



Research article

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

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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: self-shading by the standing dead biomass of a tuft, plant size, and neighbour abundance as a measure of intra-specific competition. Three indices of neighbour abundance 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. The amount of standing dead biomass increased 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, whereas the other indices of neighbour abundance had no influence on mortality rates. On a landscape level, fire significantly increased tuft mortality rates, from up to 31% for unburned tufts, to 73% for burned tufts. Fire, on the other hand, indirectly reduces the risk of future mortality by reducing self-shading and competitive pressure. Our results imply that the timing and frequency of fires is crucial for their positive indirect effects on plant fitness. As the onset of local effects on plant mortality is highly dependent on grazing pressure and stochastic rainfall, fire management should flexibly take into account the accumulation of dead plant material on a site.

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Introduction

The terrestrial surface of the southern continents is dominated by tropical and sub-tropical savannas and grasslands. In these systems, perennial grasses are crucial for the ecosystem's functioning in supporting herbivores and preventing soil erosion (Sala and Paruleo, 1997; Van Oudtshoorn, 2002). Yet, research on the grass layer in savannas has a strong system-level bias, focusing on production, composition and cover (Hodgson and Illius, 1996; Tainton, 1999; Grice and Hodgkinson, 2002; Gibson, 2008). Few studies have investigated these grasslands from a demographic perspective and studies that do consider demography typically focus on seedling establishment (e.g. Everson et al., 1988; O'Connor, 1996; Littera et al., 1997; Wan and Sosebee, 2002).

In ecosystems where grasses play an important role, few long-term studies include annual mortality rates of perennial grass individuals (e.g., Canfield, 1957; O'Connor, 1994; Fair et al.,

1999; Hodgkinson and Müller, 2005; Oliva et al., 2005) and most of them do not mention processes affecting tuft mortality, i.e. the mortality of an individual plant genet. If such processes are analysed, focus is usually on landscape-scale factors such as drought (e.g. Donaldson, 1967; Danckwerts and Stuart-Hill, 1988; Grice and Barchia, 1992; Milton and Dean, 2000; Hodgkinson and Müller, 2005), grazing (e.g. Williams, 1970; O'Connor, 1991, 1994; Briske and Hendrickson, 1998; Oliva et al., 2005) or fire (e.g. Silva and Castro, 1989; Silva et al., 1990; Boo et al., 1996) but not on local-scale factors such as competition, size or standing dead biomass.

It is known, however, that individuals continually turnover in perennial grasslands (O'Connor and Everson, 1998; Fair et al., 1999; Guàrdia et al., 2000), hence mortality is clearly an important process. It follows that an understanding of factors affecting individual mortality is crucial for understanding and managing grasslands. The broad aim of this study is to investigate local factors that affect 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.

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We examine three local-scale factors, namely self-shading, living plant size and neighbour abundance that have been suggested to influence mortality rates of perennial grasses (McGinnies, 1971; Peart and 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, 1984; Silva et al., 1990, 1991; Morgan and 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). From an energy balance perspective, the accumulation of dead culms might have the positive effect of shading living culms, but it presumably has the overall negative effect of making the plant more tuft-like which increases the leaf boundary layers causing the leaves to heat up (Jones, 1982). In perennial grasses of arid or semi-arid regions (average annual precipitation < 450 mm) the role of self-shading on plant performance has received little 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.

Studies using basal diameter or basal area as a measure of plant size typically report that small individuals are more likely to die than large ones (Peart and Foin, 1985; Silva et al., 1990; O'Connor, 1994; Oliva et al., 2005). Studies where no differences in mortality rates between grass tufts of different basal diameters were found excluded pre-reproductive or immature plants (Milton and Dean, 2000; Hodgkinson and Müller, 2005). The higher mortality of small individuals is mostly related to an increased water stress of individuals (e.g. Hodgkinson and Müller, 2005), or to an increased competition for water resources during drought times (Milton and Dean, 2000), implying that small individuals suffer more from an increased water stress, and are less competitive. This has been explained with different resource use strategies of young compared to adult grass individuals, related to the rainfall pulses typical for arid environments (Jankju-Borzelabad and Griffiths, 2006). While young individuals have an increased capacity for using pulsed resources due to their relatively higher growth rate (Grime, 2001), mature plants with well-developed roots exploit a greater soil volume. They can maintain more constant resource uptake and retention during inter-pulse periods, and their survival rates during inter-pulse (drought) times are thus higher.

