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Population ecology of a dominant perennial grass: recruitment, growth and mortality in semi-arid savanna

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Declaration

This thesis comprises three scientific studies which cover experimental approaches to identify key environmental factors influencing the demography and the individual production of a perennial savanna grass. Owing to the cumulative form of this thesis, part two, three and four are written as independent papers and do therefore overlap in the description of the study species and the study area. The idea to publish every single chapter with co-authors is the reason why the chapters are written in the first person plural. Nonetheless, all results presented here resulted from work that has been done independently by the author of the thesis.

Contents

Summary

Savannas are among the world's major terrestrial ecosystems but are also anticipated to be among the ecosystems that are most sensitive to future changes in land use and climate. Therefore, a thorough understanding of factors that structure savanna communities is required to guide management efforts.

This thesis aims to contribute to a mechanistic understanding of savanna determinants and functioning. Focus is laid on the dynamics of the perennial grass layer which has up to now mostly been regarded from a plot-level perspective, as a super-individual or as 'green slime' (an amorphous box of biomass) whose dynamics are driven solely by growth and decomposition rates. This study explores grasslayer dynamics from the perspective of the individual plant, and therefore adopts an individual-based multi-factorial approach to reveal new perspectives about the impact of ecological drivers and to fill knowledge gaps on perennial grass demography. Therefore, I experimentally explore the most important life history stages of the perennial semi-arid savanna grass *Stipagrostis uniplumis* in its natural environment (Etosha National Park), at a site where it is essentially mono-dominant. The life history stages investigated are: recruitment, growth/production and mortality.

All stages of the recruitment process were found to be highly density-dependent and triggered by events that open up the grass canopy and reduce the abundance of competitors. In contradiction to existing theory, seed and moisture availability did not constrain seedling recruitment; rather, the removal of competitors and burning exerted a crucial positive role for recruitment rates. Similarly, individual production rates were highly dependent on local density, and were higher on a recently burned site as opposed to sites with longer fire intervals. Individual mortality was substantially increased by the amounts of standing dead biomass and by competitor abundance. Fire was also found to enhance mortality.

The results highlight the importance of individual-based studies in perennial grassland, showing that perennial grass population processes in a natural environment are highly density-dependent. This role of local density cannot be assessed by plot-level approaches.

Current syntheses of savannas state fires to adversely affect the grass layer in dry savanna because of losses in cover or total biomass production. The individual-based approach of this thesis however revealed burning, by reducing density levels, to play a crucial positive role for grass health and population turnover. Reductions in total biomass or individual numbers after fire are compensated by enhanced individual production and recruitment rates. Suppressing fires will reduce the vitality of perennial grass populations. Hence, this thesis reveals new insights into how savannas function and how they should be managed. In conclusion, the results imply that current grazing and rainfall based paradigms of arid savanna functioning need to be revisited, and the factor fire as well as density-dependent processes need to be included in future mechanistic models.

Part 1

General Introduction

Savannas are among the world's major terrestrial ecosystems. They cover around 20% of the earth's land surface and 40% of the African continent (Van Wilgen *et al.* 2000; Getzin 2002). They differ from forests and deserts through the dual significance of grasses and woody plants (Walker 1985) and support a unique and large number of highly specialized plant and animal species. Savannas are of great importance to human economies as they provide a broad range of ecosystem services and are the source of livelihood of a large and rapidly growing proportion of the world's human population (Scholes & Archer 1997).

Because savannas are anticipated to be among the ecosystems that are most sensitive to future changes in land use and climate (Sala *et al.* 2000; Bond *et al.* 2003), a thorough understanding of factors that structure savanna vegetation is urgently needed to guide management efforts (Sankaran *et al.* 2005).

Two major issues challenge savanna ecologists: theoretical models focus on the determinants of savanna structure and functioning, whereas applied savanna research focuses on limits to the carrying capacity of rangeland. Both approaches have traditionally regarded the grass layer, which represents 75–90% of the total biomass in tropical savanna ecosystems (Frost *et al.* 1986 in Garnier & Dajoz 2001), as one 'super-individual' or as a 'green slime' whose dynamics are driven solely by growth and decomposition rates. Theoretical models include demographic stages of trees (e.g. Jeltsch *et al.* 1996; Higgins *et al.* 2000) but not of grasses.

Few models, however, do consider grass layer productivity on an individual level (Tews *et al.* 2006; Boulain *et al.* 2006; Meyer *et al.* 2007), but here individual productivity is often extrapolated. Empirical rangeland studies mostly adopt plot-level approaches, where changes in cover or biomass production are expressed per area but not per individual (e.g. Le Houérou 1989; Keya 1998; Fynn & O'Connor 2000; Ward & Ngairorue 2000; O'Connor *et al.* 2001; Snyman 2003, 2004b; Augustine & McNaughton 2006). Little is known about the demography of savanna grasses (O'Connor & Everson 1998; Garnier & Dajoz 2001). For southern Africa, O'Connor & Everson (1998, p. 335) go as far as to state that 'study of the population dynamics of African grasses is limited, fragmentary and still in its infancy'.

However, the demographic, individual-based perspective is needed for a predictive understanding of grass population dynamics. The few existing demographic studies on perennial grasses show how important the individual-based perspective is for understanding the dynamics of the grass layer (e.g. Silva & Castro 1989; Silva *et al.* 1990; O'Connor 1991c, 1994, 1996; Garnier & Dajoz 2001; Veblen 2008). Likewise, patterns of community dynamics and competition are most naturally modelled at the individual level (e.g. Tilman

1994; Grimm & Railsback 2005). So it is time to move beyond the 'super-individual' perspective and to gain a more mechanistic understanding of grass population dynamics. By adopting an individual-based approach, this thesis aims to contribute to a predictive understanding of grass population dynamics. Such information will not only improve management practices but will also improve the ability to predict the response of savanna grasslands to climate change. For this reason I performed a series of field experiments and explored a dominant perennial savanna grass (*Stipagrostis uniplumis*) from the individual-based, demographic perspective of population ecology.

I did this by studying environmental impacts on the most important stages in the life cycle of this grass and hence by focussing on recruitment, production and mortality. These three life stages were explored in three separate studies, which also constitute the three major parts of this thesis. The study area was chosen to lie within the semi-arid Etosha National Park in Namibia, because the aim was to investigate the species in a natural environment which is largely unaffected by anthropogenic disturbances.

In the following I will give a short introduction into savanna ecology. I will then present demographic studies on savanna grasses, point out knowledge gaps and introduce the aims of this study in more detail. Furthermore, I will introduce to the study area and the study species and present the main working hypotheses underlying this thesis.

1.1 Savannas – definition and ecological drivers

Savannas are tropical or near-tropical ecosystems which form a transient zone between rainforest and deserts (Bourlière 1983). They are structurally defined as ecosystems with a continuous herbaceous layer usually dominated by grasses or sedges and a discontinuous layer of woody species (Frost *et al.* 1986). The climatic definition of savanna comprises the chronological order of a warm wet season and a cool dry season, the latter usually being characterised by water stress (Frost *et al.* 1986; Walker 1987). In addition to these periods of water stress, consecutive years of extreme negative rainfall anomalies (meteorological drought) are more common in savannas than in adjacent forested areas (Bourlière 1983). Hence, the climate in savannas can best be described as one of extremes with contrasting climatic conditions not only within a year but also between years (Frost *et al.* 1986).

Savannas are generally found in areas receiving between 200 and 1800 mm rain per year (Johnson & Tothill 1985) and are often distinguished into high-rainfall and low-rainfall savannas. Although most authors avoid defining a clear cut-off line between the two extremes (e.g. Walker 1985; O'Connor

& Everson 1998; Sarmiento 1992), Huntley & Walker (1982) classified dry (or arid) and moist (or humid) savannas depending on the length of the dry season and the amount of annual rainfall. Hence, dry savannas are those systems that receive less than 650 mm rain per year and where the dry period lasts for at least six months. Sankaran *et al.* (2005) also found the 650 mm mean annual rainfall to cut off between stable and unstable savannas in Africa. In the dry and stable savannas (< 650 mm) the woody cover is constrained by water availability, whereas in the unstable moist (> 650 mm) savannas fire, soil properties and herbivory reduce the woody cover and hence allow grasses to persist in the presence of trees. The dry, stable savannas (< 650 mm) can be further subdivided into arid and semi-arid savannas at the 400 mm isohyets (Le Houérou 1984; Bothma 1996 in Getzin 2002).

Besides climate, there are other factors that influence savanna dynamics, namely fire, herbivory and nutrients (Frost *et al.* 1986; Frost & Robertson 1987; Skarpe 1992; O'Connor & Everson 1998; Sankaran *et al.* 2005). Fires usually occur at the end of the dry season with the start of the rains when ignition by lightning is high and when grasses are still dormant and the moisture content of the foliage is low (Siegfried 1981; Du Plessis 1997). The extended dry periods in savannas have caused fires to be an ancient phenomenon in the biome and the lack of natural firebreaks in savanna regions allows fires to cover large areas. Fire frequency decreases with decreasing rainfall from virtually annual in the moist savannas to irregular in the dry savannas with a frequency of as low as every 20 to 30 years (Walker 1985, Etosha Ecological Institute, *unpublished data*).

In natural savannas herbivory by large indigenous mammals has spatially and temporally restricted influence on vegetation dynamics (Sinclair *et al.* 2007), but today many formerly natural savannas are managed for the production of domestic livestock (Skarpe 1992). In dry savannas, livestock is in most cases supplemented with water, which leads to high animal densities and to a reduced animal mobility with strong impact on vegetation (Skarpe 1992). However, there is a lively discussion among rangeland ecologists (reviewed by Vetter 2005), whether livestock populations in arid savannas reach levels likely to cause irreversible damage to the vegetation. Disequilibrium theoreticians argue that droughts frequently cause livestock herds to collapse – enough to preclude animals from negatively influencing vegetation (Ellis & Swift 1988; Ellis *et al.* 1993).

Both, moist and dry savannas are associated with specific ecological drivers. In general, fire is proposed to be the major environmental driver in moist savannas, whereas in dry savannas precipitation and grazing are said to be the main driving events (e.g. Walker *et al.* 1981; Huntley & Walker 1982; O'Connor & Everson 1998; Fuhlendorf *et al.* 2001). Fire is rarely regarded

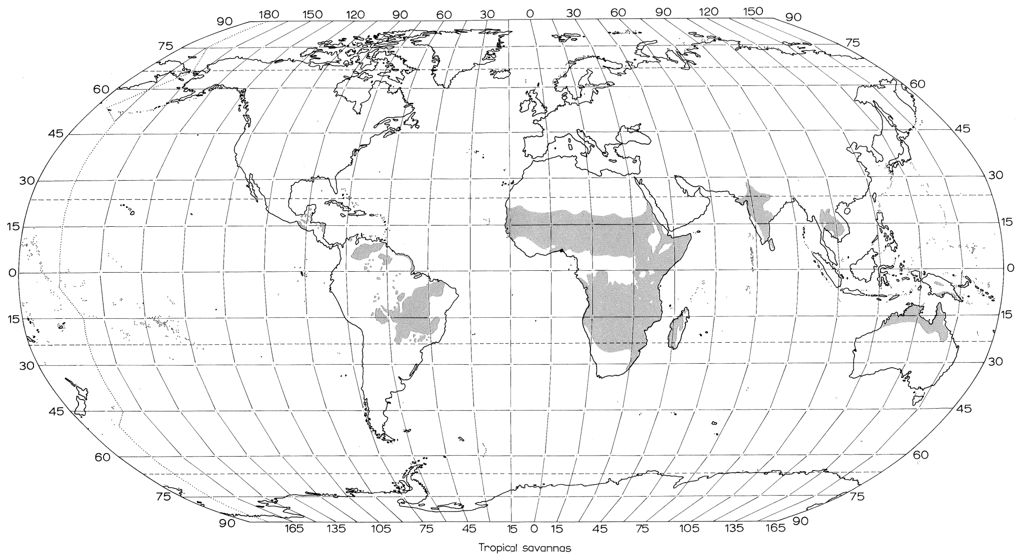

Figure 1.1: World distribution of tropical savannas (from Lamotte & Hadley (1984) after Bourlière 1983)

as an important factor in the dry savannas (Walker *et al.* 1981; Van Wilgen & Scholes 1997).

1.2 Demographic studies on perennial savanna grasses: state-of-the-art

Plant population ecology is concerned with birth and death processes (Harper 1977). Between these two events a plant grows and produces biomass. Because different kinds of plants may be most strongly regulated at different life history stages (Goldberg *et al.* 2001) it is important to understand the ecological drivers that influence the most important stages in the life cycle of a plant: birth (recruitment), growth (production) and death (mortality). The primary ecological drivers 'climate', 'fire' 'and herbivory', recognized as influencing savanna vegetation dynamics, were introduced in the previous chapter.

Although there is still a general lack of information on the impact of these drivers or other ecological factors on perennial grass population ecology (O'Connor & Everson 1998; Garnier & Dajoz 2001), some insight has accumulated which I will present regarding recruitment, mortality and production of perennial grasses:

- Recruitment is in dry grasslands primarily triggered by rainfall amounts and frequency (e.g. Potvin 1993; Lauenroth *et al.* 1994; Veenendaal *et al.* 1996; Bisigato & Bertiller 2004). Furthermore, recruitment of perennial grasses was found to be limited by competitor presence (Moloney 1990; Aguilera & Lauenroth 1993a; Defossé *et al.* 1997; Milton & Dean 2000) and seed availability (Hamilton *et al.* 1999; O'Connor 1996). Intense grazing also has a negative effect on perennial grass recruitment because grazers consume seeds and seedlings (O'Connor 1991a, 1994). The impact of fire on perennial grass recruitment was primarily studied in moist savanna, where frequent burning negatively affects recruitment rates because seedlings are killed in the fire (Mott & Andrew 1985; Silva & Castro 1989; Silva *et al.* 1990; Garnier & Dajoz 2001; Setterfield 2002).

- Mortality of perennial grass tufts is in dry savannas primarily reported after drought (Donaldson 1967; Danckwerts & Stuart-Hill 1988; Milton & Dean 2000; Hodgkinson & Muller 2005). Furthermore, intense grazing can enhance mortality rates of grass tufts (Grice & Barchia 1992; O'Connor 1993, 1994, 1995; Briske & Hendrickson 1998; Oliva *et al.* 2005). The impact of fire on tuft mortality was primarily studied in moist savanna where adult survival rates are generally high (Mott & Andrew 1985; Silva & Castro 1989; Silva *et al.* 1990; Garnier & Dajoz 2001), but where long-term fire exclusion experiments lead to enhanced tuft mortality due to plant senescence and accumulated litter which shades plants and reduces their vigor (Mott & Andrew 1985; Silva & Castro 1989; Silva *et al.* 1990).

- There are almost no data available on perennial grass production at an individual level. Studies adopting the plot level perspective found production to be primarily affected by rainfall amounts and distribution (e.g. Dye & Walker 1987; Fynn & O'Connor 2000; O'Connor *et al.* 2001), by soil nutrients (Morgan 2007) and by grazers (e.g. Keya 1998; Fynn & O'Connor 2000; Augustine & McNaughton 2006). Also on plot level, fires were found to adversely affect production in dry grasslands (Bennett *et al.* 2002; Snyman 2003, 2004b).

To sum up, a few empirical studies have examined the influence of ecological factors on individual-based processes in perennial savanna grasses but the existing knowledge is incomplete. Particularly information on individual production and density-dependence of population processes is scarce due to the tradition of plot-level studies. This is particularly surprising because in other ecosystems the role of local density in population processes, and hence, the importance of individual-based studies, is highly recognised, e.g. for tree growth (Nishimura *et al.* 2003; Newton 2006; Coomes & Allen 2007; Stoll & Newbery 2005) and tree mortality (Peters 2003; Hubbell *et al.* 2001) in forest ecosystems. Knowledge of the role of fire for grass populations in dry savannas is also fragmentary, although fires occur regularly not only in moist but also in these dry ecosystems (Everson 1999; Siegfried 1981). Since fire can be managed, a better understanding of its ecological effects would be extremely valuable (Frost *et al.* 1986).

While the previous paragraphs have reviewed the effects of several factors, it should be emphasized that most of these insights came from empirical studies that concentrate on only one or two factors in isolation, although it is known that savanna determinants interact in various ways (e.g. Frost *et al.* 1986; Skarpe 1992; O'Connor 1996; Jeltsch *et al.* 2000).

1.3 Study area and study species

Work for this thesis was conducted in the Etosha National Park (hereafter 'Etosha') which is situated in north-central Namibia and comprises an area of 22,915 km^2 (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 described as 'shrub mopane on loamy soils' (Le Roux *et al.* 1988). Du Plessis (1999) defines the area as 'shrub and low tree savanna', where woody crown cover ranges from 25 to 50%. The woody layer is almost exclusively dominated by *Colophospermum mopane* (Kirk ex Benth.) shrubs, other woody species include *Catophractes alexandri* (D. Don) and *Dichrostachys cinerea* (Forssk.). The herbaceous layer is dominated by the perennial grass *Stipagrostis uniplumis* var. *uniplumis* (Licht. ex Roem. & Schul.) which constitutes more than 90% of the herbaceous vegetation cover. The grass species *Schmidtia pappophoroides* (Steud. ex J. A. Schmidt), *Melinis repens* (Willd.), *Pogonarthria fleckii* (Hack.), and herbaceous dicotyledons such as *Commelina forskaolii* (Vahl) and *Gisekia africana* (Lour.) constitute the remaining cover. Average annual rainfall is around 380 mm and variation in annual rainfall is 30–40%, (Mendelsohn *et al.* 2002; Etosha Ecological Institute, *unpublished data*). Grazing pressure in this area is very low, as grazers occur in very low densities (Craig 1998; Erb 2000; Kilian 2002; Kolberg 2004).

