

Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability

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Summary

1. Demographic processes, particularly the recruitment of seedlings, are critical to the long-term survival and re-establishment of plant populations. In many perennial grasslands successful recruitment is a rare event that requires the simultaneous favourable alignment of several environmental variables.
2. Although a few empirical studies have examined demographic processes in perennial grasslands, most of these studies investigate the impact of only one or two environmental factors in isolation. Those studies would lead us to expect that seed availability, irrigation and burning, enhance recruitment rates whereas the presence of established competitors substantially lowers recruitment rates. But how these factors, or recruitment filters, act in concert and how they influence the different components of the recruitment process such as seedling emergence, survival and growth is not understood.
3. For this reason we explore the relative and combined influence of four factors – seed availability, irrigation, competition by the established vegetation, and fire – on the recruitment process of a perennial grass (*Stipagrostis uniplumis*) in semi-arid savanna. We used a full factorial experiment to determine how these four factors influence emergence, growth, survival and flowering of seedlings.
4. Our results show that all of the factors affected some stage of the recruitment process but not all significant effects contributed to enhancing the final number of recruits.
5. We found enhanced seed availability to significantly enhance rates of seedling emergence but to play no further role in the recruitment process. Competition by the established vegetation exerted a strong negative effect on every step of the recruitment process. Irrigation had a minor effect on recruitment. It enhanced rates of flowering and survival during the growing season but the effect of the stimulus was short-lived and did not influence later stages of the recruitment process.
6. In contradiction to existing theory, seedling recruitment does therefore not seem to be limited to above average rainfall years. Fire acted similarly to the removal of competitors; that is, it positively affected seedling emergence, growth, flowering and survival.
7. *Synthesis.* We conclude that recruitment is not limited to above average rainfall years but triggered by events that open up the grass canopy and reduce the abundance of competitors. Specifically it appears that periodic fires enable the recruitment of new individuals into the population. This study shows that fire can play an important positive role in individual turnover of semi-arid perennial grass populations.

Key-words: demography, emergence, full factorial experiment, intraspecific competition, irrigation, recruitment limitation, seed addition, seedling survival, semi-arid savanna, *Stipagrostis uniplumis*

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Introduction

A central challenge of ecology is to understand the factors that influence birth and death processes in populations (Harper 1977). The ecological significance of the complex factors influencing birth rates in particular was eloquently articulated in Grubb's concept of the regeneration niche. Grubb (1977) drew attention to the myriad of factors that could influence the journey of a seed to a recruit. Yet, in populations where individuals are capable of vegetative reproduction, individuals are potentially immortal and it is not immediately obvious that research effort should be focussed on birth or death processes. Grasslands are one such system, and research in grasslands has concentrated on biomass production rather than on demographic processes. **Despite this apparent neglect, a few studies have shown demographic processes to be important in perennial grasslands (e.g. O'Connor 1991; Lauenroth *et al.* 1994; O'Connor 1996; Fair *et al.* 1999).** In particular, seedling recruitment has been identified as critical to the long-term dynamics of grass populations (O'Connor 1991; Baskin & Baskin 1998; Lauenroth & Aguilera 1998).

Recruitment, which is the path from germination to an established, reproductive individual, includes the transition from the relatively resilient seed stage to the more vulnerable seedling stage (Grubb 1977; Kigel 1995). In many perennial grasslands successful recruitment is infrequent (e.g. Mott & Andrew 1985; Lauenroth *et al.* 1994; Ash *et al.* 1997; Lauenroth & Aguilera 1998; Orr 1998; Milton & Dean 2000; Oliva *et al.* 2005) because it depends on several environmental variables being simultaneously favourable (O'Connor 1996). Hence, the regeneration niche (Grubb 1977) in grasslands appears to be multi-dimensional. The environmental factors that define the regeneration niche vary with species (Grubb 1977) and different factors filter different stages of the recruitment process (e.g. germination, emergence, establishment) as articulated by Harper (1977).

Most studies that have investigated recruitment in perennial grasslands have explored the impact of one or two factors, or focus on only one component of recruitment, such as germination or the final number of new recruits. Thus, our knowledge of what determines recruitment success in perennial grasslands is incomplete. This study aims to fill this knowledge gap by performing a multi-factorial experiment that investigates multiple stages in the recruitment process of a perennial grass in semi-arid savanna. We are aware of only one field experiment which employed a similar multi-factorial approach, in investigating several components of the recruitment process of a perennial grass (O'Connor 1996). Here, a strong hierarchy was found amongst factors, with seed and moisture availability having an overriding effect on recruitment rates. In a similar manner to O'Connor (1996), here we focus on these factors (soil moisture, seed availability, competition and their interactions), but, in addition, we examine the effect of fire on recruitment rates. We next review the importance of these four factors.

Seed availability limits the recruitment process in many systems, particularly in those where substantial seed banks do

not exist. In perennial grasslands seed longevity is limited (Mott & Andrew 1985; Coffin & Lauenroth 1989; Pyke 1990; McIvor & Gardener 1991; O'Connor & Pickett 1992; Bertiller & Coronato 1994; O'Connor 1997) and predators such as ants and rodents are known to consume considerable amounts of seeds (Capon & O'Connor 1990; Kerley 1991; Linzey & Washok 2000; Vilà & Lloret 2000; Kelt *et al.* 2004). Hence, seed banks in grasslands are transient and we therefore expect seed availability to limit recruitment rates.

Competition from established vegetation has been demonstrated to suppress recruitment in perennial grasses of arid (Milton & Dean 2000), semi-arid (Aguilera & Lauenroth 1993; Defossé *et al.* 1997) and mesic (Moloney 1990) grasslands. These findings were attributed mostly to advantages of established individuals in competing for below-ground resources. In contrast, some studies of dry grasslands found established vegetation to exert negligible or only small effects on the early stages of seedling recruitment (O'Connor 1996; Bisigato & Bertiller 2004), and some studies report perennial grass seedlings to even survive and perform better when located close to established vegetation (Vilà & Lloret 2000; Snyman 2004a). In these cases established plants appear to act as nurse plants by providing shade.

Soil moisture availability and the positive effect of water addition on recruitment rates of perennial grasses have been emphasized by several studies. Specifically germination rates and performance of seedlings have been documented to respond positively to enhanced availability of moisture (e.g. Wilson & Briske 1979; Maze *et al.* 1993; Potvin 1993; Lauenroth *et al.* 1994; O'Connor 1996; Hamilton *et al.* 1999).

