Feature

Longevity of grass seeds in a semi-arid grassland

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Introduction

The soil seed bank plays an important role in the composition of different plant communities and thus in their conservation (Bekker *et al.* 1997). In arid and semi-arid grasslands, seed rain events are primarily driven by episodic events and secondarily by continuous trigger events such as rainfall and fire (Page and Harrington 2009). The composition of the seed bank depends on the production and composition of the present and previous communities as well as on the longevity of the seeds of each species under local conditions (Bekker *et al.* 1997; Thompson and Grime 1997).

The understanding of the function and dynamics of seed banks has become a great challenge to ecologists working in plant communities, as this understanding is necessary to determine the role of this community in ecosystem functioning and to improve the integrated management of ecosystems (Kinloch and Friedel 2005; Snyman 2009). A complete set of topics on seed banks such as the effects of environmental factors on seed bank dynamics (Baskin and Baskin 1989; Page and Harrington 2009), the spatial distribution of seeds in soil (Shaukat and Siddiqui 2004), seed persistence in soil (Luzuriaga *et al.* 2005) and the resemblance between seed species composition and the aboveground vegetation (Page and Harrington 2009) have been described. Unfortunately, there are only a few studies about the regenerative potential of seed banks (Luzuriaga *et al.* 2005), the longevity of the seeds of each species under specific climatic conditions and the quantification of seed rain in arid and semi-arid areas. This study aimed to evaluate the recruitment of grass species from the seed bank after different types of disturbance in a semi-arid grassland. The longevity of the seeds of each species under local conditions was also quantified over five seasons (2002/03 to 2006/07).

Materials and methods

The study was conducted at Bloemfontein (28^o 50'S, 26^o 15'E, altitude 1 350 m), situated in the semi-arid, summer rainfall region (mean annual rainfall 560 mm) of South Africa. Mean maximum monthly temperatures range from 17^o C in July to 33^o C in January, with a mean of 119 frost days per annum.

Grassland in good ecological condition, typical of the Bloemfontein Dry Grassland (Mucina and Rutherford 2006) in the Grassland Biome (Bredenkamp and Van Rooyen 1996) was selected for this study. The botanical composition and basal cover of the grassland in good condition was typical of that on commercial farms in the area and described in detail by Snyman (2000). The soil is a fine sandy loam of the Bloemdal form (Roodeplaat family – 3 200; Soil Classification Working Group 1991). Clay content increases with soil depth from 10% in the A-horizon (0-300 mm), to 24% in the B2-horizon (300-600 mm) and 42% in the B2-horizon (500-1 200 mm).

The research was conducted on 6 plots of 10 m x 10 m each, with a buffer zone of 5 m around each plot. The clipping treatment were clipping with and without seed removal- seed production or seed rain. The seed culms were often removed by cutting, over the growing season, as soon as the growing points began lengthening so that the seeds of the grasses never ripened. Therefore, no seed production or seed rain took place. This treatment was applied to determine the longevity of seeds in this semi-arid climate. In the control treatment, the grasses were allowed to seed and the seed to ripen and fall on the ground as seed rain. The treatments were allocated randomly to the plots with three replications for each treatment.

This research was conducted over five growing seasons (2002/03 to 2006/07). To determine the botanical composition of the field before applying the treatments, a bridge-point apparatus was used. Five hundred points (nearest plant) were recorded per plot. When the species were classified, the ecological status (Decreaser and Increaser species), as defined by Foran et al. (1978), was taken into consideration. The classification of dry *Themeda-Cymbopogon* grassland into different ecological groups as described by Fourie and Visagie (1985) was used.

