

How stable is the tuft structure of a mesic Drakensberg grassland under various burning regimes?

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Abstract

Management options to maintain the stability of Drakensberg grasslands need to incorporate their dynamic nature in response to fire. This study addressed the lack of information on the spatial and temporal changes of these grasslands at a small (tuft) scale. The basal area of every tuft in three 0.25 m² quadrats per replicate (3) of four burning treatments was mapped over two years in a long-term burning trial using a pantograph. The extent of change in size and shape of tufts indicated the dynamic nature of these grasslands from year to year. Basal cover of *Themeda triandra* was high in the annual winter (62.5%) and biennial spring (50.5%) burns, lower in the five-year burn (36.1%) and low in the biennial summer burn (11.5%). The bare area in the biennial summer burn increased by 5.6%, remained the same in the annual winter, and decreased in the biennial spring (6.1%) and five-year (7.8%) burns. The disappearance of *Stiburus alopecuroides* from the summer burn and increase in basal cover of *Tristachya leucothrix* indicates a directional change in composition which is likely to be irreversible. The biennial spring burn, where the three dominant species were in a state of equilibrium, is recommended for stability.

Keywords: Basal cover, fire, mapping

Introduction

An understanding of the dynamic response of grasses to different fire treatments is crucial for maintaining the stability of montane grasslands. However, there is little knowledge on the underlying demographic processes of the grassland, particularly on recruitment, growth, and mortality of individual grass tufts (Wiegand et al. 2003). Adult plants in montane grasslands are perennial tufted species that depend on vegetative tiller production rather than seed production for survival (Everson et al. 2009). Tufted grasses do not die after reaching a certain size but continue growing more or less indefinitely (Acocks 1990). This growth habit has led to the belief that individual grass tufts may be hundreds of years old (Ratray 1960; De Witte and Stöcklin 2010). In dense species-rich grasslands the co-existence of species will be determined by their competitive ability to access resources such as light, moisture and nutrients for growth (Lauenroth and Aguilera 1998; Peart 1989). The degree to which competition is asymmetric (unequal division of resources amongst competing plants) or symmetric (sharing of resources amongst individuals) may be determined by the nature of the resource being contested (Connolly and Wayne 1996; Freckleton and Watkinson 2001). Light may be pre-empted by larger neighbours, leading to asymmetric competition, whereas water and relatively mobile soil resources may be less so, resulting in more symmetric competition (Weiner 1986). Grasses with a large biomass can inhibit the development of seedlings as they have a competitive advantage for limited resources (Everson 1994).

Competition between different plant species within a community will be determined by a variety of processes, including the spatial distribution of individuals, the resources being competed for and the ability of the species to compete for these resources (Freckleton and Watkinson 2001). These competitive effects and responses vary between species and is not constant within a species, with shifts in resources altering competitive hierarchies (Fynn et al. 2011). Law et al. (1997) noted that asymmetrical competition can be equally strong within and between species in montane grasslands, and depends strongly, but not fully, on plant size (tiller biomass). In the dense montane grasslands of the Drakensberg, where mature tufts of *T. triandra* occupy similar niches, it is likely that both within and between species competition occurs.

Competition is not static but can depend on year-to-year temporal variation (e.g. in climate) (Herben et al. 2003) and spatial variation in competing species (Silverton et al. 1992). This is perhaps why once-off studies of tuft structure in dense grasslands have failed to detect

competition. For example, van Zyl (1998) found no evidence for inter-species competition for space using the nearest-neighbour method and concluded species are equally competitive against conspecific individuals in mesic grassland. Temporal studies on the dynamics of individuals/tufts in relation to environmental variables such as fire are therefore needed.

When there is a short-term change in resources, such as an increase in light intensity after fire, the competitive ability of a plant determines whether it will increase or decrease in abundance. *Themeda triandra*, by virtue of its high basal cover and large biomass, appears to be a vigorous competitor in regularly burnt grassland. However, the competitive superiority of *T. triandra* is not maintained with different burning regimes. This may be because fire is non-selective and its removal of all the photosynthetic tissue of all species can alter their competitiveness and competitive hierarchies in different ways (Morris and Tainton 1993; Fynn et al. 2005). The prolonged absence of fire changes the availability of resources such as light by allowing canopy development and closure resulting in dense shading.

The dominant grasses in the Drakensberg grassland vary in their shade tolerance (Everson et al. 1988) and thus respond differently to burning frequency, with shade-tolerant species such as *Tristachya leucothrix* and *Harporchloa falx* eventually replacing light-loving grasses such as *T. triandra* which become less productive and competitive and have decreased reproductive potential under self- and canopy-shading (Everson and Tainton 1984, Morris et al. this issue). These responses to defoliation depend on the position of the meristematic growing zone.

The growing zones of grass plants are situated at or immediately below the surface of the soil and are therefore protected from fire. However, if fire occurs when the meristematic zones are elevated during the growing season, the tillers of grasses such as *T. triandra* are unlikely to recover (Everson et al. 1985). Conversely, if fire or defoliation does not take place, the accumulation of organic material shades the base of the grass plant. Excessive base shading therefore leads to low tiller densities and contributes to reduced productivity (Everson et al. 1988). The objective of this study was to investigate the spatial and temporal changes over two years in the tuft size of montane grasses subjected to four burning treatments. It was hypothesized that (1) frequent fire in the dormant season would maintain a stable population of individual tufts of grasses that benefit from a high-light environment created by regular burning (e.g. *T. triandra*), (2) fire-tolerant species would be more competitive and maintain a larger populations of tufts, occupying more space, than shade-tolerant grasses (e.g. *H. falx*, *T. leucothrix*), enabling them to dominate frequently-burned grassland, and (3) burning during the

growing season or with long intervals between burns (> 2 yr.) would create instability in fire-tolerant grass populations, reducing their relative abundance in mesic montane grassland in the Drakensberg.

Methods

Study Area

The study site, situated at 1890 m asl., falls into the subalpine belt of the KwaZulu-Natal Drakensberg mountains (Killick 1963). The vegetation of the study site is classified as Northern Drakensberg Highland Grassland (Mucina and Rutherford 2006). This comprises a short dense grassland approximately 0.5 m in height (Camp 1997) dominated by *T. triandra*, *Tristachya leucothrix* and *Alloteropsis semialata*. Nearly all the Drakensberg grasses are tufted in habit (caespitose) and give the appearance of continuous cover, but after burning, the bare ground between tufts is clearly visible (Hilliard and Burt 1987). The growth of different species into these bare patches may be important in determining the spatial and temporal changes of grass tufts in response to different burning regimes.