Grass individuals may also be small because they are heavily grazed. Thus, their increased mortality may also be a consequence of subdivision or fragmentation related to the high disturbance intensity and frequency of grazing (O'Connor, 1994; Oliva et al., 2005). The impact of grazing reduces stored energy reserves, leading to a reduced resilience of individuals (Guàrdia et al., 2000). Reserve storage improves individual fitness in environments where plant individuals are likely to experience disturbance or strong fluctuations of environmental conditions, such as stochastic dynamics of a limiting resource. In arid environments, disturbances by grazing and/or fire, and stochastic dynamics of water resources usually occur together in the same habitat. The accumulation of reserve biomass in non-photosynthetic reserve organs at the plant base is an important strategy for perennial grasses to reduce plant mortality under these conditions (Müller et al., 2007; Owen-Smith, 2008).

The final local-scale factor we examine is intra-specific competition as indicated by neighbour abundance. Competition among plants has been reported to be intense in semi-arid (Fowler, 1986) and unproductive (Goldberg et al., 1999) systems.

However, few studies have explored density-dependent interactions between perennial grass individuals (Aguilera and Lauenroth, 1993; Aguiar et al., 2001; Jankju-Borzelabad and Griffiths, 2006). Mortality due to intra-specific competition has so far only been mentioned in the context of the recruitment process of perennial grasses (Aguilera and Lauenroth, 1993), or in the smallest size class of mature individuals (Peart and 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 that act at the landscape level also influence mortality in perennial grasslands. Tuft mortality has mainly been attributed to drought (e.g. Donaldson, 1967; Danckwerts and Stuart-Hill, 1988; Milton and Dean, 2000; Hodgkinson and Muller, 2005) and grazing (e.g. O'Connor, 1991, 1994; Briske and 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 many arid and semi-arid regions compared to high rainfall savanna (Bond, 1997; O'Connor and Everson, 1998) and its use as a management tool has often been questioned or neglected for these dry regions (Tainton and Mentis, 1984; Snyman, 2002, 2003; Bennett et al., 2002). However, fire is used in the arid grasslands and savannas of the southwestern United States and northern Mexico to control woody plant densities and to stimulate grass growth (McPherson, 1995).

Consequently 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 and Dajoz, 2001). The limited data available in semi-arid regions suggests that fire causes a decline in productivity and a decrease in cover, density or biomass of the grass layer (Drewa and Havstad, 2001; Bennett et al., 2002; Snyman, 2003, 2004).

The objective of our study is to contribute to the understanding of population dynamics of perennial grasses by examining the often neglected event 'mortality'. We examine local-scale factors acting at individual level: self-shading via standing dead biomass, plant size, and neighbour abundance. We also 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.

Materials and methods

Study area and study species

The Etosha National Park (hereafter 'Etosha') is situated in north-central Namibia and comprises an area of 22,915 km² (Du Plessis, 1997). Almost the whole of Etosha can be described as arid to semi-arid savanna (250–500 mm average annual rainfall) with highly variable and erratic rainfall (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 and Kok, 1988; Le Roux et al., 1988).

The research area is located in northern 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 forskoolii* 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). Grazer density and therefore grazing pressure in this area is very low (Craig, 1998; Erb, 2000; Kilian, 2002; Kolberg, 2004). Soil texture was relatively homogeneous with means of ca. 85% sand, 4% silt and 11% clay in the research area. As the study site is flat and homogeneous, plant-available water is not likely to be affected by spatial heterogeneity.

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 and Owen-Smith, 1974; Van Oudtshoorn, 2002). Because of its wide distribution and local dominance it is important for forage and soil stabilisation (Malan and Owen-Smith, 1974; Van Oudtshoorn, 2002; Klaassen and 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 known to be capable of vegetative recruitment. Although only long-term monitoring or molecular analysis can identify whether a tuft is a ramet or a genet, 4 years of monitoring (J. Zimmermann, unpublished data) and a recruitment experiment (Zimmermann et al., 2008) conducted at the same site provided not a single instance of successful vegetative reproduction but numerous instances of successful reproduction from seed. Hence, although we cannot strictly differentiate whether individual tufts at our study site are ramets or genets, circumstantial evidence suggests that most individual tufts at our study site are 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 individual, although in reality tillers within a tuft are physiologically independent (Briske, 1991).

