



## Performance of invasive alien fountain grass (*Pennisetum setaceum*) along a climatic gradient through three South African biomes



Sebataolo J. Rahlao<sup>a,\*</sup>, Suzanne J. Milton<sup>a,c</sup>, Karen J. Esler<sup>a</sup>, Phoebe Barnard<sup>b,c</sup>

<sup>a</sup> Centre for Invasion Biology, Department of Conservation Ecology and Entomology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

<sup>b</sup> Climate Change and Bio-Adaptation Division, Kirstenbosch Research Centre, South African National Biodiversity Institute, Private Bag X7, Claremont 7735, South Africa

<sup>c</sup> DST Centre of Excellence, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

### ARTICLE INFO

#### Article history:

Received 23 February 2011

Received in revised form 25 November 2013

Accepted 27 November 2013

Available online xxx

Edited by S Cilliers

#### Keywords:

Alien grass

Biological invasions

Competition

Disturbance

Seedling translocation

Transplant experiment

### ABSTRACT

The knowledge of relative performance of plants across environmental gradients is critical for their effective management and for understanding future range expansion. *Pennisetum setaceum* is an invasive perennial grass found along roadsides and other disturbed sites in South Africa. The performance of this grass in response to competition, habitat characteristics and resources was experimentally tested in three biomes (Karoo, Fynbos and Savanna) of South Africa. A total of 846 young *P. setaceum* seedlings were translocated to study sites in May 2007. The seedlings were grown in 94 plots along random transects, of which alternate halves were cleared of vegetation. Despite a variety of environmental hazards at these sites, over 30% of the transplanted seedlings survived over 15 months. Competition from resident vegetation was a major factor limiting the establishment of seedlings. However, under adequate rainfall and historical disturbance (mine dump), competition effects were overridden. Survival of seedlings was greatest in the Karoo National Park, possibly because of summer rainfall that occurred shortly after translocation. Despite differences in the survival and growth rates, seedlings remained alive at all sites, especially if they survived the first six months after translocation. *P. setaceum* is capable of persisting across a broad range of environmental conditions. Management efforts should aim to reduce seed production and establishment along roadsides that act as conduits into protected sites. This could be best achieved by maintaining as much indigenous cover along road verges as possible, as seeds survive best where competition is low.

© 2013 SAAB. Published by Elsevier B.V. All rights reserved.

### 1. Introduction

The probability of success of an invasive species into a new habitat may result from the environmental and biotic factors that prevail in that habitat (Sakai et al., 2001). These factors govern the rates of survival, establishment and spread of the invader in a new habitat (Kolar and Lodge, 2001). The success of invasive species control depends on detailed knowledge of the key processes associated with their dispersal and regeneration. The availability of propagules and habitat are regarded as factors important for plant recruitment, and thus plant persistence and spread (Kollmann et al., 2007). Moreover, the ability of a species to persist under a wide range of climatic and edaphic conditions plays a major role in its invasive potential. Phenotypic plasticity is believed to facilitate biological invasions (Williams and Black, 1993; Williams et al., 1995; Pattison et al., 1998; Milberg et al., 1999; Schweitzer and Larson, 1999; Sexton et al., 2002; Daehler, 2003; Geng et al., 2007; Lavergne and Molofsky, 2007; Hulme, 2008).

*Pennisetum setaceum* (fountain grass, Poaceae) is an apomictic, wind dispersed, C4 perennial bunch grass, native to Mediterranean parts of North Africa and the Middle East (Williams et al., 1995). Although its ecology is better known in Hawaii, where it is also invasive, little has been written about its ecology in its native range (Poulin et al., 2007) or in South Africa where it has the potential to promote fire in arid regions (Rahlao et al., 2009). Although *P. setaceum* reproduces mainly by seed, it forms pseudo-viviparous plantlets when inflorescences are inundated by water (Milton et al., 2008). Its successful spread is probably due to its popularity in horticulture, drought tolerance, unpalatability to animals, rapid growth and profuse seed production (Milton et al., 1998; Cabin et al., 2000) and the ability to thrive in a wide range of environmental conditions worldwide through phenotypic and reproductive plasticity (Williams et al., 1995; Le Roux et al., 2007). It has successfully escaped cultivation and has invaded and naturalized in a wide range of habitats worldwide including Hawaii (Williams et al., 1995), parts of southern Africa, Democratic Republic of Congo, Fiji and North America (Joubert and Cunningham, 2002; Milton, 2004). It has been found to perform better where roads interchange with rivers in the western part of South Africa, probably as a result of extra moisture, nutrients and seed exchange between the two conduits (Rahlao et al., 2010a). Although the grass performs well under high nutrient and water

\* Corresponding author at: Climate Change Monitoring and Evaluation, Department of Environmental Affairs, Private Bag X447, Pretoria 0001, South Africa. Tel.: +27 12 310 3480; fax: +27 86 595 7417.