A soil seed bank is defined as a collection of seeds, at or beneath the soil surface, which are capable of germination. Soil samples were collected randomly in eight blocks (0.5 x 0.5 m each) in every treatment to a depth of 50 mm at the end of every third month. Only the soil between the tufts was sampled up to the base of every tuft. Samples were collected into separate paper bags for immediate transport to the greenhouse for processing within 10 min of collection. In the greenhouse, soil samples were spread evenly in plastic containers (0.5 x 0.5 m) containing a 100-mm deep layer of Hygiotech growth medium (Canadian peat, polystyrene vermiculite and mono-ammonium phosphate). To measure the extent of contamination, eight additional plastic containers filled with autoclave-sterilised soil (90° C for 1 h, repeated three times over a week) were included with each set of soil samples. Seedling plastic containers were placed at random in the greenhouse. Containers were hand-watered daily, after which the seedlings were identified and counted daily over a two-month period. All identifiable seedlings were removed. Seedlings that could not be identified after two months were potted individually and grown until identification could be made. The soil medium ensured that the plants that germinated could reach a stage where they could be identified before dying down. Respective day and night temperatures of 25–30° C and 15–18° C were maintained in the greenhouse to simulate grassland conditions.

The seed bank was investigated at the beginning of October (before the new seed set), at the beginning of January (after the first seed production event) and at the beginning of April (after the second seed production event). The phenological pattern of the vegetation in the study area is characterised by these two seed setting periods every season under normal rainfall conditions. The October soil sampling, after seasonal germination had occurred and before the first spring rainfall, therefore represented the size of the persistent or potentially germinable seed bank.

Seedlings that germinated in the field in response to sufficient rainfall over the specific periods were counted over the growing seasons. This was accomplished by randomly distributing ten quadrates (0.5 x 0.5 m each) per treatment. Unfortunately, the survival of the identified seedlings was not monitored: only their emergence.

Within-year and between-year data were analysed separately. For seedling density, sub-sampling was employed where data were averaged across quadrats within plots and then analysed among treatments and sample periods. Tukey's procedure for comparison of means was applied. The Number Cruncher Statistical System (2000) software package was mainly used. Similarity between seed bank and field vegetation was tested using Sorensen's similarity index (Greig-Smith 1983).

Results

Botanical composition in field

The field's botanical composition was dominated by *Themeda triandra,* which constituted 81% of the species composition. Only 4% of the species was Increaser type II(c). This botanical composition clearly showed that the field was in a good condition at the onset of the study. Interestingly, no forbs occurred in the field. A full analysis of the species frequency can be found in Snyman (2000). Botanical composition did not vary much over the five seasons.

Seed bank germination in the greenhouse

Four days after inception of the germination study in the greenhouse, the first seedlings emerged, mostly *Eragrostis* seedlings. After seven days, most seedlings of the other grass species also emerged. Within three weeks no further seedlings emerged, although observations were still carried out for a further six weeks to identify all seedlings.