Fire can have both direct and indirect effects on the recruitment of perennial savanna grasses. Direct negative effects are due to heat damage which can cause mortality or reduce vigour (Westoby *et al.* 1988; Zacharias *et al.* 1988; Ernst 1991; Vilà *et al.* 2001). Direct positive effects are the stimulation of germination, particularly via smoke-derived compounds (Baxter *et al.* 1994; Read *et al.* 2000; Williams *et al.* 2005). Several studies describe a flush of grass seedlings after burning (e.g. Lock & Milburn 1970; Peart 1984; Whelan 1988; McDougall 1989; Snyman 2005) which can also be attributed to the indirect effects of fire. Fire indirectly influences recruitment by altering soil properties (Busso 1997; Bennett *et al.* 2002; Snyman 2002) or by changing the competitive or the resource environment seedlings are exposed to (Old 1969; Lock & Milburn 1970; Bennett *et al.* 2002; Snyman 2004a).

Our study aims to develop a detailed understanding of the recruitment filters of a dominant perennial grass (*Stipagrostis uniplumis*) in its natural environment. The study site in the Etosha National Park (Namibia) provides several advantages for our study: the grass layer is almost mono-specific, herbivores are in extremely low abundance, and human influence is non-existent. Hence, our study system allows us to ignore the role of inter-specific interactions, herbivory and human disturbance. The aim of this paper is to explore the relative importance of four factors – soil moisture, seed availability, competition and fire – in controlling different stages of the recruitment process. To achieve these aims we use a multi-factorial experiment.

Methods

STUDY AREA AND SPECIES

The Etosha National Park (hereafter simply called Etosha) is situated in north-central Namibia and comprises an area of 22 915 km² (Du Plessis 1997). Almost the whole of Etosha can be described as arid to semi-arid savanna (250–500 mm average annual rainfall) with a rainfall pattern being highly variable and erratic (Engert 1997). Rain falls during the summer months when mean monthly maximum temperatures range from 25 to 35 °C. Mean monthly minimum temperatures in winter vary from 6 to 18 °C (De Villiers & Kok 1988; Le Roux *et al.* 1988).

The research area is located in the North of Etosha, in the habitat type 'Mopane shrubs and trees on loamy sands' (Etosha Ecological Institute, unpublished data). Average annual rainfall is around 380 mm and variation in annual rainfall is between 30% and 40%, (Mendelsohn *et al.* 2002; Etosha Ecological Institute, unpublished data). Due to very low grazer densities, grazing pressure in this habitat type is very low (Craig 1998; Erb 2000; Kilian 2002; Kolberg 2004). The woody layer is almost exclusively dominated by *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard shrubs, whereas the herbaceous layer is dominated by the perennial grass *S. uniplumis* var. *uniplumis* (Licht. ex Roem. & Schul.) De Winter. *Stipagrostis uniplumis* constitutes more than 90% of the herbaceous vegetation cover. The grass species *Schmidtia pappophoroides* Steud. ex J. A. Schmidt, *Melinis repens* (Willd.) Zizka subsp. *repens* or *Pogonarthria fleckii* (Hack.) Hack., and herbaceous dicotyledon species such as *Commelina forskoolii* Vahl and *Gisekia africana* (Lour.) Kuntze, constitute the remaining cover. The canopy : gap ratio of shrubs and trees in this habitat type is 0.8–0.35 and grass green standing crop varies between 629 and 4197 kg ha⁻¹ (Du Plessis 1999).

The study species *S. uniplumis* var. *uniplumis* (hereafter simply referred to as *S. uniplumis*) is a C4 perennial tufted grass which grows on sandy soils in arid parts of Africa. It is the most common of the *Stipagrostis* species and is considered a valuable grazing grass (Malan & Owen-Smith 1974; Van Oudtshoorn 1999). Because of its wide distribution and local dominance it is important for forage and soil stabilization (Malan & Owen-Smith 1974; Van Oudtshoorn 1999; Klaassen & Craven 2003). The species is not associated with shrub or tree canopies and grows in the between-tree areas. It reproduces mainly generatively but is capable of vegetative recruitment. Generative recruitment is particularly important in this species, as we estimated that annual mortality rates exceed 20% (J. Zimmermann, S.I. Higgins, J. Hoffmann, V. Grimm & A. Linstädter, unpublished data).

SAMPLING DESIGN AND PARAMETERS

The study was conducted in the 2004/2005 growing season and subsequent dry season. The study site covered a 500 × 500 m area which burnt last in 1997 and is homogeneous in terms of soil, topography, species composition and fire history (Etosha Ecological Institute, unpublished data). The experiment was initiated at the beginning of the growing season. Perennial grass seedlings and annual plants were not present as the first rains had not yet fallen. The study site received close to the mean annual rainfall during the growing season (382 mm). We visited the study site almost weekly to check for signs of mammal grazing but found no evidence in or around any of our study plots. Hence, neither drought nor herbivory influenced the outcome of the experiment.

A full factorial experimental design was used to examine the influence of the factors Seeds (seed addition or no seed addition),

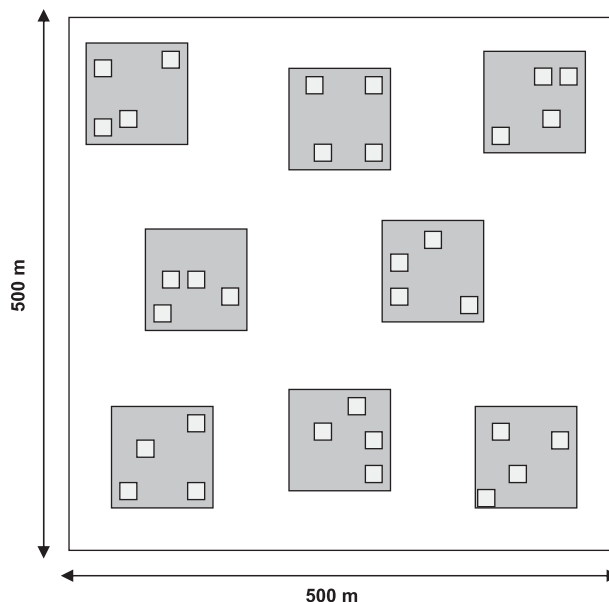


Fig. 1. Representation of the experimental layout, comprising 8 blocks (dark grey) and 32 plots (2 × 2 m, light grey) spread over a 500 × 500 m area. Figure is not drawn to scale.

Fire (burnt or unburnt), Competitors (competition by established vegetation – present or absent) and Irrigation (irrigation or no irrigation) on the recruitment process of *S. uniplumis*. Each of these four factors had two levels, resulting in a 2⁴-design (16 treatment combinations).

The full factorial design was replicated twice, resulting in 32 experimental units. Each experimental unit covered an area of 4 m² (2 × 2 m). To facilitate treatment implementation, the experimental units (from now on referred to as plots) were randomly arranged in blocks of four plots. The resulting eight blocks were randomly positioned in the 500 × 500 m area (Fig. 1). The position of each block was constrained to lie more than 100 m from the nearest road or path and more than 50 m from the nearest block. Within a block, plots were randomly placed but constrained to lie more than 5 m from each other and more than 5 m from the nearest shrub or tree, as *S. uniplumis* is generally not associated with canopies. Furthermore, only plots where the cover of *S. uniplumis* was greater than 60% were selected. We used the 60% cover threshold, as our preliminary investigations showed 60% cover to be the modal grass cover of the area (data not shown).