E-mail address: [sjahlao@gmail.com](mailto:sjahlao@gmail.com) (S.J. Rahlao).

greenhouse conditions (Rahlao et al., 2010b), the relative contribution of seed dispersal and recruitment, habitat and microsite limitation to invasion success in the field is unknown for *P. setaceum* in South Africa.

The aim of this study was to identify factors affecting the seedling establishment and recruitment of transplanted *P. setaceum* in three biomes differing in rainfall seasonality, soil type and plant community, but where the species was already present. In order to explore inter-site variation in regeneration, a factorial transplant and disturbance experiment was established and monitored for 15 months. Key questions for this study were: (i) Does seedling establishment benefit from reduced competition from indigenous vegetation? (ii) Do seedling establishment and performance rates differ among habitat types (disturbed and semi-natural)? And, (iii) is there an interaction between site (biome) and other factors influencing plant performance?

## 2. Material and methods

### 2.1. Study areas

Three sites were selected in arid and semi-arid parts of South Africa covering the current distribution range of *P. setaceum*. The altitudinal gradient ranged from 190 to 1242 m a.s.l. Rainfall seasonality and precipitation differed at all these sites (Table 1). The Karoo site was in the Karoo National Park (32°17'44.59"S, 22°33'46.71"E) near Beaufort West, in the mixed-rainfall season, semi-arid Nama-Karoo biome. This site was selected because *P. setaceum* occurs along the Gamka River, running through the park, with seeds invading from road shoulders outside the park as well as from neighbouring farms upstream. Park managers expressed the need to eradicate the grass in the park. The semi-arid summer rainfall Savanna site was situated at De Beers Mine dumps in Kimberley (28°44'17.90"S, 24°47'08.75"E). This site was selected due to the abundance of *P. setaceum* on the mine dumps where it was probably previously used for mine stabilization. The grass has escaped from the dumps into the surrounding disturbed and semi-natural areas in and near Kimberley. The semi-arid winter rainfall Fynbos biome site was situated in the Renosterveld vegetation type at PPC De Hoek Cement Mine dumps (32°55'49.09"S, 18°45'36.22"E) near Piketberg. The area was selected because *P. setaceum* is present on mine dumps and on the roadsides around the town of Piketberg. The grass has escaped into the adjacent Piketberg Mountain and could increase the fire frequency in the area. The mine authority is keen to eradicate the grass from their property given a suitable alternative; indigenous species to stabilize the mine dumps.

### 2.2. Soil properties

In February 2008, soil samples were collected at a depth of 5–20 cm from between the transect plots (described below) at all the study sites. The soil samples were pooled and oven dried at 80 °C for 2 days before

**Table 1**  
Geographic and climatic characteristics of the three (3) study sites for the study of *P. setaceum* in South Africa.

Site	Vegetation type*	Altitude (m a.s.l.)	Rainfall season	Precipitation** (mm)	Absolute air temp.*** (°C)	
					Min	Max
Karoo National Park	Upper Karoo Hardeveld	911	Mixed	259	−4	43
Kimberley	Kimberley Thornveld	1242	Summer	419	−8	47
Piketberg	Swartland Shale Renosterveld	190	Winter	447	5	49

\* Mucina and Rutherford (2006).

\*\* South African Weather Bureau—unpublished weather data, 1990–2007.

\*\*\* Measured at sites during the study period.

analyses. The soils were of sandy texture except for Piketberg, which was loamy sand. The soils were alkaline (pH 7.2–7.7) except for three transects in Kimberley that were slightly acidic (pH 5.1–6.5) with relatively high CEC (pH 7) cmol (+)/kg (4.33–9.89 ppm). Total nitrogen (0.05–0.23%) concentrations were relatively low whereas phosphorus (4–72 ppm) concentrations were highly variable. The only exception was a transect at Kimberley which had 66% sodium base saturation and <0 ppm phosphorus concentration.

### 2.3. Seed source and germination

*P. setaceum* seeds were collected from all the study sites and mixed together. The seeds were sown in a trial experiment in a greenhouse at Stellenbosch University Agronomy department where the average temperature was 38 °C. There was no germination for four weeks and the experiment was terminated. Seeds were later grown in a Forestry department greenhouse with an average temperature of 25 °C. After germination and growth for two weeks, 846 uniformly sized seedlings with at least 3–4 leaves were transplanted individually into propagation bags and left for two more weeks before translocation to the sites.

