Austral Ecology (2009) ••, ••–••

Effects of invasion of fire-free arid shrublands by a fire-promoting invasive alien grass (*Pennisetum setaceum*) in South Africa

S. J. RAHLAO,[1,3]* S. J. MILTON,[1] K. J. ESLER,[1] B. W. VAN WILGEN[2] AND P. BARNARD[3,4]
[1]*Centre for Invasion Biology and Department of Conservation Ecology and Entomology, Stellenbosch University, Private Bag X1, Matieland 7602, Stellenbosch, South Africa (Email: srahlao@sun.ac.za),* [2]*Centre for Invasion Biology, CSIR Natural Resources and Environment, Stellenbosch,* [3]*Climate Change and Bioadaptation Division, Kirstenbosch Research Centre, South African National Biodiversity Institute, Claremont,* [4]*DST Centre of Excellence, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa*

Abstract Arid shrublands in the Karoo (South Africa) seldom accumulate sufficient combustible fuel to support fire. However, as a result of invasion by an alien perennial grass (*Pennisetum setaceum*), they could become flammable. This paper reports on an experiment to assess the effects of fire following invasion by *P. setaceum*. We established 10 plots (5×10 m) separated by 2.5 m, and added grass fuel to five plots (5 and 10 tons ha^{-1} to alternate halves of the plot) leaving the remaining five plots as interspersed controls. Plots with fuel added were burnt, and fire behaviour was measured during the burns. Rates of fire spread were generally low (0.01–0.07 m s^{-1}) and did not differ significantly between burn treatments. Mean fireline intensities were higher in the high compared with the low fuel treatments (894 and 427 kW m^{-1}, respectively). We recorded plant species and their cover before and after burning on each of the plots. After 15 months of follow-up monitoring in the burn plots, only two species, the dwarf shrub (*Tripteris sinuata*) and the perennial herb (*Gazania krebsiana*) resprouted. Most individuals of other species were killed and did not reseed during the 15-month study. The mass of added fuel load (high or low) did not influence vegetation recovery rates after fire. Should future invasions by *P. setaceum* lead to similar fuel loads in these shrublands, inevitable fires could change the vegetation and may favour spread of the flammable grass. Our results have important implications for predicting the effects of invasive alien plants (especially grasses) on fire-free ecosystems elsewhere. The predicted impacts of fire may alter species composition, ultimately affecting core natural resources that support the Karoo economy.

Key words: desert vegetation survey, fire intensity, fuel load, Karoo, post-fire recovery, succulents.

INTRODUCTION

Invasive alien species are regarded as a worldwide threat to biodiversity and ecosystem functioning. One of the consequences of invasion is changes to key driving processes in ecosystems, such as fire (Smith & Tunison 1992; Mack & D'Antonio 1998; Rossiter *et al.* 2003; Brooks *et al.* 2004). Grasses have been easily moved around the world and are now common invaders that cause irreversible alterations to fire regimes in many ecosystems (D'Antonio & Vitousek 1992). Invasive perennial grasses affect fire regimes by maintaining a high standing biomass of dead material that increases the horizontal continuity between shrubs in dry habitats (D'Antonio *et al.* 2000). Invasive grasses also affect ecosystems by changing a number of fuel and fire regime properties (see Brooks *et al.* 2004).

Alien invasive grasses from around the world are common in many southern African ecosystems, especially on disturbed sites and along road verges in arid and semi-arid areas (Milton & Dean 1998; Milton *et al.* 1998; Bromilow 2001; Joubert & Cunningham 2002). However, there has been no assessment of the ecological drivers and effects of these invasive grass species in South African ecosystems (Milton 2004).

The arid and semi-arid Nama and Succulent Karoo biomes of South Africa receive very low and variable rainfall and typically comprise sparse grass, widely spaced shrubs and succulents. These have low productivity, and seldom accumulate sufficient combustible fuel to support fire (Mucina *et al.* 2006). Perennial grasses are uncommon in these biomes due to dry summers although some grass species dominate aeolian sand patches regardless of rainfall quantity and

*Corresponding author.
Accepted for publication December 2008.

doi:10.1111/j.1442-9993.2009.02000.x

seasonality (Mucina *et al.* 2006). Introduction of flammable perennial grasses to fire-free ecosystems through invasion can change the structure of the vegetation, making it more likely to burn. This, in turn, could cause local extinctions as a result of mortality in fires, and an inability to recolonize burnt sites through effective dispersal, because many plant species in these usually fire-free areas are not equipped to survive fire. The Karoo experiences a number of large scale episodic disturbances, such as locust swarms (Nailand & Hanrahan 1993), droughts (Milton *et al.* 1995) and grazing (Todd & Hoffman 1999), but not fire.

Most of the assessments of effects of perennial alien grasses have focused on the alteration of fire regimes in fire-prone vegetation (e.g. Smith & Tunison 1992; D'Antonio *et al.* 2000; Rossiter *et al.* 2003; Brooks *et al.* 2004) but not on the introduction of fire to areas that have up to now been fire-free. The combined effects of invasion and fire on the composition and dynamics of Karoo shrublands are not known, but could be significant for the biodiversity and function of these fire-free areas. In this paper, we report on an experiment to assess the introduction of invasive, flammable grasses leading to fire in an ecosystem of low and variable rainfall, where fires are absent.

