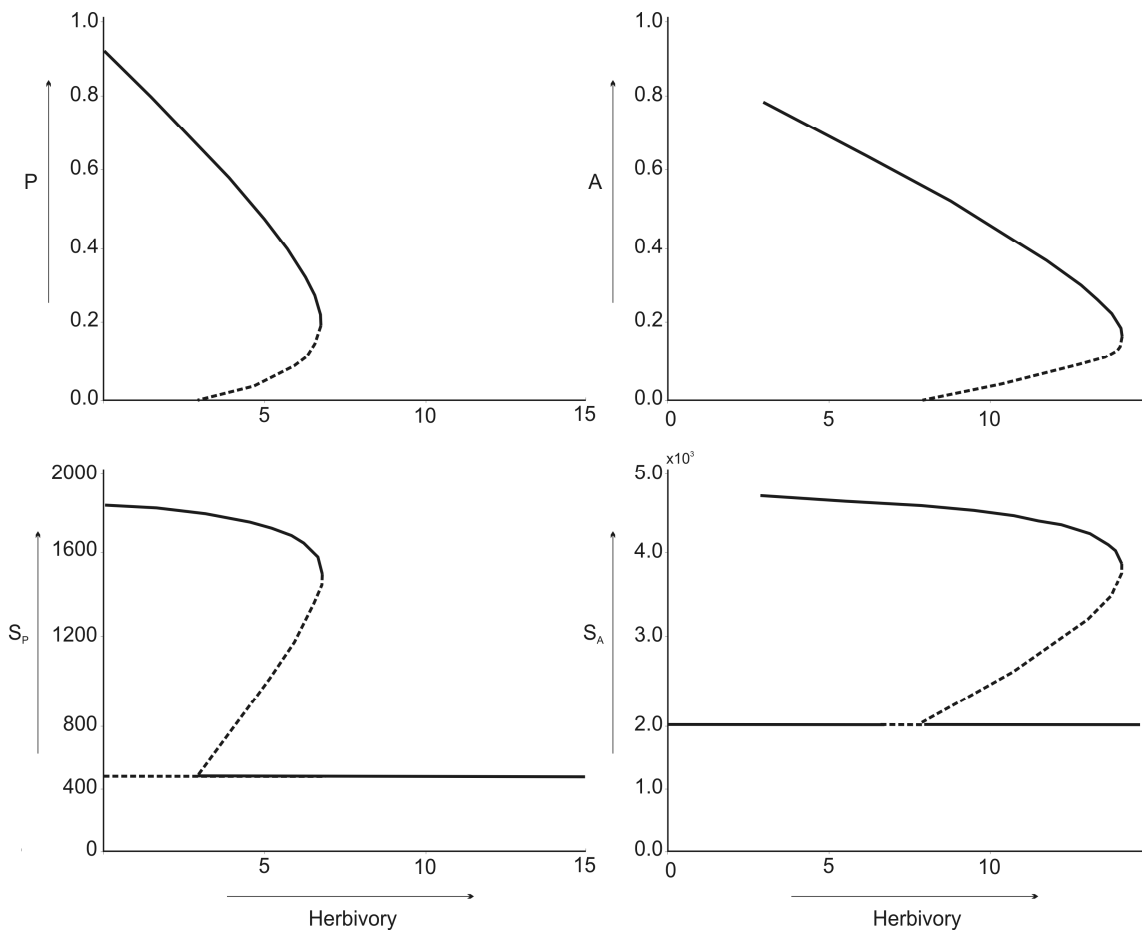
show under what conditions perennial grasses and bare soil can be found. They also give the parameter space where alternate stable states can be expected: either perennial grasses or bare soil. Because of an increase in water availability, the regions for which perennial grass and alternate stable states are predicted increase at the expense of the region without perennial grass. An increase in herbivore density increases the parameter range where bare soil and the alternate stable states can be found. The seed characteristics point in the same direction: an increase in amount of seed (increasing germination rate, decreasing seed mortality, increasing amount of influx of dispersing seeds, and increasing maximum number of seeds) leads to an increase in perennial grass cover and an increase in the region where alternate stable states can be found.



**Fig. 7.3.** Parameter planes of the water availability in the soil ( $R$ ), herbivory pressure ( $h$ ), germination rate of the seeds in the soil bank ( $g_p$ ), seed mortality ( $l_{sp}$ ), increase in the soil seed bank due to dispersing seeds ( $S_{p0}$ ), and the maximum number of seeds produced when plant cover is maximal ( $S_{pm}$ ) for three states: cover of perennial grass, bare soil and alternate stable states with either cover of perennial grass or bare soil. Parameter values are (see Table 7.1):  $c_p=0.01$ ,  $l_p=0.6$ ,  $k_p=0.1$ ,  $b_p=0.6$ ,  $k_1=1$ , (a)  $g_p=0.8 \cdot 10^{-3}$ ,  $l_{sp}=0.7$ ,  $s_{p0}=0.2$ ,  $s_{pm}=2200$ , (b)  $g_p=0.8 \cdot 10^{-3}$ ,  $l_{sp}=0.7$ ,  $R=500$ ,  $s_{pm}=2200$ , (c)  $h=0.5$ ,  $R=500$ ,  $s_{p0}=0.2$ ,  $s_{pm}=2200$ , and (d)  $h=0.5$ ,  $g_p=0.8 \cdot 10^{-3}$ ,  $l_{sp}=0.7$ ,  $s_{p0}=0.2$ .

### Perennial and annual grass cover and their soil seed banks

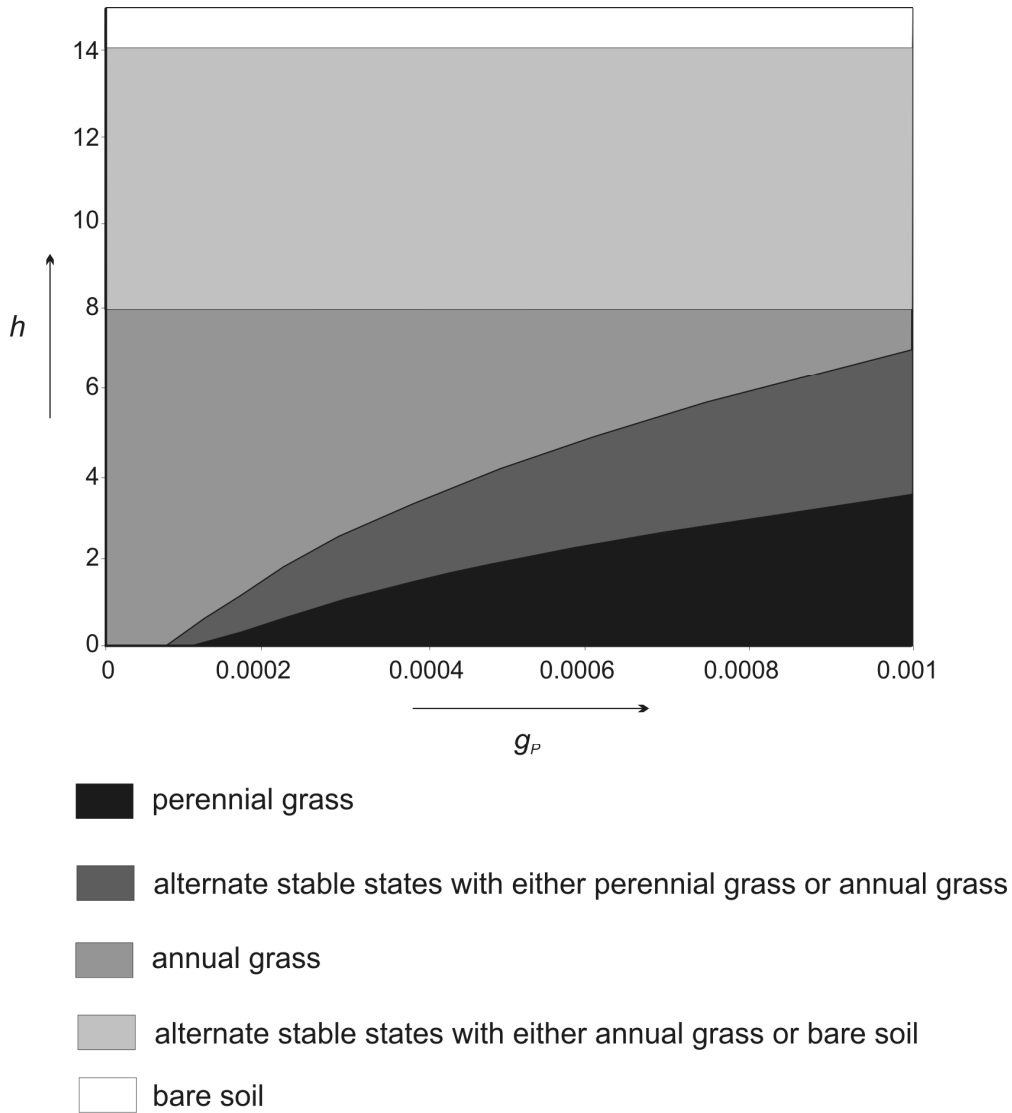
We can now analyze the model with the dynamics of both perennial and annual grass cover and their soil seed bank sizes. The equilibrium cover of perennial and annual grasses and the size of both soil seed banks decrease with increasing herbivore pressure (Fig. 7.4). Regarding the cover of annual grasses, a partly similar pattern is found as for the cover of perennial grasses, but annual grasses are absent at low herbivore density as they are outcompeted by the perennial grasses. Due to the suppression of perennial grasses by herbivores, annual grasses can occur and these grasses then also contribute their seeds to the soil seed bank. Also for annual grasses, a region of alternate stable states exists where either a state with annual grasses or a state with bare soil can occur. Again there is a threshold in annual grasses below which only the annual grasses disappear, and above which annual grasses occur. In between there might be a region where only annual grasses can occur, but where perennial grasses disappeared due to grazing (in Fig. 7.4 around  $h = 7$  to 8).



**Fig. 7.4.** Effect of herbivory  $h$  on the cover of perennial grass  $P$ , the soil seed bank of perennial grass  $S_P$ , the cover of annual grass  $A$ , and the soil seed bank of annual grass  $S_A$ . Solid lines give the stable equilibria, and dashed lines give the unstable equilibria. Parameter

values are (see Table 7.1):  $R=500$ ,  $c_p=0.01$ ,  $c_{am}=0.001$ ,  $g_p=0.8 \cdot 10^{-3}$ ,  $g_a=0.4 \cdot 10^{-3}$ ,  $l_p=0.6$ ,  $l_a=0.8$ ,  $k_a=0.1$ ,  $k_p=0.1$ ,  $s_{a0}=0.4$ ,  $s_{p0}=0.2$ ,  $l_{sa}=0.4$ ,  $l_{sp}=0.7$ ,  $s_{am}=30000$ ,  $s_{pm}=2200$ ,  $b_a=0.4$ ,  $b_p=0.6$ ,  $k_1=1$ .