### 2.4. Experimental design

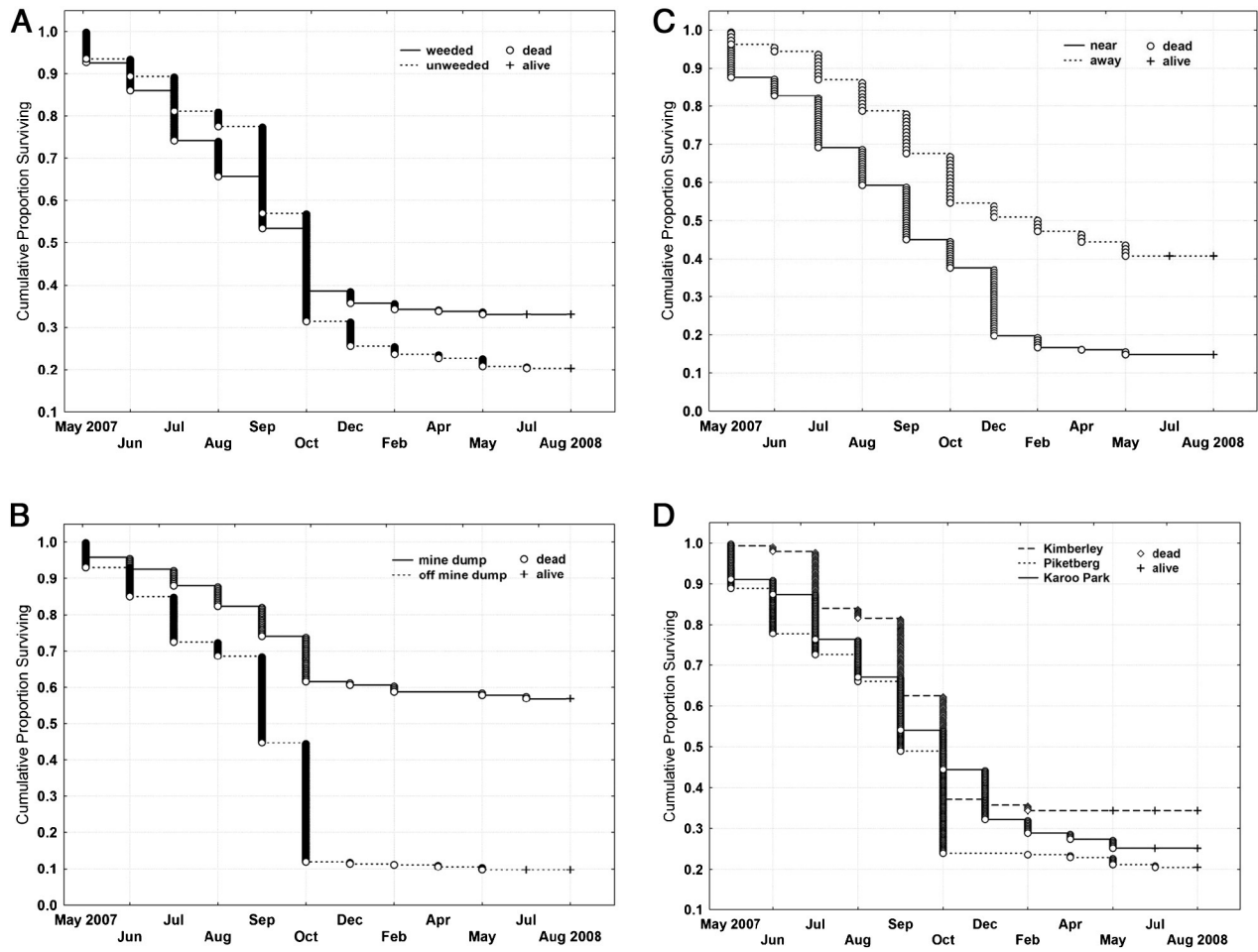
At each study site permanent pairs of 2 m<sup>2</sup> plots (cleared or uncleared) 5 m apart were established. A total of 846 young (2 months old, 0.1 m basal diameter) *P. setaceum* seedlings were translocated to the study sites in the winter of 2007. In Kimberley and Piketberg, four transects with four pairs of plots resulted in 72 seedlings per transect and 288 seedlings (4 transects × 8 plots × 9 seedlings) per site. At these sites, two transects were in the historically disturbed sites (mine dump) and two in the semi natural areas away (100 and 200 m) from the mine dump. The seedling sample size at Karoo National Park was 270 (3 transects × 10 plots × 9 seedlings). On each plot (2 × 2 m), nine (9) seedlings were placed systematically, at 0.5 m apart and 0.5 m from the plot boundaries. All seedlings were given 500 ml of water immediately after being translocated. The seedlings were grown in 94 plots, half of which were cleared of vegetation and were studied over 15 months from May 2007 to August 2008. The number of leaves, basal diameter, length of the longest living leaf and the number of inflorescences were recorded every month for each seedling.