METHODS

Study area

The study was undertaken at the 100 ha Tierberg Karoo Research Centre (33°09′S, 22°16′E) exclosure that lies inland of the Swartberg Mountains in the Sand River Valley 28 km east of Prince Albert in the Western Cape Province. The site lies within the arid transition zone between summer rainfall Nama Karoo and the winter rainfall Succulent Karoo (Milton *et al.* 2007). The climate is arid (100 year mean annual rainfall 176 mm, range 50–400 mm year^{-1}); rain is brought by cyclonic systems in the winter and is convectional in the summer. Weather variables are continuously monitored at the station and data are electronically recorded hourly (Milton *et al.* 2007). Rain can occur at any time of the year, with a higher probability in spring and autumn. Topography is flat and soils are fine textured and alkaline.

The vegetation of the plains is a sparse (25% cover), low (<0.7 m tall) shrubland dominated by succulent (Mesembryanthemaceae) and non-succulent shrubs (mostly Aizoaceae and Asteraceae). Grass and reed life-forms are confined to the vegetation of drainage lines and rocky hills. The standing air-dry above-ground plant biomass on the plains is 3.27 tons ha^{-1} (Milton 1990). Its fuel properties, however, are such that it does not carry fire. These properties include the sparse distribution of relatively course plant stems and leaves, low levels of litter production and a relatively high proportion of succulents. According to local landowners, no fires are known to have occurred in the area in the 120 years that the area has been used for sheep farming.

Experimental design

We established 10 plots of 5 × 10 m separated by 2.5 m buffer zones in natural vegetation. Grass (mixture of green and dry) fuels were added to five alternate plots (see below). Each of the fuel addition plots was split so that half was supplemented with 5 tons ha^{-1} and the other half with 10 tons ha^{-1}. The intervening five plots were retained as controls. This resulted in three treatments; no fire (control), low fuel fire and high fuel fire. No fire-breaks were made around the plots as the biomass of the natural vegetation was considered too low to carry fire. Experimental burns were all carried out on the same day (11 December 2006) by igniting the eastern end of each plot and allowing the fire to spread across the plot without further assistance.

Experience elsewhere (e.g. Govender *et al.* 2006) has shown that spreading fires are seldom possible where dry grass fuel loads are below 3 tons ha^{-1}, and that grass fuel loads seldom exceed 12 tons ha^{-1}. We added 5 and 10 tons ha^{-1} to reflect this range, using grasses harvested from dense invasions along roadsides in and near the town of Prince Albert. The tussocks had basal diameters of 0.2–0.5 m and were 0.4–0.8 m in height. These were stripped of all seed heads to reduce the possibility of invasion of natural vegetation and then transported to the study site.

Vegetation sampling

Prior to burning, herbaceous canopy cover was measured for each treatment plot (Fig. 1a). These surveys were carried out prior to experiment initiation in December 2006 and repeated in September 2007 and March 2008 to assess recovery. Projected canopy cover was measured along four 5-m long lines per plot (total 20 points per plot) using the descending point method with points at 1 m intervals. The number of contacts with plant canopies was summed for each plant species and divided by 20 to give an estimate of percentage projected canopy for each species. Total vegetation cover per plot was taken as the sum of cover values for all species. Total counts (number of individual plants per each species) were recorded for each 25 m^2 plot for each survey period.

Nomenclature follows Germishizen and Meyer (2003).