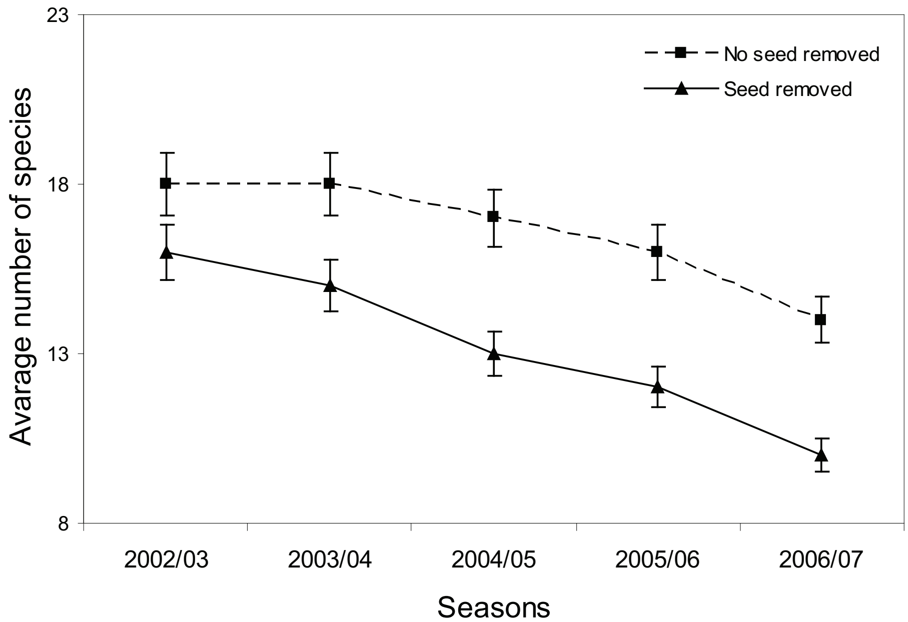
On average throughout the study period, the seedling densities of the species *Digitaria eriantha, Eragrostis chloromelas, E. superba, E. lehmanniana* and *Sporobolus fimbriatus* were similar in the seed bank, regardless of treatment applied or time of year the seed was gathered. In contrast, the seedlings of *Cymbopogon pospischilii, Panicum stapfianum* and *Triraphis andropogonoides* emerged in the seed bank only with the spring (October) soil collection. The seed of *Eragrostis plana* only germinated when the soil was collected in January, while *Agrostis lachnantha, E. obtusa* and *Elionurus muticus* only germinated with the April soil collections, over the trial period. On average over the growing seasons and regardless of treatment applied, *Themeda triandra* only germinated in the spring and autumn and not at all in the middle of the season (January). The rest of the grass species did not exhibit a clear germination pattern over the season and were also influenced to a greater or lesser extent by the different treatments. The seedling emergence of forbs and weeds was best in the autumn and poor in October.

After only four years of removing seed, no further seedling emergence of the Decreaser species (*Digitaria eriantha, Helictotrichon turgudulum, Panicum stapfianum, Pentaschistis setifolium, Sporobolus fimbriatus* and *Themeda triandra*) occurred in the seed bank and field. This cessation in seedling emergence was a marked ($p < 0.01$) occurrence as the previous season (2004/05) was characterised by seedling emergence in the seed bank in all the Decreaser species. This tendency only occurred among the Decreaser species, while the Increaser species showed almost the same germination after four years of seed removal, compared with the treatment where no seed was removed. Among the Increaser species, especially *Cymbopogon pospischilii, Eragrostis lehmanniana, E. plana* and *Heteropogon contortus* had almost no seedling emergence after four years of seed removal. Notably, the germination of *E. chloromelas* was not at all influenced by seed removal after four years and this still had a high seed presence in the seed bank. This same trend was repeated the next year. The emergence of the forb seedlings were also not significantly influenced after four years of grass seed removal. *Aristida congesta, Tragus koelerioides, Elionurus muticus* and *Bromus catharticus* are the only species emerging in the seed bank after four years of seed removal, but were not found where the seed was not removed.

The species *Digitaria argyrograpta, Setaria sphacelata var. sphacelata, Lycium tenue* and *Walafrida saxatilis* (4/27 species) only occurred in the field and never in the soil seed bank over the five years. Those species only occurring in the seed bank over the 5 years, but not in the field, included *Helictotrichon turgidulum, Panicum stapfianum, Pentaschistis setifolium, E. lehmanniana, E. superba, E. plana, Agrostis lachnantha, E. gummiflua, Cynodon dactylon, C. hirsutus, Elionurus muticus, Bromus catharticus* and *Eleusine coracana* (13/27 species). The forb species were not accounted for in the above species richness.

The species richness significantly ($P < 0.01$) declined for both seed removal and absence of seed removal for the last four years of applying the treatments (Figure 1). Notably, where the seed was removed over the five years, the species richness was significantly ($P < 0.01$) lower for all the years than in plots where it was not removed.

Figure 1: Species richness (mean number of species) for the clipping treatment for the 2002/03 to 2006/07 growing seasons. Error bars are the standard error of means (n = 3), where they are significantly different (P <0 .01). LSD0.01 = 1.3.