We can again derive a parameter plane for the model with both perennial and annual grasses and their soil seed bank as function of herbivore pressure ( $h$ ) and germination rate of the seeds in the soil bank ( $g_p$ ; Fig. 7.5). For the perennial grass cover, a similar pattern is found in relation to the herbivore density and the germination rate of the seeds of the perennial grasses compared with the model without annual grasses. Annual grasses are affected by both the presence of perennial grasses and the herbivore density. At low herbivore density and high germination rate of the seeds of perennial grasses, annual grasses disappear. When alternate stable states occur in the perennial grasses, also alternate stable states occur in the annual grasses: when perennial grasses are present, annual grasses disappear, and when perennial grasses and their soil seed bank cannot be maintained (they passed the threshold below which the supply of seeds in the soil seed bank is not sufficient anymore to maintain a perennial grass cover) then annual grasses appear (see also Fig. 7.4). When herbivore density increases further to maximally  $h=8$ , especially under conditions that the germination rate of the seeds of the perennial grasses is low, perennial grasses disappear and annual grasses can be found. With further increase of herbivore density ( $h>8$ ), the dynamics of the annual grasses is independent of the germination rate of the seeds of the perennial grasses (there are no perennial grasses anymore) and the second region of alternate stable states occur (either a state with annual grasses or a state with bare soil). Finally, annual grasses also disappear when herbivore density further increases.



**Fig. 7.5.** Parameter plane of herbivory pressure ( $h$ ) and germination rate of the seeds of the perennial grasses in the soil bank ( $g_p$ ) for the different states. Parameter values are (see Table 7.1):  $R=500$ ,  $c_p=0.01$ ,  $c_{am}=0.001$ ,  $g_a=0.4 \cdot 10^{-3}$ ,  $l_p=0.6$ ,  $l_a=0.8$ ,  $k_a=0.1$ ,  $k_p=0.1$ ,  $s_{a0}=0.4$ ,  $s_{p0}=0.2$ ,  $l_{sa}=0.4$ ,  $l_{sp}=0.7$ ,  $s_{am}=30000$ ,  $s_{pm}=2200$ ,  $b_a=0.4$ ,  $b_p=0.6$ ,  $k_l=1$ .

## Discussion

Knowledge of vegetation dynamics plays an important role in conservation, management and restoration of rangelands (Briske et al., 2005). For this reason, theoretical and empirical models have been developed to show the existence of alternative vegetation states in semi-arid grazing systems (Noy-Meir, 1975; Westoby et al., 1989; Rietkerk et al., 1996; Van Langevelde et al., 2003). Moreover, there has been an increasing recognition that vegetation changes in semi-arid grazing systems can be predicted by state-and-transition models (Walker



et al., 1981; Mayer and Rietkerk, 2004). Hence, these state-and-transition models underscore the fact that rangelands and their dynamics can be understood as a system characterised by alternate stable states that are linked by sudden transitions (Westoby et al., 1989; Bestelmeyer et al., 2003).

Therefore, previous studies have been trying to provide the underlying mechanisms behind these alternate stable states and their transitions in rangeland management. To explain observed sudden changes in the vegetation, some studies reported that water availability under the influence of grazing is the key mechanisms that determine transitions in plant communities in semi-arid areas (Rietkerk et al., 1996; Rietkerk and Van de Koppel, 1997). The positive feedback between plant cover and infiltration of rain into the soil triggers these transitions. In this paper, we considered the impact of grazing on above and belowground (soil seed bank) vegetation dynamics, and we explored the hypothesis that in addition to moisture and soil nutrients as seen in previous models, seed density in the soil and seed longevity characteristics trigger the transitions between three states: from perennial to annual grasses and from annual grasses to bare soil with an increasing grazing pressure. When grazing is absent or low, a high cover of perennial grasses and a large soil seed bank is present, whereas with increasing grazing, the high perennial cover and the size of the soil seed bank of perennial grasses declined (Tessema et al., 2011b, d). This leads a situation in which soil seed banks become a limiting factor for the existence of perennial grasses in semi-arid grazing systems (O'Connor, 1994; Sternberg et al., 2003).

We found that the positive relationship between plant cover and differences in soil seed bank dynamics between plant species, i.e., seed germination rate and seed longevity seed, trigger the transition from perennial grasses to annuals and from annual plant cover to bare soil under heavy grazing. In our model, this positive feedback is responsible for the existence of alternate stable states, which can cause shifts in vegetation composition and can explain observed sudden changes from perennial grasses to annual grasses. Rapid germination and mortality (Pons, 1991; Tessema et al., 2011e), and low seed longevity in perennial grasses (Baskin and Baskin, 2004; Tessema et al., 2011e, f) trigger the transition of herbaceous vegetation from perennial grasses to annuals. Because there is evidence that the seeds of perennial grasses do not remain viable in the soil for many years (Mott, 1978; McIvor and Howden, 2000), indicating that perennial grass seeds follow a short term colonization strategy. On the contrary, annuals can persist under heavy grazing because of their persistent soil seed banks, long longevity and relative lower palatability to herbivores compared to

perennials (O'Connor and Pickett, 1992). Our model study suggests that the system can only be restored if perennial grass cover or the size of the soil seed bank reaches a critical threshold. This means that perennial grasses may recolonize the area through seeds imported by wind, water or animals, but the recovery process may take decades (Rietkerk et al., 1996). Once perennial grasses established; their rapid growth at the onset of the first rain, give them an advantage over annual species in semi-arid grazing systems (Prins and Loth, 1989; Veenendaal et al., 1996b) and can dominate the herbaceous vegetation under low grazing pressure.

Previous studies reported the existence of alternative states and transitions in semi-arid grazing systems, with herbivores as the main driving force behind these transitions from vegetated to unvegetated states (Westoby et al., 1989; Rietkerk et al., 1996). The main explanation for these sudden changes in semi-arid grazing systems so far is the positive feedback between plant cover and infiltration of rain into the soil (Rietkerk et al., 1996, 2002; Rietkerk and Van de Koppel, 1997). This mechanism for sudden changes in the vegetation has been put forward as the explanation for desertification. The positive feedback between plant cover and size of the seed bank and seed longevity characteristics (i.e., mortality and germination) are therefore an alternative explanations for sudden vegetation changes in semi-arid grazing systems, other than the positive relationship between plant cover and infiltration of rain into the soil. In contrast to this latter positive feedback, our model can also explain changes in vegetation from perennials to annuals and vice versa.. Moreover, the infiltration of rainfall in the soil is increased by the presence of perennials, but annuals hardly increase infiltration of rain in the soil (Rietkerk et al., 2000). However, in our model, we indicated that the route to recovery is via seeds in the soil, not via infiltration, as infiltration is low in annual grasses. Hence, the seeds determine the recovery for bunch (tufted) perennial grasses, which are commonly found in semi-arid grazing systems (O'Connor and Pickett, 1992), so that we did not take into account recruitment from vegetative parts in our models.

In this paper, we show that our model can explain alternative vegetation states and transitions in semi-arid savannas as a result of soil seeds banks dynamics under the influence of grazing. Our model is alternative for the infiltration mechanism and need to be tested under which conditions the different mechanisms are valid. Our model contributes to understanding of the vegetation dynamics of semi-arid savannas, and has important implications for management and restoration of these ecosystems.

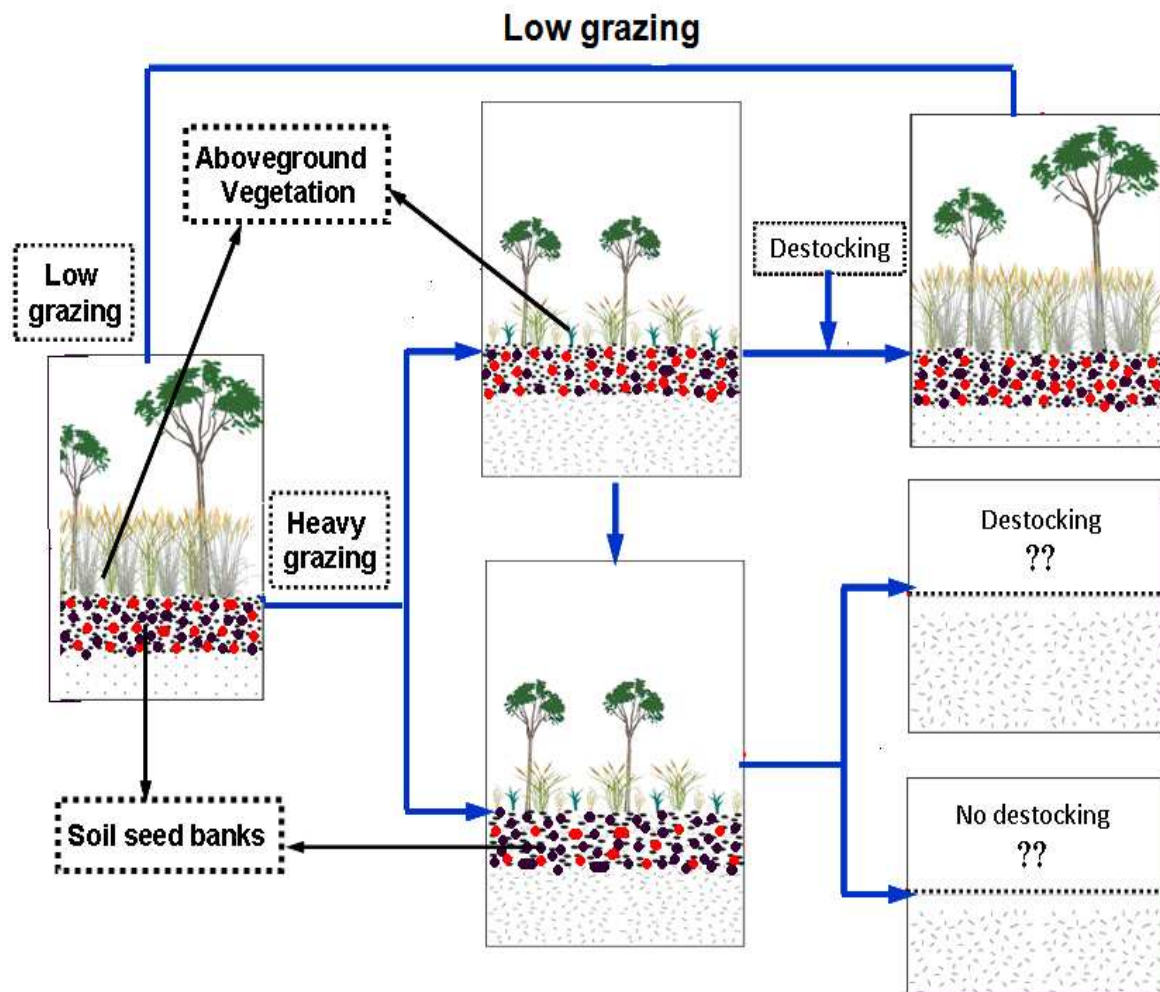
**Table 7.1.** List of the used parameters and variables, their interpretation, units, estimated values and literature sources

