Short-term influence of fire in a semi-arid grassland on (6): the soil seed bank

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Introduction

In semi-arid grassland areas of southern Africa fire is a natural phenomenon (Everson 1999) and may have a negative effect on grassland functioning by the reduction or elimination of aboveground biomass (Snyman 2003a, 2004a); the reduction of belowground physical, chemical and microbial mediated processes (Neary et al. 1999; Snyman 2003b), or altering the size and composition of the soil seed bank (Skoglund 1992). Soil seed banks are important components of vegetation dynamics affecting both ecosystem resistance and resilience (Pugnaire and Lazaro 2000). A phenomenon common to many grassland communities is the flush of germination that follows a burn (Whelan 1988; Tyler 1995). In recent years there has been an escalating interest in seed banks of grassland ecosystems. Factors affecting germination and early seedling growth are often the primary determinants of the distribution of adult plants (De Jong and Klinkhamer 1988; Mustart and Cowling 1993). Therefore, to understand the dynamics of communities, specifically in drier areas, knowledge of seedling responses to different environmental conditions is often of prime importance (De Villiers et al. 2001; Kinloch and Friedel 2005a,b). In this study the influence of a head versus a back fire on the soil seed bank of a grassland in a semi-arid climate is explored. The recruitment of grass species from the soil seed bank, after different fire treatments over two growing seasons in the greenhouse is reported.

Procedure

The study was conducted at Bloemfontein (28°50'S; 26°15'E, altitude 1350 m), situated in the semi-arid, summer rainfall region (mean annual rainfall 560 mm) of South Africa. Grassland in good ecological condition, typical of the dry Sandy Highveld Grassland in the Grassland Biome 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. The soil is a fine sandy loam Rhodic Epigleyic Luvisol. Clay content increases with soil depth from 10% in the A-horizon (0 to 300 mm), to 24% in the B1-horizon (300 to 600 mm) and 42% in the B2-horizon (600 to 1200 mm).

The research was conducted on 18 plots of 10m x 10m each, with a buffer zone of 5m around every plot. This was a one-off burn. The three treatments included fire burning against the wind (back fire), with the wind (head fire) (Trollope 1978), and a control with no burning over the last 15 years. The design was fully randomised with three replications for each treatment. Six plots were burnt on 30 August 2000 and another six on 23 August 2001. The burnt plots were therefore burnt only once during the two-year trial period. The head and back fire treatments were applied on the same day to ensure that the two types of fires were comparable. The burn treatments were applied each year at the end of August after spring rainfall thoroughly wetted the soil causing the grass sward to become relatively green. Burning was carried out in the morning with a light wind blowing. To limit the fire to every burnt plot, the plants surrounding each plot were cut short and soaked before burning. The plots were excluded from any grazing over the two-year trial period. The estimation of fuel load and fuel-water content before the burning and fire behaviour was fully discussed in previous volumes of *Grassroots*.

Botanical composition before burning was determined with a bridge-point apparatus, where 500 points (nearest plant) were recorded per plot before the fire as well as four months after the fire.

The seed bank is defined as the seeds, at or beneath the soil surface, that are capable of germination. Within each treated plot, eight soil samples of 0.5m x 0.5m each, were randomly distributed and sampled to a depth of 50mm. Only the soil between the tufts was sampled, including those of the unburnt plots. Samples were collected into separate paper bags for immediate transport to the glasshouse for processing within 10 minutes of collection. In the glasshouse, soil samples were spread evenly to a depth of 50mm in plastic containers (0.5m x 0.5m) containing a 100mm deep layer of Hygrotech growth medium (Canadian peat, polystyrene vermiculite and mono-ammonium phosphate). As a control against contamination, eight additional plastic containers filled with autoclave-sterilized soil (90°C for 1 hour – repeated three times over a week) were included with each set of soil samples. Seedling plastic containers were placed at random in the glasshouse. Seedling plastic containers were hand-watered daily, after which the seedlings were counted daily over a two-month period. Any plants that could not be identified at the seedling stage were grown on until identification was possible. Seedlings that could not be identified after two months were individually potted and grown up until identification could be made. The soil medium ensured that the plants, which germinated, could reach a stage where they could be identified before dying down. The day/night temperatures in the glasshouse were kept between 25-30/15-18°C.