Vegetation similarity between seed bank and aboveground (field)

In the perennial grassland (field) before disturbance, relatively low similarity was detected between species composition in the vegetation and in the seed bank for both treatments (Table 1). Considering the abundance of each species, vegetation was mainly dominated by perennial grasses whereas the seed bank was dominated by early succession grasses and forbs. The similarity index decreased from the first to the fifth season where seed was removed from an average of 64.28 to 35.71.

Table 1: Similarity in grass flora between seed bank and aboveground vegetation (field) by calculation of the Sorensen's similarity index for the 2005/06 season.

No seed removal	Seed removal
60.24	35.71

Seed bank size

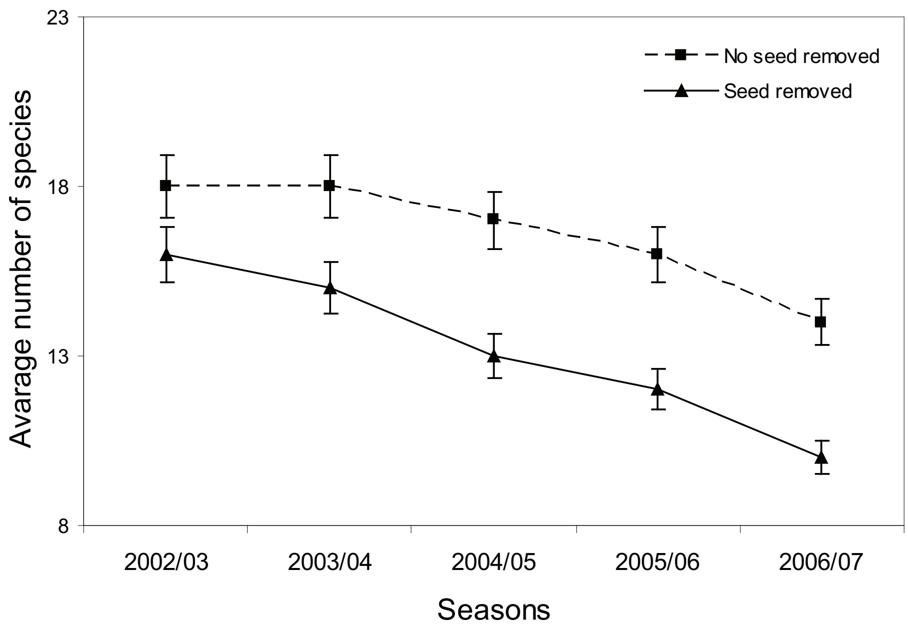
As expected, where the seed was removed a significant ($P < 0.01$) decrease in seedling density occurred in the seed bank, compared with where the grasses could produce seed undisturbed for all five seasons (Table 2). In general, the seedling density of the January soil collection was the highest, with that of October the lowest. The impact of seed removal was severe ($P \leq 0.01$) on the seedling density for all three months.

Table 2: Mean seedling density (mean number of live seedlings m-2) obtained by the seedling emergence method from soil samples of grassland for different treatments. Soil samples were taken in October, January and April for the 2002/03 to 2006/07 growing seasons, and were germinated in the greenhouse. Data are means and standard errors. Different letters indicate significant (P <0 .01) differences among clippings.

October		January		April	
No seed removal	Seed removal	No seed removal	Seed removal	No seed removal	Seed removal
132.8a ± 10.16	86.2b ± 4.14	242.2a ± 39.12	186.8b ± 21.20	128.8a ± 20.14	79.4b ± 6.26

The 2002/03 growing season was preceded by a season of well above average long-term rainfall (54% more), which could have been responsible for the favourable seedling density occurring in 2003/04 (Figure 2). The decrease in seedling density from the 2003/04 season onward, with the lowest point reached during the 2005/06 season, can largely be attributed to the extreme dry 2003/04 and 2004/05 seasons (on average 19% less than the long-term average), when the grasses could not produce large quantities of seed. The above average rainfall of the 2005/06 season, which was 30% more than the long-term average, caused the increase in seed density when the grasses could supplement the seed source in the soil seed bank. Where the seed was removed, it caused a decrease in seedling density over all the years as expected (Figure 2). Those grasses which seeded showed a variable seedling density over the five years with a very favourable seedling density in the 2003/04 growing season.