	<i>Interpretation</i>	<i>Units</i>	<i>Values</i>	<i>Sources</i>
$P$	Cover of perennial grass	-	0-1	
$A$	Cover of annual grass	-	0-1	
$S_p$	Availability of seeds of perennial grass in the soil	$m^{-2}$	0-2200	Tessema et al., 211b&c
$S_a$	Availability of seeds of annual grass in the soil	$m^{-2}$	0-5000	Vogler and Bahnisch, 2006 Tessema et al., 211b&c
$R$	Water availability in the soil	$mm\ t^{-1}$	0-500	
$c_p$	Rate of increase of plant cover due to germination of the seeds in the soil bank	$m^2$	0.01	
$c_{am}$	Maximal increase in annual grass cover when light is not limiting	$m^2$	0.001	
$g_p$	Germination rate of the seeds of grass in the soil bank per unit of water availability	$mm^{-1}$	$g_p=0.4/500$ and $g_a=0.2/500$	Tessema et al., 2011d&e at 500 mm rainfall per year
$l_p$	decrease of grass cover, for example due to death	$t^{-1}$	$l_p=0.6$ and $l_a=0.7$	
$b_p$	decrease of grass cover due to herbivory	$m^2\ g^{-1}\ t^{-1}$	$b_p=0.6$ and $b_a=0.1$	Prins, 1988 Perennial grass is more palatable than annual grass
$h$	herbivore density	$g\ m^{-2}$	0-15	
$s_{pm}$	maximum amount of seeds produced when plant cover is maximal	$m^{-2}$	$s_{pm}=2200$ and $s_{am}=30,000$	Veenendaal, 1991 Veenendaal et al., 1996b
$s_{p0}$	Fraction of amount of the maximum amount of seeds in the seed bank due to dispersal	$m^{-2}$	$s_{p0}=0.2$ and $s_{a0}=0.4$	Vogler and Bahnisch, 2006
$k_p$	plant cover where the rate of seed production is half of its maximum	-	$k_p=k_a=0.1$	
$l_{sp}$	specific loss rate of seeds	$t^{-1}$	$l_{sp}=0.7$ and $l_{sa}=0.4$	Tessema et al., 2011d&e found longevity of seed from perennial grass to be 28% and 62% for annual grass
$k_l$	plant cover where the light availability for annual grasses is half of $c_{am}$	-	0.2	



# 8

Understanding aboveground vegetation and soil seed banks in response to grazing in semi-arid African rangelands: a synthesis



Tessema Zewdu Kelkay

## **Introduction**

Rangelands comprise between 40% and 50% of the landmass of the world (Derner et al., 2006; Tennigkeit and Wilkes, 2008). It provides about 70% of the global forage for domestic livestock (Derner et al., 2006). Rangelands also provide important ecosystem services beyond forage for livestock such as biological diversity, wildlife habitat, soil protection, and greenhouse gas sequestration (Derner and Schuman 2007; Brown and Thorpe 2008). The African continent have magnificent landscapes that provide vital ecosystem services (Bongers and Tennigkeit, 2010) such as home to vast wildlife populations and yield valuable livestock products (Coppock et al., 2011). Communal rangelands provide the major feed resources for free ranging animals under pastoral production systems in East Africa (Prins, 1989). Most importantly, perennial grasses are the dominant vegetation in these ecosystems (Prins, 1988) and provide grazing for domestic and wild herbivores, as well as preventing soil erosion (Jonsson et al., 2010).

However, semi-arid rangelands in Africa experience different forms of land degradation (Snyman, 1998; Vetter, 2005), as a result of heavy grazing (Kassahun et al., 2008b). This degradation is characterized by a reduction in total vegetation cover and changes in palatable plant species (Zimmermann et al., 2010), an increase in bare soil and a reduction in soil quality (Tefera et al., 2010). The loss of herbaceous biomass and plant biodiversity are serious challenges (Kassahun et al., 2008a), causing negative impacts on the rangeland ecosystems, livestock production and livelihoods of the pastoral communities (Briske et al., 2003). Therefore, understanding the responses of vegetation to grazing is crucial to improve the management of communal rangelands in semi-arid Africa for both biological conservation and sustainable use (Snyman, 1998).

The main focus of my research is to understand the role that the soil seed banks play in the restoration of degraded semi-arid rangelands through investigating the mechanisms how grazing affects both the aboveground vegetation dynamics and the soil seed banks, with a geographical focus on semi-arid African rangelands, more specifically on Ethiopia as case study. Accordingly, the following thematic areas are covered as central discussion point to this thesis:

- (i) Impact of grazing on aboveground vegetation dynamics (Chapter 2).
- (ii) Restoration of semi-arid African rangelands from soil seed banks (Chapter 7).
- (iii) Impact of grazing on soil seed bank dynamics in semi-arid African rangelands (Chapter 3 and 4).

- (iv) The similarity of soil seed banks and aboveground vegetation in semi-arid African rangelands (Chapter 2 and 3).
- (v) Soil seed bank depletion and survival strategies of grass species in semi-arid African rangelands (Chapter 5, 6 and 7).
- (vi) Implications for the restoration of semi-arid African rangelands (Chapter 7 and 8).

In this synthesis, I show the processes how sustained heavy grazing affects the aboveground vegetation, and more specifically triggers the changes in species composition, basal cover and bare soil, and the possibility for vegetation restoration from the soil seed banks can also be deducted from the same underlying mechanisms (Fig. 8.1).

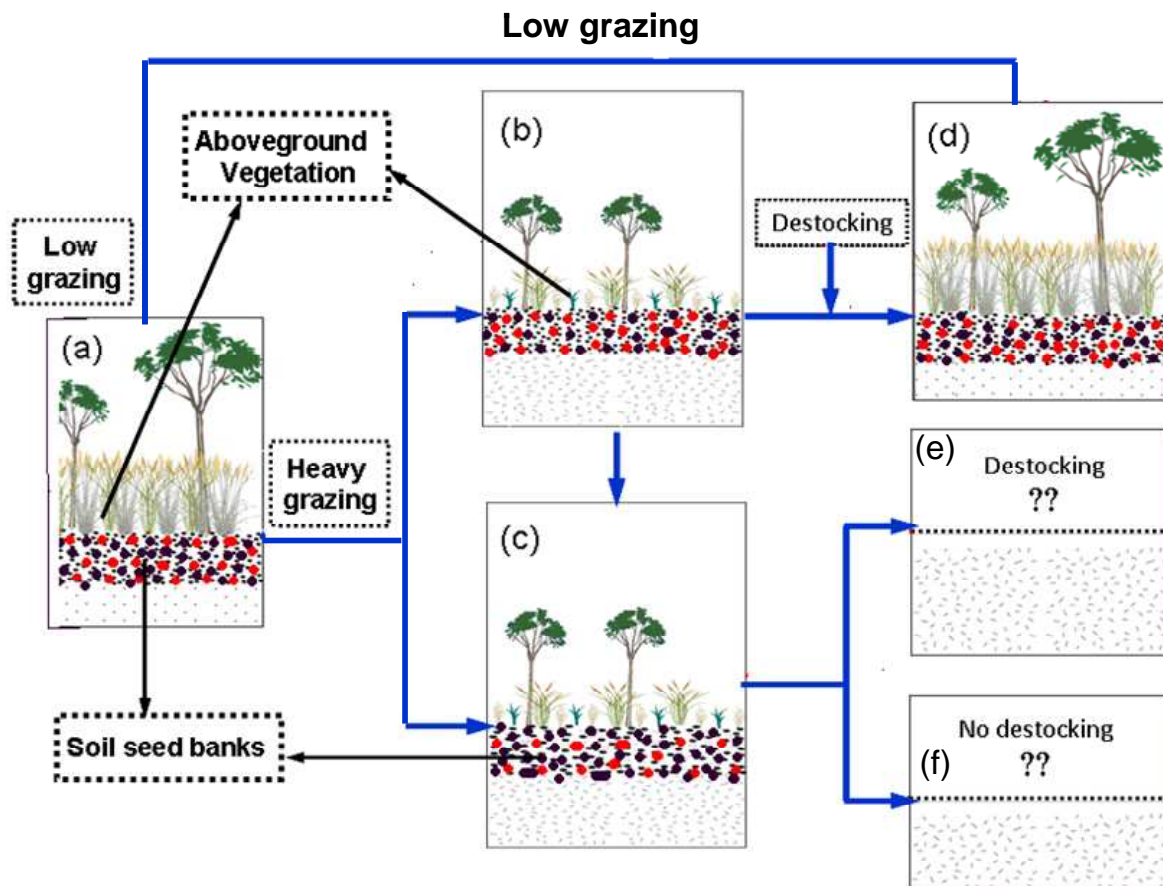
In general, I hope the work presented in this thesis will fill information gaps in our knowledge with regard to the role that soil seed banks can play in the restoration of semi-arid African rangelands, more specifically on Ethiopia under the pastoral production systems, where communal sustained heavy grazing is a typical feature of land use.

### **Impact of grazing on aboveground vegetation**

Grazing systems in Africa is as old as some 2 million years ago (Prins, 1989). The rangelands in Africa are famous for their vast number of domestic and wild herbivores (Du Toit, 2003). For millennia, domestic animals modified the vegetation to a large extent and have been exerting their impact on the grazing lands (Cumming, 1982; Sinclair, 1983). This is because of the fact that grazing lands belongs to communal property while livestock are individually owned by pastoral communities in Africa (Prins, 1992; Desta and Coppock et al., 2004). Vegetation degradation, most specifically, perennial grasses are widely put down to the existence of a ‘common property problem’ or ‘tragedy of the commons’, in pastoral communities (Dodd, 1994; IFAD, 1995). It is to be expected that each herdsman try to keep as many cattle as possible to maximize his gain on the communally owned rangeland. The herdsman concludes that the only sensible course for him to pursue is to add another animal to his herd, and another; and another (Hardin, 1968; Fratkin, 1997). Herein is the tragedy that each herdsman is locked into a system, which compels him to increase his herd without a limit-with a rangeland that is limited in area and resources (i.e., feed resources and water). This leads to a ‘free rider’ situation in such a way that individuals need to maximize their own benefit leading to vegetation degradation. Therefore, heavy grazing by livestock is considered

to be the main cause of vegetation degradation in African rangelands due to tragedy of the commons (Hardin, 1968; Fraktins, 1997).