Rainfall was measured on each block, using manual rain gauges, between October 2004 and May 2005. A gypsum block (Eijkelkamp 14.22.05) was buried at 10 cm depth on every plot to monitor soil water tension. Soil samples were taken from the first 10 cm of all 32 plots. We used the experimental design to test for differences in soil texture between plots but found no significant differences (analysis not shown). Hence, soil texture is rather homogeneous with an average of 85.4% sand (SD = 5), 3.9% silt (SD = 2.7) and 10.7% clay (SD = 4.1).

The treatments were randomly assigned and then applied to the plots at the end of October 2004, before the first rains. The treatment irrigation was applied after the first heavy rainstorm in November 2004 (Fig. 2). In the following paragraphs we describe how the treatments were implemented (note that the treatments are described in the order in which they were implemented):

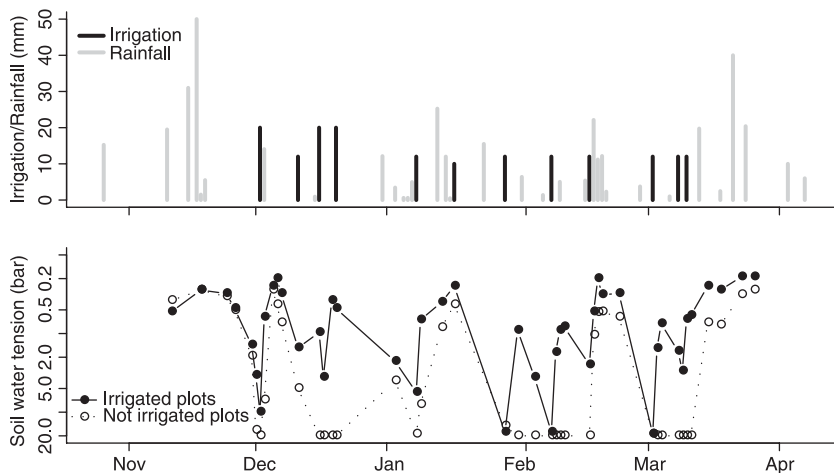


Fig. 2. The amount of rainfall and irrigation (averaged over plots) during the growing season 2004/2005 and average soil water tension (bar) of the irrigated and non-irrigated plots.

Seeds

The two treatment levels were the naturally occurring seed density in the soil seed bank and the addition of 400 seeds that were planted to the 4 m² of the plot. Seeds were planted in small spiked holes at 0.5–1 cm depth, as grass seeds are reported to emerge from the top 1 cm of the soil (Veenendaal *et al.* 1996). These seeds had been collected in the vicinity of the study area in May 2004 (after a growing season of close to average rainfall; 370.5 mm), sun dried and stored at 7 °C.

Fire

The two levels of the burning treatment were burnt and unburnt. All fires were burnt on the same morning under light wind conditions (< 2 m s⁻¹). To prevent the fire from escaping into the adjacent vegetation, we established a fire break of two 2 m width around each plot by cutting all plants to ground level. The firebreaks were located 0.5 m from the plot boundaries. The completeness of burn was 100% for each plot. Fire intensity was estimated using the Beaufait (1966) calorimetric technique. An analysis of variance revealed that fire intensity did not differ significantly between blocks or plots (analysis not shown). After the fire, all of the tufts were burned to ground level but the majority (67%) of the tufts started to resprout soon after the fire.

Competitors

The two treatment levels were no manipulation and the removal of all species. As the established vegetation was almost exclusively constituted of *S. uniplumis* individuals, the treatment involved clipping of established *S. uniplumis* individuals to ground level. We removed all basal buds but did not pull out the individuals roots to keep soil disturbance minimal. No individuals resprouted after this treatment.

Irrigation

The naturally occurring rainfall was one treatment level, whereas water addition simulating a year of above average rainfall constituted the second level. Non-irrigated plots received a total of 382 mm

rainfall (October 2004–May 2005) almost matching the long-term mean for the area (380 mm), whereas irrigated plots received an additional 166 mm, resulting in a total of 548 mm. Rainfall amounts did not vary between plots. Groundwater for irrigation was collected from a nearby borehole. The frequency and amount of irrigation (between 10 and 20 mm on 12 occasions) depended on rainfall and on soil water tension. Specifically the plots were irrigated when either the average soil water tension of the irrigated plots fell below 15 bar or when the interval between rainfall events exceeded 2 weeks. This pattern of irrigation simulated a higher rainfall year but did not prevent the soil from occasionally drying out (Fig. 2). All irrigation plots were irrigated in the afternoon of the same day and received the same amount of water. Water was supplied with a hand held sprinkler at low pressure to avoid surface flow. A water meter was used to assure that each plot received the same amount of water. The order in which we watered the plots was randomized.

Plots were not entered for treatment applications and measurements. During the study period plots were visited at least twice a week to check for rainfall, soil water potential and for newly emerged seedlings. The following parameters were measured at monthly intervals during the growing season for each seedling (first survey on 1 December 2004; last survey on 30 March 2005) and again at the start of the next growing season: the *x*, *y* coordinates to the nearest centimetre, survival (yes/no), the height (cm) and the number of tillers. Furthermore, we estimated the cover of annual vegetation (%) per plot. The first seedling mapping was conducted 12 days after the first heavy rains, as grass seedlings are reported to emerge within 3–10 days after rainstorm (e.g. O'Connor 1994, 1996; Veenendaal *et al.* 1996).

Recruitment in tropical grasslands is strongly seasonal and comprises a chronological order of several processes (O'Connor 1996). Hence, we derived the following seven response variables from the data for each plot: the number of emerged seedlings, seedling survival through the growing season (proportion surviving from the first sampling date to the later sampling dates), seedling growth through the growing season (mean number of tillers, all sampling dates), the number of flowering seedlings (recorded once at the end of the growing season), the number of reproductive tillers per seedling (mean number of reproductive tillers, recorded once at the end of the growing season), seedling survival of the dry season (proportion surviving from the start to the end of the dry season) and the number of recruits (the final number of seedlings after the dry season).