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 likely to be 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 km². 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 2 m from the edge of a tree or shrub canopy. Furthermore, we did not include juvenile individuals (basal circumference less than 3 cm); seedling mortality was explored in another experimental study (Zimmermann et al., 2008).

The following explanatory variables were recorded for each tuft at the beginning of the study (see also Table 1):

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

Table 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 neighbour's basal area	0–104 cm ²
	NA_{LBA}	The sum of all neighbour's living basal area	0–85.83 cm ²
Fire	Fire	Whether the focal tuft burned or not	True/false

dead ($n=107$). In the analyses these three categories are used to define SDB as an ordinal variable.

Plant size: The basal circumference (cm) was measured for each individual and converted into the basal area (S_{BA} , cm²) as an index of size. The living basal area (S_{LBA} , cm²) 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 distance from the focal plant (Mithen et al., 1984). In a preliminary analysis we could not statistically detect an effect of neighbouring plants on focal plant mortality beyond distances of 25 cm (J. 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} ; and NA_{LBA} , the sum of the neighbours' S_{LBA} . Note that interspecific perennial herbaceous neighbours were so rare as to be non-existent in our sample and focal plants were selected to be at least 2 m from the nearest woody plant's canopy edge. Hence neighbour abundance refers exclusively to conspecific abundances.

A management fire was ignited in the study area in October 2005 before the first rains and the onset of the growing season. It was a counter-fire (back fire) to a large wildfire with typical timing for Etosha in that most fires occur from September to December (Siegfried, 1981; Du Plessis, 1997). Before this fire, the site had not burned for the past 7 years; 3–7 years are typical fire intervals for this area (Etosha Ecological Institute, unpublished data).

The fire created a mosaic of burned and unburned patches, allowing us to include the factor fire into our analysis. We assumed that which patches burned and which did not was determined by the stochastic spread of fire (Ratz, 1995; Zinck and Grimm, 2008). Percolation theory (Stauffer and Aharony, 1992; Ratz, 1995) then predicts that the result is a mosaic of burned and unburned patches similar to what we observed at our study site. Hence, the assignment of the treatment fire was random with respect to tuft location. 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 1 year later, after the first heavy rains had induced sprouting of tillers. We then recorded whether a tuft had survived or died.

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 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 model that includes all variables and two-way interactions (the full model). This model was simplified using a stepwise selection procedure. The minimum adequate model is the simplest model that is not significantly worse (tested at the 5% level using a likelihood ratio test) than the next more complex model. The selected model is evaluated by comparing it to the simplest possible model (the null model). The null model assumes that the data can be described by the mean response across all treatment factors. 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).

Results

The total dataset describes the effects of the explanatory variables on 314 tufts. Altogether, 180 tufts (57%) died within 1 year; 73% of the burned and 31% of the unburned tufts (Fig. 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 fire all significantly influenced tuft mortality (Table 2). Graphical analysis of the residuals revealed no obvious discrepancies from the assumptions

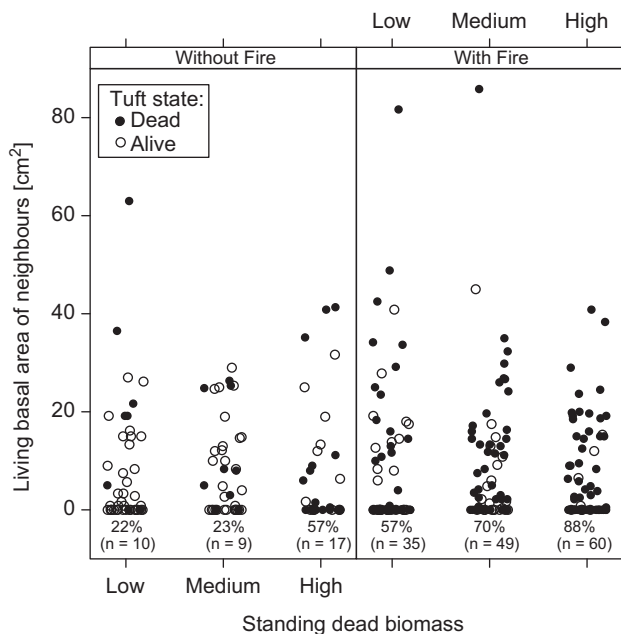


Fig. 1. Tuft mortality in relation to neighbour abundance (quantified by the living basal area of neighbours, NA_{LBA}), standing dead biomass (SDB) and fire. Noise was added to the standing dead categories in order to visualize overlaps. Percent mortality and number of dead tufts are given below the standing dead categories.