### 2.5. Microhabitat characteristics

The three sites were of different elevation (Table 1) and had different land use and soil characteristics. Percent rock cover was determined as the average rock cover for each plot (the mean percentage rock cover along three, 2 m line transects). The effect of historical disturbance (that related to past mining activities) on seedling performance was determined by placing transects on the mine dump and at different distances away from the dump (applies to Kimberley and Piketberg only). The effect of water on seedling performance was determined by placing the plots along three transects at 0, 5, 10, 15 and 20 m from the river (applies to Karoo National Park only).

### 2.6. Statistical analysis

All data were tested for normality with a Shapiro–Wilk test (Shapiro and Wilk, 1965). When data were normal, repeated measure analysis of variance (ANOVA) was used in STATISTICA 8 (Statsoft, 2007) to analyse the performance of seedlings over the study period. The seedling performance was determined by measuring their height, basal diameter and the number of leaves every month during the study period. When the data were not normal, 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



**Fig. 1.** The cumulative proportion of surviving seedlings under different variables at the three different sites. A) Weeded and unweeded plot types, B) plots on the mine dump and away (off), C) plots near (0–10 m) the river and away (12–20 m) at Beaufort West and D) different sites. The plus (+) indicates alive seedlings and the circle (o) indicates dead seedlings.

between-subject effects. The survival of transplanted seedlings was expressed as the mean number of surviving seedlings per treatment for all sites applicable to that treatment. One-way ANOVA was used to compare transplant survival and performance in weeded and unweeded plots as well as in disturbed (mine dump) and undisturbed

plots. A Bonferroni post-hoc test was performed to test the differences between and within treatments over time. Spearman correlations were calculated to detect relationships between soil characteristics, microclimate properties and plant performance. Survival analysis was performed to compare the proportion of seedlings surviving over the

**Table 2**

Repeated measures analysis of variance (ANOVA) for transplanted *P. setaceum* performance (basal diameter) across the environmental gradient and its interactions with plot type (weeded/unweeded), mine dump, distance from the river, site and time.

Variable	Sites applicable	SS	df	MS	F	p	Significance level
Site	All	580	2	290	47.61	<0.0001	***
Plot type	All	168	1	168	27.51	<0.0001	***
Mine dump	KIM & PIK	101	1	101	46.55	<0.0001	***
Distance from river	KNP	28	1	28	2.42	0.139	NS
Site × plot type	All	52	2	26	4.27	0.019	*
Site × mine dump	KIM & PIK	0.674	1	0.674	0.31	0.579	NS
Plot type × mine dump	KIM & PIK	5	1	5	2.31	0.134	NS
Site × plot type × mine dump	KIM & PIK	4	1	4	1.87	0.177	NS
Plot type × distance from river	KNP	36	1	36	3.06	0.099	NS
Time (months)	All	1214	11	110	165.17	<0.0001	***
Time × site	All	1214	22	19	28.02	<0.0001	***
Time × plot type	All	131	11	12	17.77	<0.0001	***
Time × site × plot type	All	30	22	1	2.07	0.003	*
Time × mine dump	KIM & PIK	85	11	8	36.47	<0.0001	***
Time × site × mine dump	KIM & PIK	4	11	0.33	1.55	0.109	NS
Time × plot type × mine dump	KIM & PIK	4	11	0.35	1.65	0.082	NS
Time × site × plot type × mine dump	KIM & PIK	7	11	0.61	2.88	0.001	**
Time × distance from river	KNP	130	11	12	13.21	<0.001	***
Time × plot type × distance from river	KNP	60	11	5	6.12	<0.001	***

KIM = Kimberley, PIK = Piketberg, KNP = Karoo National Park, SS = sum of squares, df = degrees of freedom MS = mean of squares, NS = not significant, \*p < 0.05, \*\*p < 0.001, \*\*\*p < 0.0001.

