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Soil seed bank dynamics under the influence of grazing as alternative explanation for herbaceous vegetation transitions in semi-arid rangelands

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ABSTRACT

Ecological studies have frequently stressed that the availability of seeds in the soil is important for the recovery of semi-arid rangelands. However, the crucial role of soil seed banks has not been incorporated into rangeland models to understand vegetation states and transitions in semi-arid rangelands. We developed and evaluated a novel model to show that the availability of seeds in the soil seed banks as a function of plant cover can trigger transitions from perennial to annual grasses and from annual grasses to bare soil with increasing grazing pressure. The model indicates that when grazing pressure is low, a high cover of perennial grasses and a large soil seed bank of these grasses may be present, whereas annual grasses with their seeds in the soil appear with increasing grazing. When grazing pressure further increases, vegetation cover and the soil seed bank size decline. We found that the positive feedback between plant cover and the size of the soil seed bank depends on seed traits, i.e., longevity and germination rate. This positive feedback is an alternative explanation for a sudden vegetation changes in rangelands, which are often explained by the positive feedback between plant cover and the infiltration rate of rain into the soil. In contrast to this latter positive feedback, our model can explain shifts in vegetation from perennials to annuals and vice versa on different soil types, which are often seen in semi-arid rangelands. Our model contributes therefore to the understanding of vegetation dynamics for the proper management and possible restoration of degraded semi-arid rangelands.

1. Introduction

Semi-arid rangelands 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 fire (Rietkerk et al., 1996; Van Langevelde et al., 2003). Semi-arid rangelands can therefore be described by state-and-transition models (Noy-Meir, 1975; Westoby et al., 1989; Rietkerk et al., 1996; Bestelmeyer et al., 2003; Briske et al., 2005). A bush encroached state of these rangelands, 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 (Roques et al., 2001; Ward, 2005). 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 cover of annual grasses, absence of perennial grasses, and bare soil (Westoby et al., 1989). Tessema et al., (2011, 2012) studied these two states and the transitions between them under the influence of grazing for semi-arid rangelands in Ethiopia: the state with perennial grass cover was found in sites with low grazing pressure, whereas the state with annual grasses and bare ground was found in sites with heavy grazing.

In semi-arid African rangelands, it has been found that intensive grazing has indeed resulted in a rapid species turn-over, reducing forage availability and forage quality to livestock (Kumar et al., 2002; Abule et al., 2005; Augustine and McNaughton, 2006; Tessema et al., 2011). Previous models showed the transitions of semi-arid rangelands due to grazing by using the relationship between water infiltration in the soil and plant cover (Rietkerk and Van de Koppel, 1997; Rietkerk et al., 2002). A reduction of aboveground biomass due to heavy grazing leads to a reduction of infiltration of rain into the soil that results in locally lower soil water availability, and consequently in reduced plant growth. However, these models do not explain the co-occurrence of annual grasses

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Table 1
List of the used parameters and variables, their interpretation, units, estimated values and literature sources.

	Interpretation	*Units*	*Values*	Sources
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	O'Connor and Pickett (1992), Tessema (2011), Vogler and Bahnisch (2006)
S_a	Availability of seeds of annual grass in the soil	m^{-2}	0–5000	Veenendaal (1991), Veenendaal et al. (1996a)
R	Water availability in the soil	$mm\,t^{-1}$	0–500	
c_p	Rate of increase in perennial grass cover due to seed germination	m^2	0.01	
c_{am}	Maximal rate of increase in annual grass cover due to seed germination when light is not limiting	m^2	0.001	
g_p g_a	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 (2011) at 500 mm rainfall per year
l_p l_a	Decrease of grass cover, for example due to death	t^{-1}	$l_p = 0.6$ and $l_a = 0.7$	
$b_p b_a$	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	
$s_{pm} s_{am}$	Maximum amount of seeds produced when plant cover is maximal	$m^{-2}\,t^{-1}$	$s_{pm} = 2200$ and $s_{am} = 30{,}000$	Veenendaal (1991), Veenendaal et al. (1996a), Vogler and Bahnisch (2006)
s_{p0} s_{a0}	Fraction of amount of the maximum amount of seeds in the seed bank due to dispersal	–	$s_{p0} = 0.2$ and $s_{a0} = 0.4$	
k_p k_a	Plant cover where the rate of seed production is half of its maximum	–	$k_p = k_a = 0.1$	
l_{sp} l_{sa}	Specific loss rate of seeds	t^{-1}	$l_{sp} = 0.7$ and $l_{sa} = 0.4$	Tessema (2011) 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	

and perennial grasses with bare soil as they only recognize the occurrence of a vegetated state alternating with bare areas. Infiltration of rain into the soil is indeed found to increase with the cover of perennials, whereas annual grasses hardly increase infiltration into the soil (Rietkerk et al., 2000). Hence, the relationship between plant cover and infiltration may be not a good mechanism to explain the transitions from perennials to annuals and from annuals to bare soil. Moreover, the feedback between plant cover and infiltration is assumed to be present on clay soils where excessive rainfall can cause crust formation (Rietkerk and Van de Koppel, 1997), whereas shifts from perennials to annuals are also found on sandy soils (Tessema et al., 2011, 2012).

A number of models of grazing lands, from savanna, grasslands to pastures, have been developed (Oomen et al., 2016). The models so far developed for semi-arid grazing systems do not explicitly include the source of recovery of grasses after they have (locally) disappeared. However, ecological studies have frequently stressed that the availability of seeds in the soil is important for the recovery of semi-arid rangelands, since the soil seed banks can serve as a buffer mechanism (Leck et al., 1989), as for example, perennial grasses after their disappearance can re-establish bare areas from their seeds in the soil (De Villers et al., 2003; Scott et al., 2010). Moreover, the importance of soil seed banks has also been frequently discussed in restoration efforts (Suding et al., 2004; Van den Berg and Kellner, 2005), but identifying the presence of annual and perennial grass seeds in the soil seed banks becomes critical in semi-arid rangelands (Müller et al., 2007; Cipriotti et al., 2012). Besides differences in seed production, seed traits like seed longevity and germination rates may determine the transition from one state to another in semi-arid rangelands (O'Connor, 1991; Pons, 1991; Sternberg et al., 2003).

Annual grass species have generally a lower germination rate than perennials (McIvor and Howden, 2000; Tessema, 2011). 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, 2011). The recovery of degraded semi-arid rangelands and the transition from one state to another are therefore thought to be determined by the intensity of grazing (Noy-Meir, 1975; Westoby et al., 1989; Stafford Smith et al., 2007) and the availability of seeds in the soil (Leck et al., 1989; De Villers et al., 2003). The crucial role of the soil seed bank for system shifts is known by rangeland ecologists but has not been incorporated into rangeland models. Therefore, we developed a model indicating that the availability of seeds in the soil seed bank as a function of plant cover can trigger transitions between three vegetation states such as from perennial to annual grasses and from annual grasses to bare soil with increasing grazing pressure, which is determined