The study was carried out in the Brotherton Burning Trial located at Cathedral Peak in the uKhahlamba Drakensberg Park. This replicated burning trial was established in 1980 to examine the influence of different burning treatments on the vegetation. The four treatments selected for this study were an annual winter burn to represent the firebreaks, which are burnt every year; a biennial spring burn, which is the present burning prescription for the area; a biennial summer burn, which is practised by rural farmers but has been shown to be detrimental to the vegetative re-establishment of grasses (Everson et al.1985); and a five-year burn to encourage the growth of woody species. Each burning treatment (25 X 25 m) was replicated three times. Three 0.25 m² quadrats were randomly located in each replicate (nine quadrats per treatment, 36 in total) and then marked with four permanent stakes in the four burning treatments. A grid subdivided into four cells of equal size (0.0625 m²) with cross wires, was fitted over the quadrat stakes. A pantograph was used to trace the basal area and create a map of all the established perennial grasses, forbs and sedges within each cell, in addition to the position of all grass seedlings. At the commencement of the study the mapping was planned to be repeated at monthly intervals. However, this was unrealistic as the first mapping operation alone took six weeks to complete. Since the mapping of the 36 plots of the burning treatments was extremely time-consuming subsequent mapping was carried out at six-weekly intervals

and was limited to mapping the precise location, number and survival of newly emerging grass seedlings. Total basal cover was mapped initially to coincide with the scheduled treatment burns (except for the five-year burn which was two years old). The removal of the above-ground biomass by fire greatly facilitated mapping and increased the accuracy of the technique. The second full mapping of all the plants took place two years later and was again timed to coincide with scheduled burns.

A Calcomp 23180 digitiser (California Computer Products, Anaheim California) was used to re-trace the hand-drawn images of every map created using the pantograph (72 in total). The software enabled the image of each tuft to be quantified by calculating its basal area (mm²). The basal areas of each species were added to enable comparisons between species in the four burning treatments for the two mapping events.

The effect of intraspecific competition on the growth and reproduction of adult plants was measured in the field using the nearest-neighbour technique of Pielou (1962). In this method the distance between a randomly chosen individual and its nearest neighbour was recorded and the size (circumference) of each tuft was measured and summed for the two tufts. Twenty-five tufts of *T. trandra* were randomly selected and the shortest distance to the nearest neighbour was measured. The circumference (mm) of each individual was measured, and the above-ground biomass was harvested from each plant at the end of the experiment. Harvested material was dried at 60⁰C to constant weight. Reproductive potential was measured as the total number of flowering culms, inflorescences and spikelets. Regression lines were plotted between the variables measured. The correlation coefficients for each regression line were compared to determine the intensity of competition between intraspecific pairs of plants.

The dynamic nature of the grasses was determined by counting the number of plants of the dominant species, *T. triandra*, *T. leucothrix* and *Stiburus alopecuroides* that changed in size over two years. If the proportion of plants increasing is equal to the proportion decreasing, then the community is in a state of dynamic equilibrium. If the proportions are not equal it is likely that a directional change is taking place and the community is not in equilibrium.

The effect of burning treatment on the basal area of each species was compared with ANOVA after applying a $\ln(x+1)$ transformation. The differences between treatments were determined by a Tukey Multiple Range test. A chi squared analysis with three degrees of freedom was used to test whether the numbers increasing, and decreasing were the same for all

treatments. To test whether the proportion of the total number of plants increasing in size in two specific treatments was significant, the following formula was applied:

$$u = \frac{P_1 - P_2}{\sqrt{\frac{P_1(1-P_1)}{n_1} + \frac{P_2(1-P_2)}{n_2}}}$$

Where u (standardized normal deviate) was significant at 5% if >1.96 and 1% if >2.54 . P_1 and P_2 were the proportions increasing and n_1 and n_2 were the total number of plants in each treatment.

Results

Mapping the vegetation in the four burning treatments showed that the competitive ability of different species changed with burning treatment. The extent of change in basal cover over two years was unexpected and showed the dynamic nature of these grasslands. An example of the maps for each treatment over the two-year period illustrates the extent of these fluctuations (Figures 1-4). The visual changes that occurred in the tuft sizes are supported by the quantitative results of the actual changes in basal area that took place in all 36 quadrats (Figure 5). In some cases, whole tufts disappeared within two years. For example, in the summer burn treatment, a large tuft of *T. leucothrix* (area = 1 052 mm²) situated at the bottom left of the plot (Figure 1a), was destroyed by this treatment (Figure 1b). In the same treatment, four tufts of *Koeleria cristata* (total basal area = 1 322 mm²) situated at the bottom right of the plot were also destroyed. Since low fire intensities occur in summer due to the high proportion of living material and high moisture content of grass fuel (Everson et al. 1985), it is likely that destruction of the elevated meristems results in loss of tufts. The dominance of wiry species that tiller below the ground (e.g. *Harporchloa falx*) is typical of this treatment. Another feature of summer burning that is clearly visible in these maps is the absence of large tufts of *T. triandra*.

The five-year burn treatment was characterized by only two species, *T. leucothrix* and *T. triandra* dominating in basal cover (Figure 2 a and b). Large bare areas between the plants were evident. Although there was a low number of tufts in this treatment, their basal area was