doi:10.1111/j.1442-9993.2009.02000.x

Experimental fires

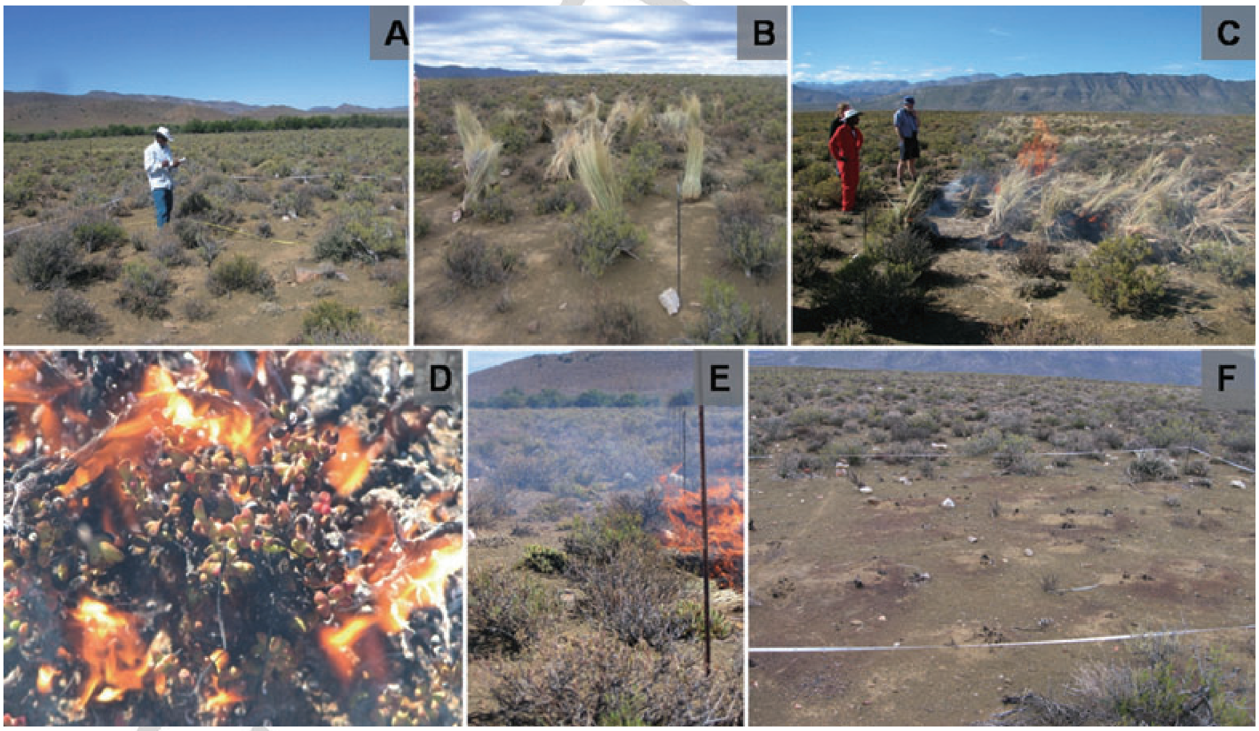
Tufts of *P. setaceum* were placed systematically within interspaces in an upright position propped up against the Karoo shrubs (Fig. 1b). This increased the total fuel load (including natural vegetation) to 8 and 13 tons ha^{-1} for the low and high fuel addition treatments, respectively. The fire behaviour characteristics were measured during the fires. The moisture content of the grass was determined by removing a sample of 10–20 g of grass material immediately prior to ignition. The samples were sealed in water-tight jars, and later weighed, oven dried (for 48 h at 60°C) and re-weighed. The heat of combustion was measured from oven dried samples using a DDS CP500 Bomb Calorimeter and was corrected for incomplete combustion to heat yield. The experimental fires were ignited across the entire 5 m edge of each plot by several people. Fires were initiated in either high fuel or low fuel loads on alternate plots. The time it took the fire to cover the first and second 5 m of the plot was recorded to determine the rate of spread in the low and high fuel sections, respectively (Fig. 1c). Fuel load and the rate of spread were used to calculate the Byram fireline intensity as follows:

$$I = Hwr$$

Where I is the fire intensity (kW m^{-1}), H is heat yield (J g^{-1}), w the mass of fuel combusted (g m^{-1}) and r the rate of spread of the fire front (m s^{-1}) (Byram 1959). As almost all of the grass fuels and other plant material were consumed in the experimental burns, we used the pre-fire grass plus the estimate for standing air-dry biomass mass, 3.27 tons ha^{-1} (Milton 1990) as equivalent to fuel consumed.

Statistical analyses

The vegetation cover data were expressed as total % projected canopy cover per plot and were arcsine ($\sqrt{x}$) – transformed before statistical analysis to achieve normality (Zar 1999). Count data were converted to density (plants m^{-2}) for both control and burned plots and then compared. A Shapiro–Wilk test was used to analyse the data for normality (Shapiro & Wilk 1965). When data were normal repeated-measures analyses of variance (ANOVA) were used in STATISTICA 8 (Statsoft 2007) to analyse the responses of vegetation to fire over the study period (15 months). When the



Colour

Fig. 1. (a) The pre-burn vegetation survey, (b) mature tussocks of *Pennisetum setaceum* were harvested along roadsides in and near the town of Prince Albert and to simulate invasion of *P. setaceum,* tufts were placed among the Karoo shrubs at a loading of 5 t ha^{-1} and 10 t ha^{-1} next to the Karoo shrubs. (c) Experimental burns were all carried out on the same day (11 December 2006) by igniting the lower end of each plot and allowing the fire to spread across the plot without further assistance. (d) Most of the Karoo species burned easily once the fire was initiated, e.g. *Ruschia spinosa*. (e) The fire did not burn beyond the plots where fuel was added. (f) Most of the area still looks bare after 15 months although some herbs, *Gazania krebsiana* and dwarf shrubs, *Tripteris sinuata* resprouted.

doi:10.1111/j.1442-9993.2009.02000.x

data were non-normal, then a non-parametric bootstrapping test (Efron 1981) was performed. Differences between means were considered significant for $P < 0.05$. Within-subject (repeated measures) effects were the sampling date and the interactions of sampling date with the between-subject effects. A Bonferroni *post hoc* test was performed to test the differences between and within treatments over time. A Student's test (*t*-test) was performed to test whether burned and unburned plots differed in total cover and density before and after fire. The *t*-test was also used to compare the rate of spread and fireline intensity between low and high fuel loads. Linear regression was used to test the relationship between rainfall and vegetation cover over the study period.

RESULTS

Fire characteristics

The heat yield (corrected for incomplete combustion) of *P. setaceum* was 15 765 J g^{-1}. The fuel moisture contents were consistently low (<1%) across all samples (Table 1). The mean rate of fire spread was also low (0.034 m s^{-1}) and did not differ ($t = -0.913$, d.f. = 8, $P = 0.39$) between low and high fuel loads. Fireline intensity (kW m^{-1}) was significantly higher ($t = -2.725$, d.f. = 8, $P = 0.026$) in high fuel loads than in low fuel loads (mean, 894 and 427 kW m^{-1}, respectively). The average air temperature during the fires was 16°C, relative humidity was 51%, and the conditions were calm, with no appreciable wind. Leaf succulent shrubs (e.g. *Ruschia spinosa*) and non-succulent shrubs (mostly Asteraceae) burned when fuel was added (Fig. 1d) and the fire did not burn beyond the plots into the surrounding natural shrubland vegetation where fuel was not added (Fig. 1e).