An analysis of soil samples revealed a relatively homogeneous soil texture of ca. 85% sand, 4% silt and 11% clay in the research area (*Part 2, this thesis*).

The study species *Stipagrostis uniplumis* var. *uniplumis* (hereafter '*S. uniplumis*') is a perennial tufted C4 grass which grows on sandy soils in arid parts of Africa. I chose this particular species because it dominates the grass layer over large areas, it is the most common of the *Stipagrostis* species and it is considered a valuable grazing grass (Malan & Owen-Smith 1974; Van Oudtshoorn 2002). Because of its wide distribution and local dominance it is important for forage and soil stabilisation (Malan & Owen-Smith 1974; Van Oudtshoorn 2002; 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.

1.4 Aims, experiments and hypotheses

This thesis aims to contribute to a predictive understanding of the dynamics of the savanna grass layer and therefore focuses on the most important stages in the life cycle of a dominant perennial savanna grass. The different parts of this thesis aim to fill knowledge gaps on demographic processes and therefore adopt an individual perspective which takes cognisance of density-dependence.

I performed multi-factorial experiments and analyses, where special focus was laid on the neglected factor 'fire' in influencing perennial grass population dynamics. Hence, I investigated the combined roles of landscape-scale (e.g. fire, rainfall) and local-scale factors (e.g. neighbour abundance, seed availability, self shading) on recruitment, production and mortality of the perennial semi-arid savanna grass *Stipagrostis uniplumis.*

The three main working hypotheses are:

- Demographic processes in savanna grasses are density-dependent.
- Productivity at the individual level is density-dependent.
- Fire is an important ecological driver also in dry savanna, which positively affects the perennial grass populations by reducing density-dependent effects.

The following three parts of this thesis focus on recruitment, production and mortality:

Part 'Recruitment'. I explored recruitment using a multi-factorial experiment that aimed to identify key factors which influence the various stages of the recruitment process. Hence, I investigated the combined roles of seed and moisture availability, fire and competitor presence on emergence, growth, flowering and survival rates of *S. uniplumis* seedlings.

Part 'Production'. The study on grass production adopted an individual-based perspective. Essential to this approach is to take cognisance of density-dependence. I hence investigated how neighbour abundance influences production and described the shape and the spatial extent of this relationship. To explore the influence of fire, I measured individual production at three sites that differ in fire history.

Part 'Mortality'. I determined mortality as influenced by fire, neighbour abundance and plant size. Furthermore, the impact of self-shading was assessed by comparing plants with different amounts of standing dead biomass.

Overall, this thesis demonstrates that the demographic, individual-based perspective is essential for a predictive understanding of the dynamics of the savanna grass layer. Current paradigms of how dry savannas function and how they should be managed are based on studies that do not consider the actual unit of a population – the individual – and hence ignore density-dependent effects. Results of this thesis will significantly challenge these paradigms by detecting the overriding effect of local density on all population processes investigated. Current synthesis suggests that rainfall and herbivory are important in determining grassland health. This thesis shows, by taking an individual-based perspective, that density-dependence and fire are in fact also critical parameters for understanding grassland health and dynamics. By revealing new insights into the relative importance of ecological drivers, particularly the role of fire, this thesis contributes to a mechanistic understanding of the ecology of dry savanna, with implications for their sustainable utilisation and management.

Part 2

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

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[*] A slightly different version of this part is published in *Journal of Ecology* (Zimmermann *et al.* 2008); http://www3.interscience.wiley.com/journal/120735539/abstract

Abstract

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.

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.

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 use a full-factorial experiment to determine how these four factors influence emergence, growth, survival and flowering of seedlings.

Our results show that all of the factors affect some stage of the recruitment process but not all significant effects contribute to enhancing the final number of recruits. 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. Fire acted similarly to the removal of competitors; that is, it positively affected seedling emergence, growth, flowering and survival.

Synthesis: we conclude that – in contradiction to existing theory – 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.

2.1 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). He 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 1991b; 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 1991b; 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 explored the impact of one or two factors, or they have focussed 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), semiarid (Aguilera & Lauenroth 1993b; 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 2003, 2004a).

This study aims to develop a detailed understanding of the combined effect of all these 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 virtually 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.

2.2 Materials and methods

2.2.1 Study area and study species

The Etosha National Park (hereafter 'Etosha') is situated in north-central Namibia and comprises an area of 22,915 km^2 (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 described as 'shrub mopane on loamy soils' (Le Roux *et al.* 1988). Du Plessis (1999) defines the area as 'shrub and low tree savanna', where woody crown cover ranges from 25 to 50%. The woody layer is almost exclusively dominated by *Colophospermum mopane* shrubs, other woody species include *Catophractes alexandri* and *Dichrostachys cinerea.* The herbaceous layer is dominated by the perennial grass *Stipagrostis uniplumis* var. *uniplumis* which constitutes more than 90% of the herbaceous vegetation cover. The grass species *Schmidtia pappophoroides*, *Melinis repens*, *Pogonarthria fleckii*, and herbaceous dicotyledons such as *Commelina forskaolii* and *Gisekia africana* constitute the remaining cover. Average annual rainfall is around 380 mm and variation in annual rainfall is 30–40%, (Mendelsohn *et al.* 2002; Etosha Ecological Institute, *unpublished data*). Grazing pressure in this area is very low, as grazers occur in very low densities (Craig 1998; Erb 2000; Kilian 2002; Kolberg 2004). An analysis of soil samples revealed a relatively homogeneous soil texture of ca. 85% sand, 4% silt and 11% clay in the research area.

The study species *Stipagrostis uniplumis* var. *uniplumis* (hereafter '*S. uniplumis*') is a perennial tufted C4 grass which grows on sandy soils in arid parts of Africa. We chose this particular species because it dominates the grass layer over large areas, it is the most common of the *Stipagrostis* species and it is considered a valuable grazing grass (Malan & Owen-Smith 1974; Van Oudtshoorn 2002). Because of its wide distribution and local dominance it is important for forage and soil stabilisation (Malan & Owen-Smith 1974; Van Oudtshoorn 2002; 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% (Zimmermann, *unpublished data*).

2.2.2 Sampling design and parameters

The study was conducted in the 2004/2005 growing season and subsequent dry season. The study site covered a 500 x 500 m area which burned 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), Fire (burned or unburned), 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 2^4 design (16 treatment combinations).

The full-factorial design was replicated twice, resulting in 32 experimental units. Each experimental unit covered an area of 4 m^2 (2 x 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 x 500 m area (Figure 2.1), but 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

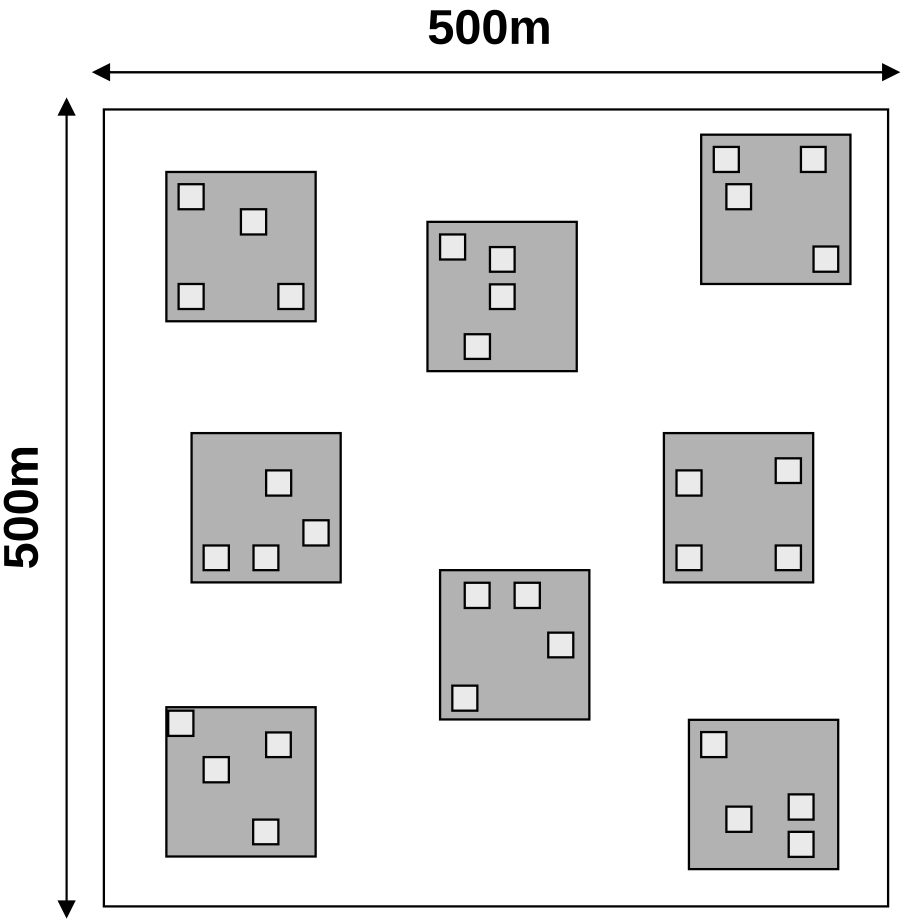


Figure 2.1: Representation of the experimental layout, comprising 8 blocks (dark grey) and 32 plots (2 x 2 m, light grey) spread over a 500 x 500 m area. Figure is not drawn to scale.

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

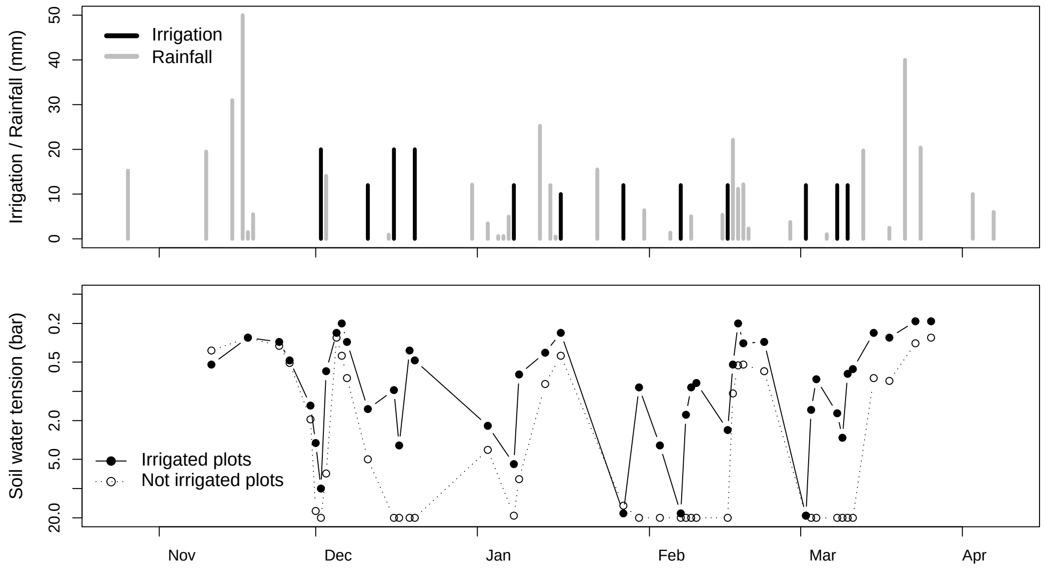


Figure 2.2: The amount of rainfall and irrigation (averaged over plots) during the growing season 2004/2005 and the consequent average soil water tension (bar) of the irrigated and non-irrigated plots

homogeneous with an average of 85.4% sand (s.d. = 5), 3.9% silt (s.d. = 2.7) and 10.7% clay (s.d. = 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 rrigation' was applied after the first heavy rainstorm in November 2004 (Figure 2.2). In the next paragraphs I describe the treatments following the order of their implementation:

Seeds. The two treatment levels were the naturally-occurring seed density in the soil seed bank, and the addition of 400 seeds that were added to the 4 m^2 of the plot. Seeds were placed 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 burned and unburned. All relevant plots were burned on the same morning under light wind conditions (< 2 m/s). To prevent the fire from escaping into the adjacent vegetation, we established a fire break of two meter 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 during the burn 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). In the fire all tufts 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 two weeks. This pattern of irrigation simulated a higher rainfall year but did not prevent the soil from occasionally drying out (Figure 2.2). All rrigation' 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. For each seedling the following parameters were measured at monthly intervals during the growing season (first survey on 01.12.2004; last survey on 30.03.2005) and again at the start of the next growing season: the coordinates, 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).

2.2.3 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 (Figure 2.1). 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 'seedling growth through the growing season' and 'survival through the growing season' included 'time' (the monthly sampling intervals) as an additional explanatory variable.

Because linear mixed effects 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 where needed to meet these assumptions ('number of emerged seedlings', 'seedling growth through the growing season' and 'number of flowering seedlings' were log transformed; 'number of reproductive tillers' and 'number of recruits' were square root transformed). Analyses of the residuals of the models fitted using these transformations revealed no deviations from the assumptions of linear mixed effects models as described by Crawley (Crawley 2002). All data were analysed using the software R 2.7.0 (R Development Core Team 2008).

2.3 Results

A total of 2649 seedlings emerged on the 128 m^2 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

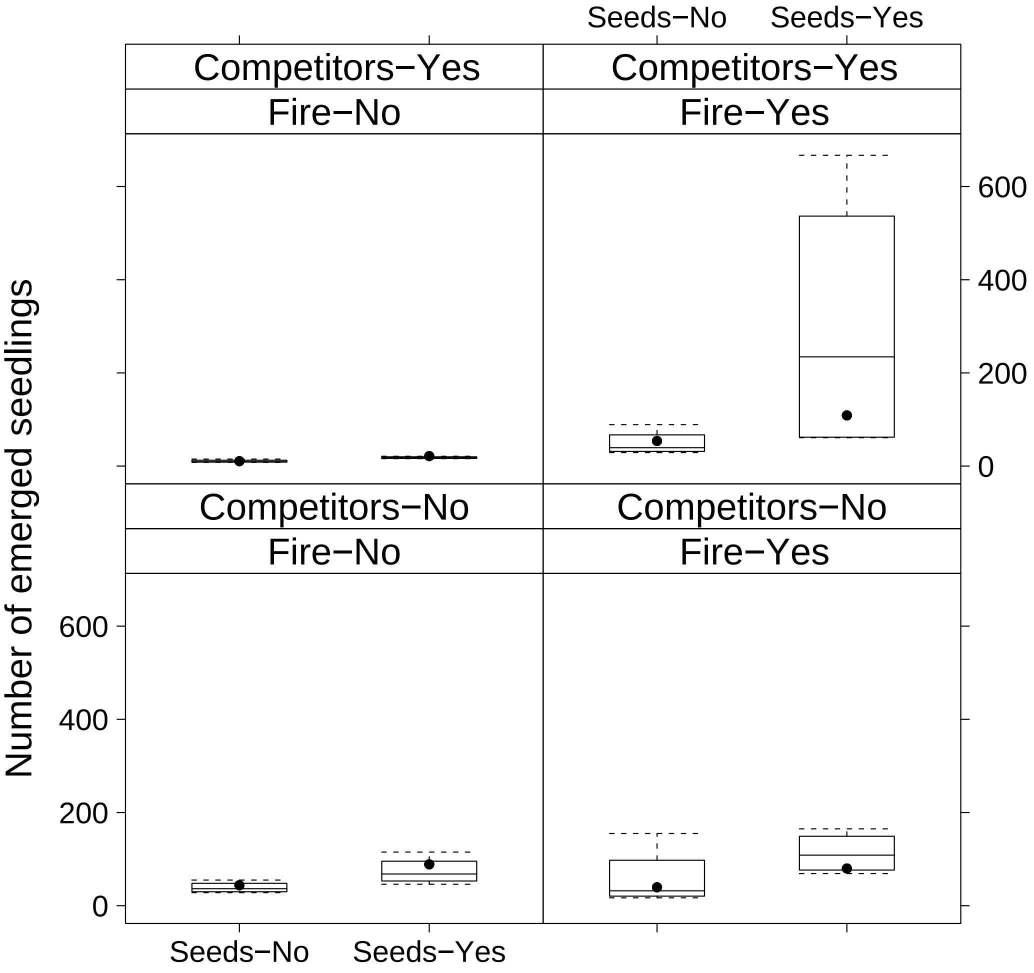


Figure 2.3: The number of emerged seedlings per plot in response to the presence of established vegetation (Competitors), burning (Fire) and seed addition (Seeds). Each variable has two levels (Yes and No). Box and whisker plots present the actual data, whereas points display predictions made using the minimal adequate model described in Table 2.1. Note that some of the variance in the data originates from the random factors which were considered in the minimal adequate model.

heavy rainstorms, at the start of the growing season (80 mm in three days, Figure 2.2). At the time of seedling emergence, the rrigation' treatment was not yet implemented. Therefore, we did not include the variable rrigation' in our statistical analysis of seedling emergence. We however emphasize that the rrigation' treatment did not trigger further seedling emergence during the course of the study.