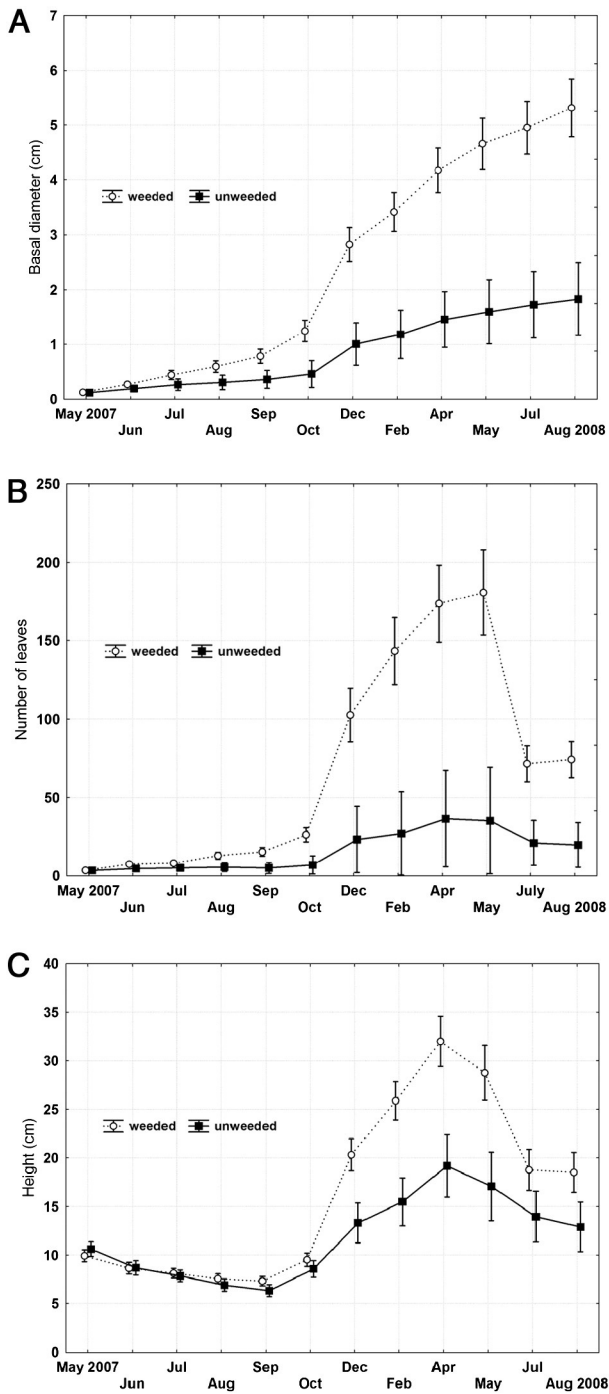


Fig. 2. Performance of transplanted *P. setaceum* seedlings at the three sites in plots cleared of vegetation (weeded) (○) and plots left unweeded (■). Performance was measured in terms of basal diameter (A), number of leaves (B) and the height of the longest living leaf, height (C). Bars indicate standard errors on all graphs.

study period at different study sites using Kaplan–Meier survival curves (Kaplan and Meier, 1958).

### 3. Results

#### 3.1. Factors affecting seedling survival and performance

A variety of habitat and environmental factors affected *P. setaceum* seedling survival and performance over the study period. Competition

from resident species affected the performance of surviving seedlings (Fig. 1A, Table 2). Seedling performance was also influenced by site disturbance history. Seedlings performed better on mine dumps than away (off) from them (Fig. 1B). At KNP seedlings performed equally well regardless of the distance from the river seedling but survived longer away from the river than near it (Fig. 1C). Climatic variables from different study sites also affected both the survival rates and performance (Fig. 1D).

#### 3.2. Effect of competition

Seedlings growing on plots from which competitors were removed (weeded plots) were larger in basal diameter and height and had more leaves throughout the study period than those growing on unweeded plots (Fig. 2). Basal diameter, number of leaves and height were positively correlated, and only ANOVA results for basal diameter are presented in this paper (Table 2). The effect of competition on seedling survival was evident across all sites throughout the study period (Fig. 3).

#### 3.3. Seedling establishment success

There were no measurable differences in performance of seedlings for five months until September 2007, when the effect of resident vegetation had an influence on growth of the transplanted *P. setaceum* seedlings. Seedlings growing in the Karoo National Park performed better (larger basal diameter) than those in other two sites (Fig. 3). This was also the case for when performance was measured as basal diameter and height (data not shown). Most transplanted seedlings that survived after six months remained alive at all sites for the rest of the study period (Fig. 1). At all sites, more seedlings growing on plots cleared of resident vegetation survived (33%) than on unweeded plots (20%) and this effect was significant (Fig. 1).

#### 3.4. Microhabitat effects

At Kimberley and Piketberg, more seedlings survived (56.9%) on mine dumps than off (9.7%) and surviving seedling performance (expressed as basal diameter) on these mine dumps was significantly better ( $SS = 101$ ,  $df = 1$ ,  $MS = 101$ ,  $F = 46.55$ ,  $p < 0.0001$ ). More seedlings (40.7%) survived away (0–10 m) from the river than those near the river at the Karoo National Park site. However, those that survived (14.8%) near the river (12–20 m) performed better in basal diameter ( $SS = 193$ ,  $df = 44$ ,  $MS = 4.395$ ,  $F = 3.319$ ,  $p < 0.0001$ ) over the study period. The effects of site, plot type and mine dump remained significant for the duration of study period (Table 2). The effects of resident vegetation removal and mine dump did not differ between Kimberly and Piketberg and over the study period. The effect of plot type did not differ with the distance from the river, or over the study period.

