Current and future vulnerability of South African ecosystems to perennial grass invasion under global change scenarios
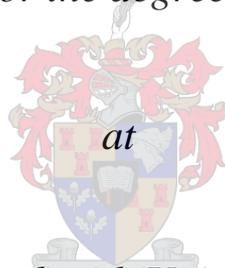
by

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at

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Date: December 2009

DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part, submitted it at any university for a degree.

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ABSTRACT

Climate change and biological invasions are major components of global change induced by human activity and are considered major drivers of global biodiversity decline in terrestrial ecosystems. These drivers interact synergistically and render ecosystems vulnerable to invasion by invasive alien species. Grasses are a group of invasive plants that easily respond to global changes and alter native plant community structure and ecosystem processes, such as fire frequency. To date there have been few studies that assess the ecological drivers and effects of invasive grass species on arid and semi-arid ecosystems of South Africa.

Fountain grass (*Pennisetum setaceum*) is a widely distributed invasive alien perennial grass from North Africa and the Middle East, valued by horticulturalists worldwide. It spreads along the edges of roads on the outskirts of most towns, and is common on mine spoil in many areas throughout South Africa. Occasionally, it escapes into natural vegetation along drainage lines or after fires. This grass can be a costly problem for agriculture and biodiversity conservation as it is unpalatable and increases fire risk. Understanding its distribution and invasive dynamics will contribute to better management and control practices.

The main objective of this study was to understand the ecology and invasion processes of *P. setaceum* across South African environmental gradients, and use it as a model to understand the synergistic relationships between biological invasions and other global change (climate and land use) scenarios. This study provides the first assessment of how *P. setaceum* overcomes different invasion barriers in South Africa as an emerging invader, in comparison with other parts of the world where it has already become problematic. A number of management and control options for this grass and other similar perennial grasses result from this study. Specifically, the study provides comprehensive understanding of: 1) the distribution and habitat preferences of *P. setaceum* in arid and semi-arid parts of South Africa, 2) environmental resources and habitat conditions that promote its invasive potential, 3) growth and reproductive performance across environmental gradients, 5) the response of an arid ecosystem to *P. setaceum* invasion and fire promotion, and 6) the predicted future distribution of this grass in South Africa under scenarios of climate change and spread.

The study has found that road-river interchanges are ideal sites for *P. setaceum* growth and that these sites should be targeted for management and control of this species. *P. setaceum* was found to persist under diverse biome environments, which is attributed to local adaptation. Disturbance was found to be a major factor promoting fountain grass invasion into semi-natural areas away from roadsides. Major clean-ups of this grass should focus on disturbed areas, especially in the fertile parts of the fynbos region where the grass has high climatic suitability. Management and control should also focus on areas with high nutrients and extra water, as these areas facilitate growth and reproduction. The dynamics of *P. setaceum* invasion and spread makes it a good model for management of similar emerging invasive perennial grasses in similar ecosystems.

OPSOMMING

Klimaatsverandering en biologiese indringing is grootskaalse komponente van mensgedrewe globale veranderinge, en kan ook gesien word as prominente drywers van die huidige afname in globale biodiversiteit van terrestriële ekosisteme. Hierdie drywers werk saam in sinergie, en laat sodoende ekosisteme kwesbaar vir indringing deur uitheemse indringerplante. Grasse is 'n groep indringerplante wat maklik reageer ten opsigte van globale veranderinge en verander inheemse plantgemeenskapstruktuur en ekosisteem prosesse, soos byvoorbeeld veldbrand frekwensie. Tot op hede is daar wynig studies gedoen wat die ekologiese drywers en effekte van indringergras spesies in droë en semi-droë ekosisteme van Suid-Afrika assesseer.

Pronkgras (*Pennisetum setaceum*) is 'n wyd verspreide meerjarige uitheemse indringergras, oorspronklik vanaf Noord-Afrika en die Midde-Ooste, en word waardeer deur tuinboukundiges wêreldwyd. Dit versprei al langs padrande aan die buitewyke van meeste dorpe, en is algemeen op ou mynhope in verskeie dele van Suid-Afrika. Somtyds ontsnap hierdie gras langs dreineringskanale of na veldbrande, en beland so in die omringende natuurlike plantegroei. Hierdie gras kan 'n duur probleem word vir landbou asook biodiversiteit bewaring omdat dit onsmaaklik is vir diere, en dit verhoog veldbrand risiko. 'n Beter begrip van pronkgras verspreiding en indringingdinamika sal bydra tot verbeterde bestuur en kontrole praktyke.

Die hoofdoel van hierdie studie was om die ekologie en indringing prosesse van *P. setaceum* regoor Suid-Afrikaanse omgewingsgradiente te begryp, en dit dan te gebruik as 'n model om die sinergistiese verhoudings tussen biologiese indringing en ander globale veranderinge (klimaat en grondgebruik) te verstaan. Die studie verskaf die eerste assessering van hoe *P. setaceum* verskillende indringing hindernisse in Suid-Afrika oormeester as 'n opkomende indringer, in vergelyking met ander dele van die wêreld waar dit al klaar problematies is. Hierdie studie verskaf uiteindelik 'n aantal bestuur en kontrole opsies vir hierdie en ander soortgelyke meerjarige grasse. Die studie verskaf spesifiek 'n deeglike verstaan van: 1) die verspreiding en habitat voorkeure van *P. setaceum* in droë en semi-droë areas in Suid-Afrika, 2) omgewingshulpbronne en habitat toestande wat hierdie plant se indringing potensiaal verhoog, 3) groei- en voortplantingsvertoning oor verskillende omgewingsgradiente,

4) die reaksie wat 'n droë ekosisteem toon teenoor *P. setaceum* indringing en veldbrand verhoging, en 5) die toekomstige verspreiding van hierdie gras in Suid-Afrika onder voorspellings van klimaatsverandering en verspreiding.

Die studie het gevind dat pad-rivier tussengange ideale liggings is vir *P. setaceum* vestiging, en dat hierdie liggings dus geteiken moet word vir bestuur en kontrole doeleindes. *P. setaceum* toon volharding onder diverse bioom omgewings, wat toegeskryf word aan plaaslike aanpassing. Daar is gevind dat versteuring 'n groot faktor is in die verhoging van pronkgras indringing in semi-natuurlike areas weg van padskouers. Grootskaalse pronkgras uitroeiing projekte moet fokus op versteurde gebiede, veral in die vrugbare dele van die fynbos streek, waar hierdie gras hoë klimaatsgeskiktheid toon. Bestuur en kontrole programme moet ook fokus op areas met hoë nutriente inhoud en ekstra water, aangesien hierdie areas groei en voortplanting vergemaklik. Die dinamika van *P. setaceum* indringing en verspreiding maak dit 'n goeie model vir die bestuur van soortgelyke opkomende meerjarige indringergrasse in soortgelyke ekosisteme.

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CHAPTER 1

INTRODUCTION

1.1   Introduction

Grasses have been identified as a major group of invasive plants that can dramatically alter native plant community structure and ecosystem processes such as fire frequency, nutrient cycling, and water circulation (D'Antonio and Vitousek 1992). Among the most significant ecological changes caused by invading alien grasses are the alteration of fire regimes (van Wilgen and Richardson 1985; D'Antonio and Vitousek 1992; Smith and Tunison 1992; Tunison 1992), the disruption of succession, and the displacement of plant and animal communities in natural rangelands (D'Antonio and Vitousek 1992). Invasive alien grasses invade an area and increase the abundance of fine fuel, which increases fire frequency, extent and in some cases intensity within what is known as grass/fire cycle (D'Antonio and Vitousek 1992). In a post-fire environment, alien grasses tend to recover more rapidly than native species and thus cause a further increase in susceptibility of the ecosystem to fire (Brooks *et al.* 2004).

Invasive grasses from around the world are prevalent in many South African ecosystems, for example on 'waste lands' (Bromilow 2001) and along roadsides in South Africa (Milton and Dean 1998; Milton *et al.* 1998) and Namibia (Joubert and Cunningham 2002) which can be viewed as conduits for invasion. A few studies (e.g. Milton 2004) have assessed habitat-specific effects of alien grasses on ecosystem function and process, but no broad-scale assessment of ecological drivers and effects has been done in South Africa. Unlike annual grasses, most perennial grass invaders are unpalatable and flammable, and hence affect fire regimes (D'Antonio and Vitousek 1992; Smith and Tunison 1992; Tunison 1992; Milton 2004). In addition, invasive grasses are widespread, effective and aggressive competitors with native species (D'Antonio and Vitousek 1992; Goergen and Daehler 2001b: 2002).

1.2   *Pennisetum setaceum*

Pennisetum setaceum (Poaceae; hereafter referred to as "fountain grass") is a widely distributed invasive C4 perennial bunchgrass species from the North African arid

Mediterranean area of the Atlas Mountains and Middle East (Williams *et al.* 1995; Milton *et al.* 1998; Henderson 2001; Milton 2004). Although the grass has a limited range within its natural range along the Sahara and Mediterranean Coast (Williams *et al.* 1995), it invades many natural habitat types (Tunison 1992; Milton *et al.* 1998; Joubert and Cunningham 2002), broad altitudinal ranges (Tunison 1992; Williams *et al.* 1995), varying rainfall and water conditions (Williams and Black 1994; Joubert and Cunningham 2002) and soil types (Milton *et al.* 1998). This grass has been introduced to many parts of the world as an ornamental plant (Williams and Black 1994; Goergen and Daehler 2002), including South Africa (Williams *et al.* 1995; Milton *et al.* 1998; Henderson 2001) and Namibia, particularly by farmers (Joubert and Cunningham 2002). It has however, escaped horticulture in arid and semi-arid parts of the world (Williams *et al.* 1995; Milton *et al.* 1998). Its popularity is probably due to its drought tolerance, unpalatability to animals, rapid growth and profuse, purple, plumose flower spikes (Milton *et al.* 1998).

In southern Africa *P. setaceum* is often found associated with roads, schist cuttings, erosion gullies, mine dumps, paths, rocky slopes, excavations and disturbances outside its natural range (Milton *et al.* 1998; Henderson 2001; Joubert and Cunningham 2002; Milton 2004) and establishes best on denuded, fertile rocky soils (Milton *et al.* 1998; Goergen and Daehler 2001b). In Hawaii, the grass has spread uncontrollably into natural vegetation (Williams and Black 1993; Goergen and Daehler 2001b). Dense stands of *P. setaceum* promote fires (D'Antonio and Vitousek 1992; Tunison 1992; Williams *et al.* 1995; Cordell *et al.* 2002) as a result of its unpalatability to livestock (Cabin *et al.* 2000; Milton 2004) and the absence of its natural enemies (Milton *et al.* 1998; Goergen and Daehler 2001a). Fires in turn may contribute to the spread and abundance of this grass (Smith and Tunison 1992).

The grass has been found to co-occur and compete with native grasses such as *Heteropogon contortus* in different habitats in Namibia (Joubert and Cunningham 2002) and Hawaii (Williams and Black 1994; Goergen and Daehler 2001b: 2002). As a result of large quantities of dead biomass accumulation on the tussocks yearly, the grass becomes highly flammable (D'Antonio and Vitousek 1992; Smith and Tunison 1992; Tunison 1992).

P. setaceum possesses a number of traits that promote its invasion into novel habitats. It has plumed seeds that are very effectively dispersed by wind and animals as feathery spikelets (Goergen and Daehler 2001: 2002), and well designed for

embedding themselves in cracks in rocks and soil. It is also easily dispersed by livestock over short distances and possibly by vehicles, water and birds over large distances (Tunison 1992). It is a drought-tolerant, fire-adapted bunchgrass (D'Antonio and Vitousek 1992; Smith and Tunison 1992; Tunison 1992) that relies on apomictic seeds for population expansion (Simpson and Bashaw 1969; Goergen and Daehler 2001b). It has high reproductive output (seeds per plant), higher reproductive potential (ovules per plant), faster seed germination, faster recovery from disturbance and higher accumulation of belowground biomass relative to the native *pili* grass (*Heteropogon contours*) on Hawaii, with which it now coexists (Goergen and Daehler 2001b). Other studies revealed that *Pennisetum setaceum* exhibits higher photosynthetic rates, greater allocation of biomass to leaves under high temperatures than lower that render it able to persist through drought but exploit water rapidly when available (Williams and Black 1994) and high phenotypic plasticity (Williams *et al.* 1995), traits which are not genetically motivated (Poulin *et al.* 2005). It flowers opportunistically in response to rain or extra water (Goergen and Daehler 2001b; Joubert and Cunningham 2002) and can flower all year, given abundant water (Goergen and Daehler 2001b). The seeds do not exhibit dormancy and most fresh seeds can germinate within 3 – 5 days of exposure to moisture. When conditions are unfavourable for germination, seeds can remain potentially viable in the seed bank for six years (Tunison 1992; Goergen and Daehler 2001b).

All of the traits that have allowed the grass to become invasive in a wide variety of habitats, particularly in Hawaii (Williams and Black 1993: 1994; Williams *et al.* 1995; Goergen and Daehler 2001b), support the concern that it may become a transformer species (*sensu* Richardson *et al.* 2000b), particularly in the sparse vegetation on fertile soils in southern Africa (Milton *et al.* 1998; Joubert and Cunningham 2002). The fynbos biome, especially Renosterveld shrublands on shale and granite soils as well as moist habitats such as drainage lines are deemed vulnerable to *P. setaceum* invasion in South Africa (Milton 2004). It is therefore useful to better understand its ecology, growth and reproductive responses and its native competitors under varying environmental conditions. This will help to better understand, predict and manage its invasion.