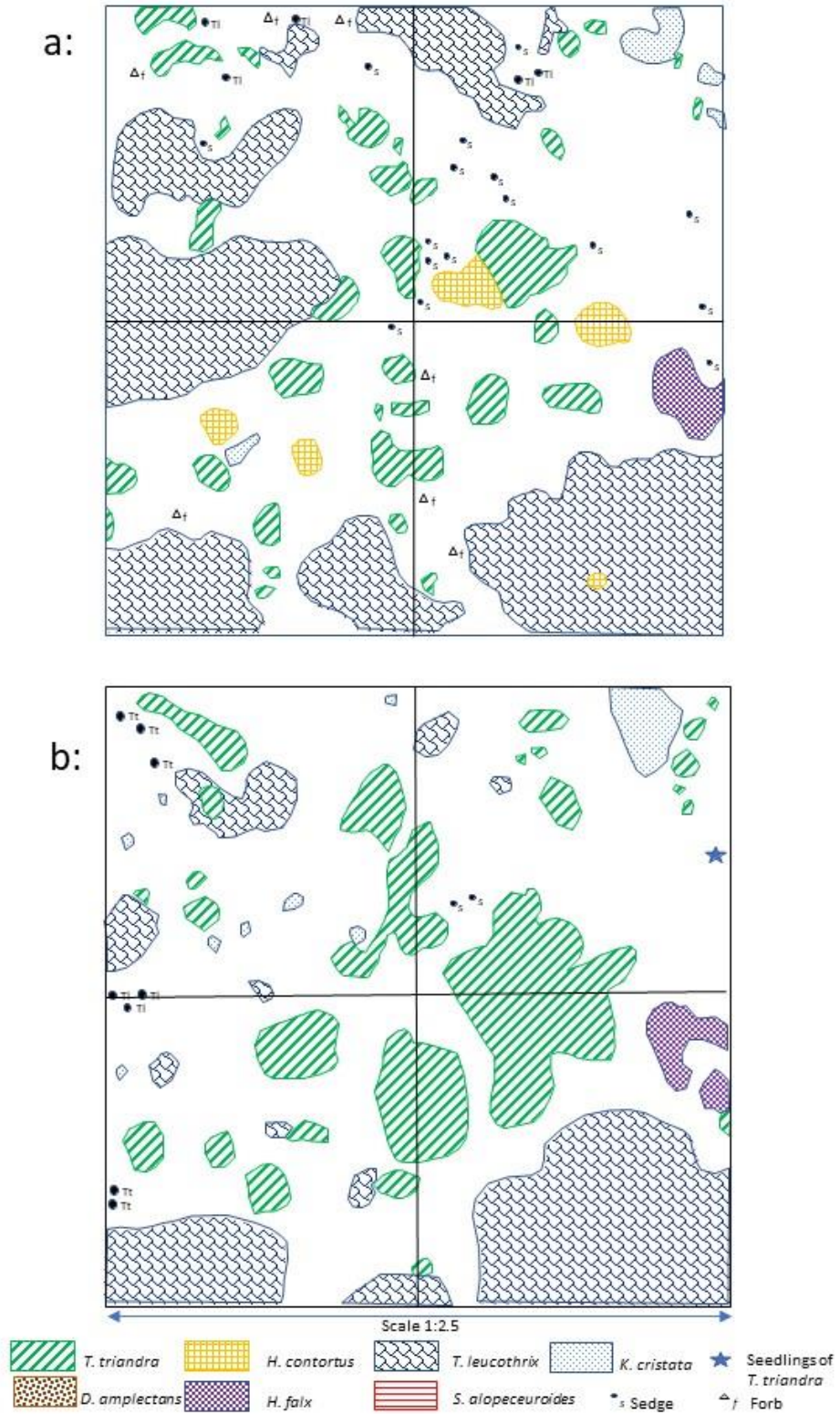


Figure 1: Typical map of the basal area of the vegetation in the 5-year burn in year 1 (a) and year 2 (b).

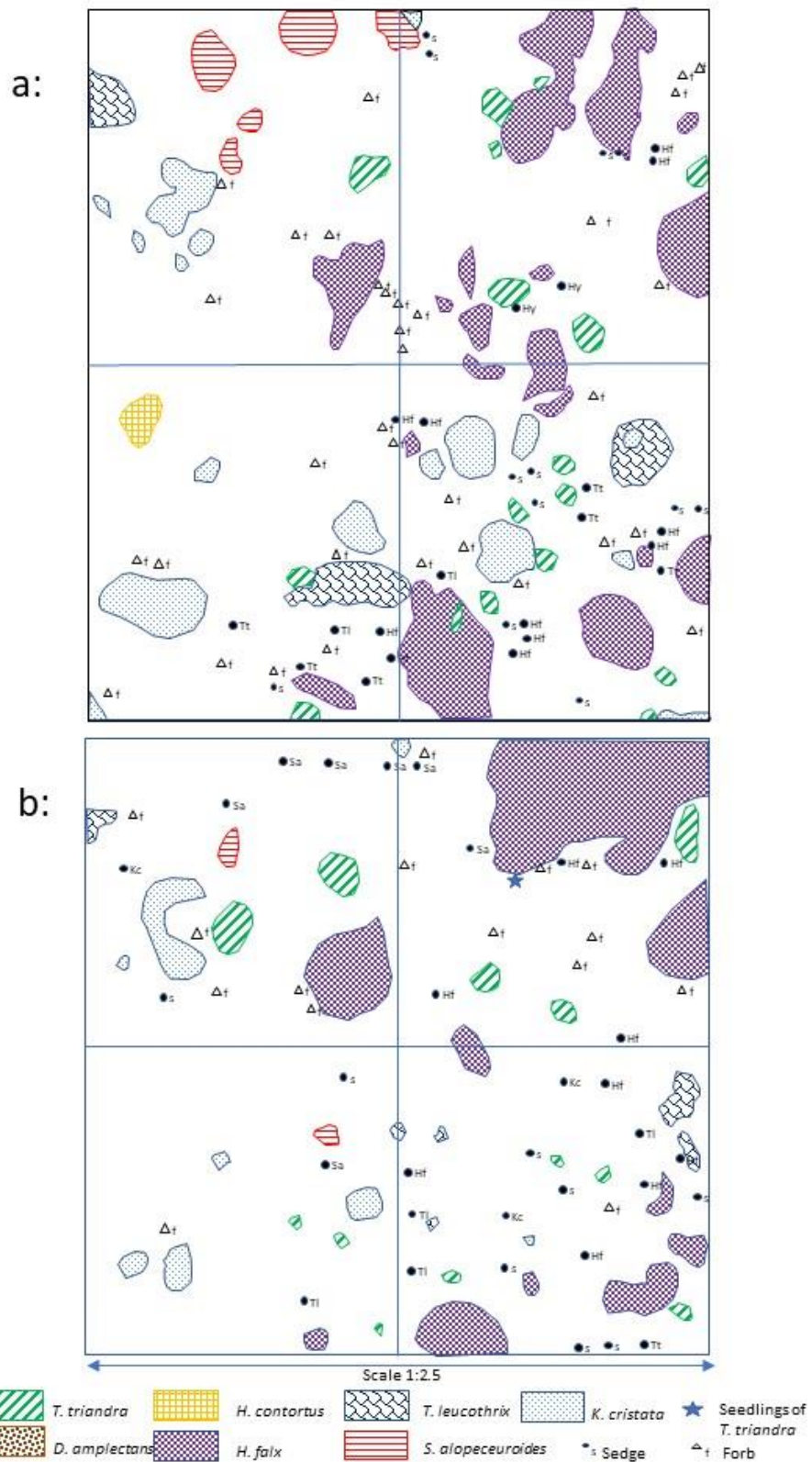


Figure 2: Typical map of the basal area of the vegetation in the biennial summer burn in year 1 (a) and year 2 (b).