The seed bank was measured two weeks after the fire (middle September – before new seed set), end of December (after producing new seeds) and end of March (after sec-

Table 1 Frequency (%) of species, ecological status and veld condition score for the grassland before and four months after burning. Percentages within a row with different superscripts differ significantly (P≤ 0.01)

Ecological status	Species	Before fire	After fire
Decreaser	*Digitaria eriantha*	5.10	4.53
	Panicum stapfianum	0.20	0.02
	Sporobolus fimbriatus	3.16[a]	2.11[b]
	Themeda triandra	49.10[a]	34.54[b]
Decreaser total		**57.56**	**41.20**
Increaser II(a)	*Cymbopogon plurinodis*	4.14[a]	0.79[b]
	Digitaria argyrograpta	7.17[a]	14.12[b]
	Eragrostis chloromelas	10.16[a]	25.29[b]
	Eragrostis lehmanniana	2.92	3.15
	Eragrostis superba	1.11[a]	2.10[b]
	Heteropogon contortus	1.31[a]	3.04[b]
Increaser II(a) total		*26.81*	*48.49*
Increaser II(b)	*Eragrostis obtusa*	0.10[a]	0.02[b]
	Elionurus muticus	6.98[a]	1.94[b]
	Triraphis andropogonoides	0.02	0.02
Increaser II(b) total		*7.10*	*1.98*
Increaser II(c)	*Aristida congesta*	2.20	2.11
	Tragus koelerioides	2.33[a]	5.22[b]
Increaser II(c) total		*4.53*	*7.33*
Increaser II total		**34.44**	**57.80**
TOTAL		**100.00**	**100.00**
Veld condition score		**796.20**	**786.32**

ond seasonal seed produced), which were considered critical periods. This was conducted one and two years after burning. The study area is characterised by these two seed production peaks under normal rainfall conditions. The purpose of the different sampling dates was to collect soil seeds at different periods to allow dormancy breaking conditions to occur in the field and to sample transient (those seeds which germinate within a year of dispersal) and persistent (those seeds which remain viable in the soil until a second or later season of germination) components of the seed bank. Therefore an estimation of the between-year (persistent) and within-year (transient) seed bank was made.

Results

Botanical composition

The average species composition and grassland condition score of the experimental plots just before the fire and four months after the fire are presented in Table 1. The experimental plots were in good condition before the fire with a grassland condition count of only 13% lower than that of a benchmark site adjacent to the burnt plots (Snyman 2000). The benchmark site was especially dominated by *Themeda triandra*, which caused this difference in grassland condition to that of the experimental sites. The grassland condition score decreased by only 1.2% (P>0.05) due to the fire (Table 1).

The botanical composition did not differ much between head and back fires and is therefore presented as average in Table 1. Where the grassland was dominated by Decreaser species before the fire, the composition after the fire is dominated by a larger percentage of Increaser IIa species. The most conspicuous decrease in frequency due to the fire was the species *Themeda triandra* (30%); *Cymbopogon plurinodis* (81%); *Elionurus muticus* (72%) and *Digitaria eriantha* (11%). The species increasing with fire were *D. argyrograpta* (97%); *Eragrostis chloromelas* (149%) and *Tragus koelerioides* (124%). The fact that these species split up into many smaller tufts after the fire, could have caused an overestimation of its frequency.

Seed bank composition and size

During the soil collections at the end of December and March for the glasshouse germinations, all the grasses were dormant and most had already dropped seed. The September collection took place right after the fire and therefore no grasses had seeded yet, and scarcely had begun sprouting. Four days after starting the germination study in the greenhouse, the first grass seeds germinated. Especially *Eragrostis* species with small seeds germinated first in the soil of the unburnt grassland. After seven days most grass seeds had germinated and the soil of the burnt grassland showed the best germination of seeds. After two weeks no further germinations took place. Observations were still carried out for a further ten weeks to identify all species.

The head fire stimulated grass seedling density more ($P<0.01$) than the back fire for all months, except for September of the first season after burning (Table 2). Due to the higher intensity of the fire close to the soil surface, more seeds could possibly have been destroyed by the back fire. Generally, fire increased ($P>0.01$) seedling germination when compared to the lower number of plants/m^2 of the unburnt plots. Most germination took place at the end of the growing seasons, with the poorest germination during December (Table 2). The highest number of seedlings of 378 plants/m^2 was noted during the March germination of the first season with the head fire. Fire stimulated the grass seedling density more during the first season following the fire and was on average for both the head and back fires 50% more than during the second season following the burning. The total grass density for the first season after the fire was 485 and 142 plants/m^2 for burnt (average head and back fire) and unburnt grassland respectively, versus the 323 and 122 plants/m^2 for the second season. The grass seedling density of the unburnt plots did not differ much ($P>0.05$) over the two growing season and therefore are given as an average in Table 2.