1.3   Hypothesis, objectives and key questions

1.3.1   Hypothesis

The general hypothesis for this study is that fountain grass has the potential to become invasive across diverse ecosystems in South Africa, and that invasiveness will be increased by climate change.

1.3.2   General objective

The combined effects of components of global change (especially climate change and land use change) render many ecosystems vulnerable to another category of global change, invasion by alien species. The main objective of this study is to understand the ecology and invasion processes of fountain grass across South African environmental gradients and to use the species as a model to understand the synergistic relationships between invasion and other global change scenarios (climate and land use changes).

1.3.3   Key research questions

The following research questions were addressed based on the above general hypothesis in order to meet the specific objectives of the study.

1. What is the distribution and habitat preference of *P. setaceum* across different biomes in South Africa?

2. What demographic attributes of *P. setaceum* and biotic factors promote or limit its invasive success in different biomes (fynbos, Nama karoo and savanna) of South Africa?

3. What are the environmental resources and habitat conditions that promote *P. setaceum* invasion?

4. What phenotypic and reproductive attributes does *P. setaceum* possess to invade a broad range of environments in South Africa?

5. What is the predicted habitat range of *P. setaceum* based on climate matching and spread dynamics in South Africa?

6. What is the possible impact of *P. setaceum* invasion in arid areas of South Africa and where it is predicted to spread?

1.4 Thesis structure

The thesis is divided into nine different chapters: three synthesis chapters (introduction, literature review and the conclusions and recommendations) and six research chapters. Two of the latter are in press, two are under review and two are at their final stages of submission. All the chapters contribute to the understanding of perennial grass invasions and their synergistic relationships with other habitat factors and global changes in affecting South African ecosystems, using *Pennisetum setaceum* as a model species. As a result of the thesis using stand-alone chapters, there is some replication in the introductory and conclusion material in Chapters 3 – 8. The relative contributions of different authors in each chapter are indicated in the chapter overview below.

Chapter 1 – The chapter introduces the key problem of biological grass invasions. It introduces fountain grass *Pennisetum setaceum* as a model species in understanding the dynamics of, and the vulnerability of ecosystems to, perennial grass invasions. It introduces the hypotheses for the study and the key research questions to address these hypotheses. The thesis structure that includes the respective contributions of all people involved in the thesis is also given in this chapter. All work on this chapter was by Mr. Sebataolo J Rahlao. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

Chapter 2 – This chapter reviews the literature on global change, especially biological invasions and climate change and their synergistic relationships in affecting biological diversity. More emphasis is put on grasses as major biological invasives. It reviews the effects of invasive alien grasses on ecosystems. It further addresses the invasion barriers on different invasive alien species and how these species overcome the barriers under different conditions and habitats. All work on this chapter was by Mr. Sebataolo J Rahlao. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

Chapter 3 – This chapter describes *Pennisetum setaceum* habitat preference and distribution, based on a paper under review: "Rahlao SJ, Milton SJ, Esler KJ and Barnard P Corridor interchanges as habitats for the invasive *Pennisetum setaceum* in semi arid South Africa" with *Weed Research* from 19 May 2009. The paper

demonstrates roads and rivers as corridor systems for *P. setaceum* dispersal, and how where these systems interchange, they provide suitable habitat for the grass propagule production. The paper further demonstrates that the presence of *P. setaceum* away from roadsides is associated with water bodies and disturbances. The paper recommends that corridor interchanges should be considered important targets for the control of alien grass invasion. Statistical verification was made by Prof. Daan G Nel of the Centre for Statistical Consultation, Stellenbosch University. All work on this chapter was by Mr. Sebataolo J Rahlao. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

Chapter 4 – This chapter deals with the performance and growth rates of translocated *P. setaceum* seedlings at three different biome environments in South Africa based on a paper under review: "Rahlao SJ, Milton SJ, Esler KJ and Barnard P, Performance of invasive alien fountain grass (*Pennisetum setaceum*) along a climatic gradient through three South African biomes" with *Biological Invasion*s from 30 March 2009. The paper demonstrates variability in performance of *P. setaceum* across environmental gradients, information which is important for the effective management of this and similar species. It further suggests that management efforts should aim to reduce seed production and seedling growth along roads especially by maintaining more indigenous cover along road verges, because seedlings survive best when competition is low. Statistical verification was made by Prof. Daan G Nel of the Centre for Statistical Consultation, Stellenbosch University. All work on this chapter was by Mr. Sebataolo J Rahlao. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

Chapter 5 – This chapter addresses the environmental resources and habitat conditions that affect *P. setaceum* invasiveness based on a paper under review: "Rahlao SJ, Esler KJ, Milton SJ and Barnard P Nutrient addition and moisture determine the invasiveness of *Pennisetum setaceum*" with *Weed Science* from 16 July 2009. The paper reports on greenhouse experiments that suggest that soil moisture and nutrient availability are important factors in promoting *P. setaceum* growth. The paper suggests that for effective management, seedling removal should be done following precipitation and in areas of nutrient enrichment such as near rivers and at road-river interchanges. Statistical verification was made by Prof. Daan G Nel of the

Centre for Statistical Consultation, Stellenbosch University. All work on this chapter was by Mr. Sebataolo J Rahlao. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

Chapter 6 – This chapter assesses the role of local adaptation in *P. setaceum* invasiveness across different biomes in South Africa. This chapter is based on a paper in preparation: "Rahlao SJ, Esler KJ, Milton SJ, and Barnard P Vegetative and reproductive adaptation of an invasive *Pennisetum setaceum* in South Africa" for submission to the *Journal of Vegetation Science*. The paper reports on comparisons of phenotypic traits among mature *P. setaceum* plants in three biome environments and the performance of its seedlings in greenhouse experiments. No differences in quantitative traits across environmental gradients were found. Furthermore, growth and reproductive responses in plant characters were not site-dependent, indicating local adaptation and environmental tolerance of *P. setaceum*. The results suggest the overriding effect of disturbance over prevailing habitat conditions on invasion processes. The study was inspired by Dr. Jaco Le Roux and all work was done by Mr. Sebataolo J Rahlao. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

Chapter 7 – This chapter is based on bioclimatic modelling of the potential future distribution of *P. setaceum,* based on its current distribution, climate matching and spread. This chapter is based on a paper in preparation: "Rahlao SJ, Roura-Pascual N, Krug RM, Esler KJ Milton SJ and Barnard P Potential distribution and spread of an invasive alien grass, *Pennisetum setaceum*, in western South Africa" for submission to the Journal of Biogeography. The primary finding is that most of South Africa's ecosystems are prone to *P. setaceum* invasion under different climate change scenarios, with the fynbos and savanna biomes predicted to be suitable for both distribution and spread. Disturbed areas provide suitable sites for the spread of this grass, especially away from roadsides where it currently occurs. Removal of standing populations along roadsides, especially those near highly disturbed areas should be of high priority. This chapter is a collaborative work by Mr. Sebataolo J Rahlao (empirical data collection, paper structure and write-up), Dr. Núria Roura-Pascual (climate-matching model) and Dr. Rainer M Krug (dynamic probabilistic spread model). Mr. Sebataolo J Rahlao carried out all the fieldwork, wrote the paper,

provided species ecology information during building of models and received specialist input on climate-matching and dynamic probabilistic spread models. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

Chapter 8 – This chapter addresses the ecosystem effects of *P. setaceum* invasion in arid shrublands. The chapter is based on a paper: "Rahlao SJ, Milton SJ, Esler KJ, van Wilgen BW and Barnard P 2009 Effects of invasion of fire-free arid shrublands by a fire-promoting invasive alien grass (*Pennisetum setaceum*) in South Africa" with *Austral Ecology*, 34 (8) 920 – 928. The paper reports on a simulated fire experiment to assess the effects of fire in fire-free shrublands following invasion by *P. setaceum*. 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 paper suggests that the predicted impacts of fire may alter species composition, ultimately affecting core natural resources that support the local karoo economy. This chapter is a collaborative work between Mr. Sebataolo J Rahlao, Dr. Brian V. van Wilgen, Prof. Karen J Esler and Prof. Suzanne J Milton. Mr. Sebataolo J Rahlao designed the field experiment, carried out all the fieldwork, collected and analysed the data, wrote the paper and received specialist input on fire temperature determination from Dr. B. van Wilgen. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

Chapter 9 – This concluding chapter summarises major findings of the entire thesis and reflects on the general problems posed by *P. setaceum* in South African landscapes. It recommends strategies for management and control of this grass and other similar grasses under disturbance and climate change scenarios. All work on this chapter was by Mr. Sebataolo J Rahlao. Prof. Karen J Esler, Prof. Suzanne J Milton and Dr. Phoebe Barnard made comments to improve it.

CHAPTER 2

LITERATURE REVIEW

2.1   Introduction

Biodiversity is under threat and changing at an alarming rate from human mediated processes such as habitat destruction (resulting from land conversion), biological invasions and global climate change. Protection of biodiversity from these factors requires costly and complex conservation actions (Sisk *et al.* 1994; Vitousek 1994; Wilcove *et al.* 1998; Dukes and Mooney 1999; Turpie 2003). Changes in land uses are predicted to exert the most impact on biodiversity. Both alone, and compounded with nitrogen deposition, atmospheric CO_2, climate change and biological invasions, land use change exert significant effects on global and local biodiversity (Sala *et al.* 2000).

This chapter reviews the impact of these global changes on biodiversity. Global climate and land use changes are discussed separately as forms of disturbance, as well as together through their synergistic interaction with biological invasions. The review also provides more details on the dynamics of biological invasions with a specific focus on invasive alien grasses as drivers of biodiversity changes worldwide.

2.2   Global climate change

Climate variability and climate change exert a dominant control on the natural distribution of species and biodiversity as a whole (Woodward 1987; Dukes and Mooney 1999; Pearson and Dawson 2003), as well as the risk of species extinction (Sala *et al.* 2000; Thomas *et al.* 2004). Warming is expected to have the greatest impact at high latitudes (Sala *et al*. 2000). Observational evidence from all continents shows that many natural systems are being affected by regional climate changes, particularly temperature increases (Parry *et al.* 2007). Anthropogenically accelerated greenhouse gas emissions lead to increases in global and regional temperatures, and these consequently have daunting effects on global biodiversity (Fischlin and Midgley 2007).

The concept of climatic envelopes can assist in predicting the future distribution of species as a result of climate changes and shifts (Pearson and Dawson

2003). This approach employs the use of species' primary occurrence data, digital maps representing environmental parameters and the conditions under which the species currently performs well (Peterson *et al.* 2001; Kriticos *et al.* 2003; Pearson and Dawson 2003; Peterson *et al.* 2003; Thuiller 2003; Thuiller *et al.* 2003; Martinez-Meyer 2005; Thuiller *et al.* 2005). However, drivers other than climate can influence systems directly or indirectly through effects on climate variables. This is because biotic interactions shift with changing environmental conditions (Davis *et al.* 1998a; Pearson and Dawson 2003), variable dispersal dynamics (Nathan *et al.* 2002; Thuiller *et al.* 2004), local geographic conditions (Davis *et al.* 1998b), and shifts in ecological barriers (Thomas *et al.* 2001). Modelling species with broad habitat ranges is more difficult than for narrow habitat specialists (Thuiller *et al.* 2004).

Although bioclimatic envelope approaches can provide useful insights into the distribution of some species at certain scales due to climate change, predictive errors in species distributions are inevitable due to the complexity of natural systems (Rutherford *et al.* 1999; Araújo *et al.* 2004; Rouget *et al.* 2004; Araújo *et al.* 2005a; Thuiller *et al.* 2005). These models correlate the observed species distributions with climate variables, assuming that current distribution is a reasonable indicator of a species' climatic requirements (Pearson and Dawson 2003).

2.3   Land use change

Land use change, particularly land conversion, has facilitated the growth of new species by disturbing natural habitats and creating openings for colonization (Goergen and Daehler 2002; Rouget *et al.* 2003). It is predicted that many biomes particularly grasslands and Mediterranean ecosystems will experience large biodiversity loss because of their sensitivity to all drivers of biodiversity change, particularly land use change (Sala *et al.* 2000). This change may interact with other global changes such as those associated with climate to facilitate invasions (D'Antonio and Vitousek 1992; Richardson *et al.* 2000a; Didham *et al.* 2005).

Human activities in the form of land fragmentation by transportation corridors such as highways and railways frequently disturbs and alters natural disturbance regimes particularly the growth and spread of invasive alien plants (Hansen and Clevenger 2005). Roadside verges generally have a higher richness of alien species than their adjacent habitats (Milton and Dean 1998; Parendes and Jones 2000;

Gelbard and Belnap 2003; Kalwij *et al*. 2008a; Kalwij *et al*. 2008b). This is because roadside conditions have been altered by increased disturbance, soil compaction, salinity (Greenberg *et al.* 1997; Gelbard and Belnap 2003; von der Lippe and Kowarik 2007), greater nutrient and water availability (Trombulak and Frissell 2000; Gelbard and Belnap 2003), increased sunlight (Parendes and Jones 2000; Watkins *et al.* 2003), traffic-borne dispersal, and alien roadside plantings (von der Lippe and Kowarik 2007). All of these factors can promote the performance of invasive alien species by disturbing natural conditions and reducing the competitive strength of the native species (Flory and Clay 2006; von der Lippe and Kowarik 2007).