In this thesis, I showed that heavy grazing sites in communal rangelands under the pastoral communities in Ethiopia results in the disappearance of perennial grass species and their replacement with annuals, a reduction in herbaceous species diversity and their plant abundance, standing biomass and basal cover compared with the lightly grazed sites (Chapter 2). Similarly, rangelands excluded from grazing had a higher plant species diversity compared with heavily grazed areas in East Africa (Mengistu et al., 2005; Yaynesht et al., 2009). The higher species diversity in areas excluded from grazing might be due to local species pools maintained in the form of soil seed banks (Snyman, 2004; Solomon et al., 2006) that recolonize the area faster as litter accumulation, organic matter and nutrient increases in the soil (Descheemaeker et al., 2006; Mekuria et al., 2007). Therefore, soil seed banks guarantee the restoration of vegetation after heavy grazing through long-term exclusion.



**Fig. 8.1.** Schematic diagram illustrating the impact of grazing on aboveground vegetation and soil seed bank dynamics in semi-arid rangelands; In the aboveground vegetation, tall herbaceous plants represent perennial grasses while short plants are annual grasses and forbs. In the soil seed banks, red dots represent seeds of perennial grasses while black dots are seeds of annual species including grasses and forbs.



Sustained heavy grazing has resulted in vegetation shifts (van Koppel et al., 1997; Rietkerk et al., 2004), showing the concept of the alternative stable states that has been frequently used to evaluate herbivore-driven vegetation changes (Westoby et al., 1989). The mechanism is the interaction between grazing and competition within the plant community in such a way that grazing intolerant species disappear because they are highly nutritious and eaten before seed setting by herbivores (Dyksterhuis, 1949; Smith, 1979). Therefore, depletion of the soil seed banks could follow due to lack of seed production from the aboveground vegetation. And in the absence of perennial grasses, the annual species will be grazed, leading to bare patches where the soil surface is exposed to water and wind erosion (Moussa et al., 2009), which changes soil structures and loss of nutrients (Mengistu et al., 2005). This, in turn, affects both the aboveground vegetation and the soil seed bank dynamics. Hence, the recovery processes of degraded semi-arid rangelands and the transition from one stable state to another could be controlled by two important factors, the intensity of grazing and the availability of persistent seeds in the soil seed banks (Chapter 7).

In this thesis, I hypothesize that the availability of persistent seeds in the soil seed banks triggers the transition of degraded semi-arid rangelands from bare ground state to annual grass state, and then to a perennial grass state since seeds buried in the soil serve as a reservoir to return to the original vegetation conditions after heavy grazing (Fig. 8.1). Moreover, stable states and transitions between states in semi-arid rangelands can probably be triggered by differences in soil seed bank dynamics between perennial and annual species, which depends on recruitment strategies. Plants facilitate their survival in semi-arid rangelands by depositing seeds into the soil seed banks. However, perennial grasses rarely recolonize bare soil in these ecosystems because their seeds are depleted in the soil seed banks due to heavy grazing, which might lead to the presence of hysteresis (Chapter 7). Moreover, the lack of recovery after resting could also related to changes in physical and chemical soil conditions due to long-term heavy grazing (Chapter 2). Therefore, resting of grazing lands may not help to the restoration of semi-arid rangelands once the seeds in the soil have been depleted unless supported with extraneous sources of perennial grass seeds through reseedling or other dispersal mechanisms.

### **Restoration of semi-arid African rangelands from soil seed banks**

Soil seed banks play an important role in maintaining the ecological and genetic diversity of the plant community (Thompson and Grime, 1979; Grime, 1989) and could guarantee the restoration of vegetation following disturbances (Bekker et al., 1998; Scott et al., 2010).

Grazing is often regarded as the most important factor responsible for large structural changes in semi-arid rangelands (Abule et al., 2005b; Kinloch and Friedel, 2005; Kassahun et al., 2009). However, vegetation studies in communal rangelands of semi-arid Africa are mostly restricted to the aboveground vegetation, and often lack the role that soil seed banks play in the restoration of degraded vegetation under influence of heavy grazing (de Villers et al., 2003; Hopfenserger, 2007; Kassahun et al., 2009).

Several hypothetical scenarios are expected to be evident in terms of changes in species composition both on the aboveground vegetation and soil seed banks under the influence of grazing in semi-arid African rangelands (Fig. 8.1). These hypotheses are:- (i) under low grazing pressure, a mosaic of growth forms including grasses, forbs and woody species are found in the aboveground vegetation, which facilitate a higher species richness, aboveground biomass and basal cover, as well as a higher seed availability in the soil seed banks (Fig. 8.1a). The continuous replenishment of new seeds from aboveground vegetation to the soil seed bank guarantees a higher similarity between the species composition of the soil seed banks and aboveground vegetation, (ii) as the grazing pressure increases, from low grazing to heavy grazing, the species composition of aboveground vegetation shifts from perennial grasses to species with an annual life history, and a reduction in herbaceous species diversity, aboveground biomass and basal cover with a higher cover of bare ground. In this situation, the seeds available in the soil seed banks could 'kick-start' the recovery of the vegetation and accelerate the transition from a degraded state to vegetation with a perennial grass cover (Fig. 8.1b) under the presence of low grazing or grazing exclusion, since the soil seed bank serves to return to the original light grazing situation (Fig. 8.1d), (iii) under sustained heavy grazing, not only the species composition in the aboveground vegetation changes but also the seeds available in the soil seed banks, more specifically, the seeds of perennial grasses may be depleted, leading to the disappearance of perennial grasses both in the soil seed banks and the aboveground vegetation (Fig. 8.1c). This hypothesis is in agreement with the finding of this thesis that sustained heavy grazing in semi-arid rangelands of Ethiopia depleted the seeds of perennial grasses in the soil seed banks (Chapter 3 and 4), which ultimately leads to the degradation of perennial grasses on the aboveground vegetation (Chapter 2 and 4); and (iv) under sustained heavy grazing, even the annual species could be severely grazed in the absence of perennial grasses, exposing the rangelands to bare patches, and consequently leading to a stably degraded rangeland conditions (Fig. 8.1e and f).

### **Impacts of grazing on soil seed bank dynamics in semi-arid African rangelands**

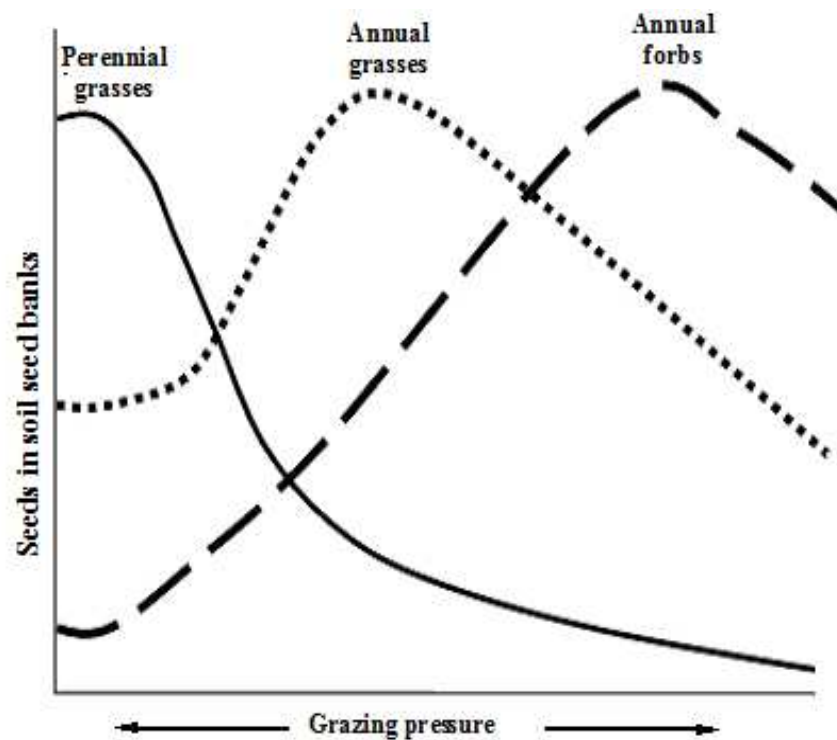
The structure of soil seed bank dynamics in semi-arid rangelands are shaped by severity of grazing over extended periods (Kinucan and Smeins, 1992; Kinloch and Friedel, 2005; Dreber and Esler, 2011). In this thesis, the soil seed banks of a semi-arid Ethiopian rangelands varied with grazing regime, with greater seedling density under light grazing than under heavy grazing (Chapter 3 and 4). The greater emerged seed densities at the light grazing sites may be due to the higher seed rain under these conditions. Other studies, however, reported that long term heavy grazing increased seed densities from the soil seed banks in southern African rangelands (Dreber and Esler, 2011; Snyman, 2004), which is contrary to the findings of this thesis. This might be due to the fact that soil disturbances by trampling may favour sometimes the germination of many small-seeded annual species in the soil seed banks leading to a greater seed density during heavy grazing conditions.

The total number of emerged seedlings from the soil seed banks increased over the first 3 months of soil sampling immediately after seed dispersal, and then decreased thereafter in semi-arid Ethiopian rangelands (Chapter 4). According to Williams et al. (2005), the temporal variation in viable seeds in the soil seed banks is a common feature of semi-arid rangelands. Scott et al. (2010) also indicated that the density of viable seeds in the soil seed banks were much higher in the early dry season compared with the late dry season in northern Australia. This higher seed density might be due to the deposition of seeds into the soils from the previous wet season's 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 (i.e., harvester ants, termites, etc.) and mortality over time due to biotic and abiotic factors.