The forb seedlings did not differ much ($P>0.05$) between the head and back fires during the first season after the fire (Table 3). The total forb seedlings germinating the first season after burning was 202.3 and 227.9 plants/m^2 respectively for burnt (average head and back fire) and unburnt grassland, compared to 259.4 and 209.9 plants/m^2 during the second season after burning. Interestingly, in both seasons, fire stimulated ($P<0.01$) seed germination during the first part of the season. In contrast, over the last half of both seasons, seedling germination was higher ($P<0.01$) on unburnt than burnt grassland. Most forb seedlings, regardless burning, germinated during December each season. Fire stimulated seedling germination of the forbs more over the second season after burning, than during the first season.

An average total for the first and second season following burning of 404 and 132 germinable grass seeds of eight and nine plant species for burnt (average for head and back fires) and unburnt grassland respectively were found in the soil cores collected. Three grass species (climax) were found in the seed bank of the unburnt grassland and not in that of burnt grassland, comparing to only two grass species (pioneer) only in the burnt and not in the unburnt grasslands seed bank. Species richness was therefore poorer with burning. All eleven plant species present in the seed bank were also present in the vegetation of the field. In contrast six species were present only in the vegetation in the field (Table 1)

Table 2: Density of grass seedlings/m for the burnt (first [1] and second [2] season after burning) and unburnt grassland estimated in September, December and March of the 2000/01 and 2001/02 growing seasons, which were germinating in the greenhouse. UB = unburnt, H = head fire and B = back fire. Numbers within a col-

Species	September				
	UB	H		B	
		1	2	1	2
Aristida congesta				2.0 ± 0.3	
Cymbopogon plurinodes	0.5 ±0.1				
Digitaria eriantha	0.9 ±0.1				
Eragrostis chloromelas	11.3 ±2.2	23.5 ±4.4	107.9 ±19.9	24.0 ±4.2	109.0 ±15.2
E. lehmanniana	1.9 ±0.3	10.8 ±2.0	6.1 ±0.8	13.5 ±3.1	2.0 ±0.1
E. superba	3.3 ±1.1	5.9 ±1.2	2.0 ±0.9	8.0 ±2.1	2.0 ±0.3
Elionurus muticus	5.7 ±1.4	4.9 ±0.9	4.0 ±0.9	5.5 ±1.4	5.7 ±0.9
Panicum stapfianum	1.9 ±0.9				
Sporobolus fimbriatus	1.9 ±0.2		2.1 ±0.3		2.0 ±0.1
Themeda triandra	24.7 ±5.4	31.2 ±3.6	9.9 ±2.1	36.0 ±1.4	11.5 ±1.3
Tragus koelerioides		2.0 ±0.3		1.9 ±0.3	
TOTAL	**52.1**[a]	**78.3**[b]	**132.0**[c]	**90.9**[b]	**132.2**[c]

umn with different superscripts for each month, differ significantly (P≤0.01). Data are means and standard error

December					March			
H		B		UB	H		B	
1	2	1	2		1	2	1	2
4.0 ±0.02		2.0 ±0.1			12.1 ±1.3		24.0 ±2.2	
				1.0 ±0.2				
42.0 ±6.5	5.0 ±2.2	13.8 ±1.1	4.0 ±0.3	38.3 ±4.6	313.7 ±30.1	136.0 ±19.4	266.0 ±29.2	122.1 ±12.4
6.0 ±2.1	1.1 ±0.2	4.0 ±0.3		1.0 ±0.1	6.1 ±0.3	10.1 ±4.6	7.9 ±0.9	12.0 ±1.3
5.0 ±1.4	2.3 ±0.9	2.0 ±0.1	2.0 ±0.1	5.0 ±0.2		2.2 ±0.9		8.0 ±1.3
16.0 ±2.4	2.0 ±0.9	8.1 ±1.0	2.0 ±0.9	3.0 ±1.0	40.1 ±1.0	33.9 ±8.4	19.9 ±3.3	8.0 ±0.9
				1.0 ±0.1				
	2.0 ±0.3	1.0 ±0.1	1.0 ±0.1	0.6 ±0.1		8.0 ±1.3		8.0 ±2.4
3.0 ±0.2	2.0 ±0.2		1.0 ±0.1	8.1 ±1.3		6.1 ±2.1		
					6.1 ±0.9		4.1 ±0.4	2.0 ±0.1
72.0^{c}	**14.4^{a}**	**28.9^{b}**	**10.0^{a}**	**58.0^{a}**	**378.1^{c}**	**196.3^{b}**	**315.9^{c}**	**160.1^{bd}**