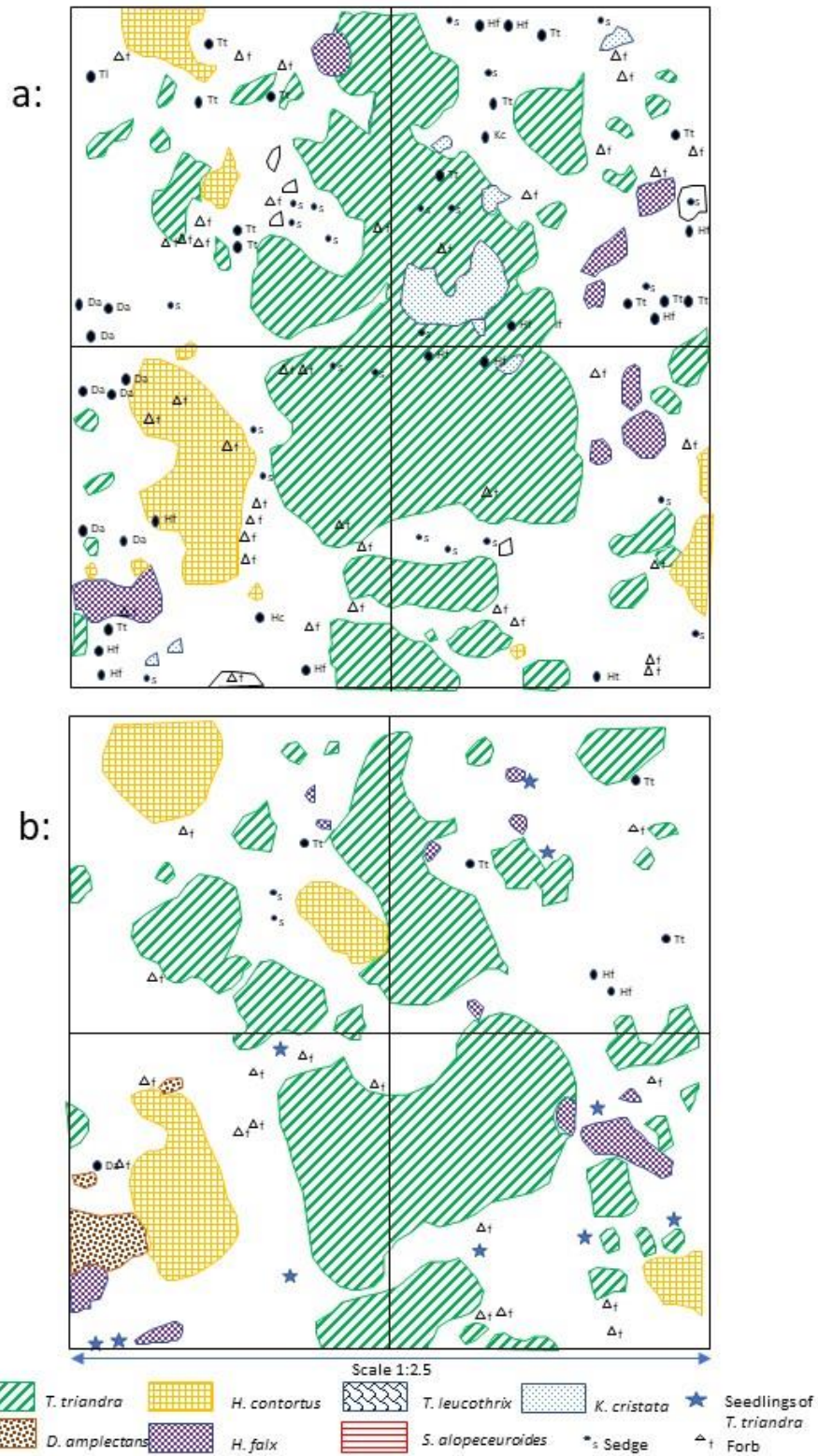


Figure 3: Typical map of the basal area of the vegetation in the biennial spring burn in year 1 (a) and year 2 (b).