Many studies have documented the ecological effects of roads, particularly on biodiversity (Forman and Alexander 1998; Trombulak and Frissell 2000), as they promote growth and spread of invasive alien species (Forman and Alexander 1998; Parendes and Jones 2000; Harrison *et al.* 2002). Transportation corridors encourage invasion by alien species by removing barriers, a) directly by altering disturbance regimes by creating gaps and changing plant composition, b) by vehicle-generated air turbulence that aid seed dispersal (Hobbs and Huenneke 1992; Greenberg *et al.* 1997; Hansen and Clevenger 2005), or c) indirectly by altering environmental conditions such as soil moisture, soil composition, and light,

Other studies have also found that roadsides facilitate invasion by alien species as a result of their disturbed soil and increased runoff (McIntyre and Lavorel 1994; Greenberg *et al.* 1997; Harrison *et al.* 2002), which allow an increase in propagule spread into the adjacent natural habitats (Gelbard and Harrison 2003).

2.4   Biological invasions

Biological invasions present one of the most significant non-climatic threats to biological diversity (Vitousek *et al.* 1997; Dukes and Mooney 1999; Dukes 2001; Richardson and van Wilgen 2004). They have serious consequences for ecological, economic and social systems worldwide (Williamson 1996; Vitousek *et al.* 1996; Dukes and Mooney 1999; Davis *et al.* 2000; DiTomaso 2000; Pimentel *et al.* 2000; Pimentel *et al.* 2001). Invasive alien species may establish in a new place through increased resource availability following disturbances such as fire and vegetation clearing (Hobbs and Huenneke 1992; Davis *et al.* 2000; Blumenthal 2006; Funk and

Vitousek 2007). The ability of a species to promote continued disturbance (such as through fire) will enable it to increase and spread (Funk and Vitousek 2007).

2.4.1 Definition of invasive alien species

Terminologies and criteria for defining alien species, especially plants, with respect to their status have evolved differently in different parts of the world (Pyšek and Richardson 2008). As a result, many definitions of invasive species exist. For the purposes of this thesis, I use Richardson *et al*. (2000b)'s concept of an alien species crossing a number of biotic and abiotic barriers in order to establish, proliferate and spread in a new environment. This definition is simple and coherent for invasions worldwide. Invasive alien species are defined as a subset of naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants and which have the potential to spread over large areas (Richardson *et al*. 2000b; Pyšek and Richardson 2008).

Major barriers through which an invasive alien species must cross on its way to invasion are discussed in detail below.

2.4.1.1 Geographic barriers

Species are transported around the world for many purposes (medicinal, horticultural, food, and agricultural), and hence geographic barriers to invasion are frequently intentionally breached. Aliens plants that have overcome geographic barriers may flourish and even reproduce occasionally outside cultivation into target areas, but that eventually die out because they do not form self-replacing populations are described as casual aliens (Pyšek *et al*. 2004). Their presence in the new area relies on repeated or continued introduction, such as escape of ornamental plants from gardens or unintentional introduction of seeds from cultivation (Richardson *et al.* 2000b; Foxcroft *et al*. 2008; Pyšek *et al*. 2008). The geographic limits of a species may be restricted by climatic conditions acting directly on the alien species, competition from other species using the same resources (e.g. space, water, light, etc) or by management and control of the species in the new locality.

2.4.1.2   *Environmental barriers*

New arrivals must cope with abiotic conditions prevailing at the new location. Many alien plant species require ecosystem degradation, such as disturbance, for recruitment of offspring (MacDougall and Tarkington 2005) through the creation of microsites for colonization (Seablom *et al*. 2003). Environmental factors, like resource availability, which favour the growth of alien propagules, are important at the point of introduction to a new locality since introduced propagules must compete with the established native species that are well adapted to this area. Moisture, light and soil properties are among the environmental barriers that limit invasion into new areas (Parendes and Jones 2000). Invasive aliens tend to favour areas where these environmental resources are in excess, especially as a result of recent by disturbance.

2.4.1.3   *Reproductive barriers*

A new species must also overcome reproductive barriers in order to produce enough offspring (propagules) to increase the chance of survival. Species that overcome reproductive barriers and produce self-replacing populations are considered naturalized (Richardson *et al*. 2000b; Pyšek *et al*. 2004). These species must undergo widespread dispersal and become incorporated within the resident flora (Richardson *et al*. 2000b). In order to be considered naturalized, an alien species should form persisting populations and reproduce in the wild without the help of humans, by recruitment from seeds or ramets capable of independent growth (Pyšek *et al*. 2004). Naturalised species need not be invasive (Pyšek *et al*. 2008).

2.4.1.4   *Local dispersal barriers*

If an alien species overcomes dispersal barriers, it is then referred to as an invasive alien species. The range of the species is then determined by the availability of suitable habitats and the presence of additional dispersal barriers. The spread of species into areas away from its point of introduction requires that it also overcomes these additional dispersal barriers, such as the absence of pollinators and dispersers, and copes with the new abiotic and biotic environments (Richardson *et al*. 2000b; Pyšek *et al*. 2008). Many species overcome dispersal barriers by having several different dispersal mechanisms (Nathan and Muller-Landau 2000).

Once an alien species has overcome these barriers (geographic, environmental, reproductive and dispersal), it is able to expand its population unaided and hence is regarded as invasive (Pyšek *et al*. 2008). Invasiveness should not be defined by impacts but by the establishment success and rate of spread of the invasive species (Ricciardi and Cohen 2007). However, Callaway and Ridenour (2004) argue that the same traits that allow a species to invade a broad range of communities could also magnify their impact. Some studies (Parker *et al*. 1999; Ricciardi 2003) suggest that the impacts of invaders are correlated with their abundance.

2.4.2 Factors promoting invasions

Invasion patterns of alien species result from a combination of many factors that include life history traits (propagule production and distribution, germination success, growth and survival requirements) and historical factors (e.g. time since introduction and geographical range of plantings) (Flory and Clay 2006). In addition to disturbance, propagule pressure is a critical determinant of invasion success (Rouget and Richardson 2003). There are three major factors that influence the invasion of an environment by new species. These include (1) propagule pressure, (2) alien species characteristics, and (3) the invasibility of the new area (Lonsdale 1999; Williamson 1999). However, some studies (Huston 1994; Davis *et al*. 2000) argue that the invasion by invasive alien species is facilitated by the same basic processes that allow colonization and/or repeated regeneration of native species.

2.4.3 Characteristics of invaders

Many hypotheses exist to explain why certain species invade new habitats. Many studies have attempted to identify characteristics of ideal invaders (Baker 1965; Crawley *et al*. 1996). However, it is unrealistic to have a general list of characteristics that explain invasiveness for all species and habitats (Perrings *et al*. 1993; Williamson 1999) due to lack of data on traits crucial for invasion success. As a result, studies have shifted in finding components of invasiveness at finer taxonomic scale or for particular life forms (Richardson and Pyšek 2006).

Adaptive traits that facilitate growth and spread of invasive alien plants in novel habitats include high seed production and germination rates (Grotkopp *et al*. 2002; Perrings *et al*. 2005), tolerance of low resource levels, and ability to flourish

with increased resources or disturbance (Milberg *et al.* 1999; Stapanian *et al.* 1999; Goergen and Daehler 2001). Success may be further enhanced by novel defensive and allelopathic biochemicals and increased competitive ability (Blossey and Notzold 1995; Callaway and Ridenour 2004), as a result of a species' release from natural enemies (Blossey and Notzold 1995; Mack *et al.* 2000; Maron and Vila 2001; Keane and Crawley 2002; Wolfe 2002; Levine *et al.* 2003; Mitchell and Power 2003; Siemann and Rogers 2003; Torchin *et al.* 2003; Callaway *et al.* 2004; Colautti *et al.* 2004; DeWalt *et al.* 2004; Muller-Scharer *et al.* 2004; Blumenthal 2006). These traits may interact with increased availability of resources (Davis *et al.* 2000; Blumenthal 2005) and tolerance of harsh environmental conditions of the new habitat (Muller-Scharer *et al.* 2004) to promote spread.

Invasion success is assumed to be governed largely by dispersal success and propagule pressure (Kolar and Lodge 2001). Lavergne and Molofsky (2007) suggest that multiple introductions of invasive species lead to high rates of phenotypic evolution after their introduction, and the species may adapt to predicted climate change in future decades.

2.4.4 *The receiving habitat (climatic and soil matching, mutualists, predators)*

The invaded ecosystem may resemble the original habitat of the alien species in terms of climate, soils, and other variables (McIntyre and Lavorel 1994; Greenberg *et al.* 1997). In some cases, small-scale disturbances may also promote the establishment success of invaders (Hobbs and Mooney 1985). However, rodents and other small herbivores may also play a role in controlling the spread of alien plants (Hobbs *et al.* 1988).

One of the most reliable indicators of whether a species will be invasive is if it has invaded elsewhere, especially under ecologically similar conditions (Reichard and Hamilton 1997; Meyer and Lavergne 2004). However, other factors such as residence time (time since introduction), chance events and propagule pressure may be more crucial for determining whether (or when) a species will invade (Rejmánek *et al.* 2005; Richardson and Pyšek 2006).

In arid parts of South Africa, the phenomenon of alien grass invasions is a relatively new and emerging problem (Milton *et al.* 2007). This may be due to arid areas being less affected by biological invasions than more mesic ecosystems,

although the established invasive alien plants have spread more rapidly in arid than in wetter parts of South Africa (Wilson *et al.* 2007). In the case of ornamentals, delayed spread might be explained by these areas being less densely inhabited and hence having less propagule pressure from gardens than more densely populated, mesic areas.

Although reproductive and vegetative advantages of invasive alien species over native competitors have been identified, these advantages may depend on factors other than plant traits. These include growing conditions such as the availability of ideal soil nutrients, moisture for germination and establishment, pollen availability and disturbance, all of which can affect the number of flowers and seeds produced by a plant (Goergen and Daehler 2001b). Success of invasive alien species is resource-dependent (Funk and Vitousek 2007), and invasive alien species are generally more productive in nutrient-rich than in nutrient-poor habitats (Daehler 2003). Availability of adequate soil moisture (not only amount, but also timing and distribution) greatly affects the survival of both native and alien plant species (Ignace *et al.* 2007). Other biotic factors such as competition with indigenous species for water, light, nutrients and suitable microhabitats for establishment play an important role in the germination and establishment success of alien plant species in their habitats (Aguiar *et al.* 1992; Daehler 2003; Fynn *et al.* 2005; Hansen and Clevenger 2005; Jongejans *et al.* 2007). In many natural systems, soils exposed by small-scale disturbances serve as important sites of recruitment, since soil water and temperature influence both the germination and decay of buried seeds (Chambers and MacMahon 1994).

2.4.5 *Propagule pressure*

Propagule pressure is one the crucial factors determining whether (or when) a species will invade a particular habitat (Rouget and Richardson 2003; Richardson and Pyšek 2006; Tanentzap, and Bazely 2009). Increasing the number of propagules increases the chances of a species establishing (Lockwood *et al.* 2005; Williamson 2006). With more individuals, there is a greater chance of some finding a suitable habitat, or avoiding difficulties from any stochastic event. The role of propagule pressure is integrated with residence time, where the longer the species is present in an area, the greater the number of propagules and their ability to be dispersed (Rejmánek *et al.* 2005; Richardson and Pyšek 2006). Establishment success usually reflects

movements of very large quantities of alien individuals usually with the purposeful or inadvertent help of humans (Lockwood *et al.* 2005). Propagule pressure can interact with other factors such as disturbance, nutrient availability and, climate to render ecosystems vulnerable to invasion (Levine and D'Antonio 2003). However, propagule pressure is increasingly seen as the null model to explain the outcome of an introduction event (Colautti and MacIsaac 2006).

2.4.6 *Spatial dispersal of seeds*

For a non-native species to cause economic or ecological harm, it must first be transported out of its native range and released within a novel locality, establish a self-sustaining population in this new location, and expand its geographical range beyond the point of initial establishment (Lockwood *et al.* 2005). There is evidence that, once a non-native population has established, proximity to a source of dispersing individuals will increase the likelihood that the invasive species will expand its geographical range (Rouget *et al.* 2004). At the global scale, the pattern of biotic exchange (deliberate or accidental introduction of plants and animals to an ecosystem) reflects the pattern of human activity (Sala *et al.* 2000), hence remote areas with little human intervention receive fewer alien species than areas that are in the middle of trade routes or that host intense human activity.

The prediction of migration rates requires an integration of the modelling of germination, growth, reproduction, dispersal, and mortality, in the context of disturbance, plant interactions, habitat loss, and landscape fragmentation (Higgins and Richardson 1999). The movement of seeds either horizontally or vertically after they have reached a surface, depends on the nature of the physical forces and the seed's physical conditions (Chambers and MacMahon 1994).

Good dispersers, however, are not necessarily good colonizers (With 2002). A certain degree of fragmentation is unlikely to affect species that are capable of long-distance movements, even though these events are rare (With 2002). Continuous tracts of favourable habitat might be required to facilitate migration and colonisation of wind-dispersed species in spite of their occasional feats of long distance dispersal, because wind is inherently random, making establishment tricky if the species drifts too far beyond its source patch.