Table 2
Minimal adequate model for tuft mortality^a.

Parameters	Estimate	SE	z-value	Pr(> z)
Intercept	-2.795	0.438	-6.384	0.000
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

^a Minimal adequate model for tuft mortality as a function of the variables SDB (an ordinal variable), fire (a factor with two levels) and the competition index NA_{LBA} (a continuous variable). Explanatory variables excluded during model simplification included 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.=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.

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. Increasing standing dead biomass (SDB) was associated with increasing tuft mortality ($P<0.0001$), both with and without the impact of fire (Fig. 2). When neighbour abundance (NA_{LBA}) was high and tufts were exposed to fire, differences between the three SDB categories were smaller (Fig. 2). Focal plant size, whether total or just living, was not important in predicting tuft mortality, and was excluded during model simplification ($P>0.05$).

Of the three neighbour abundance indices tested, the sum of the living basal area of the neighbours NA_{LBA} was identified as the most useful predictor of tuft mortality ($P<0.01$). Thus, although neighbour density (NA_{No}) and the sum of the total basal area of neighbours (NA_{BA}) were positively correlated with the sum of the living basal area of the neighbours (NA_{LBA}), they were poorer predictors of tuft mortality. Higher living basal areas of neighbours were associated with higher tuft mortality, both in the presence and absence of fire. In the absence of fire, a change in NA_{LBA} from zero to 85.8 cm² induces an increase in the probability of death by 70%, 65%, and 50% for individuals in the SDB 'low', 'medium' and 'high' categories, respectively.

Discussion

We found annual mortality rates of up to 73% for burned tufts and 31% for unburned tufts of the perennial grass *Stipagrostis uniplumis* var. *uniplumis*. These results are in line with Wright and Van Dyne (1976, in McClaran, 1995) who report mortality rates as high as 35% in a desert grassland, and Lauenroth and Adler (2008) who report mortality rates of between 37% and 70% in the Great Plains. However, our findings contrast with several studies from other arid or semi-arid grasslands which report considerably lower background mortality rates (not attributable to drought or herbivory; Fair et al., 1999; Milton and Dean, 2000; Drewa and 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%. Taken together our findings and the rates reported in the literature suggest that a large range of mortality rates is possible in arid and

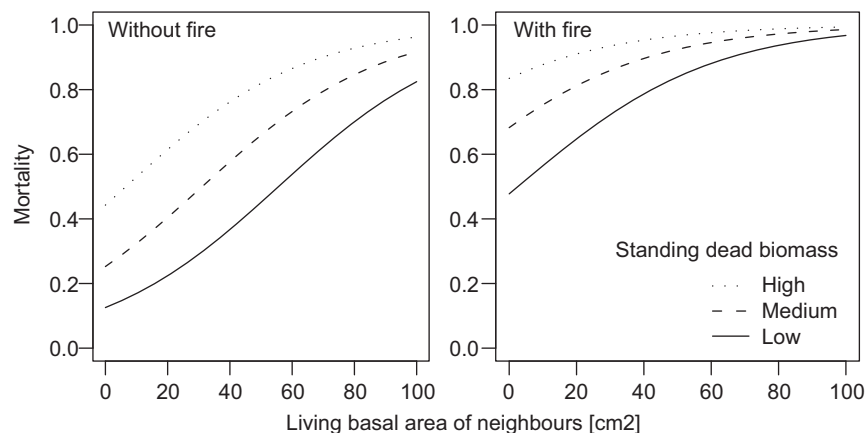


Fig. 2. Predicted tuft mortality depending on neighbour abundance quantified by the living basal area of neighbours (NA_{LBA}), standing dead biomass (SDB) and fire. Lines show the predictions made using the minimal adequate model described in Table 2.

semi-arid grasslands. This conclusion is supported by the few long-term demographic studies available for perennial grasses in arid and semi-arid environments (Austin et al., 1981). For example, Williams (1970) reports that both steady decay in population size and heavy fluctuations in mortality rates may occur for two Australian grass species, depending on environmental conditions. Mortality trends may even differ for cohorts which established in different years. He suggests that substantial fluctuations in mortality rates may be linked to changes in important environmental conditions, while stable rates reflect a consistently favourable or unfavourable environment. However, we do not fully understand yet the causes of the high variance in reported mortality rates for perennial grasses. As long-term demographic studies have only rarely been applied in the past decades because of the need to recognize plant individuals and the heavy labour requirement (Austin et al., 1981), a promising approach is using computer algorithms for tracking the identity in individual genets based on their spatial position in permanent plots (Lauenroth and Adler, 2008), and to separately analyse cohorts or populations of a particular species.