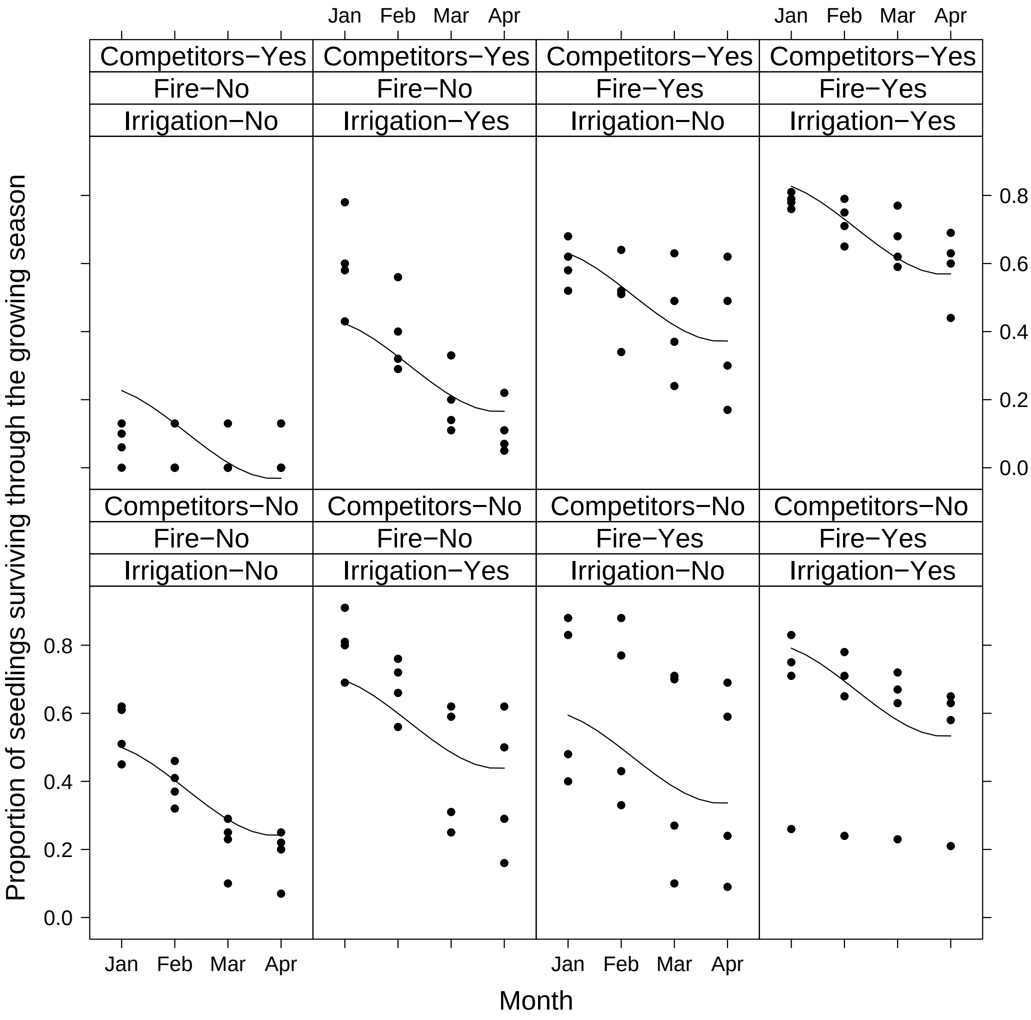


Figure 2.4: The proportion of seedlings per plot that survived through the growing season in response to the presence of established vegetation (Competitors), burning (Fire), moisture availability (Irrigation) and Time (monthly time steps). Each variable except Time has two levels (Yes and No). The points present the actual data, whereas the line displays the predictions, which are made using the minimal adequate model described in Table 2.2. Note that some of the variance in the data originates from the random factors which were considered in the minimal adequate model.

Emergence rates were significantly enhanced by the addition of seeds and severely lowered by the presence of established competitors (hereafter 'competitors') (Table 2.1, Figure 2.3). The main effect of fire was not significant, although there was a significant interaction between fire and the presence of 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 competitors (Table 2.2). Very few seedlings survived until the end of the growing season on plots where competitors were present and not burned (Figure 2.4). By contrast, irrigation as well as the combination of competitors presence and burning, significantly enhanced survival rates (Table 2.2, Figure 2.4). 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

Table 2.1: Minimal adequate linear mixed effects model (LME) 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	s.e.	d.f.	t-value	p-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

Table 2.2: Minimal adequate linear mixed effects model (LME) 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	Value	s.e.	d.f.	t-value	p-value
(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

survival through the growing season.

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 2.3). 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

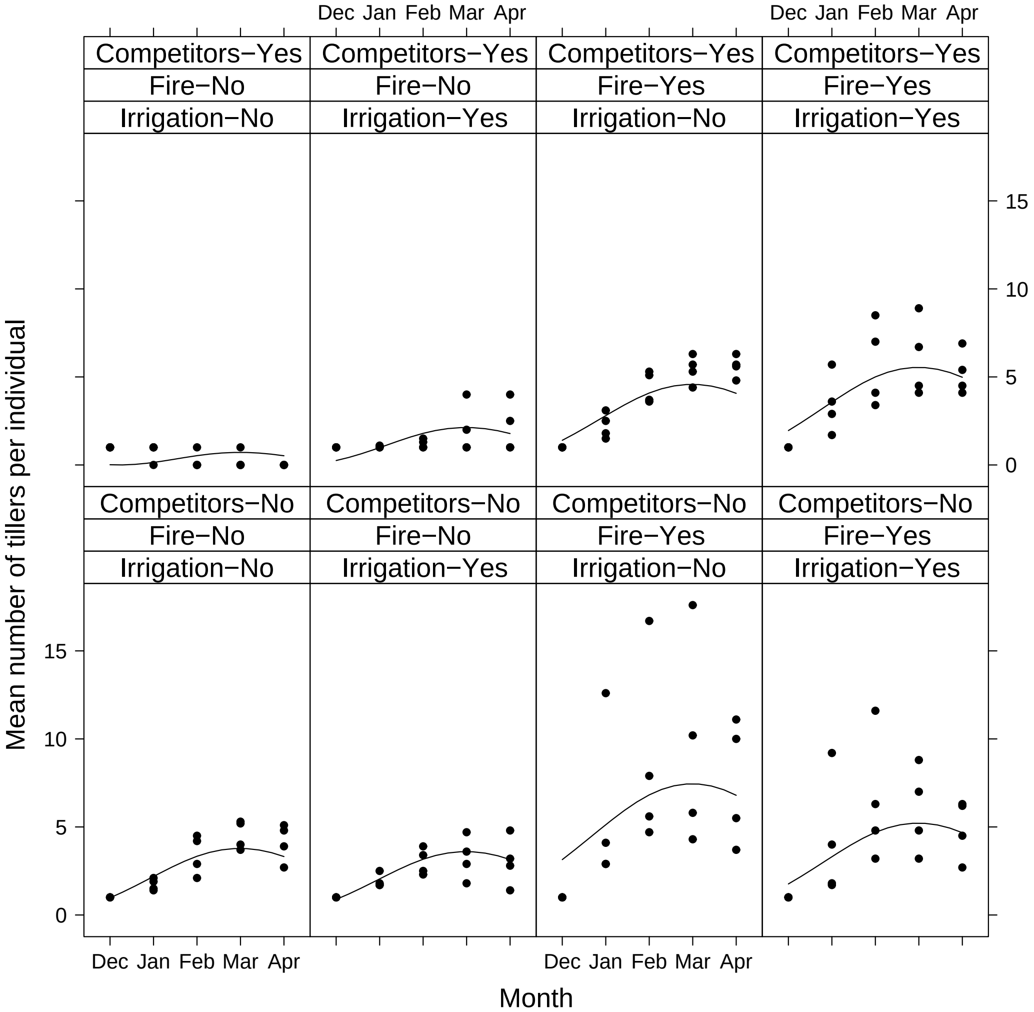


Figure 2.5: Growth as indexed by the mean number of tillers per seedling and plot, in response to the presence of established vegetation (Competitors), burning (Fire) and availability of water (Water) and Time (monthly time steps). Each variable except Time has two levels (Yes and No). The points present the actual data, whereas the line displays the predictions, which are made using the minimal adequate model described in Table 2.3. Note that some of the variance in the data origins from the random factors which were considered in the minimal adequate model.

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 competitors significantly suppressed growth (Figure 2.5). On the unburned plots, most seedlings subject to ‘competitors’ did not grow more than one or two tillers during the course of the growing season, whereas seedlings on the burned 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 burning and by irrigation, and signif-

Table 2.3: Minimal adequate linear mixed effects model (LME) 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	Value	s.e.	d.f.	t-value	p-value
(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
$\text{Competitors}_{yes}\text{:Fire}_{yes}$	0.509	0.228	19	2.229	0.038
$\text{Competitors}_{yes}\text{:Irrigation}_{yes}$	0.660	0.228	19	2.890	0.009

Table 2.4: Minimal adequate linear mixed effects model (LME) 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	Value	s.e.	d.f.	t-value	p-value
(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
$\text{Competitors}_{yes}\text{: Fire}_{yes}$	4.031	1.500	20	2.688	0.014

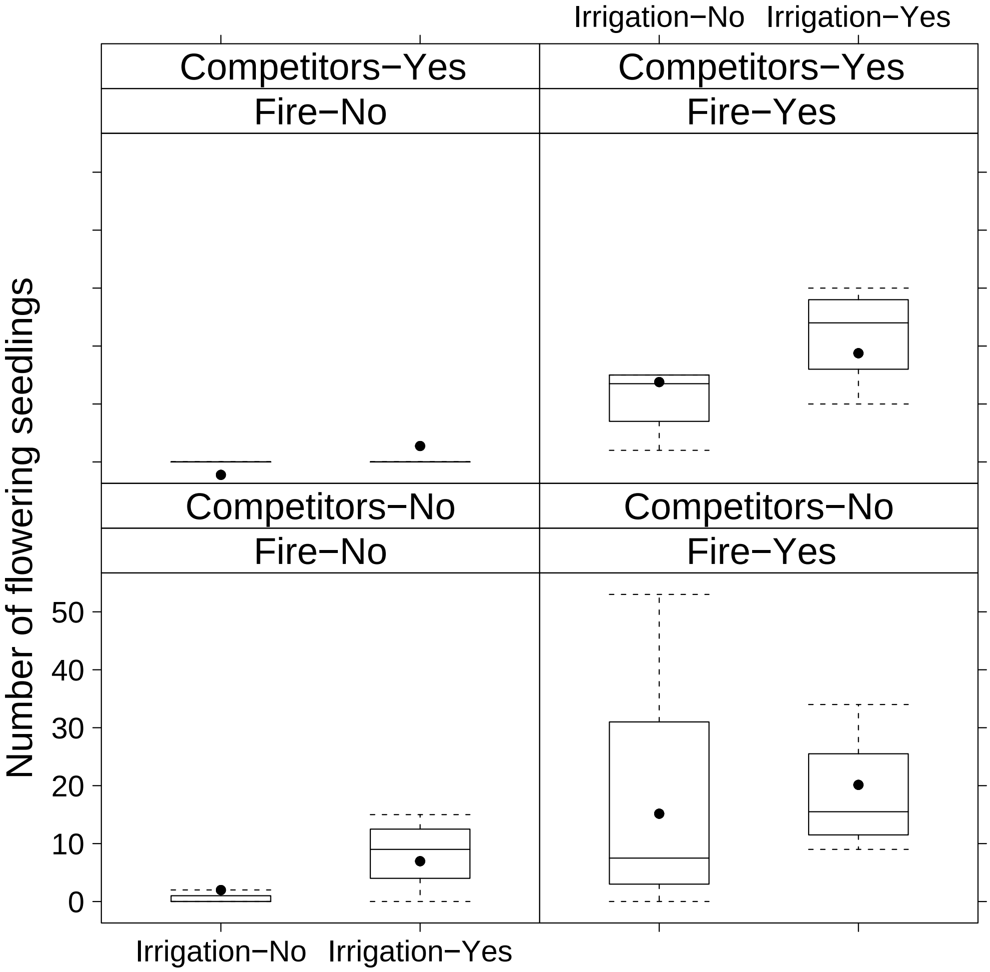


Figure 2.6: The number of flowering seedlings per plot at the end of the growing season in response to the presence of established vegetation (Competitors), burning (Fire) and irrigation. Each variable has two levels (Yes and No). Box and whisker plots present the actual data, whereas points display predictions, which are made using the minimal adequate model described in Table 2.4. Note that some of the variance in the data originates from the random factors which were considered in the minimal adequate model.

icantly reduced by the presence of competitors if the competitors remained unburned (see Table 2.4 and Figure 2.6). 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 reproduc-

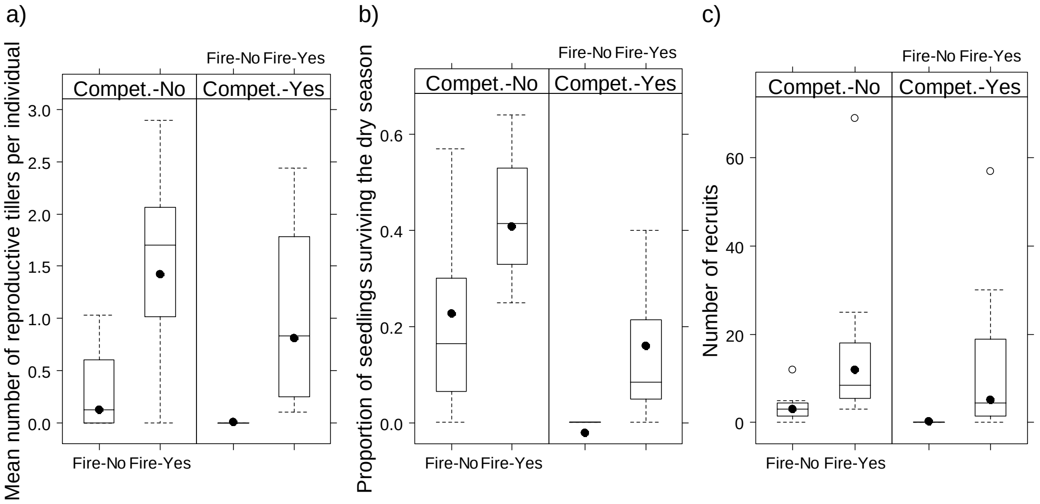


Figure 2.7: Each of the three response variables – a) mean number of reproductive tillers per seedling and per plot, b) proportion of seedlings of each plot which survived from the start to the end of the dry season and c) the number of recruits – in response to the presence of established vegetation (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 Table 2.5, Table 2.6 and Table 2.7. Note that some of the variance in the data originates from the random factors which were considered in the minimal adequate model.

tive tillers per seedling and plot ranged from 0 to 3 (Figure 2.7a). Burning significantly enhanced, and the presence of competitors significantly reduced the number of reproductive tillers per seedling (Table 2.5). 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 0–64% between plots. The factors 'fire' and 'competitors' significantly influenced seedling survival of the dry season. Burning significantly enhanced, and the presence of competitors significantly reduced seedling survival of the dry season (Table 2.6). No seedlings survived when competitors were present and fire was excluded (Figure 2.7b). By contrast, survival rates of seedlings not subject to 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 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 2.7, Figure 2.7c). Burning enhanced the number of recruits, whereas the presence of competitors reduced the number of recruits. There were no recruits at the end of the experiment on plots where 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 ($p > 0.05$).

Table 2.5: Minimal adequate linear mixed effects model (LME) 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.

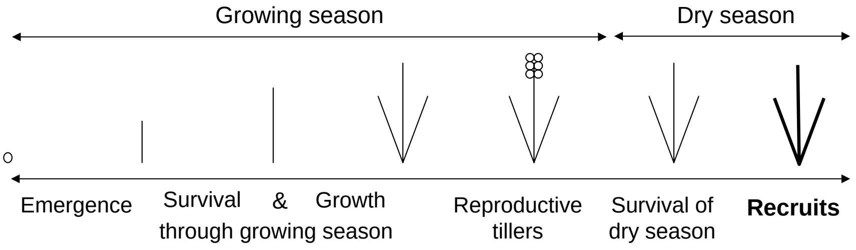
Parameter	Value	s.e.	d.f.	t-value	p-value
(Intercept)	0.349	0.130	22	2.681	0.014
Competitors$_{yes}$	-0.294	0.135	22	-2.170	0.041
Fire$_{yes}$	0.843	0.146	22	5.791	< 0.001

Table 2.6: Minimal adequate linear mixed effects model (LME) 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	s.e.	d.f.	t-value	p-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 2.7: Minimal adequate linear mixed effects model (LME) 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	s.e.	d.f.	t-value	p-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



	Emergence	Survival through growing season	Growth through growing season	Reproductive tillers	Survival of dry season	**Recruits**
Competitors	-	-	-	-	-	**-**
Fire	0	0	+	+	+	+
Irrigation		+	0	0	0	**0**
Seeds	+	0	0	0	0	**0**
Fire : Competitors	+	+	+	0	0	**0**

Figure 2.8: 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 rrigation’ was not tested for the variable ‘emergence’.

