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Species, functional groups and community structure in seed banks of the arid Nama Karoo: Grazing impacts and implications for rangeland restoration

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ABSTRACT

The regeneration potential of grazing-affected Nama Karoo vegetation was evaluated by comparing soil seed banks of different microsites across a fence-line contrast in arid Namibia. Seed banks under low and high grazing pressure reflected the condition of the standing vegetation in terms of composition, community structure and species abundance distributions. However, a close concordance between vegetation and seed bank was restricted to the herbaceous and grassy vegetation within the inter-shrub matrix.

The divergence of seed bank communities across the fence-line was low at community level but high at the level of species abundances. Continuous severe grazing increased the abundance of small-seeded, prostrate forbs with round seeds and favored unpalatable, annual grasses over palatable, perennial grasses. Microsites provided a source of small-scale variation in seed bank community composition and were dissimilar between the rangelands.

Results indicated an advanced divergence in the vegetation at the degraded site with seed banks of species common under sustainable grazing being drastically reduced. Their low abundance, even in safe sites, suggests that long-distance dispersal is one of the main limiting factors for natural re-establishment after disturbance. The inertia in recovery of Namibian degraded rangelands through seed limitation can be overcome only by active species introduction.

1. Introduction

The combination of heavy grazing and a highly variable climate has contributed to extensive environmental problems throughout southern Africa (Darkoh, 2009). In the arid Karoo, representing a significant proportion of the western part of South Africa and southern Namibia, degradation processes have been evident since the colonial occupation and the associated decrease of nomadic grazing and increase of livestock numbers in permanent settlements (Dean et al., 1995a). The reversibility of vegetation change is an important issue in these rangelands and a challenging task for land managers and restoration practitioners. There is a large body of literature on the dynamics and sustainable utilization of Karoo ecosystems (e.g. Beukes et al., 2002; Snyman, 1998; Todd and Hoffman, 2009) and the assessment of land degradation and restoration attempts (e.g. Dean et al., 1995b; Simons and Allsopp, 2007; Visser et al., 2004). However, the literature is dominated by studies focusing on aboveground assessments, often neglecting the role that soil seed banks play in ecosystem resistance and resilience. The assessment of soil seed banks is widely accepted as a valuable tool to evaluate the condition and restoration potential of African rangelands (Jones and Esler, 2004; Kassahun et al., 2009; Snyman, 2004; Solomon et al., 2006) but to date regional studies from the arid south-western zone of Africa have overlooked this aspect for the most part. Thus, soil seed bank studies constitute a large gap in rangeland knowledge, particularly in the summer rainfall portion of the Karoo constituting the Nama Karoo Biome.

The effects of grazing on the structure of soil seed banks involve quantitative and compositional shifts of species and functional groups and changes in the relative importance of species-specific regeneration strategies (Aboling et al., 2008; Kinloch and Friedel, 2005a; Sternberg et al., 2003). These changes have important implications for the long-term sustainability of the rangeland with regard to the maintenance of regeneration capacity of vegetation, recovery potential of valuable fodder species and reversibility of community shifts. Cohorts of persistent seeds are able to stabilize populations through buffering disturbance effects by allowing for recruitment of suppressed species under favorable conditions. However, in the long-term, continuous disturbance (e.g. overgrazing) can lead to local extinction of plant species (O'Connor, 1991), and can result in almost irreversible changes in vegetation, whereby a return to previous conditions from the soil seed bank is prevented (Dutoit and Alard, 1995; Kinloch and Friedel, 2005a;

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Meissner and Facelli, 1999). Therefore, a key factor in sustainable resource management is resting, which might be more important than the way rangelands are utilized (Snyman, 1998). Nama Karoo rangelands can easily deteriorate if stocking rates do not accommodate the unpredictability of the seasonal climate. Many farmers apply a rotational grazing regime, which provides resting periods for the vegetation to recover and increases ecosystem resilience (Beukes et al., 2002; Domptail et al., 2010). Resting these rangelands in the wet season proved to be most effective (Müller et al., 2007), allowing plants to germinate, establish, flower and/or replenish the soil seed bank (Esler, 1999; O'Connor, 1991). However, such adapted management strategies rely on multi-camp grazing systems, which are common on privately owned, commercially farmed land, but absent in communal, open-access areas. This has contributed to widespread land degradation in the former homelands of Namibia (Klintenberg and Seely, 2004).