Table 1. Minimal adequate linear mixed effects model of the log of seedling emergence in response to the fixed effects of competitors, fire, seeds and their two-way interactions when considering the plots nested in blocks as random effects

Parameter	Value	Standard error	d.f.	<i>t</i> -value	<i>P</i> -value
(Intercept)	3.784	0.260	20	14.570	< 0.001
Competitors _{YES}	-1.418	0.196	20	-7.258	< 0.001
Fire _{YES}	-0.105	0.223	20	-0.470	0.643
Seeds _{YES}	0.702	0.133	20	5.300	< 0.001
Competitors _{YES} : Fire _{YES}	1.727	0.290	20	5.965	< 0.001

STATISTICAL ANALYSIS

We used linear mixed-effects models (LME) to examine the influence of the fixed effects of the four treatment factors and their two way interactions on the response variables. We included plot and block as random variables in all models to account for our experimental design where 32 plots were nested in eight blocks (Fig. 1). The underlying strategy of our statistical analysis was to find the simplest model that adequately described the data, following the principle of parsimony (Crawley 2002). Thus, we first fitted a full model, including all variables and two-way interactions. Model simplification involved a stepwise backward procedure based on a likelihood ratio test. Only variables significant at the 5% level were retained in the model. The models with the response variables growth and survival through growing season included time (the monthly sampling intervals) as an additional explanatory variable.

Because LME models use maximum likelihood, it is not possible to calculate R^2 values. Linear mixed models assume a normal error distribution and constancy of the variation in the residuals. We used appropriate transformations of the response variables to meet these assumptions (number of emerged seedlings, seedling growth and number of flowering seedlings were log transformed; number of reproductive tillers and number of recruits were square root transformed; seedling survival through the growing season and seedling survival of the dry season were not transformed). Analysis of the residuals of the models fitted using these transformations revealed no deviations from the assumptions of LME models as described by Crawley (2002). All data were analysed using the software R 2.4.1 (R Development Core Team 2006).

Results

A total of 2649 seedlings emerged on the 128 m² accumulated area of the experimental plots. Of these seedlings, 1269 (48%) survived the growing season but only 273 (10%) survived the subsequent dry season.

NUMBER OF EMERGED SEEDLINGS

The density of seedlings emerging on the experimental plots varied from 2 to 167 m⁻². Only one pulse of seedling emergence occurred during the study period. This occurred shortly after heavy rainstorms, at the start of the growing season (80 mm in 3 days, Fig. 2). At the time of seedling emergence, the irrigation treatment was not yet implemented. We therefore did not include the variable irrigation in our statistical analysis

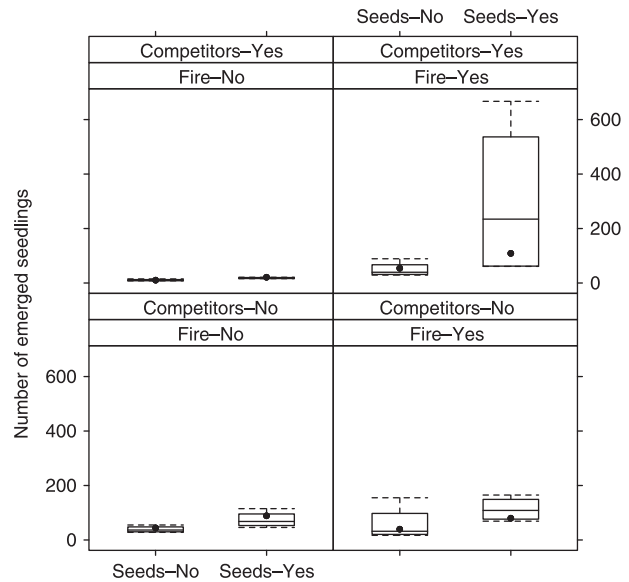


Fig. 3. The number of emerged seedlings per plot in response to the presence of established vegetation (Competitors), burning (Fire) and seed addition (Seeds). Each variable has two levels (Yes and No). Box and whisker plots present the actual data whereas points display predictions made using the minimal adequate model described in Table 1. Note that the box and whisker plots include the effects of the random factors (block and plot) on the response variable whereas the model predictions shown factor out the effects of the random factors.

of seedling emergence. We however emphasize that the irrigation treatment did not trigger further seedling emergence during the course of the study.

Emergence rates were significantly enhanced by the addition of seeds and severely lowered by the presence of established competitors (Table 1, Fig. 3). The main effect of fire was not significant, although there was a significant interaction between fire and the presence of established competitors. Specifically, when competitors were present fire significantly enhanced emergence rates. The other interaction terms did not have significant effects on seedling emergence ($P > 0.05$).

SEEDLING SURVIVAL THROUGH THE GROWING SEASON

Survival through the growing season ranged from 0% to 100% and was significantly reduced by the presence of established competitors (Table 2). Very few seedlings survived until the end of the growing season on plots where established competitors were present and not burned (Fig. 4). By contrast, irrigation as well as the combination of established competitor presence and burning significantly enhanced survival rates (Table 2, Fig. 4). The factor time had a significant negative linear effect on survival rates. We found that the factor seeds and all two-way interactions except the interaction between fire and competitors did not influence seedling survival through the growing season.

Table 2. Minimal adequate linear mixed effects model of the proportion of seedlings surviving through the growing season in response to the fixed effects competitors, fire, seeds, irrigation, their two-way interactions and the effect of time when considering the plots nested in blocks as random effects

Parameter	Standard		d.f.	t-value	P-value
	Value	error			
(Intercept)	0.358	0.057	93	6.326	< 0.001
Competitors _{YES}	-0.273	0.072	20	-3.814	0.001
Fire _{YES}	0.095	0.072	20	1.322	0.201
Irrigation _{YES}	0.197	0.051	20	3.888	< 0.001
Time	-0.199	0.015	93	-13.088	< 0.001
Time ²	0.026	0.015	93	1.688	0.095
Time ³	0.020	0.015	93	1.298	0.198
Competitors _{YES} : Fire _{YES}	0.309	0.101	20	3.049	0.006

SEEDLING GROWTH THROUGH THE GROWING SEASON

Growth was the most complex component of the recruitment process, in the sense that it was influenced by the largest number of factors and interaction terms (Table 3). The average number of seedling tillers per plot ranged from 1 to 18. We found that fire, the interaction between fire and competitors and the interaction between irrigation and competitors significantly influenced the growth of seedlings. Time had a strong linear positive effect, as well as a weaker but significant negative quadratic effect on growth. The presence of established competitors significantly suppressed growth (Fig. 5). On the unburnt plots, most seedlings subject to established competitors did not grow more than one or two tillers during the

Table 3. Minimal adequate linear mixed effects model of the log of seedling growth (mean number of tillers per seedling) through the growing season in response to the fixed effects competitors, fire, seeds, irrigation, their two-way interactions and the effect of time when considering the plots nested in blocks as random effects

Parameter	Standard		d.f.	t-value	P-value
	Value	error			
(Intercept)	1.711	0.140	124	12.233	< 0.001
Competitors _{YES}	-1.099	0.198	19	-5.557	< 0.001
Fire _{YES}	0.586	0.162	19	3.629	0.002
Irrigation _{YES}	-0.246	0.162	19	-1.525	0.144
Time	0.675	0.079	124	8.547	< 0.001
Time ²	-0.389	0.079	124	-4.931	< 0.001
Time ³	-0.031	0.079	124	-0.389	0.698
Time ⁴	0.009	0.079	124	0.117	0.907
Competitors _{YES} : Fire _{YES}	0.509	0.228	19	2.229	0.038
Competitors _{YES} : Irrigation _{YES}	0.660	0.228	19	2.890	0.009

course of the growing season, whereas seedlings on the burnt plots produced the highest numbers of tillers. The factor seeds and the associated interaction terms did not significantly influence seedling growth ($P > 0.05$).