2.4.7   Seed banking

Seed banking is important for the maintenance and management of natural populations (Chambers and MacMahon 1994; Lambers *et al.* 2005; Vosse *et al.* 2008). Chambers and MacMahon (1994) emphasize that seeds in seed banks are more dynamic than often portrayed. They are moved by animals, wind, or other physical forces, lost to consumption by animals or attacked by pathogens. They can change physiological status, or lose their germination potential because of senescence, but they are not static. Seed banking allows species to avoid density- dependent mortality when seed production is high, and to capitalize on temporally unpredictable opportunities for recruitment when seed production is low. Low seed bank densities can result from low seed production, while still accounting for a substantial fraction of seedling recruitment in any given year (Lambers *et al.* 2005).

2.5   Synergisms between global changes

Biological invasions have synergistic interactions with other global changes, including land use change (Vitousek *et al.* 1996; Hobbs 2001), climate change (Dukes and Mooney 1999; Kriticos *et al.* 2003), increased concentrations of atmospheric CO_2, and nitrogen deposition (Dukes and Mooney 1999; Dukes 2000; Weltzin *et al.* 2003a). These interactions may occur at all levels of invasion (Theoharides and Dukes 2007). Biological invasions are further promoted by habitat fragmentation due to human caused disturbances (D'Antonio *et al.* 2000; Sala *et al.* 2000). Sala *et al.* (2000) suggest that realistic projections of future biodiversity change require improved understanding about interactions among drivers of biodiversity change. Moreover, there is a need to incorporate predictive models in the assessment of invasion risk (Richardson *et al.* 2000b; Lockwood *et al.* 2005) in relation to other drivers. Removal or addition of species that interact strongly with the disturbance regime will change the state of the system structure and function (Mack and D'Antonio 1998).

Global changes (particularly land use changes and climate change) interact synergistically with biological invasions to affect biodiversity both locally and globally. For instance, in arid regions of South Africa, many aliens are confined to watercourses (Richardson *et al.* 1997) and roadsides (Milton and Dean 1998), as a result of supplementary water and nutrients (Lightfoot and Whitford 1991; O'Farrell

and Milton 2006) and vegetation clearing during road construction and maintenance (O'Farrell and Milton 2006). All these factors increase alien plant productivity on roadside habitats (Milton and Dean 1998). Plants growing along roadsides often appear larger and healthier as a result of long term increased water availability from pavement runoff and sub-pavement soil moisture retention (Lightfoot and Whitford 1991), and propagules derived from passing vehicles, wind, water or animals. Roadside surveys may provide an early warning of the presence of various alien plants species in an area (Milton and Dean 1998; Timmins *et al.* 2006). These types of surveys also provide information on the relative frequencies of alien species on roadsides and will indicate the potential of the species to naturalize if favoured by local climatic conditions and/or landuse (Jacobi and Warshauer 1992; Ullmann *et al.* 1995; Milton and Dean 1998; Addison *et al.* 2007). von der Lippe and Kowarik (2007) found the number of alien species in urban areas to be 5% more than the surrounding flora, which implies an emerging ecosystem different from the surrounding habitats.

Global environmental changes also speed up the invasion of habitats by invasive alien species (Dukes and Mooney 1999). These changes fall under the fluctuating resource availability theory (Davis *et al.* 2000) where the invasibility of habitats differs with the fluctuating availability of resources in space and/or time (Davis *et al.* 1998b) and integrates both resource availability, disturbance and the fluctuating environmental conditions. Fragmented habitats have more edges than continuous habitats and are therefore more vulnerable to invasion by invasive alien species (Vitousek *et al.* 1997).

Physical disturbance of substrates further promotes the accumulation of invasive alien species and in turn invasions can change the disturbance regimes (Hobbs and Huenneke 1992; Lake and Leishman 2004; Geiger and McPherson 2005; Hansen and Clevenger 2005). Disturbance regimes and their alteration by invasions are important in understanding the ecosystem processes and function and the impacts of single species (Vitousek 1990; Mack and D'Antonio 1998). However, Hobbs *et al.* (1988) found that disturbance in the form of gopher diggings prevented invasion of *Bromus trinii* in a serpentine community dominated by forbs. Furthermore, disturbance is in most cases considered as an important precursor to invasion (D'Antonio 1993; Davis *et al.* 2000), although many undisturbed native communities still host alien species (MacDougall *et al.* 2006).

2.6 Perennial grass invasions

2.6.1 Factors that promote perennial grass invasions

Grasses are exceptional world travellers, particularly in livestock-based economies (Milton 2004). They are introduced in many parts of the world for pasture development, rangeland improvement and revegetation (Cox *et al.* 1988; Williams and Baruch 2000) as well as for ornamental purposes (Meyer and Lavergne 2004; Dehnen-Schmutz *et al.* 2007; Tassin *et al.* 2007). The number of invasive alien plants, especially grasses, is increasing rapidly as a result of developing commercial trade, diversification of agriculture, and the growing success through nurseries, gardening and horticultural activities (Meyer and Lavergne 2004). Not all introduced grasses will become naturalized and invasive, but their invasion risk is increasing under global change. A major source of invasive alien species is ornamental plants as many alien plants today are garden escapees (Reichard and White 2001; Dehnen-Schmutz *et al* 2007).

The grass family Poaceae includes a number of species with plumose flower stalks that fragment into seed-bearing spikelets that are dispersed by wind. Some of these species have become troublesome weeds in many parts of the world. Although most produce perennial and tufted, attractive, drought-resistant plants which hence used for landscaping along walkways and roads, they are becoming widespread weeds in disturbed areas.

Grasses with extensive root systems are used to stabilize mine dumps, landslides and other human disturbed sites (Mack and D'Antonio 1998; Sharma *et al.* 2005), and also to increase rates of succession. However, some species introduced for this purpose have invaded the surrounding natural ecosystems. Perennial grasses are frequently used in rehabilitation of human-disturbed sites, probably due to their extensive root systems and rapid growth rates. The Poaceae is among the most invasive plant family globally and has potential to contribute (together with the Asteraceae and Fabaceae) heavily to the total number of invasive alien species, as it comprises the largest of the angiosperm families (Pyšek 1998). Grasses are among the invaders that affect the incidence of fire. They not only increase the frequency and sizes of fire, but also rapidly respond after fire thereby further increasing their

dominance in the system (D'Antonio and Vitousek 1992; Grace *et al.* 2000; Levine *et al.* 2003; Brooks *et al.* 2004).

In rangeland ecosystems, grasses have been introduced to develop or improve pastures. However, introduction of plants with a qualitatively different suite of traits that interact with the biological disturbance of grazing has lead to the ultimate increase of these grasses in natural pastures (Mack and D'Antonio 1998). Direct effects of grasses on ecosystem processes may appear subtle compared to the disturbance and land clearing that often precedes their invasion, although grasses may contribute a great deal to changes in ecosystem processes such as fire regimes and nutrient cycling (Williams and Baruch 2000).

Most alien grasses are too poorly known to evaluate their ecological and economic impact or to recommend control measures (Milton 2004). The objective of this study is therefore to understand the ecology and invasion dynamics of fountain grass in South Africa and recommend control measures to curb its success and invasion.

2.6.2 *Effects of perennial grass invasions*

Invasive species affect ecosystems in many different ways. These include displacing the native species, altering water and fire regimes (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998; D'Antonio *et al.* 2000; Grace *et al.* 2000; Brooks and Pyke 2001; Keeley *et al.* 2003; Levine *et al.* 2003), changing the nutrient status of the soil (Cox *et al.* 1988; Huenneke *et al.* 1990; Greenberg *et al.* 1997; Brooks *et al.* 2004), removing or introducing a food resource (Grunzweig and Korner 2000; Daehler 2003; Hunter and Omi 2006), altering the geomorphological processes (Gordon 1998; Dukes and Mooney 1999), and by reducing the aesthetic and recreational values of conservation areas (Hill *et al.* 2005).

In ecosystems that previously lacked a large grass component, the accumulation of dead biomass and a high volume ratio of leaves increase the probability of fire (Mack and D'Antonio 1998). Perennial grasses tend to produce litter that is more combustible than shrubs, therefore, fire frequency and intensity are likely to increase if grass invasive alien species are present (D'Antonio and Vitousek 1992; Milberg and Lamont 1995) and sometimes to the detriment of native species.

2.6.3   *Management of invasive perennial grass invasions*

In order to conserve biodiversity under changing climate, climate change-integrated conservation strategies need to be employed into individual regions. Management usually requires modelling of the magnitude and direction of vegetation and habitat changes as the first step (Hannah *et al.* 2002).

Management and control of invasive alien species requires an understanding of range expansion dynamics (Sakai *et al.* 2001; Pyšek and Hulme 2005; von der Lippe and Kowarik 2007). The problem has been the focus on the most heavily invaded areas and the most invaders. This study thus focuses on a relatively early stage of grass invasion in arid and semi-arid South Africa.

Understanding the relative growth and reproductive responses of invader and native competitors under varying environmental conditions may help researchers and resource managers understand, predict and better manage invasions (Parker *et al.* 1999; Goergen and Daehler 2001b). The problems caused by invasive alien species are a direct result of their success in colonizing new habitats, and understanding the mechanisms they employ is vital to controlling their spread (Blumenthal 2005).

It is clear from the literature reviewed in this chapter that the potential of *P. setaceum* to invade and transform southern African ecosystems cannot be assessed without data on its current distribution and habitat preferences, as well as the environmental resources and habitat conditions that affect its success. Knowledge of these will help identify high risk areas for invasion as well as on the likely ecosystem impacts of this grass once it has invaded. In this thesis I therefore explore these factors to contribute to a better understanding of this grass and its potential impacts on the ecosystems of southern Africa.

CHAPTER 3

CORRIDOR INTERCHANGES AS HABITATS FOR THE INVASIVE *PENNISETUM SETACEUM* IN SEMI ARID SOUTH AFRICA

3.1 Abstract

Roads and rivers may be dispersal corridors for invasive alien grass seeds that fly and float. These two systems interact at bridge interchanges that are also disturbed artificial habitats. The invasive *Pennisetum setaceum* (perennial fountain grass) establishes on roadsides and river banks and benefits from habitat conditions prevailing on these interchanges. The distribution of the grass across biomes and vegetation types and the influence of environmental variables were assessed. A road survey method was used to record and map the distribution of *P. setaceum* along 1 km roadside transects at 10 km intervals and at every corridor interchange for 5 112 km of arid and semi-arid South African national roads. *Pennisetum setaceum* populations occurred in 10 % of the total transects and interchanges. The Fynbos Swartland Shale Renosterveld was the most significantly invaded amongst the vegetation types surveyed. Our results indicate that, although *P. setaceum* performs better on the interchanges, it does not preferentially colonise them over other parts of the landscape. The presence of *P. setaceum* was closely associated with the presence of water bodies and disturbances away from the roads. Corridor interchanges should be considered important targets of both local and regional efforts to prevent and control *P. setaceum* invasions.

3.2 Introduction

Roadsides and rivers in some cases act as corridors for spread of invasive alien species into natural ecosystems (Gelbard and Belnap 2003; Christen and Matlack 2006; Jodoin *et al.* 2008). The disturbed conditions at roadsides promote the establishment of invasive species (Harrison *et al.* 2002; Dong *et al.* 2008). Rain runoff from roads (O'Farrell and Milton 2006) increases the availability of moisture and nutrients on road verges, which may increase plant success along these corridors (Lamont *et al.* 1994). The improvement of roads leads to the widening of road verges

and an increase in the number of invasive alien species in these verges that exploit disturbance opportunities (Gelbard and Belnap 2003; Kalwij *et al.* 2008b).

Rivers too are considered corridors for the dispersal of invasive alien species into ecosystems (Pyšek and Prach 1993; Johansson *et al.* 1996; Stohlgren *et al.* 1998; Foxcroft *et al.* 2007) and may also act as distinct sources of invasive alien species (Pulliam 1988; Bang *et al.* 2007). The continuous availability of water and nutrients as well as periodic flooding create disturbances that make riparian zones suitable for establishment of invasive alien plant species (Planty-Tabacchi *et al.* 1996; Stohlgren *et al.* 1998; Hood and Naiman 2000).

Fountain grass, *Pennisetum setaceum* is an invasive C4 perennial bunchgrass native to the North African arid Mediterranean area of the Atlas Mountains and Middle East (Williams *et al.* 1995). Introduced in many parts of the world as an ornamental plant and for soil stabilization, it has escaped horticulture into many natural and semi-natural habitat types (Williams *et al.* 1995; Milton *et al.* 1998; Henderson 2001; Joubert and Cunningham 2002), including broad altitudinal ranges (Tunison 1992; Williams *et al.* 1995) varying rainfall and water conditions (Williams and Black 1994; Joubert and Cunningham 2002), and varying soil types (Milton *et al.* 1998). The light seeds are dispersed in feathery spikelets, drifting in the wind or floating on water.