Table 3 Density of forb (seedlings/m²) for burnt (first and second season after burning) and unburnt grassland germinating in the glasshouse during September, December and March. Data are means and standard error. Numbers within a row with different superscripts differ significantly (P≤0.01)

	Unburnt	Burnt	
		Head fire	Back fire
First season (2000/01)			
September	$42.2^{a} \pm 3.4$	$70.3^{c} \pm 4.0$	$58.3^{b} \pm 3.8$
p-Value = 0.214			
December	$108.1^{a} \pm 6.6$	$126.5^{b} \pm 7.9$	$120.4^{b} \pm 7.2$
p-Value = 0.068			
March	$77.6^{b} \pm 4.2$	$17.3^{a} \pm 1.1$	$11.8^{a} \pm 1.0$
p-Value =0.312			
Second season (2001/02)			
September	$34.5^{a} \pm 2.6$	$42.1^{b} \pm 3.1$	$42.6^{b} \pm 3.0$
p-Value = 0.121			
December	$108.2^{a} \pm 6.8$	$165.3^{b} \pm 12.9$	$154.5^{b} \pm 6.4$
p-Value = 0.086			
March	$67.2^{b} \pm 4.0$	$59.5^{a} \pm 4.8$	$55.1^{a} \pm 4.1$
p-Value = 0.101			

but not germinating in the seed bank (Table 2).

Notable in Table 2 is that unburnt grassland is dominated by the species *Eragrostis chloromelas* and *Themeda triandra*. The pioneer grass species *Aristida congesta* and *Tragus koelerioides* occurred only in the burnt grassland during the first and second seasons following the fire. The species *Cymbopogon plurinodes*, *Panicum stapfianum* and *Digitaria eriantha* germinated only in the unburnt plots, *Elionurus muticus* increased to a great extent due to the fire, with *E. chloromelas* and *E. lehmanniana* showed the sharpest germination stimulation due to fire. Over the two seasons following the fire, 527% and 36% more seedlings/m² of *E. chloromelas* and *E. lehmanniana* respectively germinated in soil samples taken from burnt (average of head and back fire) than unburnt plots. Regardless of burning, *E. lehmanniana* and *T. triandra* germinated better at the start of the growing season. In contrast, with the exception of the second season after burning, the germination of *E. chloromelas* increased with the onset of the season, also regardless of burning. The first season following the fire, *T. triandra* showed a better germination than the second season after the fire. *Sporobolis fimbriatus* germinated only during the second season following the fire.

Panicum stapfianum was the only species in unburnt grassland occurring only in the seed bank and did not established in gaps as described by Snyman (2004b) in the same studies plots. In contrast, *Digitaria argyrograpta* and *Triraphus andropogonoides* only established in the gaps (Snyman 2004b) without being present in the seed bank.

The only forb actually occurring in the vegetation is *Geigeria aspera* that formed a small percentage (1.12%) of the botanical composition but did not germinate in the seed bank. No shrubs, namely *Lycium tenue* or *Walafrida saxatilis*, averaging 1.8% of the species composition of the vegetation in the field, germinated in the seed bank.

Discussion and conclusions

Fire may produce the post burn flush of seedlings in the seed bank by several direct and/or indirect means which include (1) direct heating of the soil and seed bank, which could affect seed germination (Ruyle et al. 1988; Zacharias et al. 1988; Zammit and Zedler 1988; Tyler 1995), change in soil structure (Adams 1996) and nutrient levels (Cavers 1995); and (2) temporary reduction in competition by removing aboveground vegetation (Tyler 1995; Edwards and Crawley 1999; Jutila and Grace 2002) thereby allowing seedlings greater access to light and water (Skoglund 1992; Snyman 2004b) and reducing allelopathic influences (Keeley et al. 1985). The relationship between fire intensity and patterns of seedling recruitment following a wildfire is still unclear (Tyler 1995).