NUMBER OF FLOWERING SEEDLINGS

Of the 1269 seedlings that were still alive at the end of the growing season 309 (24.35%) produced generative tillers which flowered. The number of flowering seedlings per plot ranged from 0 to 53 and was significantly enhanced by

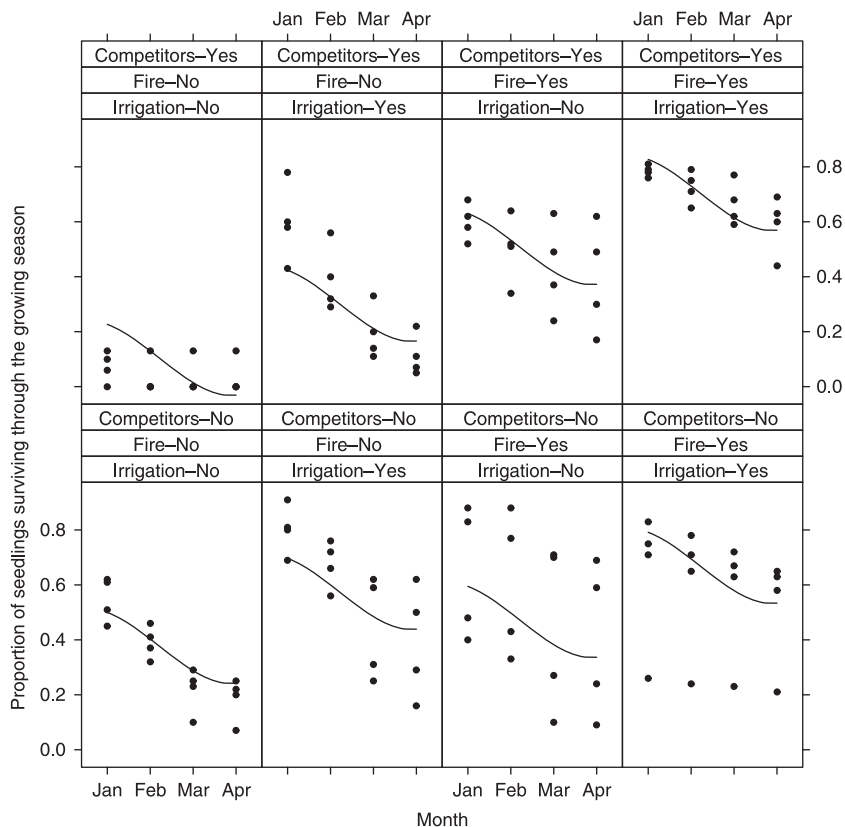


Fig. 4. The proportion of seedlings per plot that survive through the growing season in response to the presence of established vegetation (Competitors), burning (Fire), moisture availability (Irrigation) and Time (monthly time steps). Each variable except Time has two levels (Yes and No). The points present the actual data whereas the line displays the predictions, which are made using the minimal adequate model described in Table 2. Note that some of the variance in the data originates from the random factors which were considered in the minimal adequate model.

Fig. 5. Growth as indexed by the mean number of tillers per seedling and plot, in response to the presence of established vegetation (Competitors), burning (Fire) and availability of water (Water) and Time (monthly time steps). Each variable except Time has two levels (Yes and No). The points present the actual data whereas the line displays the predictions, which are made using the minimal adequate model described in Table 3. Note that some of the variance in the data origin from the random factors which were considered in the minimal adequate model.

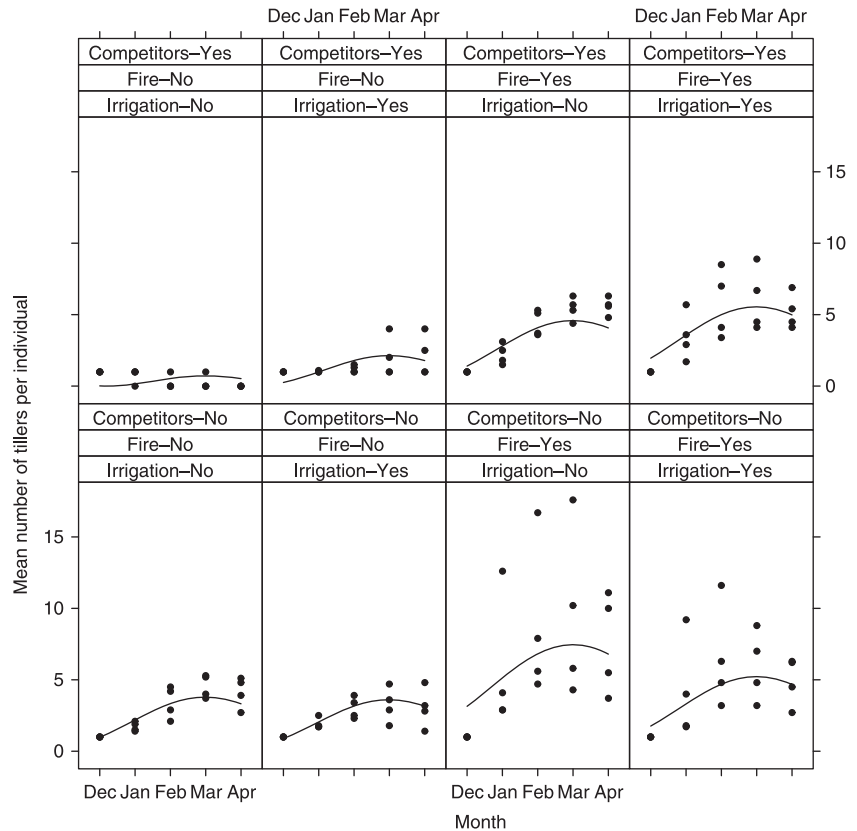


Table 4. Minimal adequate linear mixed effects model of the log of the number of flowering seedlings in response to the fixed effects of competitors, fire, seeds, irrigation and their two-way interactions when considering the plots nested in blocks as random effects

Parameter	Standard		d.f.	t-value	P-value
	Value	error			
(Intercept)	-2.171	0.839	20	-2.588	0.018
Competitors _{YES}	-3.272	1.060	20	-3.087	0.006
Fire _{YES}	3.148	1.061	20	2.968	0.008
Irrigation _{YES}	1.682	0.749	20	2.244	0.036
Competitors _{YES} : Fire _{YES}	4.031	1.500	20	2.688	0.014

burning and by irrigation, and significantly reduced by the presence of competitors, if the competitors remained unburnt (see Table 4 and Fig. 6). The factor seeds and all two-way interactions except the interaction between fire and competitors did not significantly influence the number of flowering seedlings ($P > 0.05$).