Our findings pertain to a system where large herbivore grazing was negligible. It could therefore be argued that this is an unusual situation. However, many savannas in their natural state are characterised by low herbivore numbers or cycle through periods when herbivore numbers are low. For instance the Gran Sabana has notoriously low mammal biomass, the Australian savannas, the Llanos savanna and the Cerrados had low herbivore biomasses prior to cattle and African grass introductions (Sarmiento, 1984; Huntley and Walker, 1982).

Cases where an accumulation of dead plant material leads to increased grass mortality are also not rare in Southern African savannas. In contrast, they are common in landscapes with low to moderate overall stocking rates, for example on commercially managed cattle and game farms in Namibia (A. Linstädter, unpublished data). The reason is that large herbivores, if allowed to roam freely, are highly selective in their grazing both on a local and a landscape level (Skarpe and Hester, 2008). They prefer to feed on grass regrowth following savanna fires, and avoid individuals and patches where an accumulation of dead plant material has started some time after fire (Klop et al., 2007). This promotes a shifting mosaic of patches (Archibald et al., 2005). Positive and negative feedbacks between grazing, fire, and other disturbances may create complex spatio-temporal disturbance patterns on a landscape scale (Linstädter, 2008; Fuhlendorf et al., 1999). The time elapsed since burning has been identified as the most influential parameter in determining probability of grazing

(Klop et al., 2007), which might also be the reason for the low herbivore densities recorded at our study site 7 years after the last fire.

In our study, 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. As standing dead biomass is an accumulation of old plant material from previous growing periods, dead biomass cannot be a mere symptom of a dying individual but has to be related to increased mortality through a functional mechanism. For studies reporting enhanced tuft mortality or reductions in tuft numbers in grasslands prone to fire exclusion it has been suggested that this is due to an increase in dead biomass and subsequent shading (Silva et al., 1990, 1991; Morgan and 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 individual level, supposedly through the functional mechanism of self-shading. 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 and Sosebee, 2000). The phenomenon of self-shading has to our knowledge not yet been reported for arid or semi-arid savanna (average annual precipitation < 450 mm).

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 which contradicts other studies where smaller size classes are the most susceptible to mortality (Peart and Foin, 1985; Silva et al., 1990; O'Connor, 1994; Oliva et al., 2005). Our result could be an artefact of ignoring small plants (< 3 cm circumference). Similarly to our findings, Milton and Dean (2000) found that for tuft diameters > 2 cm, drought-induced mortality was not influenced by tuft size. However, our results could also be explained by the fact that we analysed tuft mortality in a year with average rainfall, and negligible grazing. The high mortality of small individuals in other studies is either related to water stress

and an increased competition during drought times (which may be explained with different resource use strategies of young as compared to mature individuals; Grime, 2001; Jankju-Borzelabad and Griffiths, 2006), or to the impact of heavy grazing, which leads to a high mortality of individuals that have been reduced in size via fragmentation and subdivision (Oliva et al., 2005).

Two common measures of competition, the number and the sum of the basal area of close neighbours (e.g. Silander and Pacala, 1985; Aguilera and Lauenroth, 1993) had little or 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. Interestingly, the amount of standing dead biomass of focal plants had a strong effect on mortality rates, indicating that self-shading is important. Yet the shading effects of neighbours seemed less important, most probably because the neighbouring grass tufts do not cast shade on the focal tufts. This together with the fact that sum of the living basal area of neighbours positively influenced mortality rates suggests that mortality rates are influenced by competition for soil resources.

Our results add to the evidence that local density is important in arid regions (Fowler, 1986; 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 intra-specific 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 that the observed importance of intra-specific competition depends on the time since the last fire, as immediately after the fire competitors are rare due to increased fire-induced mortality. Since fire kills many individuals and stimulates recruitment (Zimmermann et al., 2008), most individuals in the post-fire environment are small. This implies that the competitive environment is relatively benign immediately after a fire, but that competition increases as the size of individuals increases with time. Consequently, rates of tuft establishment, growth and biomass production have been observed to be stimulated when competition levels are low (Aguilera and Lauenroth, 1993; Milton and Dean, 2000; Aguiar et al., 2001; Zimmermann et al., 2008).