Comparative assessments of vegetation condition between adjacent communal and commercial farmlands in Namibia revealed changes in plant species composition, cover, diversity and production as a result of contrasting grazing regimes (Domptail et al., 2010; Kuiper and Meadows, 2002; Ward et al., 2000). Observed vegetation recovery in apparently deteriorated systems after good rainfall was seen as evidence for a high resilience of arid ecosystems in Namibia to heavy grazing pressure (Kuiper and Meadows, 2002; Ward et al., 1998). However, apparent vegetation recovery is also displayed by overgrazed, persistent vegetation assemblages with seed banks dominated by grazing-adapted annuals. Visual inspections are unable to provide adequate information on the nature of rangeland deterioration, i.e. whether it is permanent or short-term, and thus reversible, as they focus solely on structural properties (*sensu* López et al., 2011) of the ecosystem. Functional indicators related to recruitment processes, such as local seed reserves of key species, are necessary to estimate ecosystem resilience and to detect negative transitions in rangeland condition, which could cross a threshold beyond which active interventions becomes indispensable for rangeland improvement (Briske et al., 2008; López et al., 2011). We addressed the issue of soil seed banks as an indicator of rangeland condition and regeneration potential using a stable fence-line contrast between a highly degraded communal rangeland and an adjacent reference site in the arid Namibian Nama Karoo. As reviewed in Domptail et al. (2010), preceding investigations at the study sites provide interdisciplinary evidence for profound impacts on soils, hydrological processes, standing vegetation, and the local fauna that have been ascribed to continuous overstocking of the communal rangeland. Our study contributes to a more comprehensive understanding of the effects of unsustainable farming in arid Namibia by analyzing, for the first time, how high grazing pressure becomes manifested in soil seed banks.

The current study's aims were twofold. First, the objective was to determine the differential response of species and their abundances to contrasting grazing regimes, i.e. the magnitude of divergence of seed bank communities across the fence-line and its linkage to the standing vegetation. The following hypothesis was tested: long-term severe and continuous grazing has altered the community structure of the soil seed bank with directional selection being evident at the level of species, functional groups and regenerative traits, and, consequently, grazing-resistant annuals are favored leading to a higher similarity between vegetation and seed bank communities under high grazing pressure. Second, the study aimed to evaluate the capacity of current seed reserves of different microsites to contribute to an improvement of the degraded rangeland. As shrubs are known to function as effective seed traps and to provide safe sites for seedling establishment, the understorey seed bank composition can be expected to be more similar to communities of the non-degraded site than the composition of seed pools of the exposed inter-shrub matrix.

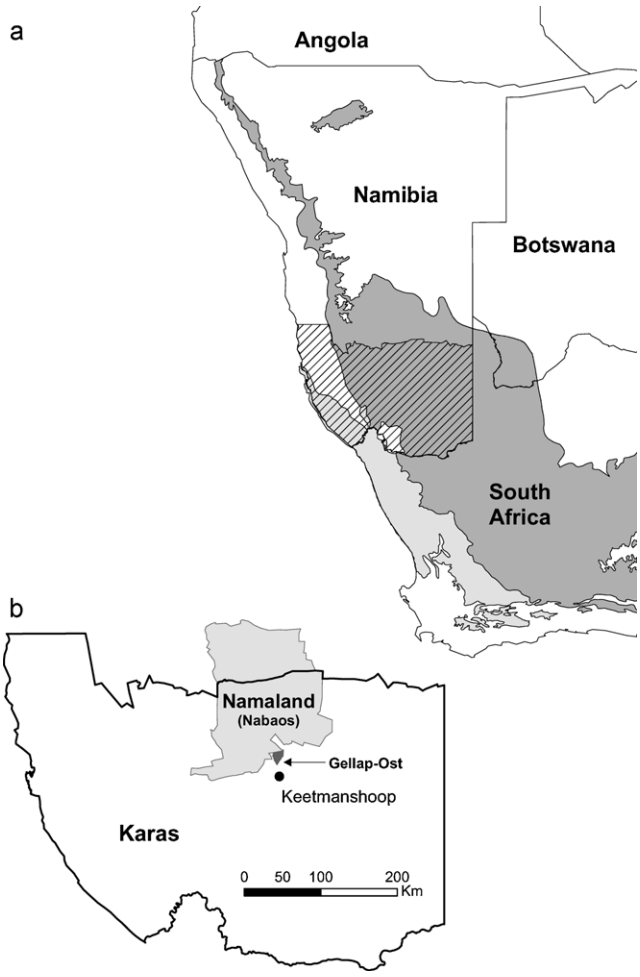

Fig. 1. (A) Geographic extent of the Karoo in south-western Africa including the summer-rainfall Nama Karoo Biome (dark gray) and the winter-rainfall Succulent Karoo Biome (light gray), and (B) location of the study sites in the Karas region of Namibia.

2. Materials and methods

2.1. Description of the study sites

The study was carried out in Nama Karoo rangelands situated in the central Karas region of southern Namibia (Fig. 1). Climate is arid with an average annual summer rainfall of 150 mm and an inter-annual coefficient of variation of 70–80%. The average annual water deficit, expressed as the difference between rainfall and rate of evaporation, exceeds 2 500 mm. Average maximum temperatures range from 34 to 36 °C in January, minimum temperatures from 4 to 6 °C in July (Mendelsohn et al., 2002). The area falls within the Namibian agro-ecological zone CPL7, which is characterized by an unreliable growing period, low biomass production and suitability for small stock farming only (Domptail et al., 2010). The adjacent study sites were located about 20 km north of the town of Keetmanshoop in two Biodiversity Observatories of the BIOTA Southern Africa project (26°24.0717′S, 18°1.2905′E, 1 100 m a.s.l.). One site was situated in a 261 ha camp of the state research farm Gellap-Ost (Fig. 1), which has a history of sustainable grazing, with mainly sheep, for several decades. Due to a sophisticated management strategy, including rotational grazing and rangeland monitoring, low stocking densities, as well as the absence of eco-