NUMBER OF REPRODUCTIVE TILLERS PER SEEDLING

As a second, quantitative measure for reproductive output we examined the number of reproductive tillers per seedling. These ranged from 0 to 22, with the majority of seedlings having no or only one inflorescence, hence the average number of reproductive tillers per seedling and plot ranged

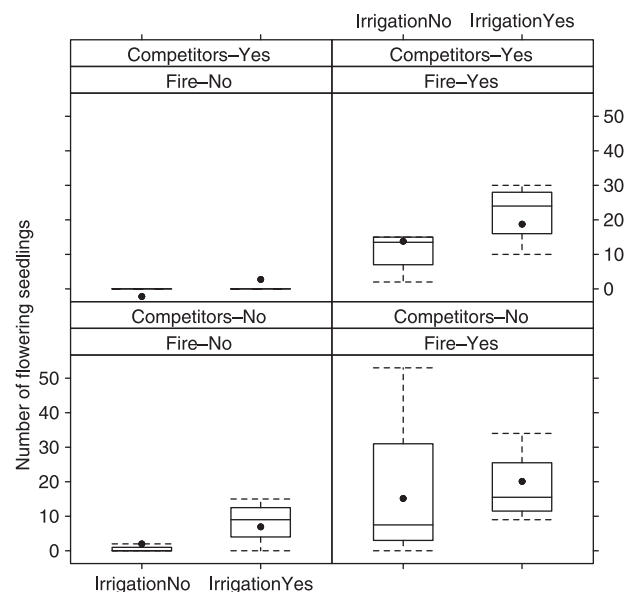


Fig. 6. The number of flowering seedlings per plot at the end of the growing season in response to the presence of established vegetation (Competitors), burning (Fire) and irrigation. Each variable has two levels (Yes and No). Box and whisker plots present the actual data whereas points display predictions, which are made using the minimal adequate model described in Table 4. Note that the box and whisker plots summarize the data and therefore include the effects of the random factors (block and plot) on the response variable whereas the model predictions shown factor out the effects of the random factors.

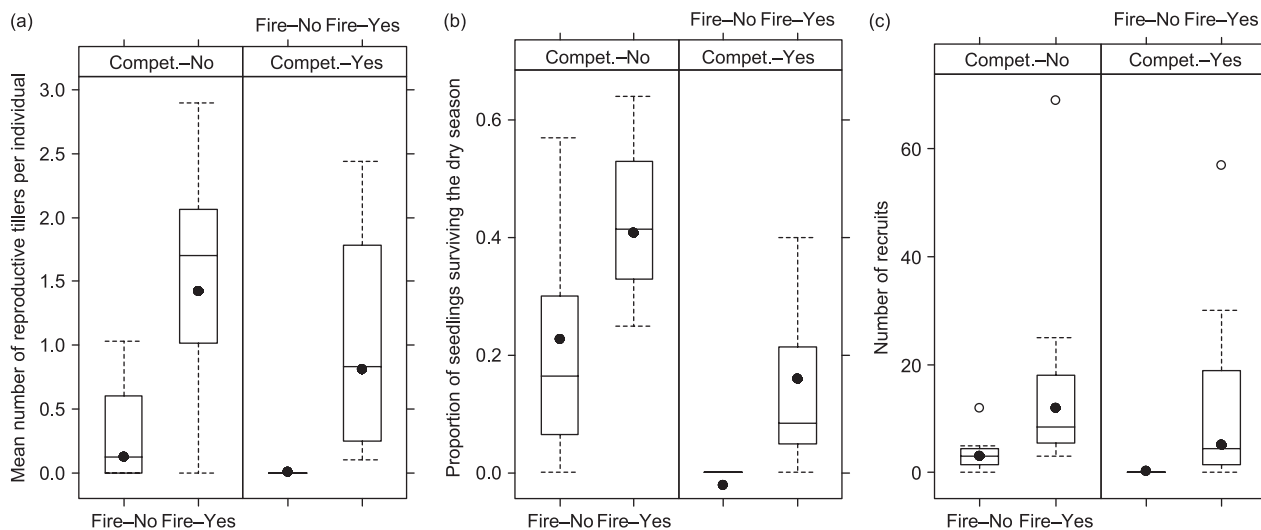


Fig. 7. Each of the three response variables – (a) mean number of reproductive tillers per seedling and per plot, (b) proportion of seedlings of each plot which survived from the start to the end of the dry season and (c) the number of recruits – in response to the presence of established vegetation (Competitors) and burning (Fire). Each of the explanatory variables has two levels (Yes and No). Box and whisker plots present the actual data whereas points display predictions, which are made using the minimal adequate models described in Tables 5–7. Note that the box and whisker plots include the effects of the random factors (block and plot) on the response variables whereas the model predictions shown factor out the effects of the random factors.

Table 5. Minimal adequate linear mixed effects model of the square root of the number of reproductive tillers (mean number of reproductive tillers per seedling) in response to the fixed effects of competitors, fire, seeds, irrigation and their two-way interactions when considering the plots nested in blocks as random effects

Parameter	Value	Standard error	d.f.	<i>t</i> -value	<i>P</i> -value
(Intercept)	0.349	0.130	22	2.681	0.014
Competitors _{YES}	-0.294	0.135	22	-2.170	0.041
Fire _{YES}	0.843	0.146	22	5.791	< 0.001

from 0 to 3 (Fig. 7a). Burning significantly enhanced, and the presence of competitors significantly reduced, the number of reproductive tillers per seedling (Table 5). The factors seeds and irrigation and all two-way interactions did not significantly influence the number of reproductive tillers per seedling ($P > 0.05$).

SEEDLING SURVIVAL OF THE DRY SEASON

The proportion of seedlings surviving the dry season ranged from 0% to 64% between plots. The factors fire and competitors significantly influenced seedling survival over the dry season. Burning significantly enhanced, and the presence of established competitors significantly reduced, seedling survival in the dry season (Table 6). No seedlings survived when established competitors were present and fire was excluded (Fig. 7b). By contrast, survival rates of seedlings not subject to established competitors were substantially higher. The factors seeds and irrigation and all two-way interactions did not significantly influence seedling survival of the dry season ($P > 0.05$).

In an additional analysis we detected a positive relationship between the proportion of seedlings surviving the dry

Table 6. Minimal adequate linear mixed effects model of the proportion of seedlings surviving from the start to the end of the dry season in response to the fixed effects of competitors, fire, seeds, irrigation and their two-way interactions when considering the plots nested in blocks as random effects

Parameter	Value	Standard error	d.f.	<i>t</i> -value	<i>P</i> -value
(Intercept)	0.226	0.041	22	5.582	< 0.001
Competitors _{YES}	-0.248	0.047	22	-5.307	< 0.001
Fire _{YES}	0.182	0.047	22	3.890	< 0.001

Table 7. Minimal adequate linear mixed effects model of the square root of the number of recruits in response to the fixed effects of competitors, fire, seeds, irrigation and their two-way interactions when considering the plots nested in blocks as random effects.