Rivers and roads also serve as reservoirs or foci of invasive alien species propagules that may eventually escape into the neighbouring landscapes (Parendes and Jones 2000; Pyšek *et al.* 2007; Richardson *et al.* 2007). Bridges link two systems that are vulnerable to invasions. Bridge construction causes more disturbance than other road building activities and involves transport of large quantities of sand that may contain seeds. Bridges therefore provide an opportunity for seed interchange between road and river systems. These multiple functions of roads and rivers in facilitating invasion have been documented independently for each corridor type. No previous studies have examined the effect of interaction of roads and rivers on invasion success. This study addresses the effect of the interaction of these corridors at the interchanges (road bridges across the river) in facilitating invasion. To determine the environmental factors that may explain the distribution of *P. setaceum* in semi-arid regions, I tested the hypotheses that *P. setaceum* 1) invasion differs among South African biomes and vegetation types, 2) performs better and is more abundant on road-river interchanges than other parts of the landscape, and 3) is

associated with disturbances such as settlements and cultivation, but not rangelands along the roads.

3.3 Methods

3.3.1 Study species

The invasive grass *Pennisetum setaceum* was introduced to South Africa before the 1930s (L. Henderson, personal communication). It is apomictic and capable of wide phenotypic variation (Williams *et al.* 1995). Although it reproduces mainly by seed, it forms pseudo-vivipary plantlets when inflorescences are inundated (Milton *et al.* 2008, see Appendix). Its popularity in horticulture and spread is probably due to its drought tolerance, unpalatability to animals, rapid growth and profuse seed production (Milton *et al.* 1998; Cabin *et al.* 2000). In South Africa, it has been declared a Category 1 invasive weed and invader that must be controlled under the South African Conservation of Agricultural Resources Act, 1983, CARA amended in 2001 (Henderson, 2001). *P. setaceum* can also be classified under the "large habitat–moderate propagule pool" of emerging invaders category of the national framework of invasive species for South Africa (Nel *et al*. 2004), and has the potential of expanding over a large part of the country if unmanaged.

3.3.2 Road survey

A single observer used the drive-by survey method (Milton and Dean 1998) that made use of repeatable overland long-distance journeys to field sites to record the presence and absence of the grass at 10 km fixed intervals for 5 112 km along the pre-selected major roads in the arid and semi-arid regions of South Africa. The survey route traversed Albany thicket (n = 21 sites), Azonal vegetation (n = 56), fynbos (n = 147), grassland (n = 86), Nama karoo (n = 187), arid savanna (n = 78), and succulent karoo (n = 51) (Figure 3−1). The survey routes were selected based on previously recorded occurrences of *P. setaceum* within South Africa (Henderson 1995; Milton *et al.* 1998; Milton and Dean 1998; Bromilow 2001).

Roadsides are surveyed because they are susceptible to invasion and are accessible for sampling (Milton and Dean 1998). Roadside surveys have been particularly useful and cost effective for large scale and rapid assessment of invasive species distribution across southern Africa (Milton and Dean 1998; Milton *et al.* 1998;

Joubert and Cunningham 2002) and elsewhere (Parendes and Jones 2000; Trombulak and Frissell 2000; Gelbard and Belnap 2003). Surveys took place for a year from October 2006 to October 2007, covered all seasons and were repeated atleast once. Each transect and interchange was classified according to biome, vegetation type/units, rainfall seasonality and annual rainfall data obtained from (Mucina and Rutherford 2006).
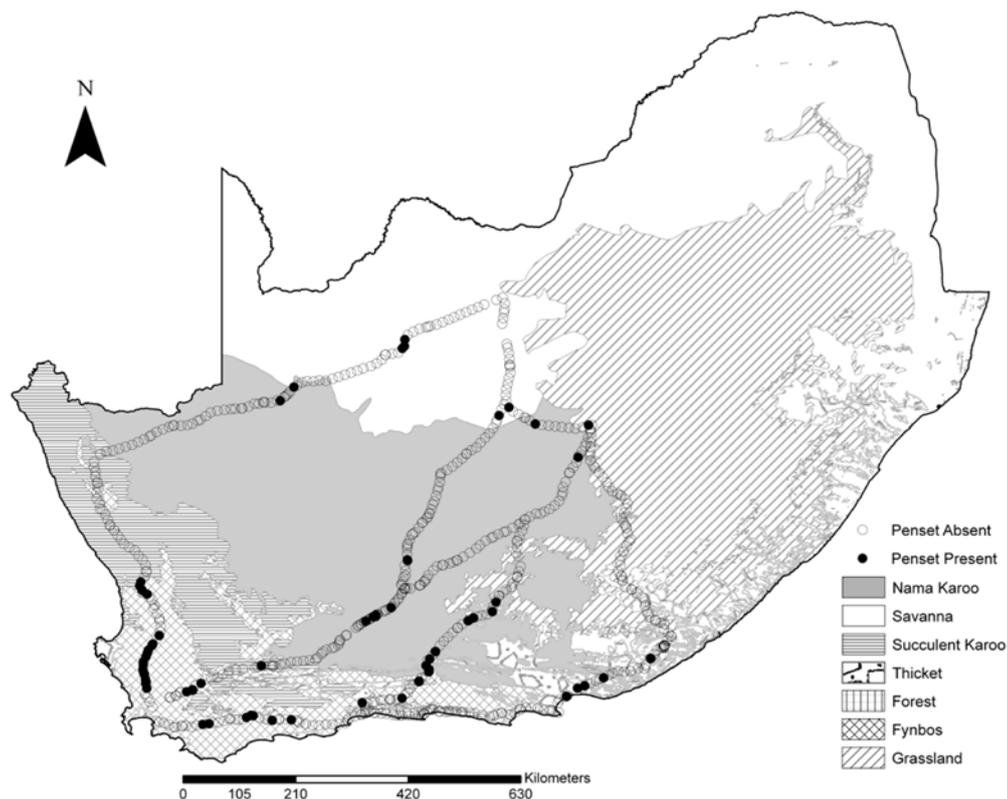
Figure 3−1: Routes travelled during the road survey and records of fountain grass (*Pennisetum setaceum*) in arid and semi-arid South Africa. Dots indicate transects and interchanges where the fountain grass was present. Open circles indicate transects and interchanges where the grass was absent.

The survey was divided into two parts; 1) in a survey every 10 km, the presence or absence of *P. setaceum* in a 1 km transect was recorded, and 2) if there was a road-river interchange before the end of 10 km, the observer surveyed the road-river interchange and began the next 10 km strip from that point. This means that the surveyed strips were sometimes less than 10 km apart if a road-river interchange was

intercepted within the strip. The road-river interchanges were considered to be part of the marked the beginning of the next ten kilometer strip. The GPS coordinates of all transects including the road-river interchanges were captured in a GPS Garmin Version 2.01. In every sample where the grass was present, additional information of the grass population density (number of individuals per square meter) and performance (basal diameter, height and number of inflorescences) was collected in a belt transect (10 x 2 m) along the road verge or road-river exchange. The basal diameter, length of the longest living leaf, and the number of inflorescences were recorded from a sample of 10 individual plants to determine growth and reproductive performance. Also recorded were the landscape features; landuse adjacent to the roadside, soil surface type, vegetation type and biome, mean annual rainfall and rainfall seasonality. The GPS coordinates and landscape features of sample sites were recorded regardless of the presence or absence of *P. setaceum*.

Analysis of variance (ANOVA) was performed in Statistica version 8 (Statsoft 2007) to assess differences between plant basal diameters, plant height, number of inflorescences and density (number of individuals per square meter). Chi-square tests were used to test for differences in the proportion of interchanges along the surveyed roads with and without *P. setaceum* and to test its association with certain vegetation types. Generalized Linear Models were used to assess the effect of road-river crossing, rainfall amount and biome type on plant performance (basal diameter). The non-parametric Mann-Whitney-U test was used to compare the performance of *P. setaceum* on the interchanges and non interchanges along the surveyed major roads when the data were not normally distributed. Differences in occurrences of *P. setaceum* per transect were compared among soil types, biomes and rain seasons using ANOVA and the post-hoc Bonferroni test. To test whether the occurrence of *P. setaceum* was strongly influenced by rain season, soil type and land use, the frequencies of occurrence were compared with distribution of transects for each of the variables.

3.4   Results

3.4.1   *Comparative reproductive performance across the landscape*

P. setaceum showed no significant habitat preference for either road-river interchanges or other parts of the landscape across biomes (Chi-square = 0.652, df =

1, $p = 0.419$). However, when the grass occurred on interchanges, it performed better ($F_{(1, 64)} = 15.618$, $p < 0.001$), with larger basal diameters than on the other parts of the landscape. In addition, the number of inflorescences per individual plant was more (Mann-Whitney U test, $Z = 3.237$, $p < 0.01$) on the interchanges than on other parts of the landscape. However, the density (number of individuals per square meter) was not different between the road-river interchanges and the rest of the landscape (Mann-Whitney U test, $Z = 0.698$, $p = 0.485$). The amount of rainfall and the biome type did not influence plant performance across the landscape in the sampled areas and during the study period (Table 3−1).

Table 3−1: Univariate test of different variable significance for plant performance (basal diameter) using Generalized Linear Models. RRC = road-river interchange

Effect	df	SS	MS	F	P	Significance
Rain (mm)	1	108.51	108.51	2.105	0.153	NS
Biome	6	252.58	42.09	0.817	0.563	NS
RRC	1	503.12	503.12	9.763	0.003	***
Biome x RRC	6	228.24	38.04	0.738	0.621	NS
Error	51	2628.09	51.53			

3.4.2   P. setaceum *distribution and frequency between biomes*

A total of 322 transects and 301 interchanges were recorded along 5 112 km of major roads in semi-arid South Africa (Figure 3−1). *P. setaceum* populations occurred in 10% ($n = 66$) of the total ($n = 629$) transects and interchanges. The number of transects surveyed differed between biomes. The percentages of transects invaded per biome were, 7% ($n = 21$) for Albany thicket, 11% ($n = 56$) for Azonal vegetation, 41% ($n = 147$) for fynbos (including Renosterveld), 3% ($n = 86$) for grassland, 5% ($n = 187$) for Nama karoo, 7% ($n = 78$) for savanna and 11% ($n = 51$) for succulent karoo. Within biomes, *P. setaceum* occurred at different frequencies among vegetation types; e.g. the Swartland Shale Renosterveld vegetation type was invaded more frequently (80%) (M-L Chi-square $= 82.322$, df $= 100$, $p < 0.001$) than other fynbos vegetation types (Table 3−2). Although highly sampled (56 transects), the Nama karoo vegetation type known as "Gamka karoo" was less invaded (2%).

Table 3−2: Vegetation types on roadsides in Albany thicket, Azonal vegetation, fynbos, grassland, Nama karoo, savanna and succulent karoo with mean annual rainfall (mm/yr), transect samples (both transect and interchanges), percentage adjoining rangeland, settlement and cultivated land and the percentage of sites invaded by fountain grass. Only vegetation types with five or more transect samples are presented here. Only the Swartland Shale Renosterveld was more significantly invaded than expected (M-L Chi-square = 82.3223, p < 0.05).

Vegetation code[*]	Vegetation type[*]	Rain (mm.y[-1])	Transect samples	% adjoining rangeland	% adjoining settlement	% adjoining cultivation	% with *Penset*
Albany Thicket							
8062	Great Fish Thicket	449	6	83	17	0	17
8066	Kowie Thicket	517	6	100	0	0	50
Azonal Vegetation							
8090	Cape Lowland Alluvial Vegetation	380	7	14	57	29	57
885	Southern Karoo Riviere	243	34	71	26	3	6
Fynbos							
22	Breede Alluvium Fynbos	480	6	33	17	50	33
9229	Central Rûens Shale Renosterveld	380	6	0	17	83	33
9228	Eastern Rûens Shale Renosterveld	384	9	22	33	44	11
8017	Garden Route Shale Fynbos	700	7	29	71	0	0
9264	Kouga Grassy Sandstone Fynbos	537	5	80	20	0	0
5556	Matjiesfontein Shale Renosterveld	297	6	67	17	17	0
8009	Swartland Shale Renosterveld	430	15	7	13	80	80
9204	Tsitsikamma Sandstone Fynbos	845	15	47	27	27	7
8003	Uniondale Shale Renosterveld	351	6	50	50	0	17
8025	Western Rûens Shale Renosterveld	490	5	20	40	40	0
Grassland							
842	Aliwal North Dry Grassland	510	14	71	29	0	0
826	Amathole Montane Grassland	672	5	80	0	20	0
830	Besemkaree Koppies Shrubland	391	6	67	33	0	0
951	Bloemfontein Dry Grassland	457	11	36	36	27	9
8050	Queenstown Thornveld	481	7	57	43	0	0
208	Stormberg Plateau Grassland	543	6	100	0	0	0
890	Tsomo Grassland	609	11	82	18	0	0
860	Xhariep Karroid Grassland	414	21	76	24	0	5
Nama Karoo							
260	Bushmanland Arid Grassland	133	32	72	22	6	3
854	Eastern Lower Karoo	247	11	73	27	0	27

306	Gamka Karoo	165	56	66	34	0	2
309	Kalahari Karroid Shrubland	156	37	84	16	0	14
284	Northern Upper Karoo	275	9	56	44	0	0
958	Upper Karoo Hardeveld	254	30	77	20	3	3
Savanna							
186	Bhisho Thornveld	717	10	70	30	0	20
1669	Ghaap Plateau Vaalbosveld	400	10	60	40	0	0
1649	Kimberley Thornveld	407	7	29	71	0	0
1647	Kuruman Thornveld	368	31	48	39	13	3
1651	Kuruman Vaalbosveld	422	6	50	50	0	0
Succulent Karoo							
879	Koedoesberge-Moordenaars Karoo	206	11	73	27	0	9
2855	Namaqualand Blomveld	145	7	14	43	43	0
2854	Namaqualand Klipkoppe Shrubland	161	17	82	12	6	0
Totals	36 vegetation types		**488**	**62**	**28**	**10**	**9**

*Based on Mucina and Rutherford (2006)

3.4.3   *Environmental factors affecting* P. setaceum *occurrence*

The results show that *P. setaceum* occurrence was not influenced (F $_{(2, 626)}$ = 2.3898, *p* = 0.092) by any of the three landuse types recorded (Table 3−3). In addition, the landuse type did not affect *P. setaceum* performance (basal diameter) (F $_{(2, 63)}$ = 0.14012, *p* = 0.870) across the landscape during the survey period. Most of the sample transects (95 %) were associated with fine-textured soil and 4 % with alluvium soils (Table 3−3) but the presence of *P. setaceum* was not statistically associated with any soil type (M-L Chi-square = 2.417, *p* = 0.490). However, plants performed better (larger in size) on alluvium soils than on fine textured soils (F $_{(1, 63)}$ = 7.1584, *p* < 0.01). The amount of rainfall in these arid areas did not influence the size of plants (basal diameter) (R = - 0.0425, *p* = 0.287) throughout the surveyed routes. Although most (56 %) sample transects occurred in the summer rainfall regions, the winter rainfall region was more invaded (39 %) than the other rain season regions (Table 3−3). Plant sizes (basal diameter) were, however, not different among the rain seasons (F $_{(2, 63)}$ = 0.32699, *p* = 0.72).