Vegetation characteristics in plots before fire

The total mean projected canopy cover of plants before the fire in December 2006 did not differ significantly ($t = -1.74$, d.f. = 8, $P = 0.17$) between plots allocated to burn and unburned treatments, and averaged 41%. The major components of cover on unburned and burned plots were respectively non-succulent shrubs (25%), leaf succulent shrubs (11%) and herbaceous and geophytic species (5%). The rest (59%) was occupied by both litter and empty spaces.

A total of 33 species was recorded on all plots, of which 15 (45%) were succulent shrubs, 11 (33%) were non-succulent shrubs and the remaining 7 (21%) herbaceous and geophytic species. The average density of plants for all plots was 6.7 plants per m^2 with *Tripteris sinuata* and *R. spinosa* more dominant (3.4 and 0.44 plants per m^2, respectively). Only one alien species (*Atriplex lindleyi*) was found at the site prior to the fire.

Responses of vegetation to fire

The mass of added fuel load (high or low) did not influence ($F = 0.24$, d.f. = 20.8, $P = 0.79$) vegetation recovery rates after fire during the study period on burned plots (Table 2). Total projected canopy cover of the control plots was similar between December 2006 and September 2007 but decreased significantly ($P = 0.007$) in March 2008. There was no significant relationship between vegetation cover and rainfall on control plots during the study period ($r^2 = 0.3882$, $P = 0.58$) and very little rainfall occurred during the post-fire monitoring period, relative to earlier rainfall records. Mean species density (plants m^{-2}) in control (unburned) and burned plots did not differ significantly ($P = 0.16$) before fire. Herbaceous and other geophytic species were reduced significantly ($P = 0.0001$) on control plots in March 2008, because of seasonal dieback of above-ground plant parts. Both the leaf succulent shrubs and non-succulent shrubs remained unchanged on these control plots (Fig. 3a,b).

The burned plots remained bare for most of the study period after fire (Fig. 1f) except for cover of the only two resprouting species (*T. sinuata* and *Gazania krebsiana*) that rapidly recovered to pre-burn levels after fire ($P = 0.68$) decreasing over time as dry con-

Table 1. Fuel and fire behaviour characteristics associated with experimental fires on 5 × 10 m plots in the Nama – Succulent Karoo interface

Fuel load	Dry mass (gm^{-2}) (±1 SE)	Fuel moisture (%) (±1 SE)	Rate of spread (m s^{-1}) (±1 SE)	Fireline Intensity (kW m^{-1}) (±1 SE)
Low	800 (5)	0.354 (0.067)	0.034 (0.007)	427 (84)
High	1271 (5)	0.354 (0.067)	0.045 (0.01)	894 (192)

The values are mean (SE) for each treatment over all the plots. The mean fuel dry mass (gm^{-2}) is the sum of the average dry mass of the natural vegetation and the added grass fuel (500 g and 1000 gm^{-2} respectively for the low and high fuel load treatments).

doi:10.1111/j.1442-9993.2009.02000.x

Table 2. Analysis of variance (ANOVA) table with *F*-ratios for effects of Plots (to which burning treatments were applied) and Time (before and after fire) on vegetation cover for burned plots

Treatments	SS	d.f.	MS	*F*-value	*P*-value	Significance level
1. Total cover						
Treatment	106.9	1	106.90	2.17	0.18	NS
Time	3042.5	2	1521.31	66.45	<0.0001	***
Treatment × Time	10.9	2	5.47	0.23	0.79	NS
2. Resprouting species						
Treatment	4.2	1	4.22	0.15	0.71	NS
Time	114.0	2	57.01	16.38	<0.001	**
Treatment × Time	3.7	2	1.87	0.54	0.59	NS
3. Succulents						
Treatment	35.3	1	35.33	0.68	0.43	NS
Time	1499.8	2	749.91	141.99	<0.0001	***
Treatment × Time	31.7	2	15.86	3.00	0.078	NS
4. Non-succulents						
Treatment	16.6	1	16.59	0.62	0.45	NS
Time	4026.5	2	2013.27	230.69	<0.0001	***
Treatment × Time	12.0	2	6.02	0.68	0.52	NS
5. Herbs						
Treatment	30.3	1	30.34	0.16	0.69	NS
Time	416.8	2	208.42	16.82	<0.001	**
Treatment × Time	11.2	2	5.60	0.45	0.64	NS

Resprouting species: *Tripteris sinuata* and *Gazania krebsiana*. * $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$. d.f., degrees of freedom; MS, mean square; significance: NS, non-significant; SS, sum of squares.

ditions prevailed (Fig. 2b). There was a slight increase ($P = 0.03$) in cover of herbaceous and geophytic species under low fuel loads in September 2007. In general, there has been a reduction and no recovery in shrubby (succulent and non-succulent) life forms and their cover remained near zero for 15 months after fire under both intensities during the study period. Herb cover on the other hand showed some recovery on burned plots during September 2007 but declined thereafter during the study period (Fig. 3c).

There was a reduction in the density of many species and most have not recovered after burning, while 18% (6/33) of species were eliminated from the burned plots during the study period (Table 3). A few new species of geophytes and hemicryptophytes (e.g. *Asparagus retrofractus* and *Drimia anomala*) were observed on the burned plots after fire during the study period.