In this thesis, I show that grazing pressure had no significant effect on species richness from the soil seed banks (Chapter 3 and 4). According to Snyman (2004), species richness of the soil seed banks declined with increasing rangeland degradation in South Africa. However, the number of species in the soil seed banks was reported to increase with grazing intensity (Dreber and Esler, 2011) which is contradictory to this thesis. The variability in local conditions between soil sampling sites in addition to grazing intensity might cause the variation in species richness in semi-arid rangelands (Kinloch and Friedel, 2005; Kassahun et al., 2008b). In this thesis, the lightly grazing sites had a higher species richness compared with the heavily grazed sites (Chapter 4), indicating that grazing indeed reduces the species richness not only in the aboveground vegetation but also in the soil seed banks (Chapter 2 and

4). For instance, in Australia and South Africa, the species richness of the soil seed banks was lower and the species composition was unstable under heavy grazing (Snyman, 2004; Kinloch and Friedel, 2005).

In this thesis, under increased grazing, the grass layer in semi-arid African rangelands changes in species compositions, leading to a change from more palatable perennial species under light grazing towards more unpalatable often annual species (forbs) in the soil seed banks (Fig. 8.2). The opening up of the vegetation layer due to heavy grazing may create establishment opportunity for annuals, especially their short life cycle, prostrate growth and small stature may help them to avoid heavy grazing stress and trampling that would facilitate easily burial of annual seeds in the soil seed banks.



**Fig. 8.2.** Schematic diagram illustrating a domestic herbivore driven transitions from perennial grass to annual grasses and annual forbs with a decrease of seeds in soil seed banks

The species composition on heavily grazed areas often do not revert to that of lightly grazed areas after good rainfall (Snyman, 2004; Kassahun et al., 2008b) indicating that the species composition on the heavily grazed areas has undergone persistent changes overtime. So that heavily grazed perennial grass species loose competitive power as opposed to grazing-tolerant annuals, and subsequently the unpalatable annual grasses become dominant on the heavily grazed patches (Chapter 2). This thesis confirms that heavy grazing causes a

persistent reduction in perennial grasses not only in the aboveground vegetation but also in the soil seed banks in semi-arid African rangelands, particularly those species with low seed dispersal potentials.

### **The similarity between soil seed banks and aboveground vegetation**

Researchers are interested in understanding mechanisms determining the similarity between the soil seed banks and aboveground vegetation for several reasons. These are to investigate: (i) the effects of disturbances such as grazing, fire, or land use changes, (ii) the impact of invasive plant species, (iii) plant succession, and (iv) the effects of restoration of degraded ecosystems (Bekker et al., 1998; Kinloch and Friedel, 2005). The primary variable that needs to be measured when studying soil seed banks and aboveground vegetation relationship is plant species similarity (Hopfensperger, 2007). For instance, if high similarity exists between soil seed banks from year one and the aboveground vegetation in year two, indicating that the soil seed banks has contributed to the composition of the aboveground vegetation in year two (Henderson et al., 1988). In this thesis, the similarity in species composition between the soil seed banks and aboveground vegetation in semi-arid Ethiopian rangelands was low under heavy grazing (Chapter 3). This dissimilarity is characterized by more frequent occurrence of perennial grasses and woody plants in the aboveground vegetation (Chapter 2), and more annual forbs in the soil seed banks (Chapter 3 and 4). Previous studies (de Villiers et al., 2003; Hopfensperger, 2007) also reported poor correlations between species in the soil seed banks and standing vegetation in grassland ecosystems. The similarity in species composition between the established vegetation and the soil seed banks in grasslands is often not more than 50% (Bakker and Berendse, 1999). This indicates that nearly half the species present in the established vegetation are not found back in the soil seed banks as a result of various disturbances, such as heavy grazing in the case of semi-arid African rangelands.

The low similarity between the soil seed banks and aboveground vegetation in terms of palatable perennial grasses might be an indicator of heavy grazing the aboveground vegetation, whereas a good similarity between the soil seed banks and aboveground vegetation is generally reported only in undisturbed (i.e. no grazing and no fire) plant communities (Hopfensperger, 2007). The low similarity observed in this thesis is due to several factors such as (i) differences in seed rain between annuals and perennials (Veenendaal et al., 1996a), (ii) depletion of seeds in the soil seed banks as a result of

germination and mortality, and/or (iii) differences in longevity and germination of seeds between species in the soil seed banks (Chapter 5 and 6).

### **Soil seed bank depletion and survival strategies of grass species**

My research confirms that the seeds of perennial grass in the soil seed banks are lacking and therefore unable to rapidly drive the transition from degraded vegetation conditions to perennial grass cover that represent better fodder value in semi-arid African rangelands (Chapter 3 and 4). Chapter 7 even shows the necessity of sufficient number of seeds in the soil seed banks to make the transition from bare soil to the two other vegetated states (“annuals” or “perennials”) possible: if the number of these seeds is below a critical threshold, the system cannot recover. Similarly, Page and Beeton (2000) and Vetter (2005) reported that semi-arid rangelands may not recover from heavy livestock grazing, even after many years of grazing exclosures.

In this thesis, the grass species showed a large variation in germination and survival (Chapter 5 and 6), in such a way that annual grasses had lower germination, higher viability, and lower mortality, and therefore maintained a higher longevity than perennial grasses. As a result, annual species are expected to dominate and form a persistent soil seed banks because of their longer longevity and lower mortality while buried in the soil (Chapter 6), coupled with good seed producing and successful seed deposition capacities, as well as the ability to complete their life cycle rapidly in one growing season. However, due to high seed germination and mortality (Chapter 5 and 6), as well as a low seed production potential (Veenendaal et al., 1996a), most perennial grass species do not form a persistent soil seed banks, and as a result these species might disappear and become locally extinct in the soil seed banks in a semi-arid savannas. Thus, perennial grass species that are palatable to herbivores (Prins, 1988), and especially those with a low seed output, as well as short seed longevity might disappear in the system due to heavy grazing. Subsequently, depletion of the soil seed banks could follow due to lack of seed production from the established plants.

The persistence of plant species and the maintenance of biodiversity in semi-arid rangelands depend on the recruitment of seedlings from annual grasses, and on the vegetative reproduction of perennial grasses (O'Connor, 1996). As a result, annual grasses are successful in disturbed habitats, such as under heavy grazing, because of a considerable amount of resources investment in their seeds, both in terms of biomass and nutrients (Veenendaal, 1991) and their large seed production efforts (Veenendaal et al., 1996b). However, most

perennial grass species also have an alternative survival strategy, such as the development and expansion of vegetative parts (i.e., tillers, rhizomes, and/or stolons) (O'Connor, 1996), horizontal growth habits and a high belowground aboveground ratio (Veenendaal, 1991). This allows perennial grasses to survive in the aboveground vegetation under unfavourable conditions, such as under the influence of high grazing pressures, drought, or fire. Consequently, perennials are at a loss if, for instance under the influence of heavy grazing, the aboveground vegetation has been removed. In this thesis, I concluded that the re-colonization strategy of perennial grasses in semi-arid African rangelands from the soil seed banks is not adapted to bridge long periods of unfavourable conditions such as sustained heavy grazing, but rapidly leading to vegetation dominated by annuals and ultimately to bare patches (Chapter 7). The re-colonization capacity of perennial grass species depends on the dispersal capacity of their seeds, recruitment strategy, soil types and length of grazing exclusion, as subsequent recovery of degraded rangelands might probably be a century old process.

### **Implications for the restoration of semi-arid African rangelands**

In this thesis, sustained heavy grazing in semi-arid African rangelands affects species composition and diversity, plant abundance, standing biomass and basal cover. Moreover, it causes the depletion of perennial grass seeds in the soil seed banks. If grazing continues at high levels, the rehabilitation of such a degraded state is unlikely to be achieved with simple reduction of heavy grazing pressure.

In a situation where perennial grasses have disappeared from the aboveground vegetation as a result of heavy grazing but ultimately their seeds are found in the soil seed banks, the perennial grasses can have a chance to recover and stabilize the degraded rangelands through grazing exclusion (destocking). Whereas, when perennial grasses are locally extinct both from the aboveground vegetation and in the soil seed banks as a result of sustained heavy grazing as confirmed in this thesis (Chapter 3 and 4), the perennial grass species recovery in degraded semi-arid African rangelands could be possible through long-term grazing exclusion (destocking) and re-introduction of seeds (re-seeding) of similar species with the participation of pastoralists. However, in a situation where perennial grass species disappeared and locally extinct both from the aboveground vegetation and in the soil seed banks, and if there is no further grazing exclusion (destocking) and seed dispersal mechanisms or external sources through re-seeding strategies, the possibility of perennial grasses recovery in semi-arid

African rangelands may be very slow or totally impossible. Therefore, these situations need to be tested in long-term studies in semi-arid African rangelands under communal grazing systems.

From this thesis, it is possible to deduce that sustained heavy grazing changes the species composition not only in the aboveground vegetation but also in the soil seed banks in semi-arid African rangelands, more specifically, perennial grass species local extinction and disappearance as opposed to annual grasses and herbs. This indicates that restoration of perennial grass species from the soil seed banks on heavily grazed sites in semi-arid African rangelands would be prevented by removal of perennial grasses on the aboveground vegetation. This, in turn, implies that restoration of perennial grasses may not be successful and slow to accomplish if they are locally disappeared. Hence, the existence of perennial grass species in semi-arid Africa depends mainly on sustainable utilization of remnant rangelands through proper conservation and grazing management. At this juncture, the seeds of perennial species under light grazing areas can also be used to re-initiate local restoration activities under the heavy grazing sites in semi-arid African rangelands through grazing exclusion. The seed-to-seedling stage is found to be the most critical transitional stage for grass survival (Chapter 4), suggesting that exclusion from huge livestock trampling effects in the early germination stage and/or supply of available water (irrigation) at this stage is important to facilitate the transition from seedling-to-established plants.