Stages of recruitment. As summarized in Figure 2.8, the presence of mature competitors significantly suppressed every single step in the recruitment process, whereas the interaction between burning and the presence of 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 of the recruitment process.

2.4 Discussion

The theoretical importance of recruitment processes for ecological dynamics is well established (Harper 1977). However, due to the intricacy of the recruitment process (Grubb 1977), quantifying the relative importance and interactive effects of the putative driving forces on recruitment processes is challenging. This study addresses 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 *et al.* 1990; Moloney 1990; Aguilera & Lauenroth 1993b; 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 that recruitment is limited by water availability – to years of above average rainfall (e.g. Potvin 1993; Lauenroth *et al.* 1994; Bisigato & Bertiller 2004) – and by seed availability (e.g. Hamilton *et al.* 1999; O'Connor 1996). Our investigation of several stages of the recruitment process demonstrates 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 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 in tropical, semi-arid grasslands has been described as having a negative effect on grassland vigour (Bennett *et al.* 2002; Snyman 2003, 2004b). In the following sections we discuss these recruitment filters and their controls on the different stages of the recruitment process.

Seedling emergence occurred in a single wave after the first heavy rainstorms of the growing season (80 mm within three days, Figure 2.2). This phenomenon has been 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 1986a; 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 1991b; Linzey & Washok 2000; Kelt *et al.* 2004).

In agreement with results from other studies on perennial grasses (e.g. Moloney 1990; Aguilera & Lauenroth 1993b) we found the presence of competitors to severely suppress seedling emergence. In semi-arid environments competition appears to be mainly for below-ground resources (Fowler 1986b; 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 1993b). 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 seven 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 has been reported to be enhanced by changes in the temperature regime (Lock & Milburn 1970; Hagon & Groves 1977; Baskin & Baskin 1998), and to be suppressed when light is filtered through green leaves (Lock & Milburn 1970; Gorski *et al.* 1977, 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 *et al.* 1990; Moloney 1990; Aguiar *et al.* 1992; Aguilera & Lauenroth 1993b; 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 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 *et al.* 1990; Moloney 1990; Aguiar *et al.* 1992; Aguilera & Lauenroth 1993b) 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 1984b; Dye & Walker 1987; O'Connor & Pickett 1992; Hamilton *et al.* 1999) and that competitors can limit flowering of perennial grasses (Gurevitch *et al.* 1990). 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 and the number of reproductive tillers, irrigation only enhanced the number of flowering seedlings, but had no effect on the number of reproductive tillers. 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 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.

2.5 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 demonstrate 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 hypothesised 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 seed availability is assumed to limit recruitment 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 may have consequences for management, in particular in conservation areas where it is difficult to manage grazing by natural herbivores and burning may be the only practical means of opening up the grass layer.

Part 3

Perennial grass production as influenced by neighbour abundance: an individual-based perspective

Abstract

Perennial grasses are a dominant component of many vegetation formations and provide important ecosystem services. Yet, most of our understanding of the factors influencing production of the grass layer in natural environments comes from plot-level studies, which ignore how local density influences production. This is particularly surprising as growth and production are recognised to be density-dependent in other ecosystems (e.g. forests).
Therefore, we use an individual-based approach to explore the aboveground net primary production of a perennial semi-arid savanna grass (*Stipagrostis uniplumis*) in its natural environment (Etosha National Park, Namibia). We describe how plant size and two measures of neighbour abundance influence individual production, and determine the shape and spatial extent of the competition kernel. Furthermore, we explore whether individual production differs at sites of different fire history and discuss whether the individual perspective reveals insights different from the plot-level perspective, regarding the role of fire.
Our results show that individual production significantly increases with plant size, whereas neighbour abundance has a significant negative impact. The data were better described by a measure of neighbour abundance that takes the size of neighbours (living basal area of neighbours) into account, than by a measure that is solely based on the number of neighbours. Concerning the role of fire, we found that production was highest for individuals at the recently burned site.
Our finding that individual production in perennial grasses is highly density-dependent suggests that the thinning of a sward can enhance its production. Burning may be an important management tool as it reduces competitive levels and enhances individual production. Due to the importance of local density for individual production, we conclude that individual-based studies are urgently needed to improve our understanding of the functioning of the perennial grass-layer in savannas and grasslands.

3.1 Introduction

Savannas and grasslands are among the world's major terrestrial ecosystems. In these systems, perennial grasses are crucial for the ecosystem's functioning in supporting herbivores and preventing soil erosion (Sala & Paruleo 1997; Van Oudtshoorn 2002). Yet, most knowledge of the grass layers functioning and productivity comes from plot-level studies, where mean field estimates of production are expressed per area and not per individual. Such plot-level approaches prevail in the context of field studies (e.g. Scholes & Walker 1993; O'Connor *et al.* 2001; Augustine *et al.* 2003), particularly in the context of range assessment (e.g. Le Houérou 1989; De Ridder & Breman 1993; Keya

1998; Ward & Ngairorue 2000; Snyman 2003, 2004b; Wessels *et al.* 2007), but also in simulation approaches (Weber *et al.* 1998; Higgins *et al.* 2000; Wiegand *et al.* 2004; Holdo *et al.* 2007; Müller *et al.* 2007). The few simulation studies that do consider individual production are forced to extrapolate because of a lack of field data (Tews *et al.* 2006; Boulain *et al.* 2006; Meyer *et al.* 2007).

The general lack of information on individual production in grasslands is particularly suprising, as only individual-based studies can take cognisance of density-dependence. In other ecosystems, the importance of individual-based studies is largely recognised and the role of local density for forest growth and production has been determined in various studies (e.g. Pacala *et al.* 1996; Huth & Ditzer 2001; Nishimura *et al.* 2003; Berger *et al.* 2004; Stoll & Newbery 2005; Rüger *et al.* 2007). Here, production is known to be maximised by thinning the stand to a density that allows each individual to grow in relatively competitor-free conditions (Newton 2006). Also in a broader context, individual-based perspectives have generated many powerful ecological insights. For instance patterns of community dynamics and intra-interspecific competition are modelled at the individual level (e.g. Tilman 1994; Grimm & Railsback 2005).

Manipulative studies have confirmed that production is also density-dependent in grasses (e.g. Duralia & Reader 1993; Aguiar *et al.* 2001). It is therefore curious that the individual perspective has been largely ignored, and that most grassland ecologists have persisted with the plot-level analysis for calculations of biomass production in the field. To provide a new perspective, our study uses an individual-based approach to understand grass production. Essential to this approach is to take cognisance of local density. We ask whether neighbour abundance influences production when production is expressed at an individual level. Additionally, we explore individual production at three sites that differ in fire history, because the importance of burning for production in dry grasslands has up to now only been evaluated on the basis of plot-level studies (Bennett *et al.* 2002; Snyman 2003, 2004b).

There are several different approaches to study how local density influences the growth and performance of plants (e.g. Hubbell *et al.* 2001; Berger *et al.* 2004; Newton 2006). One useful concept is the 'field of neighbourhood' (Berger & Hildenbrandt 2000) or more generally 'competition kernels' (Bolker & Pacala 1999; Schneider *et al.* 2006). However, most concepts were developed in the context of modelling studies, and we know very little about what these competition kernels look like, i.e. about their shape and their spatial extent. Also, it is unknown whether it is possible to detect and describe competition kernels in real field systems, as opposed to manipulative experiments.

Fire is rarely regarded as an important factor in the dry savannas (Walker *et al.* 1981; Van Wilgen & Scholes 1997), and its influence on the productivity of semi-arid grasslands is often described as negative, as it is associated with reductions in cover or biomass production at plot-level (e.g. Bennett *et al.* 2002; Snyman 2003, 2004b). However, to our knowledge no studies exist that examine the influence of burning on the production of the individual plant.

The aim of our study is to analyse grass production from an individual perspective and to explore whether neighbour abundance influences production. To achieve this aim, we describe the shape and extent of competition kernels in unmanipulated grassland. Furthermore, we investigate three sites that differ in fire history to determine whether the individual perspective reveals different insights into burning effects on grass production compared to the plot-level perspective.

3.2 Materials and methods

3.2.1 Study area and study species

The Etosha National Park (hereafter 'Etosha') is situated in north-central Namibia and comprises an area of 22,915 km^2 (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 described as 'shrub mopane on loamy soils' (Le Roux *et al.* 1988). Du Plessis (1999) defines the area as 'shrub and low tree savanna', where woody crown cover ranges from 25 to 50%. The woody layer is almost exclusively dominated by *Colophospermum mopane* shrubs, other woody species include *Catophractes alexandri* and *Dichrostachys cinerea*. The herbaceous layer is dominated by the perennial grass *Stipagrostis uniplumis* var. *uniplumis* which constitutes more than 90% of the herbaceous vegetation cover. The grass species *Schmidtia pappophoroides*, *Melinis repens*, *Pogonarthria fleckii*, and herbaceous dicotyledons such as *Commelina forskaolii* and *Gisekia africana* constitute the remaining cover. Average annual rainfall is around 380 mm and variation in annual rainfall is 30–40%, (Mendelsohn *et al.* 2002; Etosha Ecological Institute, *unpublished data*). Grazing pressure in this area is very low, as grazers occur in very low densities (Craig 1998; Erb 2000; Kilian 2002; Kolberg 2004). An analysis of soil samples revealed a relatively homogeneous soil texture of ca. 85% sand, 4% silt and 11% clay in the research area (*Part 2, this thesis*).

The study species *Stipagrostis uniplumis* var. *uniplumis* (hereafter '*S. uniplumis*') is a perennial tufted C4 grass which grows on sandy soils in arid parts of Africa. We chose this particular species because it dominates the grass layer over large areas, it is the most common of the *Stipagrostis* species and it is considered a valuable grazing grass (Malan & Owen-Smith 1974; Van Oudtshoorn 2002). Because of its wide distribution and local dominance it is important for forage and soil stabilisation (Malan & Owen-Smith 1974; Van Oudtshoorn 2002; Klaassen & Craven 2003). The species is not associated with shrub or tree canopies and grows in the between-tree areas. For the purpose of this study our definition of a *S. uniplumis* individual follows O'Connor (1994), where a tuft is considered to be a single unit, although – in reality – tillers within a tuft are physiologically independent (Briske 1991). As the grass layer in the study system is almost mono-specific, knowledge on the population dynamics of this particular grass species can be up scaled to the level of the grass layer and hence contributes to a mechanistic understanding, with implications for utilisation and management.

3.2.2 Study sites

The study was conducted in a year of medium precipitation (382 mm in the rainy season 2004/2005). Thus, neither drought nor grazers, which occur at low density, were major factors impacting on tuft performance.

Three sites of level topography were chosen which are approximately 20 km apart from each other and differ in fire history but not in botanical composition (Etosha Ecological Institute, *unpublished data*). Differences in fire history originate from differences in the sites' location between man-made and natural fire breaks (e.g. pans). Site A burned every three to five years in the past 30 years. The last fire occurred in 2004 at the end of the dry season (just before the start of the experiment); therefore, 'time since fire' is 0 years. Site B burned every 7 to 10 years in the past 30 years and last in 1997: 'time since fire' is 7 years. Site C burned last in 1975: 'time since fire' is 29 years.

3.2.3 Sampling design and parameters

For tuft selection we randomly chose points within an area of one square kilometre at each site. From each of these points a transect was laid in a random direction (0–360 °), using a 50 m tape measure. Transects that were closer than 100 m to the nearest road or path were rejected. The tuft closest to each 5 m increment on the tape measure was sampled. Because *S. uniplumis* is generally not associated with canopies, we rejected individuals that were closer than two meters from the nearest tree or shrub canopy. Furthermore, we rejected juvenile individuals (basal circumference < 3 cm).

At the beginning of the study (October 2004) we recorded the following parameters for each of the selected tufts (hereafter 'focal individual') and for all neighbouring tufts up to a distance of 50 cm: (i) the coordinates, (ii) the basal circumference and (iii) the amount of standing dead biomass. The standing dead biomass was estimated using three categories that refer to the ratio of dead to living tillers: $> 2/3$ of tillers dead; $1/3 - 2/3$ of tillers dead; $< 1/3$ of tillers dead. From these parameters we calculated the following variables:

Plant size. We first converted the basal circumference into the basal area. As we were interested in the living part of each tuft, we then inferred the living basal area of a tuft: (living basal area) = (basal area) x {1 − (standing dead biomass)}, where 'standing dead biomass' is the median value of the range of each standing dead biomass category (5/6, 3/6 and 1/6, respectively) Hence, 'plant size' in the following refers to the living basal area of a tuft.

Neighbour abundance. Tufts within a 50 cm radius of the focal individual were defined as its neighbours. We calculated two measures for neighbour abundance. The first, NA_{No}, is based on the number of neighbours, whereas the second, NA_{LBA}, is based on the sum of the living basal area of neighbours. We calculated NA_{No} and NA_{LBA} for five distance rings (0–10 cm; $>$ 10–20 cm; $>$ 20–30 cm; $>$ 30–40 cm; $>$ 40–50 cm) and normalised these indices by the area of the ring. Hence, the two measures of neighbour abundance, NA_{No} [$1/\mathrm{cm}^2$] and NA_{LBA} [$\mathrm{cm}^2/\mathrm{cm}^2$], are each described by five variables, reflecting the respective neighbour abundance index in each distance category.

All focal individuals at site B and site C were cut to just above ground level (2 cm) in October 2004 before the first rains, whereas all tufts at site A were already at ground level, because site A burned just before the start of the experiment. At the beginning of the dry season (April 2005) all focal individuals were revisited and again cut to ground level. The harvested biomass of each focal individual was oven-dried (48 h at 80 °C) and weighed, to obtain a measure for each focal individual's aboveground net primary production ('individual production') within one growing season.

To explore whether clipping of only the focal individual proves disadvantageous for its biomass production, we selected another 100 tufts at site B and C and conducted the same procedures as described above, but this time we clipped not only the focal individual but also all neighbours. We then analysed the effect of clipping (yes/no) on individual production using a generalized linear model. It was not significant ($p > 0.05$, analysis not shown).

3.2.4 Soil and plant samples

We collected plant material and soil samples in April 2005 to check for between-site differences in the chemical composition. We therefore randomly harvested plant material from the leaves of about 300 *S. uniplumis* tufts per site. We pooled these samples into a total of 15 mixed plant samples (five per site). The soil samples were taken from the upper 10 cm at 30 randomly located points at each site. These soil samples were pooled into a total of 15 mixed soil samples (five per site). Plant samples were analysed for the nutrients nitrogen, phosphorus and potassium, using the dry ashing method (Mills & Jones 1996). Soil samples were analysed for total nitrogen (Kjeldahl method, Bremner 1965), available phosphorus (Olsen method, Olsen & Dean 1965) and available potassium (atomic absorption spectroscopy, Knudsen *et al.* 1982). The analyses of plant and soil samples were conducted by the Agricultural Laboratory of the Ministry of Agriculture, Water and Rural Development in Windhoek.

3.2.5 Statistical analysis

We used generalized linear models (GLM) with a gamma error distribution and log link function to examine the influence of the explanatory variables 'plant size', 'neighbour abundance' and 'site' on individual production. We analysed the production data in two steps. In the first step, we seeked to find an adequate measure of neighbour abundance. Thus, we fitted two models (one with the NA_{LBA}, the other with the NA_{No} variables) and then selected the model with the better performance (significantly better log likelihood, Burnham & Anderson 1998). In a second step, we aimed to find the simplest model that adequately describes the data (minimal adequate model), following the principle of parsimony (Crawley 2002). Thus, the full model which included one measure for neighbour abundance as well as the variables 'plant size' and 'site' was simplified, using a stepwise-backward procedure based on a likelihood ratio test (F-test). Only variables significant at the 5% level were retained in the model. We finally aggregated the significant neighbour abundance variables to obtain a single variable for neighbour abundance which can then be graphically presented. Because generalized linear models are based on estimates of maximum likelihood, we do not present R^2-values.

We used multivariate analyses of variance (Bortz 1999) to determine between-site differences in the chemical composition of the sampled plant and soil material. All data were analysed using the software R 2.7.0 (R Development Core Team 2008).

3.3 Results

3.3.1 Individual production

The data describe the effects of ‘site’, ‘plant size’ and ‘neighbour abundance’ on the individual production of 288 tufts. Plant size ranges from 0.6 to 63.73 cm^2, and individual production (dry matter) ranges from 1.0 to 66.8 g (Fig. 3.3). The ranges of the two measures for neighbour abundance – indexed as the sum of the living basal area of neighbours (NA_{LBA}), and indexed as the number of neighbours (NA_{No}) – are presented in Figure 3.1. NA_{LBA} ranges from 0 to 0,093 $[\mathrm{cm}^2/\mathrm{cm}^2]$ and NA_{No} ranges from 0 to 0,0064 cm^{-2}. Both indices show the tendency to increase with distance to the focal individual.