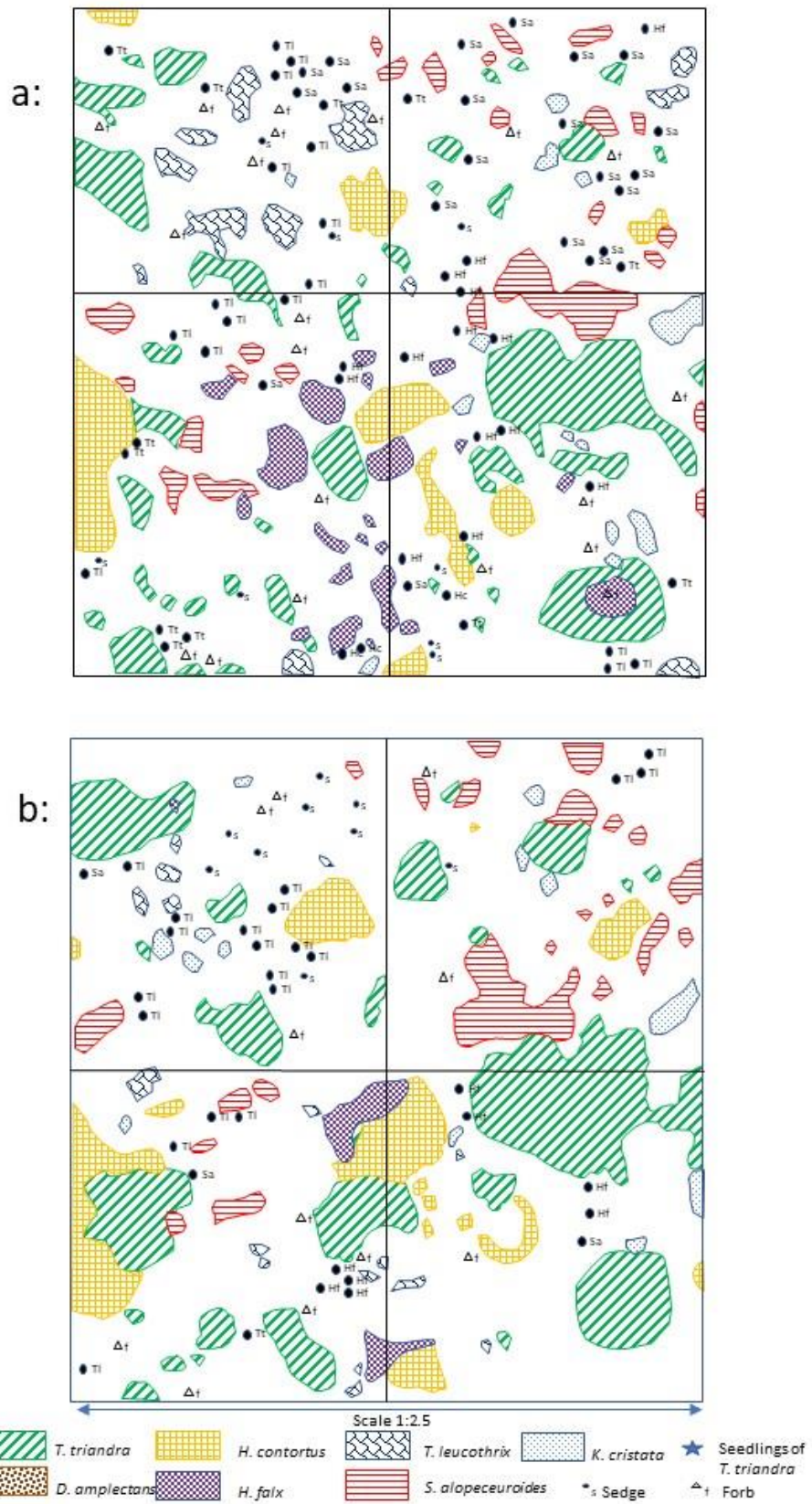


Figure 4: Typical map of the basal area of the vegetation in the annual winter burn in year 1 (a) and year 2 (b).

generally high. Changes in the shape of tufts between the two years were clearly visible showing the dynamic nature of these caespitose grasses.

By contrast, at least five species were present in the annual winter burn, with the dominant species being *T. triandra* and *Heteropogon contortus* (Figure 3 a and b). While one might expect major changes in the basal cover of plants subjected to a severe treatment such as a summer burn, the degree of change in tuft size in the regularly burnt grassland was unexpected. In both the annual winter (Figure 3 a and b) and the biennial spring (Figure 4 a and b) burn treatments tufts changed size and shape markedly over two years. This was evident in the biennial spring burn (Figure 4 a and b) where the large central tuft of *T. triandra* had broken up into two distinct tufts after two years.

The dynamic nature of the grasses was also shown by the changes in size and number of tufts of the dominant species *T. triandra*, *T. leucothrix* and *Stiburus alopecuroides* over two years (Table 1). The proportion of *T. triandra* tufts that increased in basal cover was significantly different between treatments ($\chi^2=24.00$, $P<0.001$). In the annual winter, biennial spring and five-year burns, the *T. triandra* tufts were in equilibrium with equal numbers ($P=0.47-0.51$) increasing and decreasing in area (Table 1). By contrast, in the biennial summer burn most of the *T. triandra* tufts (72%) significantly increased in area ($P=0.001$). There were, however, half the number of *T. triandra* tufts in this treatment compared to the other treatments.

In all treatments the total number of tufts of *T. leucothrix* was low (25-55) when compared to *T. triandra* (125-300) (Table 1). Treatment had a significant effect ($\chi^2=10.26$, $P<0.05$) on the proportion of *T. leucothrix* tufts that increased in basal area. In the annual winter, biennial summer and five-year burns more than half the tufts ($P=0.54-0.73$) increased in size. The greatest difference in the proportion of *T. leucothrix* tufts increasing was between the biennial summer and biennial spring burn treatments ($u=3.54$, $P<0.001$). The total number of tufts of *Stiburus alopecuroides* was low (<91) in all treatments, particularly the biennial summer burn where it was absent. There was no significant difference in the proportion of *S. alopecuroides* tufts that increased in the three treatments where it occurred.

The high number of *T. triandra* tufts in all treatments (Table 1) suggests that a positive relationship would be recorded between the distance from a tuft to its nearest neighbour and the sum of the performance of both plants. However, no such relationship was found between distance and size of adjacent tufts of *T. triandra*. Similarly, there was no correlation between

Table 1: The effect of different burn treatments on the number of plants of *T. triandra*, *T. leucothrix* and *S. alopecuroides* that increased (+) and decreased (-) in basal area over two years. *P* = proportion of plants that increase in size, NP = not present. The proportions in the row followed by different superscripts are significantly different ($p < 0.001$)

	Annual Winter	Biennial summer	Biennial spring	Five-year
<i>T. triandra</i>				
+	145	90	142	105
-	155	35	134	119
Total	300	125	276	224
<i>P</i>	0.48 ^a	0.72 ^b	0.51 ^a	0.47 ^a
<i>T. leucothrix</i>				
+	16	33	16	30
-	09	12	24	25
Total	25	45	40	55
<i>P</i>	0.64 ^a	0.73 ^b	0.40 ^a	0.54 ^a
<i>S. alopecuroides</i>				
+	59	NP	36	20
-	32	NP	30	26
Total	91	NP	66	46
<i>P</i>	0.65 ^a	NP	0.38 ^a	0.43 ^a

Table 2: Mean percentage bare area in the four burning treatments. Values in brackets represent \pm SE

Treatment	Year 1	Year 2	Sig.
Annual winter burn	81.8 (± 3.0)	82.1 (± 1.9)	NS
Biennial summer burn	85.0 (± 1.4)	90.6 (± 1.9)	**
Biennial spring burn	85.0 (± 2.9)	78.9 (± 2.9)	**
Five-year burn	74.5 (± 2.4)	66.7 (± 3.2)	***