## 4. Discussion

#### 4.1. Microhabitat limitation

Environmental stress in a new habitat has been suggested to affect the establishment of invasive species (Alpert et al., 2000). Low-stress habitats are easily invaded because many aliens are better able than natives to take advantage of high resource availability (Dukes and Mooney, 1999). The transplanted *P. setaceum* seedlings were exposed to different types of environmental stresses imposed by the three study sites. The high performance and survival on the historically disturbed mine dumps could be as a result of resource facilitation and fluctuating resources levels that promote plant invasion (Davis et al., 2000) and/or microhabitat limitation away from mine dumps (Eriksson and Ehrlén, 1992). The low performance of seedlings on unweeded plots

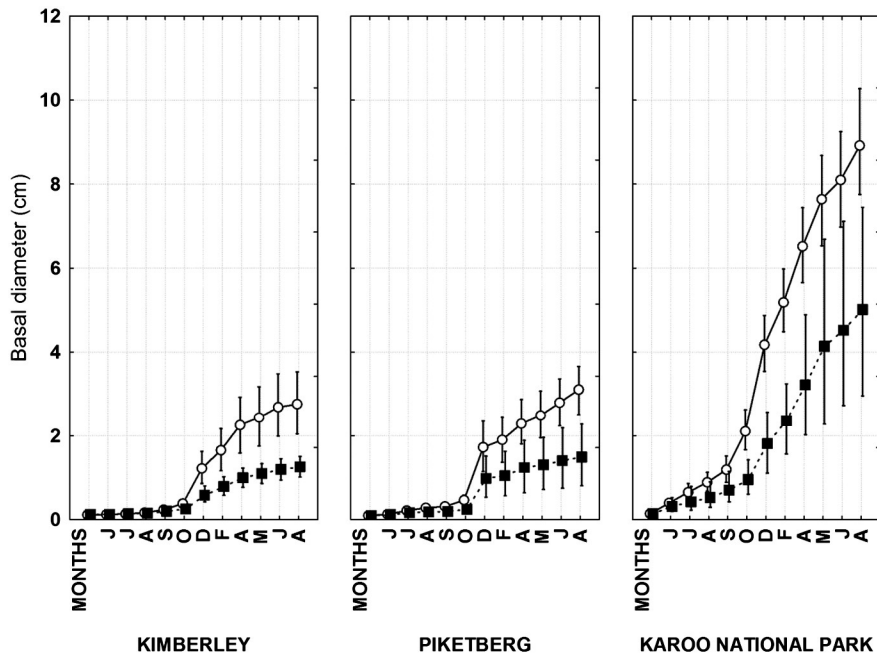


Fig. 3. Bootstrap means for basal diameters of *P. setaceum* seedlings at the three sites. Open circles (○) represent weeded plots and closed squares (■) represent unweeded plots. Bars indicate standard error on all graphs.

suggests competitive suppression by the established resident vegetation (Grime, 1973; Jutilla and Grace, 2002).

Disturbance and competition had no effect on performance and survival of *P. setaceum* in the first five months of seedling transplantation. This suggests that early survival of transplanted seedlings was not related to competitive interactions in relation to historical disturbances. However, both survival and performance of seedlings after five months was positively affected by both historical and current disturbances. This indicates that competitive suppression by resident vegetation and disturbance effects are more important for mature *P. setaceum* seedlings. Soil disturbance has been suggested to promote invasion (Hobbs and Huenneke, 1992; McIntyre and Lavorel, 1994) by increasing water and nutrient availability and other resources at disturbed and near-natural areas. Our results suggest that indigenous vegetation on undisturbed sites could suppress establishment of *P. setaceum* whereas its invasion is facilitated at both historically and currently disturbed sites.

#### 4.2. Habitat effects

In the Karoo National Park, the seedlings performed equally well regardless of the distance from the river. The interaction between the distance from the river and the removal of resident vegetation over the study period did not influence the performance of species (Table 2). This could be due to the amount of rainfall received in this area shortly after seedlings were transplanted. Although the amount of rockiness was not positively correlated with plant performance in general, most plants near rocks produced flowers and seeds before the rest of the seedlings in the Karoo National Park (SR, personal observation).