DISCUSSION

Fire characteristics

The heat yield that we found in this study (15 765 J g^{-1}) is similar to that found in savanna grasses (Govender *et al.* 2006) and of different grasses in areas commonly burned in South Africa (Trollope 1984). Despite very low fuel moisture contents, rates of fire spread were very low, probably as a result of the calm conditions under which the fires were carried out. As a result, the mean fireline intensities were also relatively low, with intensities for the low and high fuel load treatments falling into the very low and low fire intensity classes defined by Govender *et al.* (2006). Fire intensities would have been higher if the fires had occurred under hotter, drier or windier conditions. Despite these low fire intensities, the fires had marked effects on the vegetation, suggesting that the introduction of any fire could have severe effects on this ecosystem functioning.

Effects of fire on vegetation cover

This study investigated how invasion by *P. setaceum* would affect the arid Karoo shrubland vegetation as a result of fire. Plant mortality in this region is generally caused by droughts and hot summers (Milton *et al.* 1999a). Although the herbs slightly recovered on the burned plots in September 2007, they were reduced in cover during the March 2008 survey (Fig. 3c). This could probably be as a result of the hot dry summer, as they were left exposed in the absence of other large shrubs that would protect them.

The decline in total vegetation cover on control plots may be attributed to the below average total annual rainfall in the area. The total cover of resprouting species was not affected by fire over the study period, presumably because subterranean meristems were not

doi:10.1111/j.1442-9993.2009.02000.x

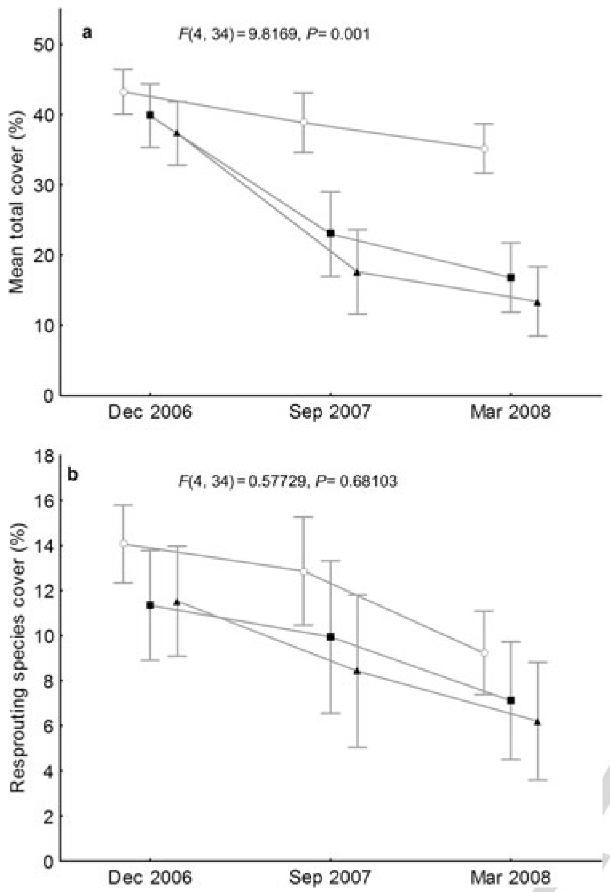


Fig. 2. Response of (a) mean total vegetation cover and (b) resprouting species (*Gazania krebsiana* and *Tripteris sinuata*) over time on burned and unburned plots and in the Tierberg Karoo Research Centre before (Dec. 2006) and after fire (Sep 2007 and Mar. 2008). (○) Control (■) low fuel load (▲) high fuel load. Error bars indicate 95% confidence interval.

damaged by the fire. *T. sinuata* resprouted vigorously on burned plots after fire and probably benefited from reduced interspecific competition which has been shown to limit shrub growth in this arid ecosystem (Milton 1995).

Tripteris sinuata, a dwarf, drought-resistant deciduous perennial shrub that is highly palatable and preferred by domestic livestock and wild mammals (Milton & Dean 1993), occurs as a climax species in the Karoo (Milton 1992; Visser *et al.* 2004). This species is resilient and tolerant to grazing and flowers successfully in the absence of all plant neighbours (Milton 1992). Dominance by the resprouting *T. sinuata* as a result of fire would provide good grazing in the short term. However, in the longer-term dominance by a single plant species that is poorly defended against herbivory is likely to reduce the resilience that plant diversity gives to grazing systems (Tilman 1996).

Furthermore, the reduction of 'nurse plants' in this dry and hot ecosystem could lead to Karoo seedlings