Though grassland condition count (Table 2) did not decrease much due to fire, the short-term botanical composition varied significantly. This change could contribute to the slight seed bank decrease in species richness (Table 1) due to the fire. In contrast, the species richness of the head and back fires remained the same throughout, in spite of higher fire intensity of the back fire close to the soil. The soil seed bank results obtained in my study are of the few which could be linked to the short-term seedling recruitment and survival in the field. Although as much as 485 and 142 seedlings/m^2 for burnt and unburnt grassland respectively germinated the first season after the fire in the seed bank in my study, only 0.48 and 0.86 seedlings/m^2 survived on the same experimental plots and over the same season from burnt and unburnt grassland respectively in the field (Snyman 2004c). The burning of semi-arid grassland did therefore have an important impact on both the seasonal survival of seedlings in the field and the seed bank over the short-term.

Caution is necessary when comparing studies of soil seed banks because of differing methods, e.g.

with respect to sample size, depth, time and number of termination cycles (Snyman 2004b). The total average seasonal seedling densities (only grasses) from burnt and unburnt grassland in this study of 404 and 132 seedlings/m^2 respectively, were extremely low when compared to other foreign seed bank results. For example, average seed densities of 4000 seeds/m^2 (McIvor and Gardener 1994) in the drier central and north-east Queensland, 7639 seeds/m^2 in Central Queensland of Australia (Bahnisch et al. 1999), 800 seeds/m^2 of *Eragrostis lehmanniana* in southern Arizona (Ruyle et al. 1988) and 2252 to 4409 seeds/m^2 for a semi-arid grassland of the western Edwards Plateau, Texas (Kinucan and Smeins 1992) were recorded. Contrarily it compares well with South African seed bank studies of 172 seedlings/m^2 in a semi-arid *Themeda triandra* grassland (Snyman 2004b), 200 seeds/m^2 in the mesic Tall Grassveld of Kwazulu-Natal (Adams 1996) and up to 350 seeds/m^2 from *Themeda triandra* rangeland in the semi-arid Savanna (O'Connor 1997). Unfortunately, little information on the influence of fire on the seed bank of grassland is available in the literature, while the savanna areas and conditions dominated by shrubs were more concentrated upon. 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. Researchers argued that species with large seed banks might be less likely to be seed limited (Crawley 1990) and therefore seeds from the seed bank fill all the establishment gaps that become available. However, some researchers suggest that this need not always be the case as the seed bank may be closed to recruitment and increases in seed production may well lead to increased seedling recruitment.

However, the influence of fire on the germination of grasses as a result of modifications to the environment and the effect of fire only on the seeds must be differentiated between. According to Zacharias *et al.* (1988) in some grass species effective burial would probably need to be achieved by some form of soil disturbance unless germination and establishment could take place before they are normally exposed to fire. In contrast, germination of *Heteropogon contortus* seed would seem to be well adapted to and indeed promoted by fire, whereas *T. triandra* responded negatively to fire (Zacharias *et al*. 1988). This response in *T. triandra* is in direct contrast to the findings in my study and to the generally held view that this species evolved under a consistent fire regime (O'Connor 1997). In summary, on the one hand *T. triandra* seedlings emerged most readily when the seed lay on the soil surface (O'Connor 1997), compared with the idea that, because of the sensitivity of this species' seeds to fire, it could be postulated that reproduction in

Themeda triandra is achieved primarily by vegetative reproduction (Zacharias et al. 1988). The evidence from studies in both semi-arid (Danckwerts 1984) and mesic (Everson 1985) environments support the last suggestion.

Only few forb seedlings were found in the seed bank in spring, but with the onset of the season they increased. The explanation for this could be that most of them flowered later over the season, where a lot of seeds distributed by wind into the rangeland. Luckily the competition of the grasses is too strong for germination and survival of these invaders in the field (Snyman 2003c).

A short-term warning trend is that the pioneer grass species *Aristida congesta* and *Tragus koelerioides* are the only two occurring in the seed bank (Table 4) in burnt and not in unburnt grassland. The second growing season following the fire, the impact of the fire on species richness and seed bank, was gradually lifted. The absence from the seed bank of several species dominating the vegetation has been reported for many grassland (Graham and Hatchings 1988; D'Angela et al. 1988; Milberg 1992). Soil seed bank is therefore an important component of vegetation dynamics affecting both ecosystem resistance and resilience (Pugnaire and Lazaro 2000).

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