Table 3.1: Full generalized linear model (GLM), relating the variables ‘site’, ‘plant size’ and five variables for NA_{LBA} at different distances to individual production. The ‘Akaike information criterion’ for this model is 1987.9 and the ‘log likelihood’ is -983.941 (d.f. = 10).

Parameter	Estimate	s.e.	t-value	p-value
(Intercept)	2.902	0.132	21.972	0.000
Site B	-1.238	0.107	-11.553	0.000
Site C	-0.444	0.109	-4.073	0.000
Size	0.023	0.004	5.349	0.000
$\mathrm{NA}_{LBA\,(0-10\,cm)}$	1.886	3.871	0.487	0.627
$\mathrm{NA}_{LBA\,(>10-20\,cm)}$	-9.271	4.526	-2.048	0.042
$\mathrm{NA}_{LBA\,(>20-30\,cm)}$	-14.674	5.695	-2.576	0.011
$\mathrm{NA}_{LBA\,(>30-40\,cm)}$	-9.230	6.035	-1.529	0.127
$\mathrm{NA}_{LBA\,(>40-50\,cm)}$	-4.649	6.400	-0.726	0.468

Table 3.2: Full generalized linear model (GLM), relating the variables ‘site’, ‘plant size’ and five variables for NA_{No} at different distances to individual production. The ‘Akaike information criterion’ for this model is 1993.6 and the ‘log likelihood’ is -986.811 (d.f. = 10).

Parameter	Estimate	s.e.	t-value	p-value
(Intercept)	2.913	0.163	17.843	0.000
Site B	-1.263	0.110	-11.463	0.000
Site C	-0.501	0.121	-4.144	0.000
Size	0.022	0.005	4.771	0.000
$\mathrm{NA}_{No\,(0-10\,cm)}$	-0.179	37.140	-0.005	0.996
$\mathrm{NA}_{No\,(>10-20\,cm)}$	-106.800	46.880	-2.277	0.024
$\mathrm{NA}_{No\,(>20-30\,cm)}$	-18.810	57.030	-0.330	0.742
$\mathrm{NA}_{No\,(>30-40\,cm)}$	-105.100	67.770	-1.550	0.122
$\mathrm{NA}_{No\,(>40-50\,cm)}$	33.910	73.210	0.463	0.644

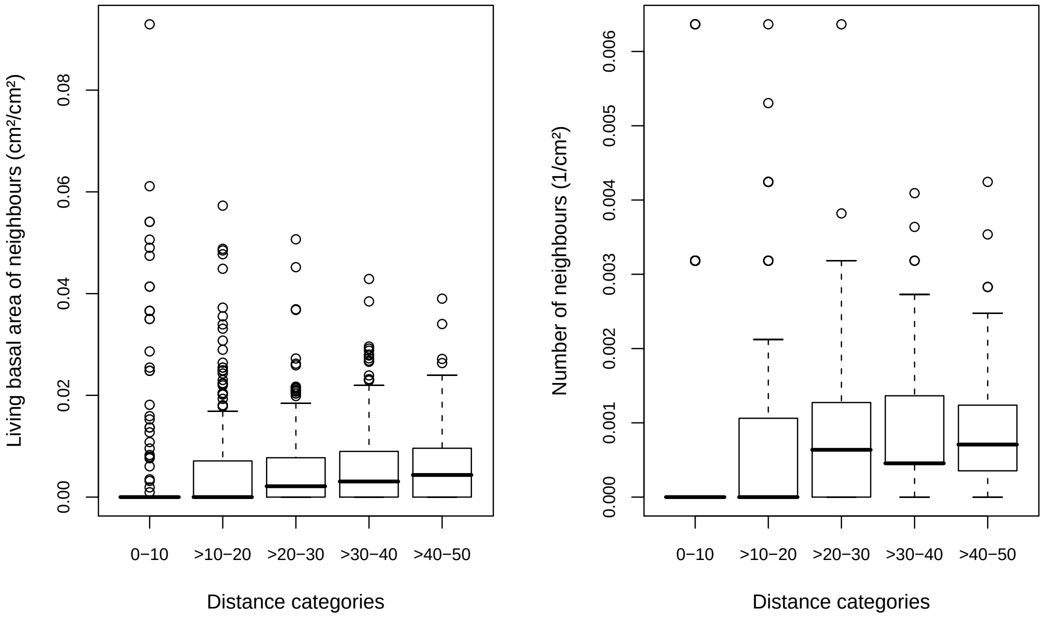


Figure 3.1: The sum of the living basal area of neighbours (NA$_{LBA}$) and the number of neighbours (NA$_{No}$) in the five distance categories from the focal individuals (n =288). In each box, the bold line shows the median, whereas the lower and upper limitations of the box show the 25 and 75 percentiles, respectively. The horizontal line joined to the box by the whisker shows 1.5 times the interquartile range of the data. Outliers are drawn individually.

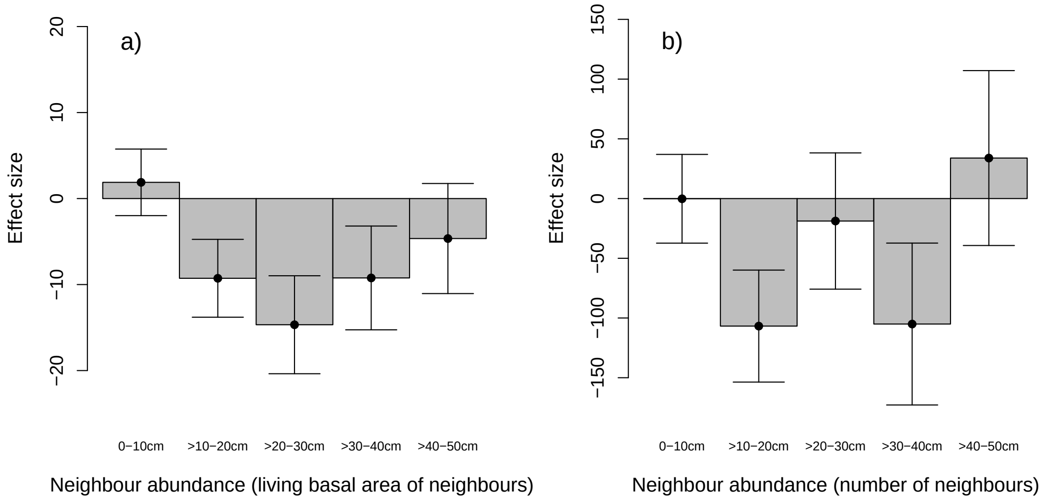


Figure 3.2: Effect sizes (estimate, slope of the regression line) of the neighbour abundance variables indexed as a) sum of living basal area of neighbours (NA$_{LBA}$) and b) number of neighbours (NA$_{No}$) for five distance categories as predicted by the full generalized linear models described in Table 3.1 and Table 3.2. Error bars indicate ± 1 standard error.

To identify the best measure for neighbour abundance we analysed the data in two steps. We first fitted two models to our set of data and compared their log likelihoods: one model included neighbour abundance indexed as NA_{LBA} (Table 3.1), the other included neighbour abundance indexed as NA_{No} (Table 3.2). Both models additionally included the variables 'plant size' and 'site' and show that neighbour abundance at $>$ 10–20 cm distance significantly reduces individual production. The model including NA_{LBA} additionally shows a significant negative influence at $>$ 20–30 cm distance. As shown in Figures 3.2a and 3.2b, the NA_{LBA} produces a unimodal prediction response which seems more ecologically plausible than the multi-modal response produced by NA_{No}. A comparison of the log likelihoods (logLik) of both models revealed that our data are significantly better described (difference in logLik > 2.55; Burnham & Anderson 1998) by the model including NA_{LBA} (logLik $=$ -983.941; d.f. $= 10$) compared to the model including NA_{No} (logLik $=$ -986.811; d.f. $= 10$). Therefore, we selected the full model including

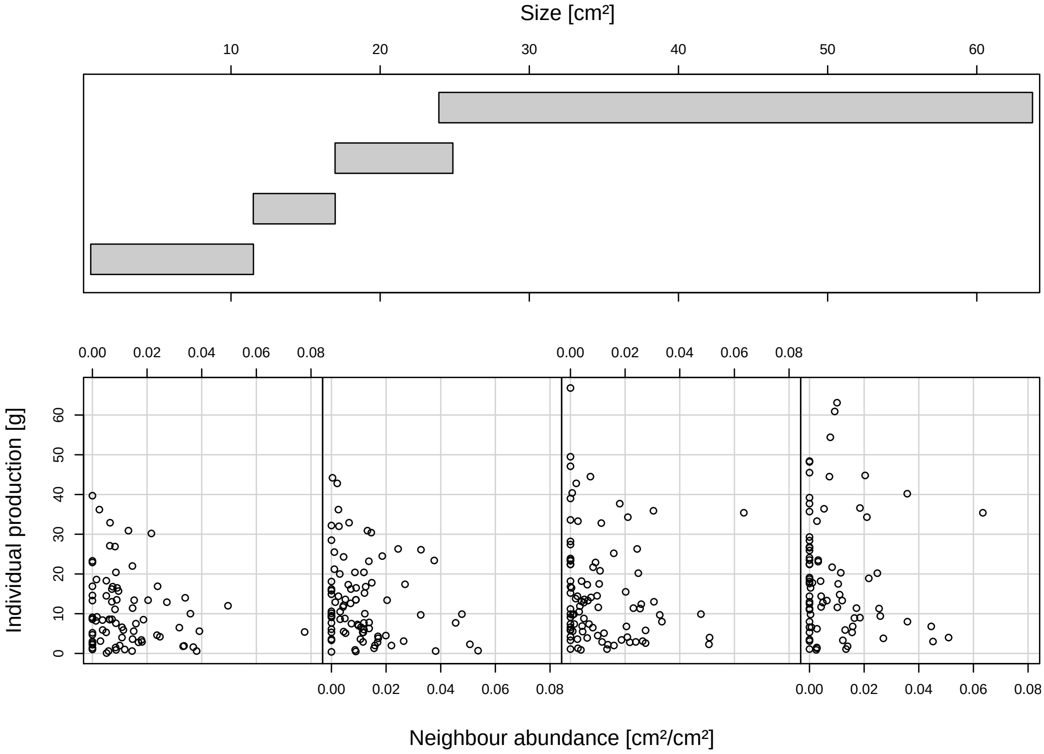


Figure 3.3: Individual production in relation to neighbour abundance (indexed as $\mathrm{NA}_{LBA\,(>10-30\,cm)}$) and plant size. The four plots are conditioned on the values of plant size shown in the top panel. The panels are ordered from left to right, from smallest plant size to largest.

the NA_{LBA} variables and determined the minimal adequate model (using likelihood ratio tests), which includes the variables 'plant size', 'site' and two levels of NA_{LBA}: $\mathrm{NA}_{LBA\ (>10-20\,cm)}$ and $\mathrm{NA}_{LBA\ (>20-30\,cm)}$. To further simplify the model, we aggregated (summarized) these two NA_{LBA} levels into $\mathrm{NA}_{LBA\ (>10-30\,cm)}$. Thus, the final model, shown in Table 3.3, relates individual production to 'site', 'plant size' and $\mathrm{NA}_{LBA\ (>10-30\,cm)}$. Individual production is highest at site A and lowest at site B. It significantly increases with 'plant size' and significantly decreases with neighbour abundance $\mathrm{NA}_{LBA\ (>10-30\,cm)}$, ranging from 0 to 0.08 [cm^2/cm^2] (Figures 3.3 and 3.4).

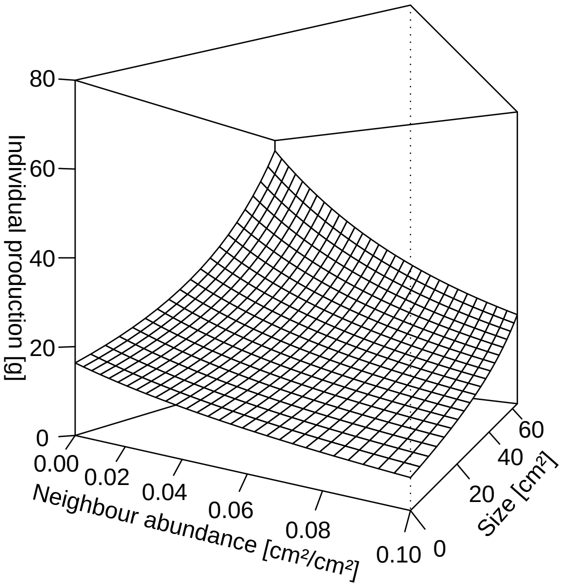


Figure 3.4: Predicted individual production in relation to plant size and neighbour abundance (indexed as $\mathrm{NA}_{LBA\,(>10-30\,cm)}$). Predictions are made using the model described in Table 3.3 and are exemplarily shown for site A.

Table 3.3: Reduced generalized linear model (GLM), relating the variables 'site', 'plant size' and $\mathrm{NA}_{LBA\,(>10-30\,cm)}$ to individual production. The 'Akaike information criterion' for this model is 1984.5 and the 'log likelihood' is -986.231 (d.f. = 6).

Parameter	Estimate	s.e.	t-value	p-value
(Intercept)	2.793	0.124	22.617	0.000
Site B	-1.217	0.108	-11.266	0.000
Site C	-0.414	0.110	-3.762	0.000
Size	0.024	0.004	5.439	0.000
$\mathrm{NA}_{LBA\,(>10-30\,cm)}$	-11.422	3.445	-3.316	0.001

3.3.2 Between-site differences

Because between-site differences in individual production are obviously not linearly linked to 'time since fire' (site B has intermediate 'time since fire', but the lowest individual production, Table 3.3), we used multivariate analyses to explore between-site differences in the chemical composition of the soil and plant material. The multivariate analyses did neither reveal significant differences between the three sites in the chemical composition of the plant material (Pillai = 0.801; approx $F = 2.448$; num d.f. = 6; den d.f. = 22; $p > 0.05$), nor in the soil properties (Pillai = 0.299; approx $F = 0.644$; num d.f. = 6; den d.f. = 22; $p > 0.05$). Mean amounts of N, P and K of the plant material and of the soil samples are given in Table 3.4 and Table 3.5. Even though these differences are not significant, the mean N, P and K in the plant material correspond to what we would expect regarding the fire history of our sites. Site A has the lowest mean values for N, P and K and burned most frequently, whereas site C has the highest mean values for N, P and K and burned only once in 30 years. However, the ranking of these nutrient differences does not correspond to the observed ranking in productivity.

Table 3.4: Mean values ($n = 5$) and standard deviation for N, P and K in the plant samples of the three sites.

Site	N (%)	s.d.	P (%)	s.d.	K (%)	s.d.
A	0.777	0.060	0.056	0.011	1.218	0.160
B	0.899	0.326	0.074	0.013	1.330	0.193
C	1.116	0.073	0.092	0.011	1.344	0.173

Table 3.5: Mean values ($n = 5$) and standard deviation for N, P and K in the soil samples of the three sites.

Site	N (%)	s.d.	P (ppm)	s.d.	K (ppm)	s.d.
A	0.029	0.015	2.314	0.848	91.800	14.618
B	0.030	0.003	2.960	0.377	110.000	35.178
C	0.028	0.001	2.478	0.724	94.600	24.775

3.4 Discussion

3.4.1 Individual production

Our individual-based study allows us to assess the importance of local density for perennial grass production in a semi-arid savanna, an aspect which is largely ignored by both applied (e.g. Scholes & Walker 1993; O'Connor *et al.* 2001; Augustine *et al.* 2003) and theoretical (e.g. Weber *et al.* 1998; Wiegand *et al.* 2004; Holdo *et al.* 2007; Müller *et al.* 2007) research on grass layer productivity. As expected from the literature on individual growth and production in forest ecosystems (e.g. Makinen 1996; Berger *et al.* 2004; Stoll & Newbery 2005), our results show that neighbour abundance has a strong negative impact on individual production in perennial grasses. Such density-dependence of grass production has, to our knowledge, only been detected in manipulative experiments (e.g. Wedin & Tilman 1993; Aguiar *et al.* 2001, but see Aguilera & Lauenroth 1993a). Our study detected the density-dependence of perennial grass biomass production in an unmanipulated field study and describes the extent and the shape of the competition kernel, which has up to now mostly been discussed in theoretical studies (e.g. Bolker & Pacala 1999; Murrell & Law 2003; Schneider *et al.* 2006). The negative impact of neighbour abundance in our unmanipulated field study is lowest in the closest vicinity of the focal plant, probably due to some historical self-thinning processes, as plants with many close neighbours are more likely to die (Mithen *et al.* 1984; Zimmermann *et al.* 2008; *Part 2 and 4, this thesis*). The negative impact then increases up to an area where this self-thinning process is active, and then decreases with increasing distance of neighbours. This 'peak' where neighbour abundance has the strongest negative impact is in our study at 10 to 30 cm distance. However, this peak is obviously not constant but rather shifts over time with stand development, as neighbours die due to density-dependent mortality (Antonovics & Levin 1980) and as the focal plant, its neighbours and their respective zones of influence grow in size (Schneider *et al.* 2006). Besides showing the importance of local density for production, our study also reveals that a measure of neighbour abundance that considers the size of neighbours is much better compared to simply counting the neighbours. Hence, our data were much better described if neighbour abundance was indexed by the living basal area of neighbours compared to neighbour numbers. Similarly, Stoll & Newbery (2005) found the sum of the basal area of neighbours to be a better measure than the number of neighbours, when analysing the density-dependence of tree growth.