We therefore propose that growth of survivors and of new recruits is enhanced immediately after a fire. In the absence of grazing, 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 intra-specific 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, especially in systems where levels of herbivory are low.

Fire increased annual tuft mortality rates of our study species by approximately 42%, which is in line with the few studies which directly relate individual tuft mortality in semi-arid grassland to fire. In these studies, mortality rates depended strongly on

species, type and timing of fire, and vegetation structure (such as the presence of shrubs). For example fire of high intensity killed 66–86% of the individuals of two perennial grass species in an Argentinian grassland whereas a fire of moderate intensity killed only 2.5% of the individuals (Boo et al., 1996). Mortality rates of other perennial grass species were in the range of 15–38% and were less affected by fire intensity. In a semidesert grassland in the North American Southwest, a fire of high intensity during the growing season killed 90% of black grama (*Bouteloua eriopoda*) individuals and 98% of another species (Cable, 1965). In contrast, two other studies report much lower values for black grama: only 31% of individuals died after a fire of moderate intensity in the growing season (Gosz and Gosz, 1996), compared to mortality rates (derived from grass densities) between 19% and 58% after a fire ignited outside the growing season, depending on the presence or absence of shrubs (Martin, 1983). 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 and Havstad, 2001; Snyman, 2004). These studies show that a focus on perennial grass density or cover may lead to an underestimation of mortality rates because old and newly established grass individuals are not distinguished (see e.g. discussion in Martin, 1983).

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 predominantly 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 their above-ground biomass 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 has been mainly discussed in the context of removing dead plant material (Bailey, 1988; O'Connor and Everson, 1998; Silva et al., 1990, 1991; Morgan and 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.

We can conceptually link different determinants of plant mortality to the phenomenon of reserve storage, a strategy of perennial grasses to increase individual fitness which is particularly important in arid environments (Wiegand et al., 2004). In our study, the local factors of self-shading and intra-specific competition for soil resources both reduce the replenishment of storage tissues, which enhances plant mortality rates. They are functionally similar to factors leading to a depletion or destruction of storage tissue. A depletion occurs if a plant resprouts after a defoliation, caused e.g. by herbivory or low-impact fires; a destruction is related to intense disturbances, mostly by fire or grazing. We conclude that in the absence of other factors affecting reserve storage, self-shading and competitive pressure may induce mortality rates of the same magnitude (exceeding 30%), because a reduced replenishment of reserve storage has a comparable impact on the size of the storage as its depletion or destruction.

Conclusions and implications for fire management

Despite high fire-induced mortality, fire might in the long term be the only management tool to maintain a healthy grass

population in savannas where grazing levels are low. 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 reduce self-shading, and to reset the competitive environment, thereby reducing the risk of future mortality. Surviving individuals may replenish their storage tissues more effectively, leading to an increased ability to survive a future drought, fire or grazing event. In systems where grazing impact on the grass layer is negligible on a landscape or a patch level, fire may therefore be the only means of increasing survival rates of perennial grasses (Everson, 1999).

The timing and frequency of fires is crucial for the success of fire management in regulating tuft grass fitness (Prober et al., 2007), because it determines whether direct or indirect effects of fire on mortality rates dominate. Replenishment of storage tissues is restricted to the growing season. Fires during this time exert stronger direct effects on grass mortality than fires before the onset of growth (Skarpe, 1992; Skarpe and Hester, 2008). In addition, fire management plans for arid and semi-arid environments should aim to avoid negative effects on plant fitness associated with the built-up of dead plant material and competitive pressure. At our study site, critical levels of standing dead biomass and competitive pressure had built-up by 7 years since the last fire. This suggests that the recommendation of Stander et al. (1993) to burn this system every 5–9 years – depending on rainfall and “time since the last burn” – is sound. The high background mortality in our study implies that the grass layer would have benefited from an earlier fire, because survival rates of perennial grasses would have been increased. We conclude that the onset of negative local effects on plant mortality is difficult to predict, because it is not only determined by the time elapsed since the last fire, but it is also highly dependent on grazing pressure and stochastic rainfall. Fire management in semi-arid savannas should flexibly take into account the accumulation of dead plant material on a site.

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