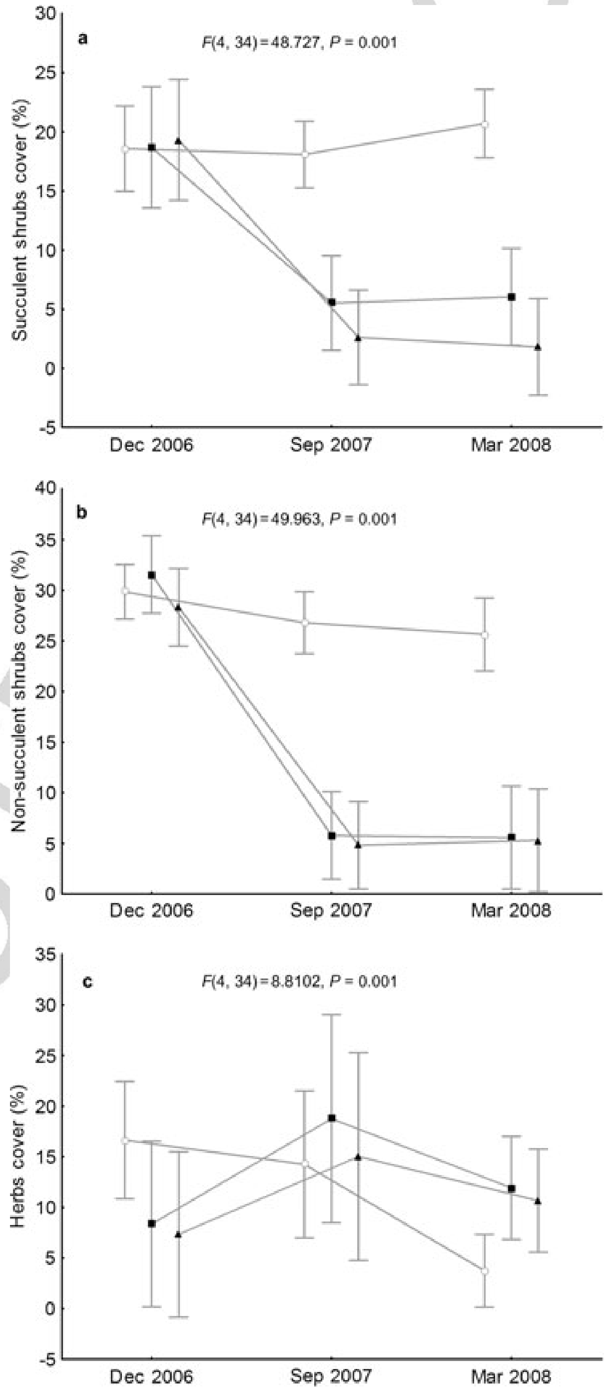


Fig. 3. Percentage cover change of total cover for three major plant life-forms: (a) leaf succulent, (b) non-succulent shrubs, (c) herbaceous and geophytic species on burned and unburned plots in the Tierberg Karoo Research Station before (December 2006) and after fire (2007 and 2008). Symbols on the graph represent (○) Control (■) low fuel load (▲) high fuel load. Error bars indicate 95% confidence interval.

doi:10.1111/j.1442-9993.2009.02000.x

Table 3. The final number of plant species in different fire survival categories on plots subjected to fire, or left unburnt, at the Tierberg Karoo Research Station

	Treatment		
Fire survival category	Low fuel load fire	High fuel load fire	No fire
All species	19	21	27
Sprout after fire	3	3	N/A
Killed by fire but seeds germinate on site	0	0	N/A
Killed by fire – no regeneration	15	18	N/A
Colonized plot after treatment	1	0	2

and shade succulents being exposed to fatal frosty conditions in winter and the summer heat (Riginos *et al.* 2005). Moreover, the reduction of vegetation cover increases run-off and erosion, leading to soil erosion and reduction in effective rainfall (Snyman & van Rensburg 1986).

Pennisetum setaceum invests in abundant opportunistic reproduction and could possibly invade this ecosystem in wet years despite the highly unpredictable and abiotically harsh conditions. Although it is largely confined to disturbed habitats, such as roadsides, cuttings and overgrazed areas, it has escaped into other habitats, including natural vegetation, perennial rivers and erosion gullies (Joubert & Cunningham 2002; Milton 2004). If widespread invasion should occur (and we see no reason why this will not happen), it will almost certainly change the vegetation structure and increase the risk of fire. Our results suggest that this will lead to adverse impacts on an ecosystem on which many plant species are ill-equipped to deal with fire.

Effects of fire on vegetation composition

Although both the leaf succulent shrubs and the non-succulent shrubs were able to burn when ignited, fire did not spread beyond the burned plots as a result of widely spaced shrubs and low fuel loads that prevented fire from spreading beyond areas to which fuel (*P. setaceum*) had been added. This suggests that the Karoo ecosystem may not support fire without grass. On the other hand, this may suggest that, in the presence of the grass, fire would be initiated and Karoo plant species could burn: however, the grass would have to be widespread to cause a continuous fire. The absence of the effect of fuel load (high or low) on vegetation recovery rates could have been due to low rainfall during the period. However, the result in this study could suggests that any amount of fire in this ecosystem would lead to detrimental impacts – particularly for succulents, most of which are endemic to the region (Mucina *et al.* 2006).

Implications for the Karoo ecosystem

Invasion of the Karoo ecosystem by *P. setaceum* could lead to increased fuel loads that may promote fire and increase fire frequency, which in turn may affect the most important natural resources that sustain the Karoo economy and ecosystem functioning (Milton *et al.* 1999b). First, reduction of forage species would lead to a decrease in the grazing potential of this area. Our study has shown a reduction in total vegetation cover and density of most species except for a few resprouting species during the study period. Second, the absence of recovery in cover of leaf succulent and non-succulent shrubs after fire during the study period might increase soil erosion rates. Although reduction in the density of established perennial shrubs has been found to improve the survival of seedlings in this vegetation type (Milton 1995), soil exposure following fire may result to an increase in run-off and sediment loss in the area as well as opportunities for further invasion. Third, loss of low growing, mound-building non-forage succulent species, such as *Brownanthus ciliatus* and *Peersia frithii*, that trap seeds and protect delicate seedlings of long-lived shrubs (Yeaton & Esler 1990; Milton & Hoffman 1994) from abiotic stress during seedling stages (Dean & Yeaton 1992) could be devastating in this ecosystem in that the seedlings could be exposed and may die from the harsh and stochastic environmental conditions in the area.