3.4.2 The role of fire

Nitrogen cycling is thought to be tightly coupled to fire frequency (Reich *et al.* 2001) and frequent fires have been associated with reduced nutrient status in grasslands (Turner *et al.* 1997; Ojima *et al.* 1994) or forests (e.g. Thornley & Cannell 2004; McIntosh *et al.* 2005). This was also observed in our study where nutrient levels of the plant material corresponded well with fire frequency. That is, the site with a high fire frequency had the lowest and the site with the lowest fire frequency had the highest proportion of nutrients in the plant samples. Nevertheless, the ranking of the nutrient differences between the three sites does not correspond to the observed ranking in productivity. Turner *et al.* (1997) made similar observations in tallgrass prairie where they discovered a general lack of relationship between N availability and productivity. In their study too, production was highest in burned plots although total extractable N was lower compared to unburned plots. We suggest two possible explanations for the observed phenomenon of high productivity after burning despite low levels of nutrients. Firstly, the soil and plant samples were taken several months after the fire event at site A and might therefore have failed to detect a short-term or post-fire nutrient pulse often observed after burning (Radho-Toly *et al.* 2001; Bennett *et al.* 2002; Castelli & Lazzari 2002; Rau *et al.* 2007). A second and more plausible explanation is that plant productivity responses are due more to biophysical effects (Ojima *et al.* 1994). Thus, in tallgrass prairie, enhanced productivity after burning was related to litter removal and associated increases in soil temperature (Hulbert 1988) and to increased photosynthetically active radiation (Knapp 1984a, 1985).

Although our study could not describe the influence of 'time since fire' in detail (as we used only three data points with relatively long intervals), we found that burning promotes, at least in the short term, individual biomass production. This result ist supported by findings of our experiment on recruitment filters (Zimmermann *et al.* 2008; *Part 2, this thesis*), where seedling growth was significantly enhanced on recently burned plots. Our results therefore suggest that burning of dry grassland cannot simply be regarded as negative. Nonetheless the impact of fire on the grass layer is complex. Both, the plot-level and the individual perspective are important to understand this complex relationship. In the short term, fire reduces production at plot level (Bennett *et al.* 2002; Snyman 2003, 2004b), probably due to a reduction in individual numbers (*Part 4, this thesis*). This loss in production at plot level is on a slightly longer time scale supposedly compensated by the observed recruitment wave and the enhanced growth of seedlings and survivors after fire (Zimmermann *et al.* 2008; *Part 2, this thesis*).

3.5 Conclusions

Both applied and theoretical research on grass productivity should incorporate the individual perspective, because perennial grass production is highly density-dependent, as neighbour abundance has a strong negative impact on individual production. Therefore, our study sheds a new light on management options, in so far as thinning of a sward/stand can – not only in forests but also in grassland ecosystems – lead to enhanced individual production. Fire, which reduces competitive levels, might therefore be an important management tool.

Part 4

Grass mortality in semi-arid savanna: the role of fire, competition and self-shading*

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*A slightly different version of this part has been submitted to *Perspectives in Plant Ecology, Evolution and Systematics* (authors: Zimmermann, J., Higgins, S. I., Grimm, V., Hoffmann, J., & Linstädter, A.)

Abstract

Perennial grasses are a dominant component of many vegetation formations and provide important ecosystem services including supporting herbivores and preventing soil erosion. Despite their importance, our understanding of the processes that influence their mortality rates is surprisingly limited.

This study explores the effects of local and landscape-scale processes on mortality of a perennial grass (*Stipagrostis uniplumis*) in semi-arid savanna. We focussed on three local-scale factors acting at the level of the individual: self-shading by the standing dead biomass of a tuft, plant size, and neighbour abundance. To characterize neighbour abundance, three indices were calculated: number of neighbours, sum of the neighbours' basal area, and sum of the neighbours' living basal area. At the landscape scale, we explored the influence of fire on tuft mortality.

We found the amount of standing dead biomass to substantially increase the mortality rates of tufts. Neighbour abundance, indexed as the sum of the living basal area of neighbours, was also associated with higher mortality rates. On a landscape level, we found that fire significantly influenced tuft mortality rates. The number of neighbours, the sum of neighbours basal area and the size of a plant had no influence on mortality rates.

The relationships between these determinants of mortality are, however, complex. That is, although fire is an important direct source of mortality, it indirectly reduces the risk of mortality by reducing the amount of standing dead biomass and competitive pressure. Our results imply that avoiding fire will reduce the vitality of perennial grass populations.

4.1 Introduction

The terrestrial surface of the southern continents is dominated by tropical savannas and grasslands. In these systems, perennial grasses are crucial for the ecosystem's functioning in supporting herbivores and preventing soil erosion (Sala & Paruleo 1997; Van Oudtshoorn 2002). Yet, research on the grass layer in savannas has a strong system bias, focussing on production, composition and cover. Few studies have investigated these grasslands from a demographic perspective and studies that do consider demography focus on seedling establishment. Mortality is largely ignored, perhaps because the capacity of many perennial grasses for vegetative reproduction is interpreted as evidence that, once established, grasses can be assumed to be immortal.

Evidence for our assertion that studies of savanna grassland largely ignore mortality are the numerous entries in the index of standard rangeland management texts (e.g. Hodgson & Illius 1996; Tainton 1999; Grice & Hodgkinson 2002) for biomass production, decomposition, tiller dynamics, species composition, but no entries for mortality or death. Seedling establishment, in the context of grasses, receives only brief mention. Even the primary literature on grass demography in savannas has focussed on tiller dynamics, recruitment and establishment (e.g. Everson *et al.* 1988; O'Connor 1996; Laterra *et al.* 1997; Wan & Sosebee 2002).

In ecosystems where grasses play an important role only few long-term studies include annual mortality rates of perennial grass individuals (e.g. Canfield 1957; O'Connor 1994; Fair *et al.* 1999; Hodgkinson & Muller 2005; Oliva *et al.* 2005) and most of them do not mention processes affecting tuft mortality. If such processes are analysed, focus is usually on landscape scale factors such as drought (e.g. Donaldson 1967; Danckwerts & Stuart-Hill 1988; Grice & Barchia 1992; Milton & Dean 2000; Hodgkinson & Muller 2005), grazing (e.g. O'Connor 1991a, 1994; Briske & Hendrickson 1998; Oliva *et al.* 2005) or fire (e.g. Silva & Castro 1989; Silva *et al.* 1990; Boo *et al.* 1996) but not on local scale factors (i.e. competition effects, size or standing dead biomass).

Even though mortality is largely ignored, it is known that there is a continual turnover of individuals in perennial grasslands (O'Connor & Everson 1998; Fair *et al.* 1999), hence mortality is clearly an important process. It follows that an understanding of factors affecting whole plant mortality is crucial for understanding and managing grasslands. The broad aim of this study is to investigate factors other than drought and grazing that affect tuft mortality of perennial grasses in a semi-arid savanna. Our study focuses on both, local-scale factors acting at the level of the individual plant, but also on a large scale process that acts at landscape level – fire.

We examine three local-scale factors, namely self-shading, plant size and neighbour abundance, which have been suggested to influence mortality rates of perennial grasses (McGinnies 1971; Peart & Foin 1985; Silva *et al.* 1990; O'Connor 1994). Self-shading describes the negative impact of the amount of standing dead biomass on perennial grasses and has been reported in savannas subject to fire exclusion (Knapp 1984a; Silva *et al.* 1990, 1991; Morgan & Lunt 1999). Self shading occurs if tufts are not defoliated. This allows dead biomass to accumulate, which decreases irradiance and subsequently suppresses initiation and survival of tillers (Coughenour *et al.* 1984; Deregibus *et al.* 1985; Everson *et al.* 1988). Although this process is well known on tiller level, we are aware of no studies explicitly examining the impact of standing dead biomass on whole plant mortality. Particularly in perennial grasses of arid or semi-arid regions (average annual precipitation $< 400\,\text{mm}$) the role of self-shading on plant performance received considerably less attention, compared to regions of higher rainfall regimes. We speculate that this is because self-shading is ignored in systems where growth rates and hence rates of accumulation of dead plant material are low.

It is unclear how plant size influences mortality rates in perennial grasses. Some studies in grasslands report that small individuals are more likely to die than large ones (Peart & Foin 1985; Silva *et al.* 1990; O'Connor 1994; Oliva *et al.* 2005), whereas other studies found no differences in mortality rates between grass tufts of different basal diameters (Milton & Dean 2000; Hodgkinson & Muller 2005).

The final local-scale factor we examine is competition, or neighbour abundance. Competition among plants has been reported to be important in semi-arid (Fowler 1986b) and unproductive (Goldberg *et al.* 1999) systems. However, few studies have explored density-dependent interactions between perennial grass individuals (Aguilera & Lauenroth 1993a; Aguiar *et al.* 2001). Mortality due to intraspecific competition has so far only been mentioned in the context of the recruitment process of perennial grasses (Aguilera & Lauenroth 1993a), or in the smallest size class of mature individuals (Peart & Foin 1985). Evidence for mortality of mature individuals induced by high densities of conspecifics, as has been found in tropical forest tree populations (Condit *et al.* 1994; Hubbell *et al.* 2001; Peters 2003), has, to our knowledge, not yet been discovered in perennial grasses.

Factors which act at landscape level also influence mortality in perennial grasslands. Tuft mortality has mainly been attributed to drought (e.g. Donaldson 1967; Danckwerts & Stuart-Hill 1988; Milton & Dean 2000; Hodgkinson & Muller 2005) and grazing (e.g. O'Connor 1991a, 1994; Briske & Hendrickson 1998; Oliva *et al.* 2005). However, information on the effects of fire on tuft mortality in dry grasslands remains anecdotal. Fire as an ecological process is considered less important in arid and semi-arid regions compared to high rainfall savanna (Bond 1997; O'Connor & Everson 1998) and its use as a management tool has been questioned or neglected for these dry regions (Tainton & Mentis 1984; Snyman 2002, 2003; Bennett *et al.* 2002). However, little information is available on the impact of fire on vegetation of arid and semi-arid regions. Its impact on grass populations has predominantly been investigated in moister savannas (e.g. Silva *et al.* 1990, 1991; Garnier & Dajoz 2001). When studied in semi-arid regions, the impact of fire on the grass layer has mostly been described as negative, suggesting that fire causes a decline in productivity and a decrease in cover, density or biomass (Drewa & Havstad 2001; Bennett *et al.* 2002; Snyman 2003, 2004b).

The objective of our study is to contribute to the understanding of population dynamics of perennial grasses by examining the neglected event 'mortality'. We examine local-scale factors acting at individual level: self-shading via standing dead biomass, plant size, and neighbour abundance. We include fire as a landscape-scale process, impacting tuft mortality and the local-scale factors, to test our hypothesis that fire is an ecological driver also in dry savannas.

4.2 Materials and methods

4.2.1 Study area and study species

The Etosha National Park (hereafter 'Etosha') is situated in north-central Namibia and comprises an area of 22,915 km^2 (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 described as 'shrub mopane on loamy soils' (Le Roux *et al.* 1988). Du Plessis (1999) defines the area as 'shrub and low tree savanna', where woody crown cover ranges from 25 to 50%. The woody layer is almost exclusively dominated by *Colophospermum mopane* shrubs, other woody species include *Catophractes alexandri* and *Dichrostachys cinerea.* The herbaceous layer is dominated by the perennial grass *Stipagrostis uniplumis* var. *uniplumis* which constitutes more than 90% of the herbaceous vegetation cover. The grass species *Schmidtia pappophoroides*, *Melinis repens*, *Pogonarthria fleckii*, and herbaceous dicotyledons such as *Commelina forskaolii* and *Gisekia africana* constitute the remaining cover. Average annual rainfall is around 380 mm and variation in annual rainfall is 30–40%, (Mendelsohn *et al.* 2002; Etosha Ecological Institute, *unpublished data*). Grazing pressure in this area is very low, as grazers occur in very low densities (Craig 1998; Erb 2000; Kilian 2002; Kolberg 2004). An analysis of soil samples revealed a relatively homogeneous soil texture of ca. 85% sand, 4% silt and 11% clay in the research area (*Part 2, this thesis*).

The study species *Stipagrostis uniplumis* var. *uniplumis* (hereafter '*S. uniplumis*') is a perennial tufted C4 grass which grows on sandy soils in arid parts of Africa. We chose this particular species because it dominates the grass layer over large areas, it is the most common of the *Stipagrostis* species and it is considered a valuable grazing grass (Malan & Owen-Smith 1974; Van Oudtshoorn 2002). Because of its wide distribution and local dominance it is important for forage and soil stabilisation (Malan & Owen-Smith

1974; Van Oudtshoorn 2002; Klaassen & Craven 2003). The species is not associated with shrub or tree canopies and grows in the between-tree areas. The species reproduces mainly generatively but is also capable of vegetative recruitment. Hence, only long-term monitoring or molecular analysis can identify whether a tuft is a ramet or a genet. We therefore did not differentiate between ramets and genets. For the purpose of this study our definition of a *S. uniplumis* individual follows O'Connor (1994) where a tuft is considered to be a single unit, although in reality tillers within a tuft are physiologically independent (Briske 1991).

4.2.2 Sampling design and parameters

The study was conducted in a year of medium precipitation (382 mm recorded at the study site in the rainy season 2004/2005). Thus, neither drought nor grazers, which occur at low density, were major factors impacting on tuft mortality during our study.

We selected 314 tufts and registered their coordinates at the beginning of the rainy season 2004/2005. For tuft selection we randomly chose points within an area of 9 km^2. From each of these points a transect was laid in a random direction (0–360 °), using a 50 m tape measure. Transects that were closer than 100 m to the nearest road or path were rejected. The tuft closest to each 5 m increment on the tape measure was sampled. Because *S. uniplumis* is generally not associated with canopies, we rejected individuals that were closer than two meter from the nearest tree or shrub canopy. Furthermore, we rejected juvenile individuals (basal circumference less than 3 cm) in our sample, as seedling mortality is explored in another experimental study (Zimmermann *et al.* 2008; *Part 2, this thesis*).

The following explanatory variables were recorded for each tuft at the beginning of the study (see also Table 4.1):

Standing dead biomass (SDB). The accumulated standing dead biomass of a tuft was described using three categories, that refer to the ratio of dead to living tillers: high $> 2/3$ of tillers dead ($n = 98$); medium 1/3–2/3 of tillers dead ($n = 109$); low $< 1/3$ of tillers dead ($n = 107$).

Plant size. The basal circumference (cm) was measured for each individual and converted into the basal area (S_{BA}, cm^2) as an index of size. The living basal area (S_{LBA}, cm^2) of a tuft was inferred from the proportion of the standing dead biomass (SDB), using the average proportion of dead tillers within each SDB category: $S_{LBA} = S_{BA} * (1 - SDB_x)$, where SDB_x is the average SDB for the SDB category (1/6, 3/6 and 5/6 respectively for the categories 'low', 'medium' and 'high').

Neighbour abundance. We assume that competitive effects decrease with

Table 4.1: Definition of the explanatory variables used in this study.

Factor category	Acronym	Description	Range
Standing dead biomass	SDB	Proportion of dead tillers of the focal tuft	$> 2/3$ high 1/3–2/3 medium $< 1/3$ low
Plant size	S_{BA}	The focal tuft's basal area	0.7–140.4 cm^2
	S_{LBA}	The focal tuft's living basal area	0.7–63.75 cm^2
Neighbour abundance	NA_{No}	The number of neighbours	0–7
	NA_{BA}	The sum of all neighbours' basal area	0–104 cm^2
	NA_{LBA}	The sum of all neighbours' living basal area	0–85.83 cm^2
Fire	Fire	Whether the focal tuft burned or not	True–False

distance from the focal plant (Mithen *et al.* 1984). In a preliminary analysis we found the effect of neighbouring plants on the focal plant's mortality to be important at distances up to 25 cm (Zimmermann, *unpublished data*). The focal tuft was therefore in the centre of a circle with a radius of 25 cm, other tufts in this circle are termed neighbours of the focal plant. For each of these neighbours, we recorded the relative coordinates, the SDB category and the size (S_{BA} and S_{LBA}). We calculated three different cumulative indices for neighbour abundance from the data: NA_{No}, the number of neighbours; NA_{BA}, the sum of the neighbours' S_{BA}; NA_{LBA}, the sum of the neighbours' S_{LBA}.

A fire was ignited in the study area in October 2005 before the first rains and the onset of the growing season. The fire was a back fire, and its timing was typical for Etosha in that most fires occur from September to December (Siegfried 1981; Du Plessis 1997). Also, the site had not burned for the past seven years, and three to seven years are typical fire intervals of this area (Etosha Ecological Institute, *unpublished data*).