Table 3−3: Relative frequencies (%) of *Pennisetum setaceum* occurrence with respect to the different variables along the sample transects and interchanges (river crossings) in arid and semi-arid parts of South Africa.

Variable		Transect samples	Occurrence		Invaded		% total invaded
			River crossing	Non-river crossing	River crossing	Non-river crossing	
Rain season							
	Mixed	25	32	19	31	29	30
	Summer	56	50	62	31	29	30
	Winter	19	18	19	37	42	39
Soil							
	Alluvium	4	8	1	6	0	3
	Fine	95	92	98	91	100	96
	Rock	0	0	0	0	0	0
	Sand	1	0	0	3	0	1
Biome							
	Albany Thicket	3	4	3	9	6	7
	Azonal Vegetation	9	15	3	14	6	11
	Fynbos	23	23	24	31	52	41
	Grassland	14	13	15	3	3	3
	Nama karoo	30	32	28	26	13	20
	Savanna	12	5	19	3	13	7
	Succulent karoo	8	8	8	14	6	11
Landuse							
	Cultivated	12	11	12	29	39	33
	Ranched	59	56	63	37	32	35
	Settled	29	33	25	34	29	32

3.5   Discussion

3.5.1   Distribution of P. setaceum *between biomes and vegetation types*

P. setaceum has only invaded a small proportion (10 %) of surveyed distance/points suggesting that it is an emerging invader in South Africa. This is despite it being classified as a category 1 weed and invader (Henderson 2001). The results show the fynbos biome to be relatively more invaded (41 %) by *P. setaceum* and this is in agreement with Milton and Dean (1998) who found *P. setaceum* mostly in the fynbos biome. A feature of this biome is its winter rainfall, Mediterranean-type climate that closely matches the conditions from which this grass originates (Milton *et al.* 1998).

More specifically, the abundance of *P. setaceum* in the fynbos biome Swartland Shale Renosterveld could be attributed to this vegetation type receiving winter rainfall, and being nutrient-rich and highly transformed due to prime quality of the land for agriculture into cropland and vineyards (Mucina and Rutherford 2006).

This result is also in agreement with other studies that found *P. setaceum* to be confined largely to shale and granite formations along the Cape Peninsula (Milton *et al.* 1998).

3.5.2   Factors affecting P. setaceum *performance on the interchanges*

Although the occurrence of *P. setaceum* was not determined by the presence of road river interchanges, the grass growth (basal diameter) and reproductive (inflorescence number) performance was higher for plants on these interchanges than on other parts of the landscape. A number of factors could support this improved performance of *P. setaceum* on the interchanges. Firstly, the maintenance of the road network (mowing and ditch digging) could facilitate resource availability and hence rapid growth of the grass.   These activities create disturbances for establishment of openings for colonization and if soil conditions and climate are suitable, *P. setaceum* will establish if propagules arrive there. Secondly, the soil used as land fill for bridge construction over rivers might have contained or have been suitable for the establishment of *P. setaceum* propagules. Thirdly, the introduction of soil from elsewhere into the new location during road and bridge construction brings unsuitable conditions for indigenous species and hence *P. setaceum* may establish without any competition. Fourthly, there could be a continuous supply of moisture, due to drainage ditches along roads (Jodoin *et al.* 2008) and possibly nutrients as a result of debris deposited on the side bridge, particularly during flooding, which might support *P. setaceum* growth on these interchanges.   Lastly, the road-river interchanges are relatively inaccessible and hence protected from continuous roadside management and once *P. setaceum* populations establish, they may persist for years and utilize resources in the detriment of other species.

The construction of roads and the improvement of existing ones have been highlighted as important factors in the ongoing spread of invasive alien plant species elsewhere (Greenberg *et al.* 1997; Forman and Alexander 1998; Trombulak and Frissell 2000; Gelbard and Belnap 2003). These findings are consistent with the idea that the effect of road improvement on plant cover and richness is due to factors associated with road construction and road maintenance, and not to differences in site characteristics (there was no relationship between soil type and *P. setaceum* occurrence).

3.5.3   *Environmental factors and conditions affecting distribution*

A large number of factors have been identified that influence the spread and success of invasive species along roads (Milton and Dean 1998; Gelbard and Belnap 2003) and rivers (Johansson *et al.* 1996) in different biomes. The hypothesis that *P. setaceum* would be more prevalent near human settlements where it originates as an ornamental was tested. Contrary to other findings that housing density and their distance from the roads were found to play a major role in explaining alien plant species presence along roads (Harrison *et al.* 2002; Gelbard and Harrison 2003; Pauchard and Alaback 2004; Kalwij *et al.* 2008b), *P. setaceum* did not show any preference to any of the land use types recorded. This suggests that the grass has the potential to disperse and establish far away from the point sources and could invade natural areas in other parts of South Africa.

Although the occurrence of *P. setaceum* was not influenced by soil type, plants in alluvial soils were larger (basal diameter) than on other soil types. This suggests the influence of extra moisture and nutrients as well as the possible influence of floods that decrease the strength of competitive interactions on these alluvial plains (Hood and Naiman 2000; Parendes and Jones 2000; Richardson *et al.* 2007). This provides an indication of the magnitude of distribution this grass could have particularly along tributaries and roads that traverse natural areas (Joubert and Cunningham 2002; Milton 2004) and into disturbed or sparse vegetation on fertile soils (Williams *et al.* 1995; Milton *et al.* 1998). The results support the idea that roads act as disturbances that promote invasive species (Harrison *et al.* 2002; Dong *et al.* 2008), especially at their interchanges with rivers where more propagules are produced.

The presence of *P. setaceum* away from the road was associated with the presence of water bodies such as river systems and animal drinking points. These points provide extra moisture that plants need for continued growth and persistence especially away from the roads where disturbances may not be prevalent. Disturbances, such as overgrazing, that occur away from the roadsides also facilitate the presence of *P. setaceum* especially if it also occurs on the roadside nearby.

There are some important caveats to the results. Major roads in South Africa are heavily managed and the grass is cut regularly along the road verges, which means that some populations might have been missed during sampling. Timing of sampling

might have played a role in the presence of the grass, the grass is usually visible when it has flower heads (inflorescences) and during dry periods some populations might have been missed. However, this repeatable method ensured that the same routes were surveyed more than once at different times of the year during visits to experimental sites. Some biomes were under-sampled and hence the results obtained may not be generalized. Despite these caveats, this highly repeatable method could be used for monitoring the spread of this grass and other alien plants in South Africa and elsewhere, especially along roads and rivers.

Alien perennial grasses pose a number of problems to many ecosystems as a result of their efficient growth and dispersal mechanisms. I suggest that the presence of *P. setaceum* along roadsides will pose a major problem of being able to produce more propagules that will eventually fly and/or float along rivers and roads and establish further, hence expanding the grass invasion range. Problems will also arise when colonies expand out from roadsides into agricultural lands and rangelands. The findings suggest that road-river interchanges should be considered important targets of both local and regional efforts to prevent and control this grass.

Management efforts to prevent or slow down the spread of invasive alien species must also recognize that, communities with fertile rocky soils such as the fynbos Swartland Shale Renosterveld vegetation type are particularly vulnerable to invasion by *P. setaceum* and possibly other similar alien grasses. These results indicate the importance of road-river interchanges as important habitat for the invasive *P. setaceum* hence can provide information on its potential distribution and range expansion. Small populations of this grass from the interchanges can easily spread through the same corridors over the landscape, so their early detection is crucial to land managers. The results suggest that the availability of propagules and the ideal conditions (mesic and disturbed) at these interchanges will facilitate the proliferation of *P. setaceum*. Management of this grass should focus on spot infestations of these interchanges for the better control of this invasive alien grass.

CHAPTER 4

INFLUENCE OF HABITAT AND COMPETITION ON PERFORMANCE OF THE INVASIVE *PENNISETUM SETACEUM* ALONG A RAINFALL SEASONALITY GRADIENT

4.1   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 establishment of two month old seedlings 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 germination along roadsides that act as conduits into protected sites. This can best be done by maintaining as much indigenous cover along road verges as possible, as seeds survive best where competition is low.

4.2   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 allows invaders to succeed in a wider range of environments (Williams and Black 1993; Williams *et al.* 1995; Pattison *et al.* 1998; Milberg *et al.* 1999; Schweitzer and Larson 1999; Sexton *et al.* 2002; Geng *et al.* 2007; Lavergne and Molofsky 2007, although it is not a requirement within any single, defined environment (Daehler 2003; Richardson and Pyšek 2006).

Pennisetum setaceum (fountain grass, Poaceae) is an apomictic, wind dispersed, C4 perennial bunchgrass, 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-vivipary plantlets when inflorescences are inundated by water (Milton *et al.* 2008). Its 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 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 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). The relative contribution of seed, habitat and microsite limitation to invasion success is unknown for many invasive grass species including *P. setaceum* in South Africa.

The aim of this study was to identify factors affecting the survival and growth of transplanted two month old *P. setaceum* seedlings 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 growth benefit from reduced

competition from indigenous vegetation? (ii) does performance of established seedlings differ among habitat types (disturbed and semi-natural)? and (iii) is there any relationship between site (biome) and other factors influencing plant performance?

4.3   Methods

4.3.1   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 – 1 242 m a.s.l. Rainfall seasonality and precipitation differed at all these sites (Table 4−1). 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 mine dumps.

4.3.2   Soil properties

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

4.3.3 Seed source and germination

P. setaceum seeds were collected from all the study sites and mixed together since origin did not influence their aspects of reproduction (see Chapter 6) and the populations do not differ genetically in South Africa (le Roux *et al.* 2007). The seeds were sown in a trial experiment in a greenhouse at Stellenbosch University Agronomy Department where the average temperature was 38°C (31 – 45°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. This greenhouse was safer for seedling germination and is representative of the conditions where *P. setaceum* grows in the field (see chapter 7). 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 2 more weeks to harden before translocation to the sites.

4.4   Experimental design

At each study site permanent pairs of 2 m^2 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 x 8 plots x 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 x 10 plots x 9 seedlings). On each plot (2 x 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.

4.4.1 Microhabitat characteristics

The three sites were of different elevation (Table 4−1) and had different landuse 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 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).

Table 4−1: Geographic and climatic characteristics of the three 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. (^{o}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)

4.4.2 Statistical analysis

All data were tested for normality with a Shapiro – Wilk test (Shapiro and Wilk 1965). When data were normal, repeated-measures analysis of variance (ANOVA) was used in Statistica 8 (Statsoft 2007) to analyse the performance of seedlings over 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 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 study period at different study sites using Kaplan-Meier survival curves (Kaplan and Meier 1958).