Pennisetum setaceum has been found to threaten biodiversity in other desert regions of the world (Brooks & Esque 2000; Williams & Baruch 2000; Brooks & Pyke 2001). There are other perennial grasses (e.g. Spanish reed *Arundo donax*, marram grass *Ammophila arenaria* and tussock grass *Stipa tenuissima*) that have potential to invade riparian or high-altitude communities in the Karoo ecosystem (Milton 2004) and this study may provide an indication for their possible effects on plant communities. This study has provided an indication that *P. setaceum* may increase the frequency and intensity of fires in the arid ecosystem. It would therefore, be appropriate to devise eradication strategies especially in areas where it

doi:10.1111/j.1442-9993.2009.02000.x

proliferates near road verges and other disturbed areas. Manual clearing or application of herbicides would probably control *P. setaceum* along roadsides and river banks, but would be costly.

The limitations of this study are that the results are based on only 15 months of observations and the outcomes might differ with environmental fluctuations in this arid ecosystem. The fire characteristics found here are for one fire event at a particular time and venue, and this may vary with temporal and spatial variation in conditions that could affect resprouting, mortality of species and fire behaviour.

Our results have important implications for quantifying the effects of invasive alien plants (especially grasses) on fire-free ecosystems elsewhere. These include the possibility of native species extinctions, changes in resource regimes, ecosystem services reduction and the ultimate opportunities for further invasion by other invasive alien species. Further evaluation of fire behaviour (especially under more extreme fire weather conditions) and fire effects (especially across a range of post-fire weather conditions) following invasion by *P. setaceum* would improve our understanding of potential impacts of this invader on a species-rich succulent desert.

ACKNOWLEDGEMENTS

This study was funded by DST – NRF Centre of Excellence for Invasion Biology, Stellenbosch University, South Africa. We thank D. G. Nel for statistical assistance. Many thanks to Mr Jacobus Minnaar of the Prince Albert Primary School and Mr Henry Lekay of the Prince Albert Municipality for their assistance during fire experiment.

REFERENCES

Bromilow C. (2001) *Problem Plants of South Africa: A Guide to the Identification and Control of More than 300 Invasive Plants and Other Weeds*. Briza Publications, Pretoria.

Brooks M. L. & Esque T. (2000) Alien grasses in the Mojave and Sonoran deserts. *Proceedings of the California Exotic Pest Plant Council Symposium* **6,** 39–44.

Brooks M. L. & Pyke D. A. (2001) Invasive plants and fire in the deserts of North America. In: *Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management* (eds K. E. M. Galley & T. P. Wilson) pp. 1–14. Allen Press, Tall Timbers Research Station, Tallahassee.

Brooks M. L., D'Antonio C. M., Richardson D. M. *et al.* (2004) Effects of invasive alien plants on fire regimes. *Bioscience* **54,** 677–88.

Byram G. M. (1959) Combustion of forest fuels. In: *Forest Fire: Control and Use* (ed. K. P. Davies) pp. 61–89. McGraw-Hill, New York.

D'Antonio C. M. & Vitousek P. M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **23,** 63–87.

D'Antonio C. M., Tunison J. T. & Loh R. K. (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral Ecol.* **25,** 507–22.

Dean W. R. J. & Yeaton R. I. (1992) The importance of harvester ant *Messor capensis* nest-mounds as germination sites in the southern Karoo, South Africa. *Afr. J. Ecol.* **30,** 335–45.

Efron B. (1981) Nonparametric estimates of standard error: the Jackknife, the Bootstrap and other methods. *Biometrika* **68,** 589–99.

Germishizen G. & Meyer N. L. (2003) *Plants of Southern Africa: An Annotated Checklist*. Strerilitzia 14, National Botanical Institute, Pretoria.

Govender N., Trollope W. S. W. & van Wilgen B. W. (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *J. Appl. Ecol.* **43,** 748–58.

Joubert D. & Cunningham P. L. (2002) The distribution and invasive potential of fountain grass *Pennisetum setaceum* in Namibia. *Dinteria* **27,** 37–47.

Mack M. & D'Antonio C. M. (1998) Impacts of biological invasions on disturbance regimes. *Trends Ecol. Evol.* **13,** 195–8.

Milton S. J. (1990) Above-ground biomass and plant cover in a succulent shrubland in the southern Karoo, South Africa. *S. Afr. J. Bot.* **56,** 587–9.

Milton S. J. (1992) Effects of rainfall, competition and grazing on flowering of *Osteospermum sinuatum* (Asteraceae) in arid Karoo rangeland. *Afr. J. Range Forage Sci.* **9,** 158–64.

Milton S. J. (1995) Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *J. Appl. Ecol.* **32,** 145–56.

Milton S. J. (2004) Grasses as invasive alien plants in South Africa. *S. Afr. J. Sci.* **100,** 69–75.

Milton S. J. & Dean W. R. J. (1993) Selection of seeds by harvester ants (*Messor capensis*) in relation to condition of arid rangeland. *J. Arid Environ.* **24,** 63–74.