The fire created a mosaic of burned and unburned patches, allowing us to include the impact of burning into our analysis. Which patches burned and which did not burn are assumed to be randomly assigned, which is exactly what percolation theories of fire spread would predict (Stauffer & Aharony 1992; Ratz 1995). Specifically, percolation theory predicts that a fire percolates through a homogeneous fuel layer as a stochastic process.

Because the fuel layer at our site is homogeneous, the burned and unburned patches were spatially interspersed, and the assignment of the fire treatment was, with respect to tuft-location, random.

After the fire, all focal tufts were revisited and it was noted whether a tuft had burned or not. Hence, the factor ‘fire’ had two levels, ‘true’ and ‘false’. All tufts were remapped one year later, after the first heavy rains had induced sprouting of tillers. We then recorded whether a tuft had survived or died.

4.2.3 Statistical analysis

We used generalized linear models (GLM) with a binomial error distribution and logit (logistic) link function to relate the seven explanatory variables (Table 4.1) to tuft mortality. The underlying strategy of our statistical analysis was to find the simplest model that adequately describes the data (minimal adequate model), 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. Because logistic regressions are based on estimates of maximum likelihood we do not use R^2-values to evaluate the goodness of fit of our models. All data were analysed using the software R 2.7.0 (R Development Core Team 2008).

4.3 Results

The total dataset describes the effects of the explanatory variables on 314 tufts. Altogether, 180 tufts (57%) died within one year. These were 73% of the burned and 31% of the unburned tufts (Figure 4.1). The minimal adequate model indicated that standing dead biomass (SDB), neighbour abundance indexed as the sum of the living basal area of neighbours (NA$_{LBA}$), and

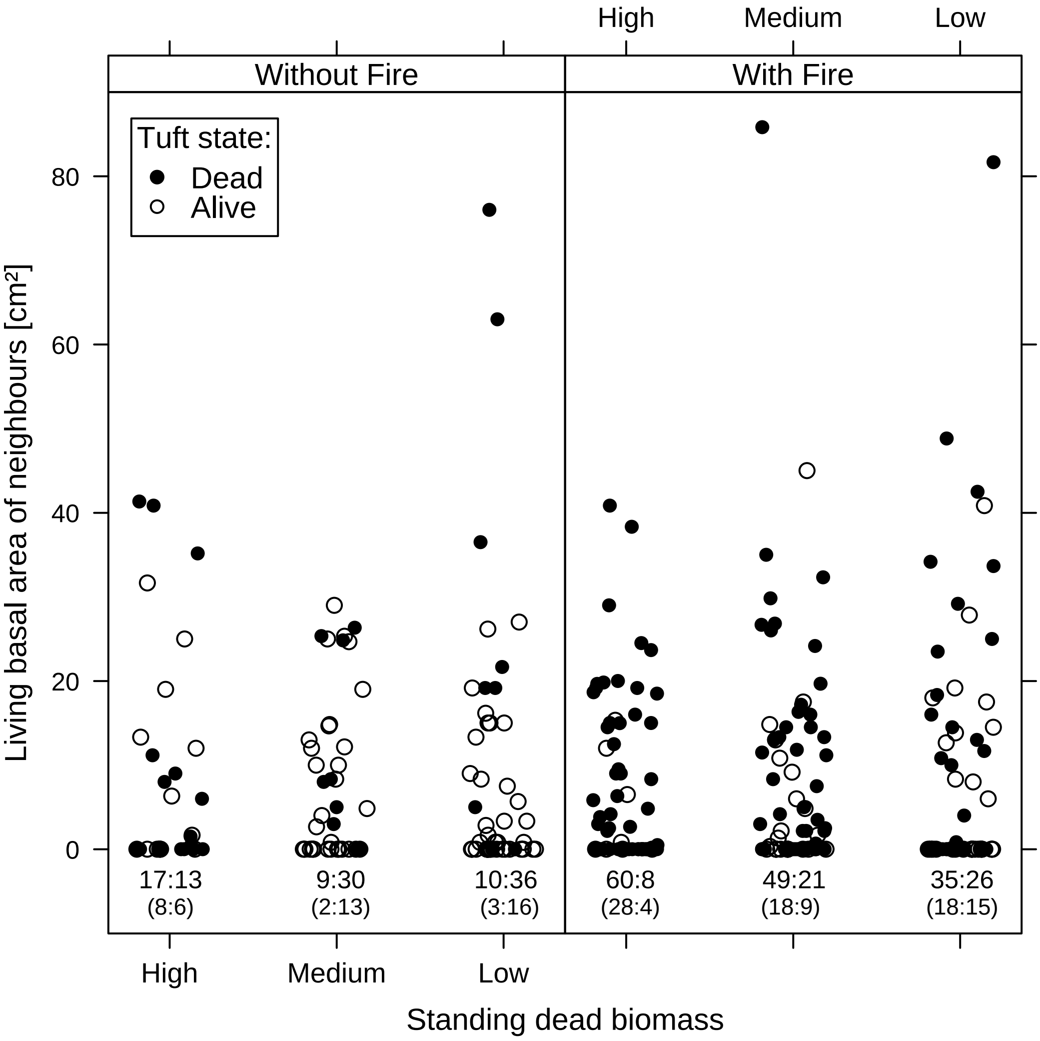

Figure 4.1: Tuft mortality in relation to neighbour abundance (quantified by the living basal area of neighbours, NA$_{LBA}$), standing dead biomass (SDB) and fire. Noise was added to the standing dead categories in order to visualize overlaps. The dead:alive ratio of tufts is given below the standing dead categories. Furthermore, the dead:alive ratio of tufts within the '0' range of the y-axis is shown in brackets.

fire significantly influenced tuft mortality (Table 4.2). Graphical analysis of the residuals revealed no obvious discrepancies from the assumptions for generalized linear models. The minimal adequate model differed significantly (deviance = 87.436; d.f. = 3; $p < 0.0001$) from the null model. Furthermore, the minimal adequate model fitted well to our set of observations, because it did not differ significantly (deviance = 41.158; d.f. = 40; $p = 0.4200$) from the saturated model. Both tests (minimal adequate model versus null model and minimal adequate model versus saturated model) were based on log-likelihood ratios. The model selection procedure showed that none of the interaction terms significantly ($p > 0.05$) influenced tuft mortality.

The importance of the amount of standing dead biomass (SDB) for tuft mortality was indicated by a strong positive relationship ($p < 0.0001$). We found that tufts with high levels of SDB (> 2/3 SDB) were more likely to die than tufts with medium or low levels of SDB (< 2/3 SDB or < 1/3 SDB) both with and without the impact of fire (Figure 4.2). When neighbour abundance (NA_{LBA}) was high and tufts were exposed to fire, differences between the three SDB categories were smaller (Figure 4.2). Plant size ranged from 0.7 to 140.4 cm^2 for S_{BA} and from 0.7 to 63.75 cm^2 for S_{LBA}. Both indices were not important in predicting tuft mortality, and were excluded during model simplification ($p > 0.05$). Of the three neighbour abundance indices tested, only NA_{LBA} was identified as an important predictor of tuft mortality ($p < 0.01$). Thus, neighbour abundance affects tuft mortality neither by the number of neighbouring tufts (NA_{No}) nor by the sum of the basal area of the neighbours (NA_{BA}), but only by the sum of the living basal area of the neighbours (NA_{LBA}). NA_{LBA} ranged from 0 to 85.83 cm^2 (Figure 4.1). Higher levels of living basal area of neighbours were associated with increased

Table 4.2: Minimal adequate generalized linear model (GLM) for tuft mortality as a function of the variables SDB (continuous), Fire (two levels) and the competition index NA_{LBA} (continuous). Explanatory variables excluded during model simplification were S_{BA} ($p = 0.611$), S_{LBA} ($p = 0.932$), NA_{No} ($p = 0.699$), NA_{BA} ($p = 0.083$) and all interaction terms ($p > 0.05$). The minimal adequate model is different from the null model (deviance = 87.436; d.f. $\doteq$ 3; $p < 0.0001$). The minimal adequate model does not significantly differ from the saturated model (deviance = 41.158; d.f. = 40; $p = 0.420$). Both tests are based on log-likelihood ratios. All variables besides fire were treated as being continuous variables.

Parameter	Estimate	s.e.	z-value	p-value
Intercept	0.625	0.402	1.552	0.121
SDB	0.855	0.171	4.987	0.000
Fire_{True}	1.850	0.279	6.64	0.000
NA_{LBA}	0.035	0.011	3.097	0.002

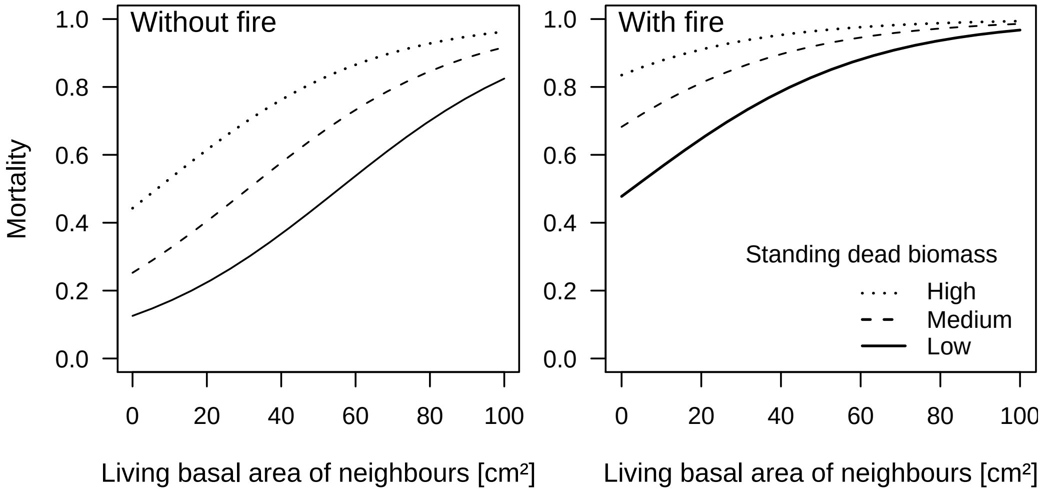

Figure 4.2: Predicted tuft mortality depending on neighbour abundance quantified by the living basal area of neighbours (NA$_{LBA}$), standing dead biomass (SDB) and fire. Lines show the predictions made using the minimal adequate model described in Table 4.2.

levels of tuft mortality, both in the presence and absence of fire (Figures 4.1 and 4.2). In the absence of fire NA$_{LBA}$ increased the probability of death by respectively 70, 65 and 50% for individuals in the SDB 'low', 'medium' and 'high' categories.

The factor fire significantly increased rates of tuft mortality ($p < 0.0001$), irrespective of standing dead biomass and competitive neighbourhood (Figure 4.2). Its impact was particularly severe on individuals with low NA$_{LBA}$, where it increased the probability of death by around 40%. However, with an increase of NA$_{LBA}$ the relative impact of fire was gradually reduced.

4.4 Discussion

We analysed the influence of processes affecting tuft mortality of the perennial grass *Stipagrostis uniplumis* var. *uniplumis*. We focussed on factors acting on the local scale (standing dead biomass, plant size and neighbour abundance) as well as on one landscape-scale process (fire). We found annual mortality rates of up to 73% for the burned tufts and 31% for the unburned tufts. Studies from other arid or semi-arid grasslands have reported considerably lower background mortality rates (Fair *et al.* 1999; Milton & Dean 2000; Drewa & Havstad 2001; Oliva *et al.* 2005). In these studies, the average annual decrease in tuft numbers, frequency or density was, in the absence of large scale disturbances, less than 5%. Mortality rates or decreases in density or frequency exceeding 30% have only been reported after large scale disturbances such as drought (Donaldson 1967; O'Connor 1994; Milton & Dean 2000), intensive grazing (Briske & Hendrickson 1998) or fire (Wright 1971; Boo *et al.* 1996; Snyman 2004b). Hence, the background mortality rates reported here are considerably higher than previously reported.

We found that standing dead biomass (SDB), neighbour abundance by the living basal area of neighbours (NA$_{LBA}$) and fire influenced tuft mortality rates. The amount of standing dead biomass strongly influenced tuft mortality. Studies reporting enhanced tuft mortality or reductions in tuft numbers in grasslands prone to fire exclusion have postulated their observations to be due to an increase in dead biomass and subsequent shading (Silva *et al.* 1990, 1991; Morgan & Lunt 1999). However, these ideas have never been explicitly tested. Our individual-based approach – which directly relates the amount of standing dead biomass to the mortality risk faced by individual tufts – provides evidence that the amount of standing dead biomass does influence mortality rates at the whole plant level. These results are consistent with tiller level experiments, where reductions in light quality and quantity were found to suppress growth, initiation and survival of tillers (Deregibus *et al.* 1985; Everson *et al.* 1988; Wan & Sosebee 2000). This phenomenon of self shading has to our knowledge been ignored in arid or semi-arid savanna (average annual precipitation < 450 mm), apparently because it is assumed that biomass accumulation of standing dead material is low. For instance in moist, productive savanna, a single year of fire exclusion is suggested to allow sufficient dead biomass to accumulate to cause self-shading induced mortality (Silva *et al.* 1990, 1991). Thus, the annual rate of litter accumulation might vary between grasslands and savannas of different rainfall regimes, but our results show that given enough time (in our case 7 years of fire exclusion) sufficient standing dead biomass can accumulate, even in semi-arid systems, to induce high mortality rates.

Individual plant size did not significantly influence tuft mortality. However this result could be an artefact of ignoring small plants (< 3 cm circumference) in this study. It is known that the smaller size classes are the most susceptible to mortality (Peart & Foin 1985; Silva *et al.* 1990; O'Connor 1994; Oliva *et al.* 2005). Similarly to our findings, Milton & Dean (2000) found that for tuft diameters > 2 cm drought-induced mortality was not influenced by tuft size.

Two common measures of competition, the number and the sum of the basal area of close neighbours (e.g. Silander & Pacala 1985; Aguilera & Lauenroth 1993a) showed no effect on mortality of the focal plant in our study. We found that an index, which incorporates not the sum of the whole basal area but only the sum of the living basal area (NA$_{LBA}$), explained significantly more variance in mortality rates. Such an approach, where dead plant parts are not considered but only the 'active' size of the neighbours is accounted for, seems particularly appropriate for tufted grasses which accumulate dead tillers.

Our results add to the evidence that local density is important in arid regions (Fowler 1986b; Goldberg *et al.* 1999). While previous studies in arid regions have shown that competition influences growth and production (e.g. Aguiar *et al.* 2001), this study is the first to show that mortality can be density-dependent in mature perennial grasses. Similar results of intraspecific density-dependent mortality of mature individuals have been documented for woody species in tropical forests (Condit *et al.* 1994; Hubbell *et al.* 2001; Peters 2003).

Our results suggest the observed importance of intraspecific competitive effects to vary as a function of the time since the last fire, as immediately after the fire competitors are rare due to enhanced fire-induced mortality. Rates of tuft establishment, growth and biomass production have been observed to be stimulated when competition levels are low (Aguilera & Lauenroth 1993a; Milton & Dean 2000; Aguiar *et al.* 2001; Zimmermann *et al.* 2008; *Part 2 and 3, this thesis*). We therefore propose that growth of survivors and of new recruits is enhanced immediately after a fire. At some point in time after the fire, resources are depleted and competitive effects are severe enough to lead to enhanced mortality of individuals. Such a phenomenon was also observed after a fire in woody species of Brazilian Cerrado, where enhanced initial plant recruitment and growth was followed by strong intraspecific competition and subsequent reduction in the number of individuals (Soares *et al.* 2006). We suggest that our research area was in the second stage of the process at the beginning of our study, which would explain the strong impact of neighbour abundance on the mortality rates observed. We recommend that this build-up of competitive pressure with 'time since fire' be incorporated into models and management plans for populations of perennial savanna grasses.

Fire increased annual tuft mortality rates of our study species by approximately 42%. We are aware of only one study that directly related individual tuft mortality to fire in semi-arid grassland (Boo *et al.* 1996). In that study, mortality rates depended strongly on species and type of fire: fire of high intensity killed 66–86% of the individuals of two perennial grass species, whereas a fire of moderate intensity killed only 2.5% of the individuals. Mortality rates of other perennial grass species were in the range of 15–38%. Other studies with repeated surveys of the frequency or density of perennial grass tufts in dry environments also report low abundance (approx. 40%) after fire (Drewa & Havstad 2001; Snyman 2004b). The high mortality observed in our study might also be due to the type of fire and the pre-fire condition of the grass layer. Back fires are more damaging to the grass layer than head fires, as they release their heat at or near the soil surface in contrast to head fires where the heat is predominately transferred away from the soil surface (Trollope 1999; Snyman 2003). Furthermore, fire has been reported to be more damaging when the grass canopy is dense and moribund (Wright 1971; Everson 1999). In our study area, approximately 60% of all grass tufts had more than 1/3 of tillers dead. However, the reduction in tuft numbers due to fire needs to be interpreted in the context of competitive interactions between tufts. So far, the positive impact of fire on the grass layer was mainly discussed in the context of removing dead plant material (Bailey 1988; O'Connor & Everson 1998; Silva *et al.* 1990, 1991; Morgan & Lunt 1999). Our study additionally shows that fire leads to a reduction in the number of individuals in a population. This in turn reduces the average level of competition between individuals in the population and hence increases the survival rates and productivity of the survivors.