4.5 Results

4.5.1 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 (Figure 4−1). Basal diameter, number of leaves and height were positively correlated, and only ANOVA results for basal diameter are presented in this chapter (Table 4−2). 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. Thereafter, the effect of competition was evident across all sites throughout the study period (Figure 4−2).
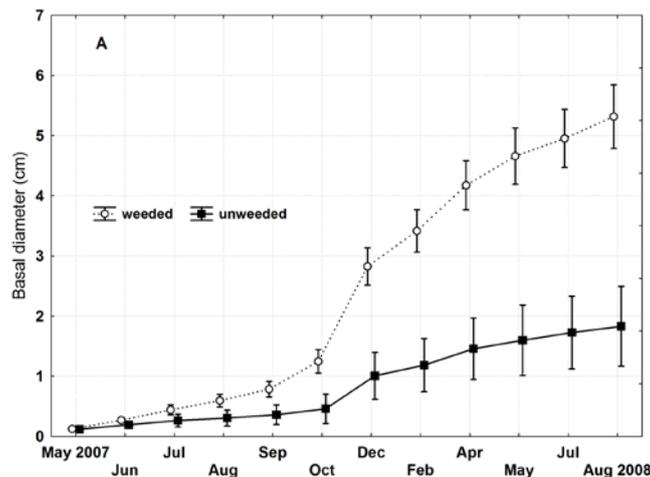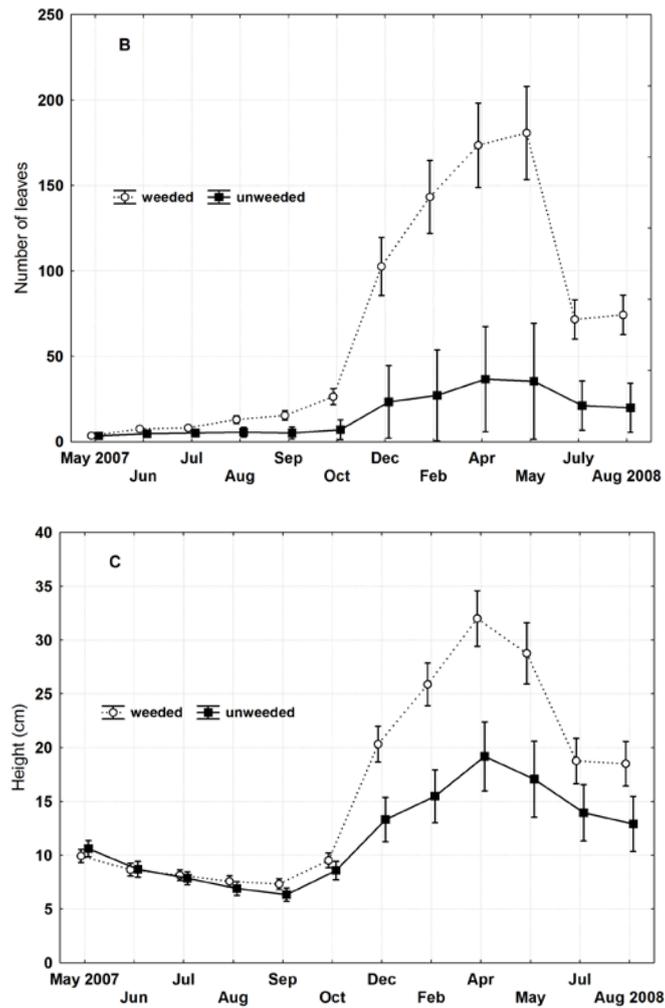
Figure 4−1: Performance of transplanted *P. setaceum* seedlings at the three sites in plots cleared of vegetation (weeded) (○) and plots left unweeded (■). Performance was measured in terms of basal diameter (A), number of leaves (B) and the height of the longest living leaf, height (C). Bars indicate standard errors on all graphs.

4.5.2   Survival and growth of transplants

Seedlings growing in the Karoo National Park performed better (larger basal diameter) than those in other two sites (Figure 4−2). This was also the case for when performance was measured as basal diameter and height (data not shown). Transplanted established seedlings that survived the first six months remained alive at all sites for the rest of the study period (Figure 4−3). At all sites, more seedlings growing on plots cleared of resident vegetation survived (33%) than on unweeded plots (20%) and this effect was significant (Table 4−2).
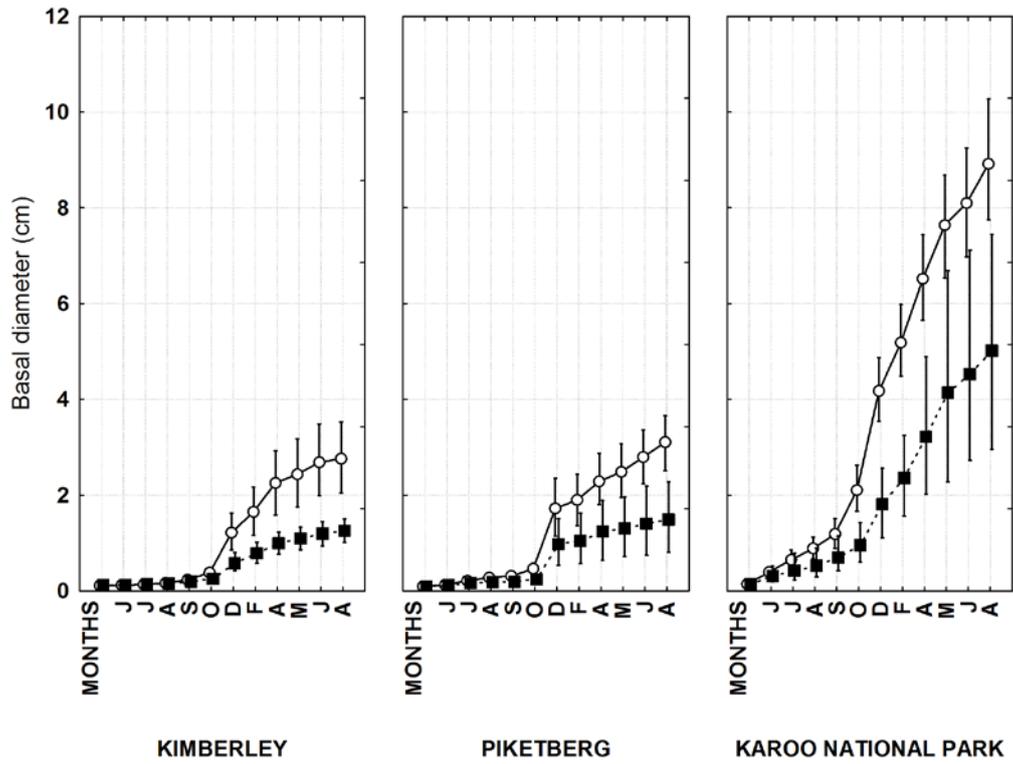
Figure 4−2: Bootstrap means for basal diameters of *P. setaceum* seedlings at the three sites. Open circles (○) represent weeded plots and closed squares (■) represent unweeded plots. Bars indicate standard error on all graphs.
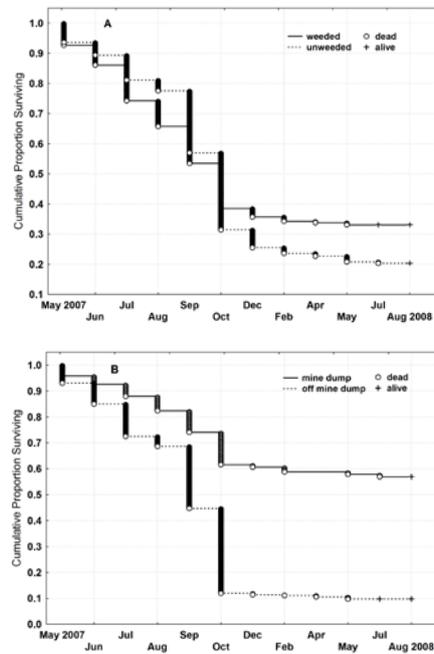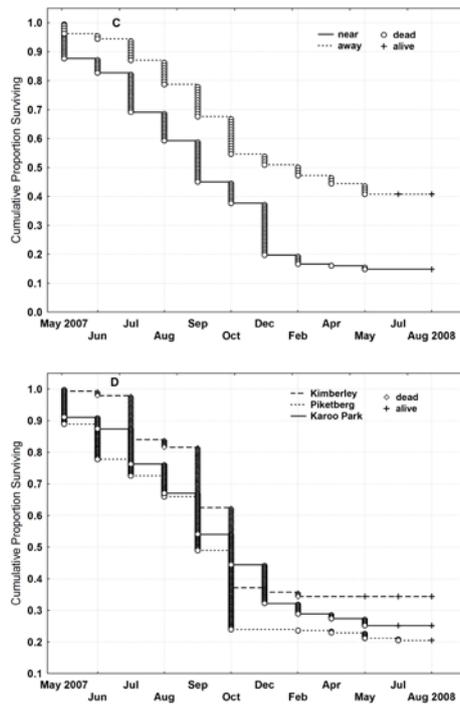
Figure 4−3: The cumulative proportion of surviving seedlings under different variables at the three different sites. A) weeded and unweeded plot types, B) plots on the mine dump and away, C) plots near (0 – 10 m) the river and away (12 – 20 m) at Beaufort West and D) different sites. The plus (+) indicates alive seedlings and the circle (○) indicates dead seedlings.

4.5.3 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 4−2). 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.

Table 4−2: 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
Site	All	580	2	290	47.61	<0.0001
Plot type	All	168	1	168	27.51	<0.0001
Mine dump	KIM and PIK	101	1	101	46.55	<0.0001
Distance from river	KNP	28	1	28	2.42	0.139
Site x plot type	All	52	2	26	4.27	0.019
Site x mine dump	KIM and PIK	0.674	1	0.674	0.31	0.579
Plot type x mine dump	KIM and PIK	5	1	5	2.31	0.134
Site x plot type x mine dump	KIM and PIK	4	1	4	1.87	0.177
Plot type x distance from river	KNP	36	1	36	3.06	0.099
Time (months)	All	1,214	11	110	165.17	<0.0001
Time x site	All	1214	22	19	28.02	<0.0001
Time x plot type	All	131	11	12	17.77	<0.0001
Time x site x plot type	All	30	22	1	2.07	0.003
Time x mine dump	KIM and PIK	85	11	8	36.47	<0.0001
Time x site x mine dump	KIM and PIK	4	11	0.33	1.55	0.109
Time x plot type x mine dump	KIM and PIK	4	11	0.35	1.65	0.082
Time x site x plot type x mine dump	KIM and PIK	7	11	0.61	2.88	0.001
Time x distance from river	KNP	130	11	12	13.21	<0.001
Time x plot type x 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

4.6   Discussion

4.6.1   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 these three 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 suggests competitive suppression by the established resident vegetation (Grime 1973; Jutila 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. The results suggest that indigenous vegetation on undisturbed sites could reduce growth and survival of established *P. setaceum* seedlings, whereas its invasion is facilitated at both historically and currently disturbed sites.

4.6.2 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 4−2). 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 (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 this 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) (3.42cmol (+)/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 number of

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

4.6.3 Influence of environment on survival and performance

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, *P. setaceum* seedlings that survived after six months persisted for the rest of the study period. Most desert plants experience high seedling mortality in the first two months. This suggests that once the *P. setaceum* seedlings have survived for two months, they are able to grow 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.

4.6.4 Conclusions

This study demonstrated that established seedlings of the invasive alien *P. setaceum* are able to survive, grow and reproduce in three biomes with distinct climatic characteristics. At all three sites *P. setaceum* performed well under reduced competition from resident indigenous species although the performance rates differed between sites. However, other habitat conditions such as soil and moisture availability could override competition effects and lead to seedling growth. 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 nearby natural areas if it is not managed effectively. Both biotic and abiotic factors and their interactions promote *P. setaceum* growth. Reduction in human induced disturbances is recommended, especially land cover change, which reduce

competition with indigenous species and hence promote *P. setaceum* performance. Management efforts should also aim to reduce seed production and *P. setaceum* growth 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, the results contribute significantly to the 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 invader weed that must be prohibited and controlled in South Africa.

CHAPTER 5

NUTRIENT ADDITION AND MOISTURE DETERMINE THE INVASIVENESS OF *PENNISETUM SETACEUM*

5.1   Abstract

A conducted a greenhouse study to examine the effects of different habitat conditions and environmental resources on growth rates of fountain grass *Pennisetum setaceum,* an invasive alien perennial grass in South Africa. To help understand the factors promoting the spread of this emergent alien grass, I investigated the effects of temperature regimes, nutrient and moisture addition, and soil type on seedling growth rates and biomass allocation. The results suggest that fountain grass seedlings do not tolerate drought, as they died within one month without water. Additional nutrients and extra water increased seedling growth rates over the study period. Higher temperatures with extra moisture increased seedling growth rates and the development of below-ground biomass over the study period. This study demonstrates the importance of available environmental resources and their interactions with some habitat conditions in promoting fountain grass growth. I suggest that soil moisture and nutrient availability are critical factors affecting performance of fountain grass in arid environments. Managers should target seedlings for removal following precipitation and in areas of nutrient enrichment, such as near rivers and at road-river crossings.

5.2   Introduction

The success of invasive alien plant management partly depends on the knowledge of factors limiting their recruitment (Alvarez-Aquino *et al*. 2004). The performance of alien species in new habitats depends on habitat conditions and available environmental resources, where resource-poor environments often support natives over aliens (Daehler 2003). The availability of resources in a new habitat and reduced competition from resident species renders plant communities vulnerable to invasion. Fluctuations in resource availability may occur due to their reduced uptake by resident vegetation or an increased supply and facilitation relative to their uptake (Davis *et al*. 2000). For example, in dry regions, augmentation of water supply increases the

invasibility of vegetation, either as a direct effect of water supply or through improved access to mineral nutrients (Dukes and Mooney 1999; Davis *et al.* 2000). Soil moisture is the primary ecological driver in many environments, especially in deserts, due to the low frequency and high variability of precipitation, and to high potential evapotranspiration (Noy-Meir 1973; Reynolds *et al.* 2004).