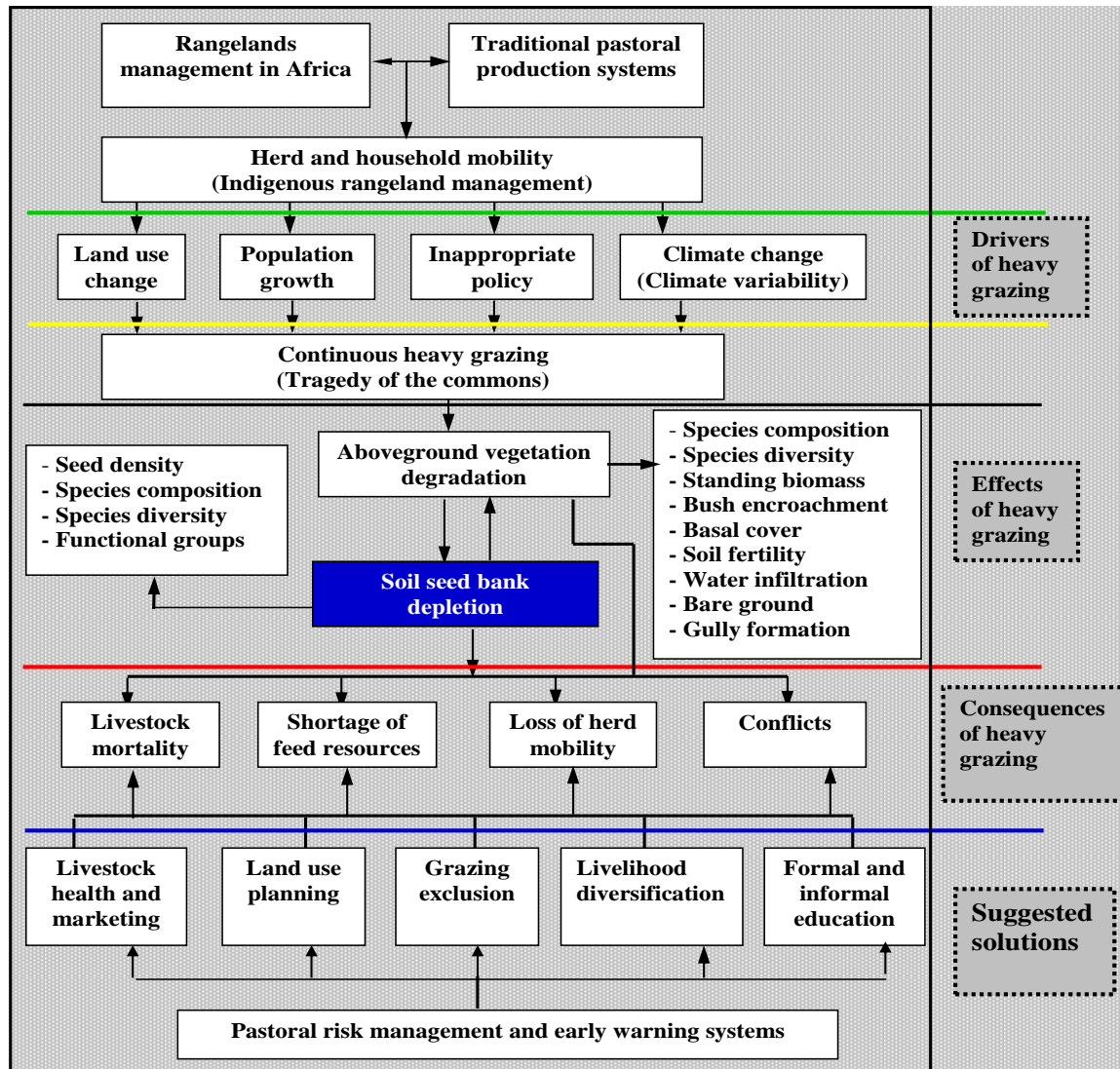
Pastoral production systems by definition are dependent on the mobility of herds in search of rangeland resources (i.e., good grazing sites and watering points), which is assumed to lead to the sustainability of semi-arid rangelands (Desta and Coppock, 2004; Coppock et al., 2011). Traditionally, African pastoralists have been dependent on large herds of livestock that roamed widely over diverse grazing areas (Coppock, 1994). This mobility of herds over diverse areas provides rangelands resting opportunity for a certain period that would facilitate vegetation restoration either from the soil seed banks and/or from vegetative structures, most specifically, in perennial grasses and woody species. Moreover, the heterogeneous grazing and resting of livestock in bomas (kraals) at night during mobility creates the spatial heterogeneity of soil nutrient in African rangelands via deposition of faeces and urine. Therefore, herd mobility has been considered as a traditional rotational grazing system under pastoral communities in Africa. In addition, the ingestion of seeds by livestock and the subsequent disposal via faeces during herd mobility could enhance the restoration of degraded rangelands. However, herd mobility has been curtailed or limited to short distance



grazing areas due to various reasons under pastoral systems (Mesele et al., 2011), and in recent decades, the situations in semi-arid African rangeland become more difficult for pastoralists to subsist largely on livestock production due to shortage of feed resources as a result of rangeland degradation (Coppock et al., 2011).

Several factors could contribute to the collapse of the sustainability of pastoral systems and leading towards its extinction in most East African countries. These factors include rapid human population growth, land use changes, loss of herd mobility, shortage of feed resources expansion of crop agriculture and conflicts (Cotula et al., 2009; Mesele et al., 2011). In this thesis, I indicated in a schematic diagram the drivers of heaving grazing leading towards vegetation degradation and soil seed bank depletion, as well as its consequences on pastoral communities together with some suggested solutions (Fig. 8.3). Accordingly, in this schematic diagram, I showed that the soil seed banks play the central role in the restoration of aboveground vegetation in degraded semi-arid African rangelands through proper land use planning and grazing management such as grazing exclusions and re-seeding strategies (Fig. 8.3).

Pastoralists in semi-arid Africa have long traditions in excluding their rangelands seasonally from grazing (Gemedo et al., 2006; Angassa and Oba, 2010). These exclosures are often only grazed at the time of forage scarcity and in dry seasons for lactating and pregnant cows. Therefore, these seasonal grazing exclosures can also play an important role in the conservation of grass species diversity that are intolerant to grazing and can be used for sustainable rangelands utilization. The traditional exclosure system of grazing lands by pastoralists can represent the hump-back model developed for explaining plant species diversity under the influence of grazing (Oba et al., 2001). The hump-back model suggests that species diversity reaches maximum at the intermediate biomass levels that could be obtained under the traditional grazing exclosures in pastoral systems (Angassa and Oba, 2010).



**Fig. 8.3.** Schematic diagram showing the drivers of heavy grazing leading towards vegetation degradation and soil seed bank depletion in semi-arid African rangelands with some recommended suggestions

Traditional grazing exclusions are ecologically important in maintaining species diversity, as well as the functioning and stability of rangelands under pastoral systems. For instance, in rangelands with greater species diversity, the loss of standing biomass and vegetative cover are far less and even its recovery after grazing is much faster than degraded rangelands with fewer plant species. The loss of each plant species as a result of heavy grazing can decline the resilience of rangelands to droughts, leading to further degradation. However, traditional grazing exclusions in pastoral areas can facilitate plant species diversity, more specifically grasses with good fodder value that can sustain livestock production. Therefore,

understanding these long traditions and indigenous knowledge of pastoral communities can benefit in the conservation of rangelands from further degradation and for the restoration of previously degraded rangelands in Africa.

I only focused on heavy grazing but understanding the factors contributing to the heavy grazing levels, which ultimately leads to the degradation of rangelands is crucial, although these issues are beyond the scope of this thesis. The government blames climatic variability (drought), and the non-governmental organizations blame inappropriate policies and strategies for the causes of rangeland degradation in Africa (Desta and Coppock, 2004; Coppock et al., 2011). However, rangeland degradation is increasing over time as a result of heavy grazing and pastoralists are under pressure and their livelihood is in continuous vulnerable situations in eastern Africa.

This thesis provides information about the impacts of grazing on aboveground vegetation and soil seed bank dynamics, as well as other important issues in semi-arid rangelands in Ethiopia in particular and in Africa in general for researchers, development workers and policy makers, to design appropriate policies and strategies, as well as developing technologies adapted to local conditions, to improve the quality of life of the pastoral communities.



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## Summary

Rangelands in Africa provide important forage resources for herbivores; particularly perennial grasses provide grazing for domestic and wild herbivores. However, semi-arid rangelands in Africa experience different forms of soil and vegetation degradation, as a result of continuous heavy grazing. This degradation is characterized by a reduction in vegetation cover and changes in palatable plant species and an increase in bare soil. The loss of herbaceous biomass and plant biodiversity are serious challenges, causing negative impacts on the rangeland ecosystems, livestock production and people's livelihoods. Therefore, understanding the responses of vegetation to grazing is crucial to improve the management and restoration of degraded communal rangelands in semi-arid Africa for both biological conservation and sustainable use.

This thesis aims to fill important information gaps about the role that soil seed banks play in the recovery and possible restoration of degraded rangelands, with a geographical focus on semi-arid African rangelands, more specifically on Ethiopia. This was done through investigating the mechanisms of how heavy grazing affects the soil seeds bank dynamics so as to understand stable states and transition processes of aboveground vegetation. In this thesis, aboveground vegetation and soil seed bank dynamics were studied under heavy and light grazing pressures in a field study and under experimental conditions. I hypothesized that plant species that disappeared from the aboveground vegetation due to heavy grazing can, however, recolonize these areas from soil seed banks in rangelands, since the soil seed bank can serve as a reserve to return to the original vegetation conditions. Accordingly, the following research questions are addressed as central to this thesis:

- (i) How does grazing influence both the aboveground vegetation and soil seed bank dynamics in semi-arid African rangelands?
- (ii) Can the seeds, available in the soil seed banks, drive the transition from degraded conditions to a vegetation with perennial grass species?
- (iii) What is the similarity between the species composition of the aboveground vegetation and soil seed banks? and
- (iv) Can the germination and longevity of grass species contribute to vegetation restoration of degraded rangelands?

In this thesis, heavy grazing resulted in the disappearance of perennial grasses, a reduction in herbaceous species diversity and their plant abundance, standing biomass and basal cover, as well as a higher percentage of bare ground, leading to rangeland degradation (Chapter 2). In contrast, light grazing sites had a higher organic carbon, phosphorus and exchangeable bases, and therefore a higher pH and higher electrical conductance, indicating an improved soil nutrient conditions compared with heavy grazing sites, mainly attributed to the higher basal cover and standing biomass at light grazed sites, and the export of nutrients through grazing and dung collection from the heavily grazed sites. In addition, these rangelands seem to confirm the existence of two stable states under influence of grazing (Chapter 2). The first state is typical for sites with a low grazing pressure, characterized by ample herbaceous cover (basal cover), perennial grasses with scattered trees, and good soil conditions, and the second states found at sites with heavy grazing, with poor annual grasses, absence of perennial grasses, and a high proportion of bare ground.. The rehabilitation of such a degraded state is unlikely to be achieved spontaneously with simple reduction of the heavy grazing pressure because these areas may develop feedback loops that inhibit rehabilitation due to changes in vegetation structure and composition, as well as changes in soil nutrients associated with heavy grazing. Hence, changes in herbaceous vegetation, standing biomass and soil composition are caused by interactions between grazing, soil and vegetation, and these interactions determine these rangeland transitions.