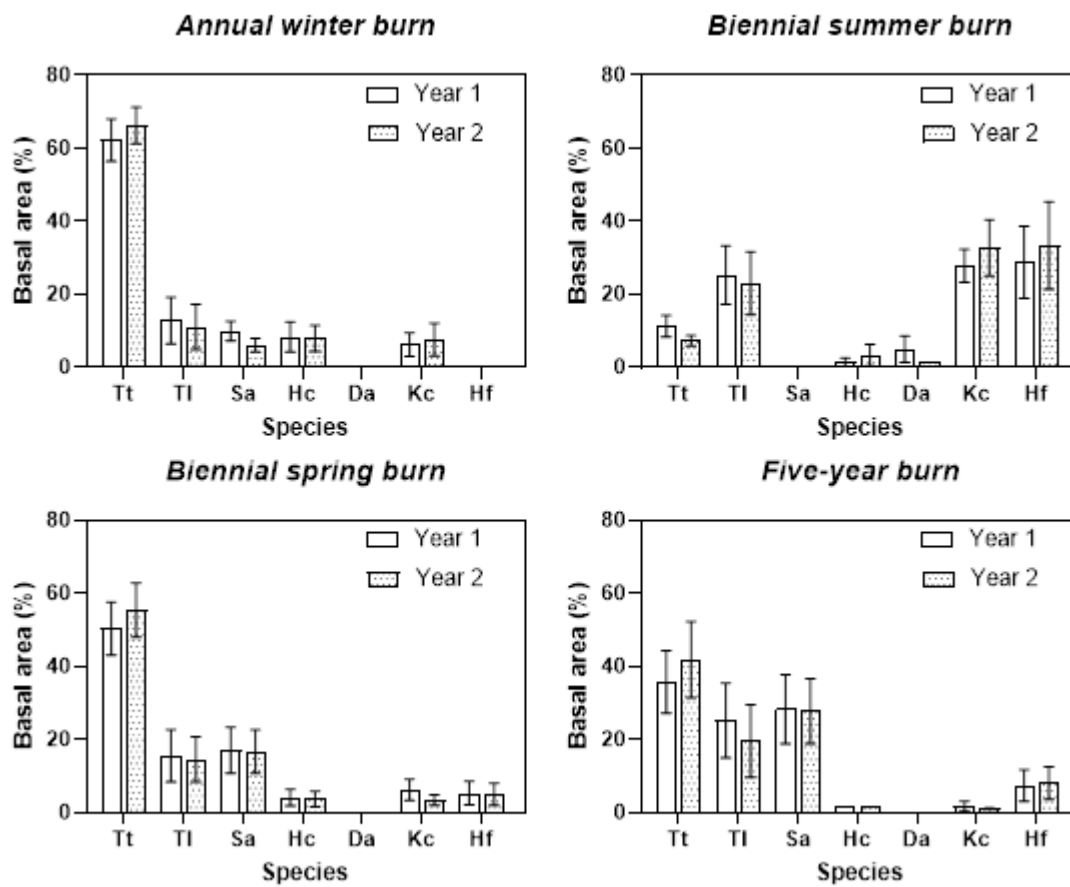


Figure 5: Percentage basal area of the seven most dominant species in four burning treatments in year 1 and year 2. Vertical bars represent standard errors. Tt – *T. triandra*, Tl – *T. leucothrix*, Sa – *S. alopecuroides*, Hc – *H. contortus*, Da – *D. amplexans*, Kc – *K. cristata*, Hf – *H. falx*. Treatment means were significantly different ($P < 0.01$) for *S. alopecuroides*, *T. triandra* and *K. cristata*.

distance and number of inflorescences, distance and number of spikelets and distance and dry mass.

The percentage basal area of the seven most abundant grass species (*T. triandra*, *T. leucothrix*, *S. alopecuroides*, *Heteropogon contortus*, *Diheteropogon amplexans*, *Koelaria cristata* and *H. falx*) was significantly different between the four burning treatments (Figure 5). For example, in year one the basal area of *T. triandra* was high in the annual winter (62.5%) and biennial spring (50.5%) and lower in the five-year burn (36.1%) treatments. By contrast, *T. triandra* only contributed <11.5% of the total basal area in the summer burn treatment. The species that dominated this treatment were *T. leucothrix*, *K. cristata* and *H. falx* with basal covers ranging from 25.2-28.9%. These three species contributed <16% basal cover in the annual winter and biennial spring burn treatments. Amongst the most striking changes that occurred in the summer burn was the disappearance of *S. alopecuroides*. This species was most abundant in the five-year burn where it contributed 28.4% of the basal cover. The results of the ANOVA indicated a significant effect of treatments on the mean basal cover of *S. alopecuroides*, *K. cristata* and *T. triandra*.

Percentage bare area differed significantly between treatments ($P < 0.01$, Table 2). In the annual winter burn, there was no significant difference in bare area between years (81.8-82.1%). By contrast, the biennial summer burn resulted in a significant 5.6 percentage point increase in bare area between the two years. The biennial spring burn reduced the extent of bare area from 85% to 78.9%, while the five-year burn resulted in the greatest reduction of bare area (7.8 percentage point decrease).

Discussion

With an increasing focus on the role of grasslands and savannas in biodiversity conservation and the provision of ecosystem services other than as a forage source, comprehensive information on keystone species is invaluable as a means of developing management and conservation strategies for these vegetation types (Snyman et al. 2013; Bengtsson et al. 2019). This study was initiated to address the lack of information on the demographic processes of keystone species in montane grasslands, particularly on recruitment, growth, and mortality of

individual grass tufts subjected to different burning treatments. The maps produced over the two-year period for the four burning treatments enabled the quantification of these processes.

The most notable result was the extent of change in size and shape of tufts of the different species. Our hypothesis that a stable population of fire-tolerant grasses would be maintained by regular burning was confirmed since the response of these species to their spatial environment indicated that they were in equilibrium. Since tufted grasses such as *T. triandra* have no means of spreading significant distances by rhizomes or stolons (O'Connor 1993) and are poorly adapted to reproducing via seed (Everson et al. 2009), little change in tuft sizes were expected. However, the dynamic nature of these grasslands was evident from the expansion of tufts through basal tiller production and the increase in the number of tufts through fragmentation.

Clonal fragmentation of tufts into smaller collections or units of ramets (new tufts) was common among the perennial caespitose grasses in this study. For example, the large tuft of *T. leucothrix* that was present in year one (see the left of the map of the five-year burn treatment, Figure 1a) had fragmented into seven smaller tufts by year two. Briske and Derner (1998) highlighted the need for a greater understanding of the fate of clonal fragments to determine their longevity. Briske and Anderson (1990) stated that a greater ramet recruitment would be expected from a high number of smaller clones due to the greater clonal circumference than with larger tufts. This was supported by Tomlinson et al. (2007) who noted that lots of small tufts can expand and occupy new ground more effectively than a population of large tufts. However, Oborny (2000) stated that the value of splitting into new tufts compared to staying as an integrated tuft depended on the spatial distribution of resources (patches). The clone site can therefore influence competitiveness for resources and tiller recruitment.