Soil type plays a major role in the distribution and community structure of plants (Wilson et al., 1992; Gelbard and Harrison, 2003). Resource-poor soils appear to be more resistant to invasion, particularly in semi-arid systems (Harrison, 1999; Belnap and Phillips, 2001; Stohlgren et al., 2001; Gelbard and Harrison, 2003). In our study, *P. setaceum* seedling survival and performance was minimal (<1%) in saline (pH = 7.4) soils along a transect near the Kimberley mine dump. Soil at this site had the highest levels of sodium (Na) (44.36 cmol (+)/kg) and potassium (K) (3.42 cmol (+)/kg). This effect could not be detected until the sixth month when seedlings began to die off. Stohlgren et al. (1998) found a positive relationship between exotic

species (and cover) to percent soil silt and percent soil nitrogen. Most seedlings (90) in our study died off at the soil with the highest clay content (6.0%).

#### 4.3. Establishment success across environments

The overall good survival rates of *P. setaceum* across three climatically distinct environments demonstrate the species' ability to adjust to different conditions prevailing at new locations. Despite differences in survival rates at early stages, *P. setaceum* seedlings that survived the six months persisted for the rest of the study period. This suggests that once the seedlings have overcome the critical seedling stage they are able to establish despite harsh environmental conditions. Flowering occurred after six months in the Karoo National Park; this could be as a result of extra moisture from the river where *P. setaceum* is prevalent. Seedlings at other sites took more than 12 months before flowering could occur. The interaction between abiotic and biotic processes at these sites played a major role in the survival rates of *P. setaceum* seedlings.

#### 5. Conclusion

Our study demonstrated that the invasive alien *P. setaceum* is able to thrive and establish in three biomes with distinct climatic characteristics. We found evidence for microsite limitation at different stages of its regeneration process. At all three sites *P. setaceum* performed well under reduced competition from resident indigenous species although the establishment and performance rates differed between sites. However, other habitat conditions such as soil and moisture availability could override competition effects and lead to successful establishment. This study has demonstrated that *P. setaceum* has a high growth and invasion potential in historically disturbed habitats (mine dumps) as well as in sites with current disturbances. Conservation authorities concerned with management of *P. setaceum* invasion need to give more attention to these historical disturbances that act as hotspots for seed production. *P. setaceum* is already present at these sites and will easily invade near natural areas if it is not managed effectively. Both biotic and abiotic factors and their interactions promote the establishment and growth of *P. setaceum*. We recommend reduction in human induced disturbances, especially land cover change, which reduce

competition with indigenous species and hence promote *P. setaceum* establishment. Management efforts should also aim to reduce seed production and establishment of *P. setaceum* along roadsides that act as conduits into near-natural sites. This can best be done by maintaining as much indigenous cover along road verges as possible as competition reduction favours seedling survival. Finally, our results contribute significantly to our understanding of basic processes that affect emerging invaders, especially grasses in new environments in South Africa. Results confirm the status of this grass as an important emerging weed and invader that must be prohibited and controlled in South Africa.

### Acknowledgements

This study was funded by the DST-NRF Centre for Invasion Biology at Stellenbosch University, South Africa. We are grateful to De Beers (Kimberley), PPC De Hoek Cement Mine (Piketberg) and SANParks (Karoo National Park) for providing permission on their land for this study. Malebogo Thabong, Napo Khasoane and Thabiso Mokotjomela are greatly thanked for their assistance in the field.