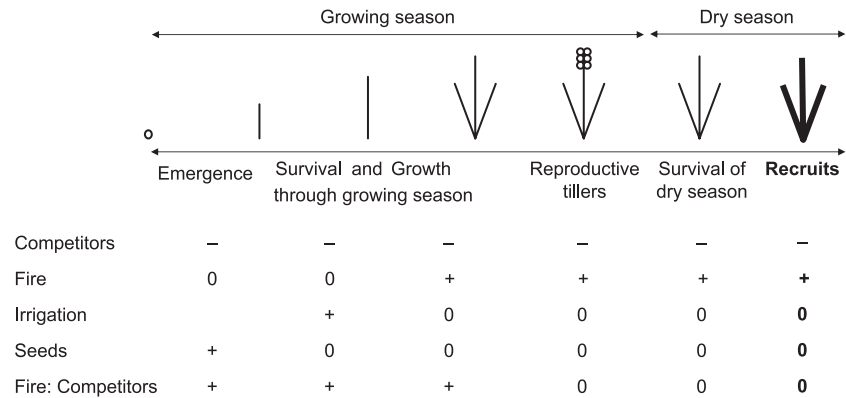
Parameter	Value	Standard error	d.f.	<i>t</i> -value	<i>P</i> -value
(Intercept)	1.750	0.605	22	2.891	0.009
Competitors _{YES}	-1.190	0.489	22	-2.432	0.024
Fire _{YES}	1.703	0.581	22	2.934	0.008

season and seedling size, indexed as the average number of tillers per seedling ($F_{1,23} = 23.7$, $P = 0.0001$).

NUMBER OF RECRUITS

The final number of seedlings at the end of the experiment ranged from 0 to 69 between plots. The factors fire and competitors significantly influenced the number of recruits (Table 7, Fig. 7c). Burning enhanced the number of recruits

Fig. 8. Summary of the influence of the presence of competitors, fire, irrigation, seed addition and the interaction between competitors and fire on different stages in the recruitment process from the start of the growing season to the end of the dry season and on the final number of recruits. It is shown which of the experimental factors significantly ($P < 0.05$) act on the different components of the recruitment process. '+' indicates a positive effect whereas '-' indicates a negative effect; '0' indicates no significant effect ($P > 0.05$). The factor irrigation was not tested for the variable emergence.



whereas the presence of established competitors reduced the number of recruits. There were no recruits at the end of the experiment on plots where established competitors were present and where fire was excluded. The number of recruits was not significantly affected by the factors seeds and irrigation or by the two-way interactions ($P > 0.05$).

STAGES OF RECRUITMENT

As summarized in Fig. 8, the presence of mature competitors significantly suppressed every single step in the recruitment process, whereas the interaction between burning and the presence of established competitors had a positive effect particularly during early stages of the recruitment process. Seed addition positively affected the first stage (emergence) but played no further role in the following stages of the recruitment process. Similarly, the positive influence of irrigation on survival in the growing season did not influence survival rates over the dry season. By contrast, the positive effect of burning was particularly apparent during the later stages in the recruitment process.

Discussion

The theoretical importance of recruitment processes for ecological dynamics is well established (Harper 1977). The intricacy of the recruitment process (Grubb 1977), however, ensures that quantifying the relative importance and interactive effects of the putative driving forces on recruitment processes is challenging. In this study we address these difficulties by using a full factorial experimental design to elucidate the interactive effects of fire, competitors, irrigation and seed availability on different stages of the recruitment process in a semi-arid savanna.

As expected from the literature on recruitment in perennial grasses (e.g. Gurevitch 1986; Moloney 1990; Aguilera & Lauenroth 1993; Defossé *et al.* 1997; Milton & Dean 2000), the presence of established vegetation severely hindered every stage of the recruitment process. An unexpected result was that irrigation and seed addition did not stimulate recruitment. This finding contradicts the literature on recruitment in dryland grasses, which has shown water availability to limit recruitment to years of above average rainfall (e.g. Potvin

1993; Lauenroth *et al.* 1994; Bisigato & Bertiller 2004) and to seed availability (e.g. O'Connor 1996; Hamilton *et al.* 1999). Our investigation of several stages of the recruitment process allows us to demonstrate that seed addition only enhanced recruitment at the emergence stage, whereas irrigation only affected seedlings during the growing season. Both factors are of subordinate importance in our study system as they had no effect on the final number of recruits and did hence not sustain their positive influence throughout the recruitment process. The strong positive influence of burning on the recruitment process is somewhat surprising, particularly because burning has in tropical, semi-arid grasslands been described as having a negative effect on grassland vigour (Bennett *et al.* 2002; Snyman 2004b). In the sections that follow we discuss these recruitment filters and their controls on the different stages of the recruitment process.

Cues of seedling emergence found in our study mostly agree with findings from other studies. We observed a single wave of seedling emergence after the first heavy rainstorms of the growing season (80 mm within 3 days, Fig. 2), a phenomenon also reported from other grass species where most germination occurs in response to the first major rainfall event (e.g. Mott 1978; McIvor & Gardener 1991; Ash *et al.* 1997), stressing the importance of soil moisture availability for grass seeds to germinate and emerge (e.g. Wilson & Briske 1979; Maze *et al.* 1993; Defossé *et al.* 1997; Hamilton *et al.* 1999). After this event, not even rainstorms of 40 mm triggered emergence, even though it is known that 40 mm can trigger seedling emergence of *S. uniplumis* in semi-arid Kaokoland (Zimmermann, unpublished data).

Our result that the addition of seeds enhanced emergence rates is in agreement with other experimental studies in perennial grasslands (Fowler 1986b; O'Connor 1996; Hamilton *et al.* 1999; Wilsey & Polley 2003). This phenomenon is often attributed to limited seed set in the previous year or to seed predation (Capon & O'Connor 1990; Kerley 1991; O'Connor 1991; Linzey & Washok 2000; Kelt *et al.* 2004).