Leafy grasses with many tillers such as *T. triandra* are best able to prevent other species invading their space (Fynn et al. 2009). Bigger tufts are likely to survive better than smaller tufts, especially under stress (drought). New tillers developing on well-established large tufts will have access to limiting nutrients through the plant. However, smaller tuft fragments are more vulnerable and are therefore more likely to die (O'Connor 1994). This then poses the question – are big tufts better at holding their ground and expanding than smaller tufts? Mapping the changes in basal area of grass tufts of all species over two years provided evidence of the effect of different burning treatments on clonal expansion and fragmentation.

In the dense grasslands of this study, the small distances between tufts suggests that plants were competing primarily for space in terms of available light and nutrients. However, we found no correlation between distance and size of individual tufts of *T. triandra*, possibly because under crowded conditions, neighbourhood effects are much more apparent at the population level. This corroborates evidence from a larger catchment scale study in the Drakensberg mountains, where Gordijn et al. (2018) showed that distance-to-tuft measurements increased non-linearly with longer burning rotations. Thus longer fire return intervals at this scale were associated with lower basal cover, increased bare ground and greater distance-to-tuft, which increased from a minimum of 100 mm under annual burning to a maximum of 240 mm in a five-year burn interval.

The five-year burn was characterized by a dominance of large tufts, with few smaller-sized plants occurring (Figure 2). This may be due to the increased litter and aerial cover in this treatment shading out smaller plants. Everson (1999) recorded an accumulation of moribund material of up to 6 000 kg ha⁻¹ after five years in the same grassland. The reduction of bare area recorded in the five-year burn (Table 1) may have been due to smaller tufts of *T. triandra* expanding in the absence of neighbours. Although Wiegand et al. (2003) reported that large tufts of the perennial climax and subclimax grasses do not die directly, this did not appear to be the case in the five-year burning treatment, where local extinction of tufts was recorded. For example, the five tufts of *H. contortus* recorded in Figure 2a had disappeared two years later (Figure 2b). However, the small size of these tufts (0.8% basal cover) compared to those in the biennial spring burn (8.3% basal cover; Figure 5) indicated that these tufts were already fragmented into smaller tufts and were therefore prone to mortality when stressed (Wiegand et al. 2003). This supports the view that big tufts are better at holding their ground and expanding than smaller tufts, and that smaller tufts are more vulnerable when stressed (O'Connor 1994). However, the equal number of tufts increasing and decreasing in the plots burnt regularly in the dormant season (Figures 3 and 4) indicated that tuft integrity was largely maintained irrespective of the spatial patterns.

The high number of *T. triandra* tufts that increased in size in the severe summer burn treatment was unexpected (Figure 2; Table 1). Although this implies an increase in *T. triandra*, this treatment only had half the number of *T. triandra* plants when compared to the other treatments, severity of treatment having caused a 50% mortality of the plants. This reduced the competition from neighbours and may account for the unexpected increase in size in many of the surviving plants. These results support those of McDougall (1989) who found that *T.*

triandra plants released from competition (using herbicides) were larger with a greater tiller area and tiller production compared to control plants. The disappearance of *S. alopecuroides* from the summer burn plots and the increase in species such as *T. leucothrix*, indicated a directional change in species composition which was likely to be irreversible (Figure 5). Summer burning should therefore be discouraged to prevent further loss of species.

The most favourable burning treatment for stability in this grassland community was the biennial spring burn (Figure 3). In this treatment, the three dominant species were in a state of equilibrium, with the proportion of plants increasing being approximately equal to the proportion decreasing (Table 1). Although the size and shape of the tufts of these species were dynamic, with some tufts increasing in basal area and others fragmenting into two or more smaller tufts (Figure 3), the plants were in equilibrium with equal numbers increasing and decreasing in area. While the temporal range of the study was only two years, the results support those of Morris et al. (this issue) where the biennial spring burn resulted in a stable species composition over the last 40 years. The dominance of *T. triandra* in the plots burnt regularly in the dormant season may be attributed to the fact that it is relatively intolerant of shading compared to species that tiller below the soil surface such as *H. falx* (Everson et al. 1998; Fynn et al. 2011). Therefore, longer burning regimes, such as the five-year burn, which result in an accumulation of the previous season's dead material, creating lower light intensities than with regular burning, do not favour light sensitive species such as *T. triandra*.

Themeda triandra was also close to equilibrium in the annual winter burn which was characterized by a high number of species (Figure 4). There was also a greater proportion of *S. alopecuroides* as well as shade tolerant species such as *T. leucothrix* increasing in size. A similar trend was apparent in the five-year burn except for *S. alopecuroides*, which had a greater number of plants decreasing in size.

One of the key observations following the local extinction of a tuft of a species, was the low number of seedlings establishing in the gaps. Seedling establishment in the study was dominated by the most abundant grass species, *T. triandra*. However, competition and high seedling mortality (80%) accounted for their low survival in all the treatments (Everson et al. 2009). This may be attributed to root competition which has been shown to limit grass seedling establishment in mesic grasslands (Tedder et al. 2011). There was also an absence of alien invasive species establishing in the gaps resulting from tuft attrition. Frankow-Lindberg (2012) reported that species-rich plant communities provide resistance against invasive species. This

was supported by this study where the gaps created in the summer burn were filled by two species already present in the vegetation, *K. cristata* and *H. falx*.

Conclusions

The labour intensive nature of this research means that few (if any) other attempts have been made to map grasslands in South Africa at such a fine scale. Our study revealed surprising inter-annual variability in populations of tufts of mesic grassland, with tufts changing markedly in size and spatial distribution between one year and the next even for dominant species such as *T. triandra*. Since once-off studies as well as periodic monitoring do not reveal the dynamic nature of mesic montane grass populations at small (tuft) scales, this work fills a critical gap in knowledge on the demographic processes of montane grasslands at the individual plant scale. The long-term stability of the tufts, particularly in the five-year cycle warrants further investigation to assess whether patterns of tuft growth and disintegration are random, directional or cyclical. However, a constraint to extending this research is the time-consuming process of mapping all the tufts using a pantograph. Top-down photography and satellite imagery were initially tested in this study but were unsuccessful because species identification at this level was not possible in these dense grasslands. Alternative technologies therefore need to be investigated to aid such research.