### References

- Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3, 52–66.
- Belnap, J., Phillips, S.L., 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* 11, 1261–1275.
- Cabin, R.J., Weller, S.G., Lorence, D.H., Flynn, T.W., Sakai, A.K., Sandquist, D.R., Hadway, L.J., 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation of and restoration of a Hawaiian tropical dry forest. *Conservation Biology* 14, 439–453.
- Daehler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics* 34, 183–211.
- Davis, M.A., Grime, P.J., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88, 528–534.
- Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? *Trends in Ecology & Evolution* 14, 135–139.
- Efron, B., 1981. Nonparametric estimates of standard error: the jackknife, the bootstrap and other methods. *Biometrika* 68, 589–599.
- Eriksson, O., Ehrlén, J., 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91, 360–364.
- Gelbard, J.L., Harrison, S., 2003. Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. *Ecological Applications* 13, 404–415.
- Geng, Y.P., Pan, X.Y., Xu, C.Y., Zhang, W.J., Li, B., Chen, J.K., Lu, B.R., Song, Z.P., 2007. Phenotypic plasticity rather than locally adapted ecotypes allows the invasive alligator weed to colonize a wide range of habitats. *Biological Invasions* 9, 245–256.
- Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347.
- Harrison, S., 1999. Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia* 121, 99–106.
- Hobbs, R.F., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6, 324–337.
- Hulme, P.E., 2008. Phenotypic plasticity and plant invasions: is it all Jack? *Functional Ecology* 22, 3–7.
- Joubert, D., Cunningham, P.L., 2002. The distribution and invasive potential of fountain grass *Pennisetum setaceum* in Namibia. *Dinteria* 27, 37–47.
- Jutila, H.M., Grace, J.B., 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *Journal of Ecology* 90, 291–302.
- Kaplan, E.L., Meier, P., 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53, 457–481.
- Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16, 199–204.
- Kollmann, J., Frederiksen, L., Vestergaard, P., Bruun, H.H., 2007. Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biological Invasions* 9, 31–42.
- Lavergne, S., Molofsky, J., 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. *PNAS* 104, 3883–3888.
- Le Roux, J.J., Wieczorek, A.M., Wright, M.G., Tran, C.T., 2007. Super-genotype: global monoclonality defies the odds of nature. *PLoS ONE* 2 (7), e590. <http://dx.doi.org/10.1371/journal.pone.0000590>.
- McIntyre, S., Lavorel, S., 1994. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. *Conservation Biology* 8, 521–531.
- Milberg, P., Lamont, B.B., Perez-Fernandez, M.A., 1999. Survival and growth of native and exotic composites in response to a nutrient gradient. *Plant Ecology* 145, 125–132.
- Milton, S.J., 2004. Grasses as invasive alien plants in South Africa. *South African Journal of Science* 100, 69–75.
- Milton, S.J., Hoffmann, J.H., Bowie, R.C.K., D'Amico, J., Griffiths, M., Joubert, D., Loewenthal, D., Moinde, N.N., Seymour, C., Toral-Granda, M.V., Wiseman, R., 1998. Invasive fountain grass on the Cape Peninsula. *South African Journal of Science* 94, 57–59.
- Milton, S.J., Dean, W.R.J., Rahlao, S.J., 2008. Evidence for induced pseudo-vivipary in *Pennisetum setaceum* (Fountain grass) invading a dry river, arid Karoo, South Africa. *South African Journal of Botany* 74, 348–349.
- Mucina, L., Rutherford, M.C., 2006. Vegetation map of South Africa, Lesotho and Swaziland. *Strelitzia*.
- Pattison, R.R., Goldstein, G., Ares, A., 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117, 449–459.
- Poulin, J., Sakai, A.K., Weller, S.G., Nguyen, T., 2007. Phenotypic plasticity, precipitation, and invasiveness in the fire-promoting grass *Pennisetum setaceum* (Poaceae). *American Journal of Botany* 94, 533–541.
- Rahlao, S.J., Milton, S.J., Esler, K.J., Wilgen, B.W.V., Barnard, P., 2009. Effects of invasion of fire-free arid shrublands by a fire-promoting invasive alien grass (*Pennisetum setaceum*) in South Africa. *Austral Ecology* 34, 920–928.
- Rahlao, S.J., Milton, S.J., Esler, K.J., Barnard, P., 2010a. The distribution of invasive *Pennisetum setaceum* along roadsides in western South Africa: the role of corridor interchanges. *Weed Research* 50, 537–543.
- Rahlao, S.J., Esler, K.J., Milton, S.J., Barnard, P., 2010b. Nutrient addition and moisture promote the invasiveness of Crimson fountain grass (*Pennisetum setaceum*). *Weed Science* 58, 154–159.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32, 305–332.
- Schweitzer, J.A., Larson, K.C., 1999. Greater morphological plasticity of exotic honeysuckle species may make them better invaders than native species. *Journal of the Torrey Botanical Society* 126, 15–23.
- Sexton, J.P., McKay, J.K., Sala, A., 2002. Plasticity and genetic diversity may allow saltcedar to invade cold climates in North America. *Ecological Applications* 12, 1652–1660.
- Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52, 591–611.
- Statsoft, I., 2007. STATISTICA 8 (data analysis software). [www.statsoft.com](http://www.statsoft.com).
- Stohlgren, T., Bull, K., Otsuki, Y., Villa, C., Lee, M., 1998. Riparian zones as havens for exotic plant species in the central grasslands. *Plant Ecology* 138, 113–125.
- Stohlgren, T.J., Otsuki, Y., Villa, C.A., Lee, M., Belnap, J., 2001. Patterns of plant invasions: a case example in native species hotspots and rare habitats. *Biological Invasions* 3, 37–50.
- Williams, D.G., Black, R.A., 1993. Phenotypic variation in contrasting temperature environments: growth and photosynthesis in *Pennisetum setaceum* from different altitudes on Hawaii. *Functional Ecology* 7, 623–633.
- Williams, D.G., Mack, R.N., Black, R.A., 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. *Ecology* 76, 1569–1580.
- Wilson, J.B., Rapson, G.L., Sykes, M.T., Watkins, A.J., Williams, P.A., 1992. Distributions and climatic correlations of some exotic species along roadsides in South Island, New Zealand. *Journal of Biogeography* 19, 183–193.