In agreement with results from other studies on perennial grasses (e.g. Moloney 1990; Aguilera & Lauenroth 1993) we found the presence of established competitors to severely suppress seedling emergence. In semi-arid environments competition appears to be mainly for below-ground resources (Fowler 1986a; Casper & Jackson 1997), and some studies

have attributed reduced seedling emergence to below-ground competition and associated reductions in resources (e.g. Moloney 1990; Aguilera & Lauenroth 1993). It is unlikely that reduced soil moisture due to below-ground competition would have limited seedling emergence in our experiment. This is because perennial grasses have been reported to germinate when the soil remains wet for two to four consecutive days (Wilson & Briske 1979; Lambert *et al.* 1990) and in our study the soil remained saturated for more than 7 days preceding emergence. We therefore suggest above-ground competition to have limited emergence rates in our experiment. When the above-ground vegetation was removed by either burning or complete removal of competitors, more seedlings emerged. This might be because open habitat patches enhance light availability and create more heterogeneous temperatures compared to a closed vegetation canopy (Old 1969; Lock & Milburn 1970). Germination of several grass species have been reported to be enhanced by changes in the temperature regime (Lock & Milburn 1970; Hagon & Groves 1977; Baskin & Baskin 1998) and suppressed when light is filtered through green leaves (Lock & Milburn 1970; Gorski *et al.* 1977; Gorski *et al.* 1978) or litter (Wilsey & Polley 2003).

In contrast to other studies reporting either stimulation of seedling emergence via smoke-derived compounds (Baxter *et al.* 1994; Read *et al.* 2000; Williams *et al.* 2005), or suppression by dry heat which destroys seeds (Westoby *et al.* 1988; Zacharias *et al.* 1988; Ernst 1991), our study reveals no such direct impact of fire. **Fire stimulated seedling emergence only indirectly by the removal of above-ground vegetation, which is consistent with findings reported for other perennial savanna grasses such as *Themeda triandra* (Lock & Milburn 1970) and *Heteropogon contortus* (Tothill 1969).**

The survival of seedlings through the growing season was, in our study, significantly affected by irrigation. In agreement with findings of other studies on perennial grass seedlings, irrigation significantly enhanced survival rates through the growing season (Potvin 1993; O'Connor 1996). Because irrigation treatments were applied in periods of low rainfall, these results support the conclusion of Lauenroth *et al.* (1994) that it is not only the annual amount of rainfall but also the intra-seasonal distribution of rainfall that affects seedlings.

The survival of seedlings through the growing season was negatively affected by the presence of competitors. Reduced survival rates of grass seedlings in the presence of competitors is generally related to water limitations due to below-ground competition (Gurevitch 1986; Moloney 1990; Aguiar *et al.* 1992; Aguilera & Lauenroth 1993; Defossé *et al.* 1997).

We found, as have others, that fire significantly enhanced seedling growth (Scanlan 1980; Silva *et al.* 1990). This may be an effect of enhanced light availability due to the removal of above-ground vegetation (Old 1969; Lock & Milburn 1970) or an effect of chemical changes in the soil and its nutrient status (Daubenmire 1968; Blank *et al.* 1994; Busso 1997). Although grass seedling growth is reported to be enhanced by water supplementation (O'Connor 1996), irrigation had no major effect on seedling growth rates in our study. Irrigation

only enhanced seedling growth if the seedlings were subject to the presence of established competitors. Hence it appears that the amount and distribution of rainfall was sufficient for seedling growth. The negative impact of competitor presence on growth rates observed in our experiment was also reported in other studies in dry grasslands (Cook & Ratcliff 1984; Gurevitch 1986; Moloney 1990; Aguiar *et al.* 1992; Aguilera & Lauenroth 1993) and these authors attribute the effects to below-ground competition for water or nutrients.

The number of flowering seedlings was positively influenced by burning and irrigation and suppressed by the presence of competitors. These findings are in agreement with studies reporting fire to enhance the reproductive output of perennial grasses (Old 1969; Scanlan 1980; Silva *et al.* 1990; Sarmiento 1992; Vilà *et al.* 2001), with studies that have shown that lower amounts of rainfall can limit seed set (Knapp 1984; Dye & Walker 1987; O'Connor & Pickett 1992; Hamilton *et al.* 1999) and that competitors can limit flowering of perennial grasses (Gurevitch 1986). Most of these studies however investigated mature individuals, whereas we found perennial grass seedlings to flower in the first season.

Similarly, the number of reproductive tillers per seedling was influenced by burning and by the presence of competitors, irrigation, however, had no effect. While burning enhanced both the number of flowering seedlings as well as the number of reproductive tillers, irrigation only enhanced the number of seedlings that flower but had no quantitative effect. Because irrigation neither enhanced growth rates nor survival of the dry season, most of the irrigated seedlings that were not subjected to other treatments remained small, produced only one reproductive tiller and then died during the dry season, hence performing the life cycle of an annual grass plant. This strategy under a scenario of above average rainfall, stresses the importance of generative recruitment in this species. The survival of seedlings from the start to the end of the dry season and the final number of seedlings was in our study solely influenced by fire and by competitors. Hence, the positive effects of seed addition and irrigation observed on earlier stages of the recruitment process were not sustained throughout the recruitment process. In principle, as large grass seedlings have better survival rates because they are more resistant to desiccation (Fowler 1988; Silva & Castro 1989; O'Connor 1996), growth responses occurring in the growing season indirectly influence survival over the dry season. But since irrigation during the growing season promoted only survival but not growth, it probably only delayed the fate of seedlings but did not alter it. McDougall (1989) reports similar results where irrigation improved seedling performance during the watering period but did not enhance the number of new recruits. By contrast, fire enhanced growth and hence size of seedlings. In our study, no seedlings survived the dry season if competitors were present and fire was excluded. Seedling recruitment is therefore predominately hindered by the presence of competitors, even in a year of average amounts of rainfall. Previous studies (McDougall 1989; Moloney 1990; Potvin 1993) found few or no perennial grass seedlings to establish amongst mature individuals.

Conclusions

This study shows for the first time how the factors fire, competitors, moisture and seed availability, each of which is known to influence recruitment in grasslands, interactively influence different stages of the recruitment process. Our results point to the overwhelming negative influence of the presence of established vegetation on almost every stage of the recruitment process investigated. The factorial nature of our experimental design allowed us to show how fire and the removal of established vegetation served to open up the grass canopy and thereby enhance almost every step in the recruitment process. Seed addition and irrigation influenced only early stages in the recruitment process, but did not influence the final number of recruits produced. **The weak effect of irrigation was particularly surprising, because numerous previous studies have hypothesized recruitment in arid systems to be limited to above average rainfall years.** Our study is the first to suggest that average rainfall is adequate for recruitment in arid systems. Similarly, while seeds are assumed to be limiting in arid grasslands, we show that although seed addition influenced the number of seedlings, it did not influence the final number of recruits.

Our results imply that infrequent fires in semi-arid regions can be used to remove above-ground vegetation and thereby enhance rates of recruitment. **In these systems a reduction in perennial grass cover or mortality of mature individuals due to fire seems to be demographically compensated by more frequent grass seedling recruitment.** Hence fire can play an important role in population turnover in perennial grasses. Our findings have consequences for management, in particular in conservation areas where it is difficult to manage grazing by natural herbivores and burning is the only practical means of opening up the grass layer.

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