References

- Acocks JPH. 1990. *Acocks' Notes: key grasses of South Africa* (ed. PJK Zacharias), Grassland of southern Africa, Howick.
- Bengtsson J, Bullock JM, Egoh B, Everson C, Everson T, O'Connor T, O'Farrell PJ, Smith HG, Lindborg R. 2019. Grasslands—more important for ecosystem services than you might think. *Ecosphere* 10(2):1-20.
- Briske DD, Anderson VJ. 1990. Tiller dispersion in populations of the bunchgrass *Schizachyrium scoparium*: implications for herbivory tolerance. *Oikos* 59(1) 50-56.
- Briske DD, Derner JD. 1998. Clonal biology of caespitose grasses. In: Cheplick GP (ed). *Population biology of grasses*. Cambridge: Cambridge University Press. pp 106-117.
- Camp KG. 1997. The Bioresource Groups of KwaZulu-Natal. Unpublished Cedara Report N/A/97/6.
- Connolly J, Wayne P. 1996. Asymmetric competition between plant species. *Oecologia* 108:311-320.
- De Witte LC, Stöcklin J. 2010. Longevity of clonal plants: why it matters and how to measure it. *Annals of Botany* 106: 859-870.
- Everson CS. 1999. Veld burning in different vegetation types: Grassveld. In: Tainton NM (ed), *Veld management in South Africa*. Pietermaritzburg: University of Natal Press. pp 228-235.
- Everson TM. 1994. Seedling establishment of *Themeda triandra* Forssk. in the Montane grasslands of Natal. PhD thesis, University of Natal, Pietermaritzburg.
- Everson CS, George WJ, Schulze RE. 1989. Fire regime effects on canopy cover and sediment yield in the montane grasslands of Natal. *South African Journal of Science* 85(2):113-6.
- Everson CS, Tainton NM. 1984. The effect of thirty years of burning on the highland sourveld of Natal. *Journal of the Grassland Society of Southern Africa* 1(3):15-20.
- Everson TM, Yeaton RI, Everson CS. 2009. Seed dynamics of *Themeda triandra* in the montane grasslands of South Africa. *African Journal of Range and Forage Science* 26(1): 19-26.
- Frankow-Lindberg BE. 2012. Grassland plant species diversity decreases invasion by increasing resource use. *Oecologia* 169:793–802. doi:10.1007/s00442-011-2230-7.
- Freckleton RP, Watkinson R. 2001. Asymmetric competition between plant species. *Functional Ecology* 15: 615–623.
- Fynn RW, Morris CD, Edwards TJ. 2005. Long-term compositional responses of a South African mesic grassland to burning and mowing. *Applied Vegetation Science* 8(1):5-12.

- Fynn RWS, Morris C, Ward D, Kirkman K. 2011. Trait–environment relations for dominant grasses in South African mesic grassland support a general leaf economic model. *Journal of Vegetation Science* 22: 528–540.
- Fynn RW, Wragg PD, Morris CD, Kirkman KP, Naiken J. 2009. Vegetative traits predict grass species' invasiveness and the invasibility of restored grassland. *African Journal of Range and Forage Science* 26(2):59-68.
- Gordijn PJ, Everson TM, O'Connor TG. 2018. Resistance of Drakensberg grasslands to compositional change depends on the influence of fire-return interval and grassland structure on richness and spatial turnover. *Perspectives in Plant Ecology, Evolution and Systematics* 34:26-36.
- Herben T, Krahulec F, Hadincová V, Pecháčková S, Wildová R. 2003. Year-to-year variation in plant competition in a mountain grassland. *Journal of Ecology* 1:103-13.
- Hilliard OM, Burt BL. 1987. The botany of the southern Natal Drakensberg (ed. JN Eloff). *Annals of Kirstenbosch Gardens* No 15, National Botanic Gardens, Cape Town.
- Killick DJB. 1963. *An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg*. Botanical Survey of South African Memoirs, No. 34. Pretoria: Government Printer.
- Lauenroth WK, Aguilera MO. 1998. Plant-plant interactions in grasses and grasslands. Population biology of grasses. Cambridge University Press, Cambridge. 28:209-30.
- Law R, Herben T, Dieckmann U. 1997. Non-manipulative estimates of competition coefficients in a montane grassland community. *Journal of Ecology* 1: 505-17.
- McDougall KL. 1989. The re-establishment of *Themeda triandra* (kangaroo grass): implications for the restoration of grassland. Technical Report Series no. 89. East Melbourne: Department of Conservation, Forests, and Lands.
- Morris CD, Everson CS, Everson TM, Gordijn PJ. In press. The stability of Drakensberg grassland under consistent burning regimes. *African Journal of Range and Forage Science*
- Morris CD, Tainton NM. 1993. The effect of defoliation and competition on the regrowth of *Themeda triandra* and *Aristida junciformis* subsp. *junciformis*. *African Journal of Range and Forage Science* 10(3):124-8.
- Mucina L, Rutherford MC, Powrie LW. 2006. The Vegetation of South Africa, Lesotho and Swaziland'. (Eds Mucina L and MC Rutherford.) pp. 748-89.
- Oborny B, Kun Á, Czárán T, Bokros S. 2000. The effect of clonal integration on plant competition for mosaic habitat space. *Ecology* 81(12):3291-304.
- O'Connor TG. 1993. The influence of rainfall and grazing on the demography of some South African savanna grasses: a matrix modelling approach. *Journal of Applied Ecology* 30: 119–132.
- O'Connor TG. 1994. Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology* 31: 155–171.

- Peart DR. 1989. Species interaction in a successional grassland. II. Colonization of vegetated sites. *Journal of Ecology* 77:252-266.
- Silvertown J, Holtier S, Johnson J, Dale P. 1992. Cellular automaton models of interspecific competition for space--the effect of pattern on process. *Journal of Ecology* 1:527-33.
- Snyman HA, Ingram LJ, Kirkman KP. 2013. *Themeda triandra*: a keystone grass species. *African Journal of Range and Forage Science* 30(3): 99–125.
- Tedder MJ, Morris CD, Fynn RWS, Kirkman KP. 2011. Grass-on-grass competition along a catenal gradient in mesic grassland, South Africa. *African Journal of Range and Forage Science* 28 (2): 79-85.
- Tomlinson KW, Dominy JG, Hearne JW, O'Connor TG. 2007. A functional-structural model for growth of clonal bunchgrasses. *Ecological Modelling* 202(3-4):243-64.
- Van Zyl DD. 1998. Aspects of the invasion of southern tall grassveld by *Aristida junciformis* subsp. *junciformis* Trin. et Rupr (MSc) University of Natal, Pietermaritzburg.
- Wiegand T, Snyman HA, Kellner K. 2003. From individual scale to population and community scale: modeling dynamics of the semi-arid grasslands of South Africa. International Rangeland Conference.
- Weiner J. 1986. How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. *Ecology* 67: 1425–1427.