Figure 2: Mean grass seedling density (number of live seedlings m-2) for the clipping treatment for the 2002/03 to 2006/07 growing seasons. Vertical bars are standard errors of means.



Discussion

This study clearly showed that the longevity of the Decreaser grass species was very poor as after only four years of seed removal, no more seed was present in the seed bank. The results of seed removal support the contention that *Themeda triandra* is prone to failed seedling recruitment under sustained defoliation, because of elimination of the seed bank (O'Connor 1994). In contrast, *Themeda triandra* showed considerable annual seed turnover when the seed was not removed. If Decreaser grass species cannot seed for whatever reason in this semi-arid grassland, the potential of the seed bank decreases linearly until it is suddenly depleted after four years. At that time, only 11 out of 27 grass species were present in the seed bank in the field where seed was permanently removed, of which the remaining grasses were those with very small seeds. According to O'Connor (1997) *T. triandra* does not have a seed bank older than one year, which is debatable when compared with these results. In a Montana grassland of South Africa, a high predation of seeds (70-98%) and low viability (37% in 15-

month-old seeds) contributed to poor representation of T. triandra in the seed bank (<1.2%) when compared with the aboveground vegetation (<29.2%; Everson et al. 2009). These attributes, together with its poor dispersal, indicate that seed dynamics of *T. triandra* will play a limited role in the restoration of grassland in degraded areas (Everson *et al.* 2009). The availability of seed therefore depends on seed production by the established population in the preceding year (O'Connor and Pickett 1992) and also the maintenance of its viability in the seed bank over time. The paucity of seed carry-over by grasses from season to season has also been reported by Russi et al. (1992).

The *Eragrostis* species, especially *Eragrostis. chloromelas,* still had a good seedling emergence in the seed bank after four years of removing the seed from the plants. These very small seeds of the *Eragrostis* species therefore have a good survival ability. The dominance of *Eragrostis* species after four years in the seed bank is supported by studies finding that small seeds, like those of *Eragrostis spp.* dominated as they are more persistent because they can bury into the soil faster and escape predation (Snyman 2004; Fenner and Thompson 2005). According to Jones (1968) sub-climax grasses such as *Eragrostis* can yield an immense quantity of seed (up to 21 000 seeds m-2). Perennial grasses, especially the larger-seeded species, do not, in general, form persistent seed banks even in the absence of seed predation, because of poor seed survival (Williams 1983). Snyman (2004) also argued that the larger a grass seed the shorter its longevity.

The seedlings of the seed bank mainly consisted of forbs as well as early succession species, while those established in the field were more dominated by climax plants. The disturbed habitat of the greenhouse seedlings was therefore more beneficial for species with a lower ecological status. The same explosion of pioneer plants is found in practice when soil is cultivated or mechanically disturbed for the first time (Snyman 2003). Climax plant species therefore prefer a more natural and undisturbed habitat for successful establishment and survival (Snyman 2003). According to Wolfson and Tainton (1999), the relative importance of seed to the survival of *T. triandra* populations varies according to the ecological conditions of the site. Seeds of perennial grasses are usually scarce in the soil and this would explain, at least partly, the slow recovery of disturbed perennial rangelands (Snyman 2004). Not only did the Decreaser species decrease drastically after four years of seed removal, but so did the species richness.

Conclusion

This study clearly demonstrated that the composition of the seed bank depends on the composition and production of the present and previous plant communities, as well as on the longevity of the seeds of each species under local conditions. If there is a disturbance to the plant community, the seed bank might intervene in re-establishing the original community. This relationship between the composition of the seed bank and the vegetation is particularly important for the vegetation that appears under different management regimes.

References

Baskin CC and Baskin JM 1998. Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination. Academic Press, New York.

Bekker RM, Verweij GL, Smith REN, Reine R, Bakker JP and Schneider S 1997. Soil seed banks in European grasslands: does land use affect regeneration perspective. Journal of Applied Ecology 34: 1293 – 1310.