Milton S. J. & Dean W. R. J. (1998) Alien plant assemblages near roads in arid and semi-arid South Africa. *Divers. Distrib.* **4,** 175–87.

Milton S. J. & Hoffman M. T. (1994) The application of state-and transition models to rangeland research and management in arid succulent and semi-arid grassy karoo, South Africa. *Afr. J. Range Forage Sci.* **11,** 18–26.

Milton S. J., Dean W. R. J., Marincowitz C. P. & Kerley G. I. H. (1995) Effects of the 1990/91 drought on rangeland in the Steytlerville Karoo. *S. Afr. J. Sci.* **91,** 78–84.

Milton S. J., Hoffmann J. H., Bowie R. C. K. *et al.* (1998) Invasive fountain grass on the Cape Peninsula. *S. Afr. J. Sci.* **94,** 57–9.

Milton S. J., Davies R. A. G. & Kerley G. I. H. (1999a) Population level dynamics. In: *The Karoo: Ecological Patterns and Processes* (eds W. R. J. Dean & S. J. Milton) pp. 183–207. Cambridge University Press, Cambridge.

Milton S. J., Zimmermann H. G. & Hoffmann J. H. (1999b) Alien plant invaders of the karoo: attributes, impacts and control. In: *The Karoo: Ecological Patterns and Processes* (eds W. R. J. Dean & S. J. Milton) pp. 275–87. Cambridge University Press, Cambridge.

Milton S. J., Dean W. R. J., O'Connor T. G. & Mills A. J. (2007) Scaling up from site-based research to a national research

doi:10.1111/j.1442-9993.2009.02000.x

and monitoring network: lessons from Tierberg Karoo Research Centre and other design considerations. *S. Afr. J. Sci.* **103,** 311–17.

Mucina L., Rutherford M. C., Palmer A. R. *et al.* (2006) Nama-karoo biome. In: *The Vegetation of South Africa, Lesotho and Swaziland* (eds L. Mucina & M. C. Rutherford). Strelitzia 19, National Biodiversity Institute, Pretoria.

Nailand P. & Hanrahan S. A. (1993) Modelling brown locust, *Locustana pardalina* (Walker), outbreaks in the Karoo. *S. Afr. J. Sci.* **89,** 420–4.

Riginos C., Milton S. J. & Wiegand T. (2005) Context-dependent interactions between adult shrubs and seedlings in a semi-arid shrubland. *J. Veg. Sci.* **16,** 331–40.

Rossiter N. A., Setterfield S. A., Douglas M. M. & Hutley L. B. (2003) Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Divers. Distrib.* **9,** 169–76.

Shapiro S. S. & Wilk M. B. (1965) An analysis of variance test for normality (Complete Samples). *Biometrika* **52,** 591–611.

Smith C. W. & Tunison J. T. (1992) Fire and alien plants in Hawaii: research and management implications for native ecosystems. In: *Alien Plant Invasions in Native Ecosystems of Hawaii* (eds C. P. Stone, C. W. Smith & J. T. Tunison) pp. 394–408. University of Hawaii Press, Honolulu.

Snyman H. A. & van Rensburg W. L. J. (1986) Effect of slope and plant cover on run-off, soil loss and water use efficiency of natural veld. *J. Grassland Soc. S. Afr.* **3,** 153–8.

Statsoft I. (2007) STATISTICA 8 (data analysis software). [Cited •• •• ••.] Available from URL: http://www.statsoft.com 3

Tilman D. (1996) Biodiversity: population versus ecosystem stability. *Ecology* **77,** 350–63.

Todd S. W. & Hoffman M. T. (1999) A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecol.* **142,** 169–78.

Trollope W. S. W. (1984) Fire behaviour. In: *Ecological Effects of Fire in South African Ecosystems* (eds P. d. V. Booysen & N. M. Tainton) pp. 199–217. Springer-Verlag, Berlin. 4

Visser N., Botha J. C. & Hardy M. B. (2004) Re-establishing vegetation on bare patches in the Nama Karoo, South Africa. *J. Arid Environ.* **57,** 15–37.

Williams D. G. & Baruch R. A. (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biol. Invasions* **2,** 123–40.

Yeaton R. I. & Esler K. J. (1990) The dynamics of a succulent Karoo vegetation. *Plant Ecol.* **88,** 103–13.

Zar J. H. (1999) *Biostatistical Analysis*. Prentice Hall, Upper Sadle River.

doi:10.1111/j.1442-9993.2009.02000.x

SNP Best-set Typesetter Ltd.	
Journal Code: AEC	Proofreader: Jason
Article No: 2000	Delivery date: 7 May 2009
Page Extent: 9	Copyeditor: Eric

AUTHOR QUERY FORM

Dear Author,

During the preparation of your manuscript for publication, the questions listed below have arisen. Please attend to these matters and return this form with your proof.

Many thanks for your assistance.

Query References	Query	Remark
1	AUTHOR: Please confirm the affiliation of '4' is correct.	
2	AUTHOR: Please provide the abbreviated journal title for **Brooks & Esque, 2000.**	
3	AUTHOR: Please provide the date you accessed this article online and check this website address/URL and confirm that it is correct (Please note that it is the responsibility of the author(s) to ensure that all URLs given in this article are correct and useable.) for for **Statsoft, 2007.**	
4	AUTHOR: Please confirm that the editor's name P. d. V. Booysen is correct for **Trollope, 1984.**	