4.5 Conclusions

Despite high fire-induced mortality, fire might in the long term be the only management tool to maintain a healthy grass population. The high mortality observed (31%) even in the absence of fire is due to high levels of standing dead biomass and competitive pressure which builds up with time since fire. Both standing dead biomass and competitive pressure are reset by fire. Hence, although fire has the direct effect of increasing mortality rates, it also serves to reset the competitive environment and thereby indirectly reduces competitive pressure. In systems where grazing impacts on the grass layer are negligible, fire may therefore be the only means of maintaining the vitality of the grass layer (Everson 1999). At our study site, critical levels of competitive pressure had built up by seven years since the last fire, suggesting that the recommendation of Stander *et al.* (1993) to burn this system every five to nine years is sound.

Part 5

General discussion

This thesis investigates the perennial savanna grass layer from an individual perspective and aims to contribute to a predictive understanding of perennial grass populations and to a mechanistic understanding of the ecology of arid savanna.

Current assumptions and syntheses on how the savanna grass layer functions and how it should be managed are predominately based on plot-level studies which do not consider the actual unit of a population – the individual –, and therefore ignore the importance of local density (e.g. Le Houérou 1989; Scholes & Walker 1993; Keya 1998; Fynn & O'Connor 2000; Ward & Ngairorue 2000; O'Connor *et al.* 2001; Augustine & McNaughton 2006).

By adopting an individual-based approach, this thesis aims to define the role of local density for perennial grass population dynamics. Hence, the main working hypotheses were, that (i) demographic processes and (ii) production at individual level are highly density-dependent, and that (iii) fire by reducing density dependent effects plays a positive role for grassland health and population turnover. The multi-factorial nature of the experiments additionally provides new insights into the combined impact of ecological drivers on perennial grass populations.

Because different kinds of plants may be most strongly regulated at different life history stages, it is important to know which factors affect the population at a particular life history stage or with regard to particular demographic parameters (Goldberg *et al.* 2001).

Therefore, I conducted a series of field experiments focusing on the most important stages in the life cycle of the perennial grass *Stipagrostis uniplumis*: recruitment, growth/production and mortality. These three life stages were investigated in detail, each in a separate study. Concerning recruitment, a full-factorial experimental design explored the combined roles of seed and moisture availability, fire and competitor presence on emergence, growth, survival and flowering. Individual production was measured as affected by neighbour abundance, plant size and fire history. Mortality rates were assessed in relation to self-shading, neighbour abundance, plant size and fire. In the paragraphs that follow I discuss the main findings of each of the component studies.

Recruitment. All of the factors investigated affected some stage of the recruitment process, but not all significant effects contributed to enhancing the final number of recruits. Seed availability significantly enhanced rates of seedling emergence but played no further role in the recruitment process. Competition by the established vegetation exerted a strong negative effect on every step of the recruitment process, whereas burning positively affected seedling emergence, growth, flowering and survival. In contradiction to existing theory, irrigation had a minor effect on seedling recruitment and recruitment did therefore not seem to be limited to above average rainfall years. Rather, recruitment was triggered by events that open up the grass canopy and reduce the abundance of competitors. The results imply that infrequent fires in semi-arid regions may create a recruitment niche for perennial species. Fires can be used to remove aboveground vegetation, thereby reducing local density and enhancing rates of recruitment.

Production. Individual production was found to be highly dependent on neighbour abundance, which had a strong negative impact. The data were better described by a measure of neighbour abundance that considered the size of neighbours than by just counting neighbour individuals. Burning promoted individual production at least in the short term. Because perennial grass production is highly density-dependent, the results suggest that thinning of a sward can enhance individual production and that periodic fires can promote individual production by reducing competitive levels.

Mortality. All factors investigated (burning, neighbour abundance and the amount of standing dead biomass) substantially increased the mortality rates of individuals. The relationships between these determinants of mortality are, however, complex. That is, although fire is an important direct source of mortality, it indirectly lowers the risk of mortality by reducing the amount of standing dead biomass and competitive pressure. My results therefore imply that avoiding fire will reduce the vitality of perennial grass populations.

The individual-based approach of this study reveals a new perspective on the dynamics of the savanna grass layer. Because the grass layer in the study system is almost mono-specific, knowledge on the population dynamics of this particular grass species can be up scaled to the level of the grass layer and hence contributes to a mechanistic understanding, with implications for utilisation and management.

Most of the current knowledge on the grass layer's functioning and productivity comes from plot-level studies (e.g. Scholes & Walker 1993; Fynn & O'Connor 2000; O'Connor *et al.* 2001; Augustine & McNaughton 2006) which ignore the importance of local density and fail to define the role of ecological factors for perennial grass population dynamics. The results of this thesis however point to the overwhelming negative influence of local density on crucial stages in an individual's life cycle. All stages of the recruitment process as well as individual production and mortality were highly density-dependent. This thesis hence demonstrates the importance to consider local density in both applied and theoretical studies.

Knowledge on density-dependence of grass population processes also allows a new interpretation of ecological drivers. Rangeland ecologists consider fires as unimportant or even unwanted in dry grasslands because plot-level studies found fires to reduce cover or total amounts of biomass in these systems (e.g. Bennett *et al.* 2002; Snyman 2003, 2004b).

Results of these individual-based studies however suggest that avoiding fire will adversely affect grassland health in a natural dry savanna. The results imply that accumulated standing dead plant material and high competitive levels – if not reset by fire – enhance mortality rates, reduce individual production and entirely restrain recruitment of new individuals into the population. Hence, fire affects the grass layer not only indirectly via its influence on tree cover (Sankaran *et al.* 2005) as argued in the discussion on bush encroachment (Van Langevelde *et al.* 2003; Ward 2005; Britz & Ward 2007) but additionally plays a direct and important positive role in grassland health and in population turnover in perennial grasses. Negative effects of reduced cover or biomass after fire (Bennett *et al.* 2002; Snyman 2003, 2004b) are, as suggested by this thesis, due to losses in individual numbers and seem to be demographically compensated by enhanced recruitment rates but also by enhanced productivity of survivors. For simple demographic processes my results suggest that with fire grass has higher fitness (more offspring) than without fire. Fires occur less frequently in dry savannas, but they seem to be of no less importance for grassland health compared to more moist savannas where long term fire exclusion is known to adversely affect grass population dynamics (Mott & Andrew 1985; Silva & Castro 1989; Silva *et al.* 1990). The positive effect of burning might have been neglected for arid savannas because these systems are mostly used as rangelands where frequent grazing by livestock might to a certain extend replace the positive impact of fires. Similar to fires, grazers remove above-ground biomass. Nevertheless, grazer densities in natural savannas are low (Oesterheld *et al.* 1992, and burning and grazing are not functionally equivalent. While grazers avoid patches where a large amount of moribund material has already accumulated (Augustine & McNaughton 1998; Belsky & Blumenthal 1997; Kraaij & Ward 2006), fires depend on such fuel accumulation and reset these unproductive patches (this thesis).

The multi-factorial nature of the experiments allowed to detect the relative and interactive influence of several factors on the demographic stages of a grass individual and allowed a wider interpretation as opposed to single-factor experiments (O'Connor 1996). Also, the investigation of several life history stages revealed the hierarchical importance of the putative driving factors. Hence, rainfall and seed availability affected early stages of the recruitment process such as emergence or growth but did not influence the final number of recruits. This result contradicts other studies that found recruitment to be limited by seed availability (e.g. Hamilton *et al.* 1999; O'Connor

1996) and it also contradicts existing theory that recruitment is limited to above average rainfall years (e.g. Potvin 1993; Lauenroth *et al.* 1994; Bisigato & Bertiller 2004).

The general consensus in the literature is that rainfall and grazing are the most important factors for grass layer dynamics in dry regions, whereas fire is rarely regarded as an important factor (e.g. Walker *et al.* 1981; Van Wilgen & Scholes 1997; O'Connor & Everson 1998; Fuhlendorf *et al.* 2001). This thesis, however, found by adopting an individual-based perspective, that the neglected factors 'local density' and 'burning' are in fact crucial for understanding grassland health and dynamics. This is because fire acts to reduce the negative effect of local density and therefore enhances rates of recruitment and individual production.

5.1 Outlook

Grazing. This thesis investigated the population dynamics of a perennial grass in its natural environment. At the study site, large herbivores occur in very low abundance and human influence is almost non-existent. Hence, this study system allows to ignore the roles of herbivory and of human disturbance. However, today many savannas are managed for the production of domestic livestock (Skarpe 1992). In dry savannas, livestock is in most cases supplemented with water which leads to high animal densities and to reduced animal mobility resulting in high grazing pressures (Skarpe 1992; Oesterheld *et al.* 1992). *Stipagrostis uniplumis* is known to decrease in abundance with increasing grazing pressure and to become locally extinct in areas with a history of prolonged heavy grazing (Schulte 2002; Müller *et al.* 2007). Knowing that all *Stipagrostis uniplumis* population processes are highly density-dependent, it would be interesting to experimentally define levels of grazing that do not harm the population but instead have the positive role of reducing individual numbers and hence the negative effect of local density. Furthermore, it would be of interest to experimentally investigate whether a certain grazing regime can to some extent replace the role of fire for maintaining a healthy grass population. Thus, we need a more mechanistic understanding of the indirect and interactive effects of fire and grazing on the grass layer. Up to now, effects of fire and grazing on savanna dynamics have been studied with a clear focus on the tree layer (Van Langevelde *et al.* 2003; Higgins *et al.* 2007; Nefabas & Gambiza 2007). Similar approaches are needed for the grass layer.

Rainfall. I found the role of rainfall not to be as crucial for grass recruitment as previously reported (e.g. Potvin 1993; Lauenroth *et al.* 1994; Bisigato &

Bertiller 2004), as average rainfall amounts were adequate for recruitment in my experiment. It was however beyond the financial and logistical scope of this thesis to conduct large-scale irrigation experiments to investigate the role of rainfall distribution and amounts on production and on mortality rates. Although rainfall is suggested to be a main determinant of dry savanna (e.g. Walker *et al.* 1981; O'Connor & Everson 1998; Sankaran *et al.* 2005), I am not aware of any study that experimentally investigates the role of moisture availability on individual mortality and production rates of perennial savanna grasses in a natural environment. Reports on rainfall effects on savanna vegetation are based on precipitation monitoring and the majority of the studies on rainfall–vegetation interaction adopts plot-level approaches (e.g. Pandey & Singh 1992; Augustine & McNaughton 2006; Kraaij & Milton 2006, but see O'Connor 1994; Milton & Dean 2000) and does often not distinguish between annual and perennial vegetation. Also, changes in cover or biomass – the results of plot-level studies – may reflect recruitment or growth (Milton & Dean 2000) and can therefore not contribute to a comprehensive understanding of population responses to rainfall amounts and distribution.

However, the few existing individual-based monitoring studies found prolonged periods of low rainfall amounts or droughts to affect perennial grass populations by enhancing mortality rates (Milton & Dean 2000; O'Connor 1994). It would be of interest to experimentally define the levels of rainfall amount and distribution that harm the population. Together with results from this thesis, such information would improve knowledge on the dynamics of the perennial grass layer, its reaction to extreme events such as fire or drought and the ability to predict the response of savanna grasslands to climate change.

Recruitment filters. The aim of the recruitment experiment was to define the major recruitment filters. The large number of factors investigated in the experiment however logistically restricted every single factor to only two levels (present/absent). The next step would be a more detailed assessment of the most important factors. It would hence be interesting to find critical levels at which the established competitors harm recruitment rates. Also, a more detailed experiment on the factor 'fire' would particularly help to improve management practices. Here, it would be interesting to vary fire type (burning with or against the wind – 'head fire' or 'back fire'), fire timing and fire intensity. It would also be good to experimentally define whether the positive effect of burning is related to biophysical effects (Ojima *et al.* 1994) or to changes in soil chemistry (Radho-Toly *et al.* 2001; Bennett *et al.* 2002; Castelli & Lazzari 2002; Rau *et al.* 2007).

Decomposition. Initially, this study aimed to also investigate annual decomposition rates of *S. uniplumis.* Unfortunately, an unplanned fire destroyed the experiment and the unburned samples were too few to assess the impact of various factors on the annual decomposition rate which was around 20% (Zimmermann, *unpublished data*). Still, information on decomposition is needed for management reasons (e.g. to assess the accumulation rate of fuel load) but also for a systems understanding (Pütz 2006).

Last but not least. Knowledge is missing on several parameters, which are important for predicting the long term population dynamics of the species. Information on for example seed longevity or maximum age of individuals are crucial particularly for simulation models which aim to predict population dynamics under scenarios of different land use practices or climate change (Müller *et al.* 2007). Such parameters can be assessed via long term experiments and monitoring programmes.

5.2 Conclusions

This thesis demonstrates that the demographic, individual-based perspective is essential for an understanding of the dynamics of the savanna grass layer. The results challenge current paradigms of how savannas function and how they should be managed. The current synthesis of rainfall and grazing being the major environmental drivers in dry savanna needs to be revisited. The recruitment experiment found average amounts of rainfall to be sufficient for perennial grass recruitment, hence recruitment was not – as suggested by current syntheses – restricted to above average rainfall years. Rather, results from this thesis suggest another environmental factor to play a crucial role in natural dry savanna. A factor whose importance for dry grasslands has largely been ignored or neglected, namely fire. This thesis suggests that fire, in reducing local density, plays an important positive role for perennial grass' population turnover. Hence, the proposed avoidance of burning adversely affects the vitality of perennial grass populations. This thesis thus implies that fire is – amongst rainfall and grazing – one of the major environmental drivers not only in moist but also in dry savanna. The individual perspective and the multi-factorial nature of the experiments provide new insights and allow a new interpretation of environmental factors, which were not detected by plot-level or single-factor studies. Results of this thesis point to the overwhelming negative influence of local density on all perennial grass life history stages investigated. Both applied and theoretical research should therefore incorporate the individual perspective, if the aim is to contribute to a mechanistic understanding of the ecology of arid savanna.

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Zusammenfassung

Savannen zählen zu den größten und zugleich am stärksten durch Landnutzung und Klimawandel bedrohten terrestrischen Ökosystemen. Die Entwicklung adäquater Managementstrategien und Vorhersagen zu den Auswirkungen des Klimawandels ist daher dringend nötig, setzt jedoch ein prozessbasiertes Verständnis dieser Ökosysteme voraus. Die bisherige Kenntnis von Savannendynamiken, vor allem solchen der Grasschicht, beruht größtenteils auf Studien mit Flächenansatz. Diese untersuchen die Gesamtbiomasse einer Fläche, lassen aber keine Aussagen über elementare populationsökologische Prozesse wie Etablierung und Mortalität zu. Zum Verständnis der Populationsdynamik sind daher individuenbasierte Studien unabdingbar.

Diese Arbeit konzentriert sich auf die wichtigsten Stadien im Lebenszyklus eines dominanten, ausdauernden Grases (*Stipagrostis uniplumis*) in einer anthropogen weitgehend ungestörten Savanne (Etosha National Park). Ich untersuche den Einfluss biotischer und abiotischer Faktoren auf 'Etablierung', 'Produktion' und 'Mortalität' mittels eines multifaktoriellen, experimentellen Ansatzes. Anhand einer Gegenüberstellung von Ergebnissen meiner individuenbasierten Studien mit solchen von flächenbasierten Studien diskutiere ich aktuelle Theorien zur Savannendynamik.

Ich konnte zeigen, dass entgegen bisheriger Annahmen die Etablierungsrate von *S. uniplumis* nicht allein durch Wasser- oder Samenverfügbarkeit limitiert ist. Vielmehr sind nicht nur sämtliche Stadien der Etablierung, sondern auch die Produktions- sowie die Mortalitätsrate stark dichteabhängig: Eine hohe Dichte an Nachbarindividuen verhindert Etablierungsereignisse, reduziert die Produktion auf der Individuenebene und erhöht die Mortalitätsrate. Feuer hingegen beseitigt moribundes Pflanzenmaterial und reduziert durch Verringerung der Individuendichte den Konkurrenzdruck. Die hohe Mortalitätsrate bei Feuer wird durch erhöhte Produktion der Überlebenden sowie durch verstärkte Keimlingsetablierung kompensiert.

Meine Arbeit trägt mit neuen Erkenntnissen, welche in individuenbasierten Studien gewonnen wurden, zum Verständnis der Populationsdynamik von Savannengräsern bei. Die Ergebnisse zeigen, dass gängige Theorien zur Rolle ökologischer Faktoren in semi-ariden Savannen hinterfragt werden müssen. Insbesondere kann Feuer – entgegen bisheriger Annahmen – hier eine fundamentale und positive Rolle in der Populationsdynamik spielen. Diese Erkenntnis ist besonders interessant, da Feuer in Savannen als Management-Werkzeug eingesetzt werden kann.