In this thesis, a total of 103 species (15 perennial and 29 annual grasses, 6 legumes, 52 forbs and 1 woody species) emerged from all soil seed bank samples collected over the nine months sampling period in Ethiopia (Chapter 3 and 4). The soil seed bank composition was correlated to differences in grazing pressure, with a greater seedling density under light grazing compared with heavy grazing. Immediately after seed dispersal, the seedling density increased over the first 3 months of soil sampling during the long dry season and remained relatively stable until the short rainy season and decreased thereafter at the start of the rainy season (Chapter 4). Under light grazing, perennial grass species dominated, whereas annual species were abundant at the heavily grazed sites, indicating that perennial grasses, with good fodder value, are replaced by annual species in the soil seed banks due to heavy grazing. With increasing soil depth, the seedling density and its species richness declined. Moreover, the seeds of perennial grasses were less abundant in the soil seed banks under heavy grazing. The similarity in species composition between the soil seed banks and the aboveground vegetation was low, which can be attributed to the impact of heavy grazing (Chapter 2 and 3). Results



show that most perennial grasses germinate rapidly after initial seed dispersal at the first rains early in the year, whereas annual grasses show a linear germination pattern over time, indicating that perennial grasses have a different survival strategy than annuals (Chapter 5). Moreover, annual grasses had a lower germination rate, a higher viability, and a higher mortality rate, leading to a longevity of 62%, which was high compared to the 28% for perennials (Chapter 6). As a result, annual species are expected to dominate the soil seed banks, whereas most perennial grass species do not form persistent soil seed banks. The mean mortality from the seedling stage to adult plants in grass was 64.5%, and the seed-to-seedling stage was found to be the most critical transitional stage for grass survival on these rangelands, suggesting that exclusion from grazing and trampling in the early germination stage is important to facilitate the transition from seedling to established plants (Chapter 4). Depletion of perennial grass seeds in the soil due to heavy grazing coupled with high seedling mortality leads to a strong decrease in perennial grasses both in the soil seed banks, as well as in the aboveground vegetation. Moreover, I found that the positive relationship between plant cover and differences in soil seed bank dynamics, i.e., seed density, seed germination rate and longevity, trigger the transition from a system with three stable states, from perennial grasses (state 1) to annuals (state 2) and from annual plant cover to bare soil (state 3) under heavy grazing in these savannas (Chapter 7).

I hypothesize that the restoration of perennial grasses from the soil seed banks in heavily grazed areas in semi-arid African rangelands cannot be successful without an extraneous source of perennial grass seeds and without protecting the young plant's regrowth from trampling and grazing. Therefore, the persistence of species and maintenance of biodiversity in semi-arid rangelands depend mainly on the recruitment of seedlings from annual species, and on vegetative reproduction of perennial grasses and woody species. These findings have important implications for the management, conservation and restoration of semi-arid African rangelands.



## **Samenvatting- Dutch summary**

Holddroge graasgebieden in Afrika vormen een belangrijke voedselbron voor herbivoren; in het bijzonder overblijvende grassen zijn een belangrijke voedselbron voor gedomesticeerde en wilde herbivoren. Deze graasgebieden in Afrika zijn echter onderhevig aan verschillende vormen van bodem en vegetatie degradatie als gevolg van een hoge graasdruk. Deze degradatie wordt gekenmerkt door een achteruitgang in vegetatie bedekking, veranderingen in eetbare plantensoorten, en een toename van het percentage kale grond. Het verlies van kruidachtige vegetatie en plantenbiodiversiteit vormen een grote uitdaging, met negatieve gevolgen voor de grasland ecosystemen, de veestapel, en het inkomen van mensen. Daarom is het van belang om de effecten van begrazing op de vegetatie te begrijpen om zo het beheer en herstel van gedegradeerde graasgebieden in Afrika te verbeteren, zowel voor natuurbescherming als voor duurzaam gebruik.

Dit proefschrift heeft tot doel om inzicht te verschaffen in de rol van zaadbanken in het herstel en de restauratie van gedegradeerde halddroge Afrikaanse graasgebieden, met Ethiopië als geografisch studiegebied. Er is onderzoek gedaan naar de mechanismes hoe graasdruk de zaadbank dynamiek beïnvloedt om zo inzicht te verschaffen in stabiele evenwichten en transitie processen die kunnen optreden in de bovengrondse vegetatie. In dit proefschrift zijn de bovengrondse vegetatie en de dynamiek van zaadbanken bestudeerd onder zware en lichte graasdruk in een veldsituatie en in een experimentele situatie. Mijn hypothese is dat plantensoorten die verdwenen zijn van de bovengrondse vegetatie als gevolg van zware graasdruk, deze gebieden weer kunnen koloniseren vanuit de zaadbank in de bodem, omdat de zaadbank functioneert als een toevluchtsoord van waaruit de originele vegetatie weer kan herstellen. De volgende onderzoeksvragen staan centraal in dit proefschrift:

- (i) Hoe beïnvloedt begrazing de bovengrondse vegetatie en de dynamiek van de zaadbank in halddroge Afrikaanse graasgebieden?
- (ii) Kunnen de zaden aanwezig in de zaadbanken zorgen voor een transitie van gedegradeerde omstandigheden naar een vegetatie bestaande uit overblijvende planten?
- (iii) Is de soortensamenstelling in de bovengrondse vegetatie vergelijkbaar met de soortensamenstelling van de zaadbank?
- (iv) Kan de kieming en levensduur van grassoorten bijdragen aan het herstel van de vegetatie in deze gedegradeerde graasgebieden?

Zware graasdruk resulteerde in het verdwijnen van overblijvende grassen, een vermindering in het aantal en de diversiteit van de kruidachtige vegetatie, een vermindering van staande biomassa en bodembedekking, evenals een hoger percentage kale grond. Dit alles leidde tot een degradatie van de graasgebieden als gevolg van zware begrazing (hoofdstuk 2). Lage graasdruk, echter, resulteerde in een hoger gehalte organische koolstof, stikstof en uitwisselbare basen in de bodem, en dus tot een hogere pH en elektrisch geleidingsvermogen, wat wijst op een verbeterde nutriëntenhuishouding van de bodem in vergelijking met zwaar begraasde bodems. Dit is voornamelijk het gevolg van meer bodembedekking en een grotere staande biomassa onder lage graasdruk, in combinatie met de afvoer van nutriënten door begrazing en het verwijderen van mest in gebieden met een hoge graasdruk. Deze halfdroge Afrikaanse graasgebieden lijken het bestaan van twee alternatieve stabiele evenwichten onder invloed van begrazing te bevestigen (hoofdstuk 2). Het eerste evenwicht is typisch voor gebieden met een lage graasdruk, en wordt gekenmerkt door een hoog percentage aan kruidachtige vegetatie en een grote bodembedekking, overblijvende grassen met her en der bomen, en goede bodemomstandigheden. Het tweede evenwicht is typisch voor gebieden met een hoge graasdruk, en wordt gekenmerkt door de aanwezigheid van veel, kwalitatief laagwaardige, eenjarige grassen, de afwezigheid van overblijvende grassen en een hoog percentage kale grond. Het is onwaarschijnlijk dat dergelijke gedegradeerde gebieden te herstellen zijn door simpelweg de graasdruk te reduceren, omdat er als gevolg van veranderingen in vegetatiestructuur en samenstelling, en veranderingen in de bodemnutriënten feedback loops zijn ontstaan die herstel verhinderen. Dus veranderingen in de kruidachtige vegetatie, staande biomassa, en bodemsamenstelling worden veroorzaakt door de interactie tussen begrazing, bodem en vegetatie, en deze interacties bepalen de transitie van halfdroge Afrikaanse graasgebieden.

In dit proefschrift zijn in totaal 103 soorten (15 overblijvende en 29 eenjarige grassen, 6 leguminosen, 52 kruidachtige en 1 boomsoort) gevonden in de monsters van alle zaadbanken verzameld over een periode van 9 maanden in Ethiopië (hoofdstuk 3 en 4). De samenstelling van de zaadbanken in de bodem was gecorreleerd met verschillen in graasdruk: er was een hogere dichtheid aan kiemplanten bij een lage graasdruk dan bij een hoge graasdruk. De eerste drie maanden na de zaadverspreiding nam de dichtheid aan kiemplanten toe, maar na 3 maanden nam de dichtheid af (hoofdstuk 4). Bij een lage graasdruk domineerden overblijvende planten, terwijl eenjarige soorten domineerden in gebieden met een hoge graasdruk. Dit wijst erop dat overblijvende planten met een hoge voedingswaarde vervangen worden door eenjarige soorten in de zaadbank in de bodem als gevolg van zware begrazing.

De dichtheid en soortenrijkdom van kiemplanten nam af met een toename van de bodemdiepte. Verder waren er minder zaden aanwezig van overblijvende grassen in de zaadbanken van zwaar begraasde gebieden. Er was een lage overeenkomst in de soortensamenstelling van de zaadbank en de bovengrondse vegetatie, als gevolg van een hoge graasdruk (hoofdstuk 2 en 3). Na de initiële zaadverspreiding, kiemen de meeste overblijvende grassen snel bij de eerste regenval vroeg in het jaar, terwijl eenjarige grassen een lineair kiemingpatroon volgen, wat er op wijst dat overblijvende grassen een andere overlevingsstrategie hanteren dan eenjarige grassen (hoofdstuk 5). Verder hadden eenjarige grassen een lager kiemingpercentage een hogere levensvatbaarheid en een hogere sterftekans, resulterend in een overlevingskans van 62%, tegenover 28% voor overblijvende planten (hoofdstuk 6). De verwachting is dus dat eenjarige soorten domineren in de zaadbank, en de meeste overblijvende grassoorten niet langdurig aanwezig zijn in de zaadbank. De gemiddelde sterftekans van het kiemstadium naar een volwassen plant was 64.5% in grassen, en de transitie van zaad naar kiemplant was de meest kritische transitie voor de overleving van grassen in deze graasgebieden. Dit suggereert dat preventie van begrazing en vertrapping in het vroege kiemstadium belangrijk is om de transitie van kiemplant naar volwassen plant te faciliteren (hoofdstuk 4). Een afname van zaden van overblijvende grassen als gevolg van zware graasdruk in combinatie met een hogere sterftekans van kiemplanten resulteerde in een sterke afname van overblijvende grassen, zowel in de zaadbank in de bodem, als in de bovengrondse vegetatie. Daarnaast toonde ik aan dat er drie stabiele evenwichten bestaan in deze graasgebieden, namelijk een gekarakteriseerd door meerjarige grassen, een ander door eenjarige grassen en een derde door kale grond. De transitie tussen deze stabiele evenwichten wordt sterk beïnvloed door de vegetatiebedekking en de dynamiek van de zaadbank, onder invloed van verschillen in zaaddichtheid, kiemingspercentages en overleving van deze grassen (hoofdstuk 7).