Bredenkamp G and Van Rooyen N 1996. Dry Sandy Highveld Grassland, In: Low AB and Rebelo AG (eds) Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, pp. 41.

Everson TM, Yeaton RI and Everson CS 2009. Seed dynamics of *Themeda triandra* in the Montana grasslands of South Africa. African Journal of Range and Forage Science 29: 19 - 26.

Fenner M, and Thompson K 2005. The Ecology of Seeds. Cambridge University Press, Melbourne.

Foran BD, Tainton NM and Booysen P de V 1978. The development of a method for assessing veld condition in three Grassveld types in Natal. Proceedings of the Grassland Society of Southern Africa 13: 27 – 34.

Fourie JH and Visagie AFJ 1985. Weidingswaarde en ekologiese status van grasse en karoobossies in the Vrystaatstreek. Glen Agric 14: 14 – 18.

Greig-Smith P 1983. Quantitative Plant Ecology. Butterworths, Washington.

Jones RM 1968. Seed production of species in the Highveld secondary succession. Journal of Ecology 56: 661 – 666.

Kinloch JE and Friedel MH 2005. Soil seed reserves in arid grazing lands of central Australia. Part 1: seed bank and vegetation dynamics. Journal of Arid Environments 60: 133 – 161.

Luzuriaga AL, Escudero A, Olano JM and Loidi J 2005. Regenerative of seed banks following an intense soil disturbance. Acta Oecologica 27: 57 – 66.

Mucina L and Rutherford MC 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African national Biodiversity Institute, Pretoria, South Africa.

O'Connor T.G 1994. Composition and population response of an African savanna grassland to rainfall and grazing. Journal of Applied Ecology 31: 155 – 171.

O'Connor T.G 1997. Microsite influence on seed longevity and seedling emergence of a bunch-grass (*Themeda triandra*) in a semi-arid savanna. African Journal of Range and Forage Science 14: 7 – 11.

O'Connor TG and Pickett GA 1992. The influence of grazing on seed production and seed banks of some African savanna grasslands. Journal of Applied Ecology 29: 247 – 260.

Page MJ and Harrington RA 2009. Fourteen months of seed rain in three Australian semi-arid communities. Austral Ecology 34: 294-305.

Russi L, Cocks S and Roberts EH 1992. Seed bank dynamics in a Mediterranean grassland. Journal of Applied Ecology 29: 763 – 771.

Shaukat SS and Siddiqui IA 2004. Spatial pattern analysis of seeds of an arable soil seed bank and its relationship with above ground vegetation in an arid region. Journal of Arid Environments 57: 311 – 327.

Snyman HA 2000. Soil-water utilisation and sustainability in a semi-arid grassland. Water South Africa 26: 331 – 341.

Snyman HA 2003. Revegetation of bare patches in a semi-arid rangeland of South Africa: an evaluation of various techniques. Journal of Arid Environments 55: 417 – 432.

Snyman HA 2004. Short-term response in productivity following an unplanned fire in a semi-arid rangeland of South Africa. Journal of Arid Environment 56: 265 – 185.

Snyman HA 2009. Root studies on grass species in a semi-arid South Africa along a degradation gradient. Agriculture, Ecosystems and Environment 130: 100 – 108.

Soil Classification Working Group 1991. Soil Classification: A Taxonomic System for South Africa. Pretoria, South Africa. Department of Agriculture Development. 262 pp.

Thompson K and Grime JP 1979. Seasonal variation in seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67: 893 – 921.

Williams ED 1984. Changes during 3 years in the composition of the seed bank beneath a long-term pasture as influenced by defoliation and fertilizer regime. Journal of Applied Ecology 21: 603 – 615.

Wolfson MM and Tainton NM 1999. The morphology and physiology of the major forage plants, In: Tainton NM (ed) Veld Management in South Africa. University of Natal Press, Scottsville, South Africa, pp. 54 – 90.