Ik stel me op het standpunt dat het herstel van overblijvende grassen van de zaadbank in de bodem in zwaar begraasde gebieden in halfdroge Afrikaanse graasgebieden niet succesvol kan plaatsvinden zonder een externe bron van zaden van overblijvende grassen en zonder bescherming van de jonge planten tegen vertrapping en begrazing. Daarom hangt het behoud van soorten en het behoud van biodiversiteit in halfdroge graasgebieden af van de vestiging en overleving van kiemplanten van eenjarige soorten en van vegetatieve reproductie van overblijvende grassen en houtachtige soorten. Deze bevindingen hebben belangrijke implicaties voor het beheer, behoud en herstel van halfdroge Afrikaanse graasgebieden.



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## **Affiliations of co-authors**

Robert M.T. Baars, Larenstein University of Applied Sciences, Wagenigen University,  
Droeveendaalsesteeg 2, 6708 GA, Wageningen, The Netherlands.

Willem F. de Boer, Resource Ecology Group, Wageningen University, PO Box 47, 6700AA  
Wageningen, The Netherlands

Tessema Zewdu Kelkay, Resource Ecology Group, Wageningen University, PO Box 47,  
6700AA Wageningen, The Netherlands and School of Animal and Range Sciences, Haramaya  
University, PO Box 138, Dire Dawa, Ethiopia

Frank van Langevelde, Resource Ecology Group, Wageningen University, PO Box 47,  
6700AA Wageningen, The Netherlands

Herbert H.T. Prins, Resource Ecology Group, Wageningen University, PO Box 47, 6700AA  
Wageningen, The Netherlands



## Curriculum Vitae



Tessema Zewdu Kelkay was born on 19 March 1969 in Gondar, Ethiopia. After his high school, he joined the Alemaya University of Agriculture in 1988 to study Agriculture, specializing in Animal Sciences, which was completed in 1991 with BSc degree. After graduation, Tessema started his career at the Adet Agricultural Research Centre, the Ethiopian Institute of Agricultural Research (EIAR), as a researcher in the Department of Animal Feeds and Nutrition Research in 1992. He served as a Head of the Department of Animal Feeds and Nutrition Research from 1992-1998 and 2001-2002. During this time, Tessema has conducted several research projects in Forage and Pasture Crops breeding, agronomy, nutrition, food and forage crops integration, natural pasture assessment and improvement, as well as farming systems in different parts of Ethiopia. In 1999, Tessema enrolled at the Alemaya University of Ethiopia for his MSc degree in Animal Production (Pasture management), which was completed in 2000. He did his MSc thesis research on “Productivity and nutritional quality of Elephant grass (*Pennisetum purpureum* (L. Schumach.) as influenced by height of harvesting and different sources of fertilizer application” under the supervision of Dr. Robert M.T. Baars, Van Hall Larenstein University of Applied Sciences, Wageningen University of the Netherlands and Associate Prof. dr. Alemu Yami, Ethiopian Institute of Agricultural Research. After his MSc degree, Tessema was employed as a lecturer in the Department of Animal Sciences at Haramaya University (the then Alemaya University) of Ethiopia. Tessema has been worked as an assistant professor in the Department of Animal Sciences at Haramaya University of Ethiopia from April 2006 until he joined Wageningen University of The Netherlands for his PhD study in December 2007. Tessema has been teaching different courses for undergraduate and MSc students. Moreover, he has supervised several MSc thesis research in Range Ecology and Management, Animal Production and Animal Nutrition at Haramaya University. From this onwards, Tessema has developed a research interest working in rangeland evaluation, management and restoration in semi-arid areas under the influence of various biotic and abiotic factors. Furthermore, Tessema has served in various positions at Haramaya University of Ethiopia in his best capacity as Head of the Department of Animal Sciences (2003-2006), member of the Council of Graduate Studies of Haramaya University (2003-2006), member of the Academic Commission of the College of Agriculture (2003-2006) and Chairman of the Graduate Committee of the Department of Animal Sciences at Haramaya University of Ethiopia (2003 – 2006).

In December 2007, Tessema joined the Resource Ecology Group at Wageningen University and Research (WUR) in The Netherlands to study his Doctor of Philosophy (PhD) degree under the supervision of Prof. Dr. Herbert H.T. Prins and co-supervision of Dr. Willem F. de Boer and Dr. Robert M.T. Baars. His PhD thesis focuses on the **“RECOVERY OF RANGELANDS: The Functioning of Soil Seed Banks in a Semi-arid African Savanna”**, through investigating the mechanisms how grazing pressure affects both the aboveground vegetation dynamics and availability of persistent viable seeds (seedling density), species diversity and functional groups in the soil seeds banks, as well as the germination ecology of grass species, in a typical semi-arid African rangelands, with particular emphasis on Ethiopia. Tessema completed his PhD study in October 2011 and the result of his research conducted is included in this thesis.

Tessema has conducted different research projects in relation to the management of improved pasture and rangelands in semi-arid parts of Ethiopia and he published more than 60 papers in different journals, conference proceedings, chapter(s) in a book and one book as a sole author. Moreover, Tessema is a member of different professional societies such as International Rangeland Society (2011), The Grassland Society of Southern Africa (2010 and 2011), The Ethiopian Society of Animal Production (since 1993), The Agronomy and Crop Physiology Society of Ethiopia (since 1995), The Crop Science Society of Ethiopia (since 1993), The Netherlands Ecological Research Network (2008-2010) and The Association for Tropical Biology and Conservation (2010 and 2011-student member). Last but not least, Tessema has participated in several national and international conferences, workshops and symposia in his field of profession.



## List of Publications

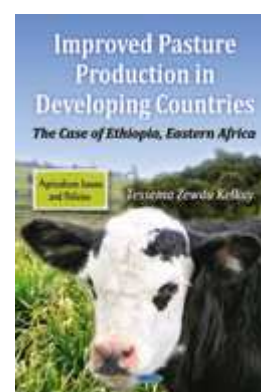
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## PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC), which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



### Review of literature (5.6 ECTS)

- Soil seed bank dynamics in semi-arid rangeland ecosystems (2008)

### Writing of project proposal (7 ECTS)

- The role of soil seed banks in herbaceous vegetation recovery in semi-arid savanna grazing systems (2008)

### Post-graduate courses (9.6 ECTS)

- Advanced statistics; PE&RC (2008)
- Long term dynamics of food and human development; PE&RC (2008)
- Biodiversity and ecosystem services in a sustainable world; PE&RC (2008)
- Consumer resource interactions: danger, disease and density-dependence; PE&RC and SENSE (2010)
- Multivariate analysis; PE&RC (2008)
- Survival analysis; PE&RC (2009)

### Laboratory training and working visits (1.5 ECTS)

- ArcGIS 9.3 software training; Larenstein University of Applied Sciences, Netherlands and Haramaya University, Ethiopia (2009)

### Invited review of (unpublished) journal (7 ECTS)

- Animal nutrition; South African Journal of Animal Science (2008)
- Rangelands, pasture & apiculture; East African Journal of Sciences (2009)
- Improved pasture management; Grassland Science (2010)

### Deficiency, refresh, brush-up courses (2.8 ECTS)

- Ecological methods I; REG (2008)

### Competence strengthening / skills courses (3.5 ECTS)

- Scientific writing; WGS (2010)
- Communication in interdisciplinary research methods; WGS (2008)
- Information literacy, including endnote; WGS (2008)

### PE&RC Annual meetings, seminars and the PE&RC weekend (2.7 ECTS)

- PE&RC Day: biodiversity challenge (2008)
- PE&RC Weekend (2008)
- Farming futures in sub-Saharan Africa (2008)
- Biodiversity workshop (2009)
- Symposium of the 92th Dies Natalis of Wageningen University: a world in transition (2010)

- Mini-symposium on spectro-directional sensing of vegetation (2010)
- How to write a world-class paper (2011)

#### **Discussion groups / local seminars / other scientific meetings (6.3 ECTS)**

- Ecological Theory and Application; PE&RC discussion group (2008, 2010 & 2011)
- The 16<sup>th</sup> annual conference of the Ethiopian Society of Animal Production (2008)
- The 17<sup>th</sup> annual conference of the Ethiopian Society of Animal Production (2009)
- Multi-Stakeholder Workshop on Farmers Entrepreneurship in Ethiopia, Addis Ababa, Ethiopia (2009)

#### **International symposia, workshops and conferences (10 ECTS)**

- The Netherlands Ecological Research Network annual meeting (2008)
- The Netherlands Ecological Research Network annual meeting (2010)
- The 45<sup>th</sup> annual Grassland Society of South Africa (GSSA) Congress: Sustainable and Adaptive Practices in Range and Pasture Systems, with an Emphasis on Arid Regions; Kimberley, Northern Cape, South Africa; poster presentation (2010)
- The 5<sup>th</sup> conference of the All African Society of Animal Production (AASAPP and the 18<sup>th</sup> Ethiopian Society of Animal Production (ESAP); United Nation Conference Centre; Addis Ababa, Ethiopia; oral and poster presentation (2010)
- The IX International Rangeland Congress: Diverse Rangelands for a Sustainable Society; Rosario, Argentina; oral presentation (2011)

#### **Lecturing / supervision of practical's / tutorials (6 ECTS)**

- Range and forage production and management; 10 days (2008)
- Feed resources development and management; 10 days (2008)

#### **Supervision of 12 MSc students; 30 days per six months (36 ECTS)**

- Rangeland degradation and livelihood vulnerability among pastoralists
- Rangeland resource utilization and condition assessment
- Spatial variation in range dynamics in relation to *Prosopis juliflora* invasion
- Range condition, biomass production and plant biodiversity of the rangelands
- Pastoralists perception towards range resource utilization and range condition assessment
- Natural pasture condition, utilization practice and improvement methods
- Indigenous conflict management and resolution mechanisms in relation to range resources utilization
- Effect of nitrogen fertilizer and harvesting stage on yield and quality of natural pasture
- Stubble height and defoliation frequency on growth dynamics, yield and chemical composition of Napier grass (*Pennisetum purpureum* Schumach L.)
- Supplementation of Greenleaf Desmodium or Lablab to Napier grass on feed intake, digestibility and live-weight change of sheep
- Efficiency of livestock feed resources utilization and forage development
- Tree crown density in vegetation productivity, plant functional type composition and other selected ecosystem parameters in relation to grazing.