Prevention of invasion into natural habitats is constrained by a lack of knowledge about requirements of invasive species for recruitment, growth and survival. The perennial fountain grass *Pennisetum setaceum* is an invasive C4 bunchgrass native to the North African arid Mediterranean area of the Atlas Mountains and Middle East (Williams *et al.* 1995). It invades many natural habitat types (Tunison 1992; Milton *et al.* 1998; Joubert and Cunningham 2002) that include broad altitudinal ranges (Tunison 1992; Williams *et al.* 1995), varying rainfall and water conditions (Williams and Black 1994; Joubert and Cunningham 2002), and varying soil types (Milton *et al.* 1998). In South Africa, it has been declared a Category 1 weed and invader under the Conservation of Agricultural Resources Act, 1983 (amended in 2001) that must be prevented and controlled. This is as a result of its promotion of fire in other parts of the world, such as Hawaii (Williams *et al.* 1995) and South Africa (Rahlao *et al.* 2009). Understanding and identifying environmental resources that promote the success of invasive alien species during the critical life stages can be used to focus their management (Ward *et al.* 2006).

The objective of this study was to experimentally assess seedling survival and growth of *P. setaceum* under differing environmental resources. The hypothesis that seedlings will perform better in nutrient-rich soils and high soil moisture availability was tested under two temperature alternatives. The experiment was performed by establishing seedlings in two greenhouse environments and monitoring their survival and growth over a period of eight months. Based on other studies on this species, as well as generalizations about known invaders, I predicted that 1) *P. setaceum* seedlings would perform better with high than low water and nutrient availability, 2) nutrient-rich soils would promote the growth of *P. setaceum* more than nutrient-poor soils, and 3) *P. setaceum* seedlings would perform better in moderate than high temperatures.

5.3   Methods

5.3.1   Experimental design

P. setaceum seeds were collected from Prince Albert (33^0 10' S, 22^0 17' E), Western Cape Province, South Africa, during December 2006. *P. setaceum* occurs along roadsides in this arid area, and has the possibility of invading semi-natural areas away from roadsides (see Rahlao *et al*. 2009 for more details). The seeds were later germinated in soil trays in a greenhouse (natural lighting, 31^oC, mean maximum, and 18^oC, mean minimum temperatures) until they germinated by end of April 2007. The germinated seedlings were transplanted into 1.2 L plastic bags and maintained at ambient temperatures without watering for two weeks. In June 2007, a total of 120 seedlings were then translocated into 3.9 L pots containing two different types of soil (Table 2). Two separate greenhouse treatments were conducted to determine the effect of temperature, water, nutrients and soil type on *P. setaceum* seedling growth and reproductive rates. Seedlings were randomly assigned to four different treatments in a factorial design, with two alternatives of greenhouse conditions (n = 2 x 60) to assess temperature effects, two alternatives of fertilizer addition (n = 2 x 60), three alternatives of moisture content (n = 3 x 40), and two alternatives of soil type (n = 2 x 60), including five replicates (Table 5−1). The experiment was conducted under two temperature ranges in greenhouses located at the South African National Biodiversity Institute (SANBI) in Cape Town, South Africa from June 2007 to January 2008. The typical temperatures in the greenhouses ranged between 30 – 45 ^{o}C (mean = 33^oC) for hot and between 15 – 30 ^{o}C (mean = 21.6 ^{o}C) for moderate greenhouses respectively.

The watering treatments were divided into high-water plants that received 150 mL three times a week (1 045 mm/year), low-water plants that received 150 mL once a week (348 mm/year) and no-water plants that did not receive water, to estimate soil moisture effects on growth. These treatments simulate rainfall patterns within the full range of regions that are at high risk of invasion by *P. setaceum* (see Chapter 8 for more details). The dry treatment simulates a prolonged drought following seedling growth. These three soil moisture treatments were achieved by the use of overhead automatic sprinklers in each greenhouse. The system has been used in similar studies (Goergen and Daehler 2001; Daehler and Goergen 2005; Poulin et al. 2007) and has been effective in ensuring slow water absorption and less runoff.

Table 5−1: Factorial experimental design, where 120 potted (3.9 L pots) *P. setaceum* seedlings were randomly assigned to treatments in two different greenhouses to determine the effect of temperature, water, nutrients and soil type. Seedlings were assigned to four different treatments with two alternatives of greenhouse conditions (n = 2 x 60), two alternatives of fertilizer addition (n = 2 x 60), three alternatives of moisture content (n = 3 x 40) and two alternatives of soil type (n = 2 x 60). All treatments were replicated five times. See text for more details.

Soil moisture (M)	Soil type (S)	Nutrient (N)	Temperature (T)
450 ml [(150 ml x 3)/ week] (n = 40)	Nutrient poor sand (n = 60)	Nutrients (20 g m^{-2}) (n = 60)	Hot = 30 – 45 ^{o}C (n = 60)
150 ml/ week (n = 40)	Nutrient rich sand (n = 60)	No nutrient (n = 60)	Moderate = 15 – 35 ^{o}C (n = 60)
No moisture (n = 40)			

Seedlings assigned to nutrient/fertilization treatments received the slow release fertilizer N:P:K = 7:1:3 (21) added in aqueous form (Table 5−1). The soil effects were tested with two different soil types, one rich in phosphorus, potassium, nitrogen and calcium as determined by a professional laboratory analysis (BEMLAB, cc.), and another soil was untreated sand, poor in all nutrients. Both soils had a high sand component (Table 5−2). The nutrient rich soil was similar to soils where *P. setaceum* occur in the field (near roadsides and on road-river crossings).

At the end of the experiment, inflorescences of the grass were removed and burned to reduce the possibility of invasion from the greenhouses. The roots and leaves were then harvested and oven-dried to a constant mass for 48 hours under 60 ^{o}C, and weighed to estimate the root and shoot biomass.

5.3.2   *Data collection and statistical analyses*

Seedling height, stem basal diameter and number of leaves were monitored every month for eight months (June 2007 to January 2008), the time it took for the leaves to begin dying off after producing inflorescences. Seedling survivorship was estimated as the proportion of seedlings surviving at each time interval.

Table 5−2: Properties of the two soil types used for growing *P. setaceum* seedlings in the two temperature regimes (greenhouses) at the Kirstenbosch Research Centre, South Africa.

Soil properties	Stellenbosch	Kirstenbosch
Soil pH	5.9	6.3
N total (%)	0.038	0.152
P (ppm)	2	178
K (cmol/kg)	0.08	0.49
Ca (cmol/kg)	0.33	6.51
Mg (cmol/kg)	0.37	1.27
CEC (cmol/kg)	1.55	5.34
Clay (%)	2.0	1.4
Silt (%)	3.6	6.0
Sand (%)	94.4	92.6
Mechanical classification	Sand	Sand

Repeated measures analysis of variance (ANOVA) was performed to analyze effects of the environmental resource conditions (moisture, fertilization, soil type and temperature regimes) on growth rates, root and shoot biomass. Survival of transplanted seedlings was measured as the mean count of surviving seedlings for each treatment. Survival analyses were done to compare groups in a generalized non-linear model of Statistica, to compare the cumulative proportion of seedlings that survived per treatment over the study period. All data were tested for normality and variance before further analyses. Statistical analyses were performed using STATISTICA (Statsoft 2007) version 8.

5.4 Results

5.4.1 Seedling growth rates

Seedlings that received no water died within a month in both greenhouses and were excluded from further analysis. Seedlings with added nutrients had larger basal diameters than those without nutrients throughout the study period ($F_{(45.6, 45.63)} = 25.8$, df = 1, p < 0.0001). Soil type did not influence seedling growth rates over the study period ($F_{(1.7, 1.68)} = 0.9$, df = 1, p = 0.335). Seedlings grown in conditions of high soil moisture were consistently larger than those grown in low-moisture conditions under moderate temperature (Figure 5−1).

Table 5−3: Repeated measures analysis of variance (ANOVA) for *P. setaceum* performance (basal diameter) under different environmental resource regimes, habitat conditions and their interactions during the study period (June 2007 – January 2008). Significant effects and interactions are in bold.

Effect		SS	df	MS	F	p	Significance level
(1)	Temperature	0.3	1	0.28	0.2	0.692	NS
(2)	Soil type	1.7	1	1.68	0.9	0.335	NS
(3)	**Nutrients**	**45.6**	**1**	**45.63**	**25.8**	**<0.0001**	*******
(4)	**Moisture**	**39.9**	**1**	**39.85**	**22.5**	**<0.0001**	*******
	Temperature x Soil type	1.3	1	1.31	0.7	0.395	NS
	Temperature x Nutrients	1.3	1	1.31	0.7	0.395	NS
	Soil type x Nutrients	1.4	1	1.37	0.8	0.384	NS
	Temperature x Moisture	**36.5**	**1**	**36.55**	**20.7**	**<0.0001**	*******
	Soil type x Moisture	5.3	1	5.29	3.0	0.091	NS
	Nutrients x Moisture	0.7	1	0.68	0.4	0.540	NS
	1 x 2 x 3	0.1	1	0.15	0.1	0.772	NS
	1 x 2 x 4	0.1	1	0.08	0.0	0.830	NS
	1 x 3x 4	6.0	1	6.01	3.4	0.072	NS
	2 x 3 x 4	0.0	1	0.02	0.0	0.907	NS
	1 x 2 x 3 x 4	3.1	1	3.13	1.8	0.190	NS
	Error	76.1	43	1.77			
(5)	**Time**	**305.0**	**7**	**43.57**	**182.9**	**<0.0001**	*******
	Time x Temperature	**7.5**	**7**	**1.08**	**4.5**	**<0.0001**	*******
	Time x Soil type	2.1	7	0.31	1.3	0.256	NS
	Time x nutrients	**52.0**	**7**	**7.42**	**31.2**	**<0.0001**	*******
	Time x moisture	**23.4**	**7**	**3.34**	**14.0**	**<0.0001**	*******
	5 x 1 x 2	1.7	7	0.24	1.0	0.425	NS
	5 x 1 x 3	1.0	7	0.14	0.6	0.771	NS
	5 x 2 x 3	2.2	7	0.31	1.3	0.242	NS
	5 x 1 x 4	**20.2**	**7**	**2.89**	**12.1**	**<0.0001**	*******
	5 x 2 x 4	3.2	7	0.45	1.9	0.070	NS
	5 x 3 x 4	1.1	7	0.16	0.7	0.703	NS
	5 x 1 x 2 x 3	0.2	7	0.04	0.1	0.994	NS
	5 x 1 x 2 x 4	0.8	7	0.11	0.5	0.864	NS
	5 x 1 x 3 x 4	**6.1**	**7**	**0.87**	**3.6**	**<0.001**	******
	5 x 2 x 3 x 4	0.0	7	0.01	0.0	1.000	NS
	5 x 1 x 2 x 3 x 4	2.2	7	0.31	1.3	0.246	NS
	Error	71.7	301	0.24			

SS = sum of squares, df = degrees of freedom MS = Mean of squares, NS = Not significant, **$p<0.001$, ***$p<0.0001$

5.4.2 Environmental resources and habitat condition interactions

The interaction of temperature and soil moisture affected the seedlings growth rates throughout the study period (Table 5−3). Under moderate temperatures, seedlings growing in high-water conditions were consistently larger than ($F_{(35.04, 5.01)} = 11.08$, df = 7, p = <0.0001) those in low-water conditions (Figure 5−1A). However, under hotter conditions, the amount of water did not have an impact on seedling growth rates over the study period ($F_{(0.38, 0.05)} = 0.11$, df = 7, p = 0.997, Figure 5−1B).
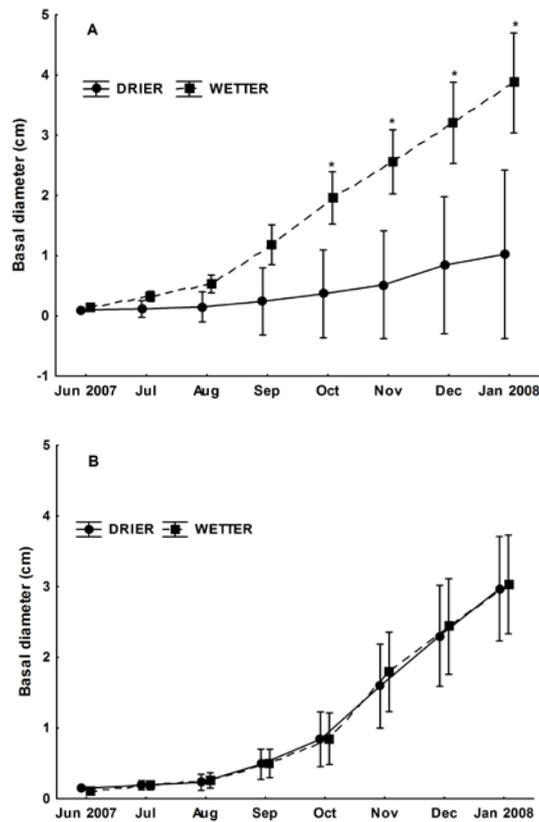
Figure 5−1: Performance (basal diameter) of *P. setaceum* seedlings under drier and wetter conditions in two temperature treatments of A) moderate (15 – 35°C) and B) hotter (30 – 45°C) temperatures. * denotes significant differences. Bars indicate standard deviation from the mean.

5.4.3 Biomass responses

Addition of nutrients significantly increased both above- and below-ground biomass (Table 5−4). Under high temperature regime, *P. setaceum* seedlings developed significantly more ($F_{(1, 58)} = 4.2638$, $p = 0.04341$) below-ground biomass than under a moderate temperature (Figure 5−2 A & B). However, there was no difference ($F_{(1, 63)} = 2.5116$, $p = 0.11802$) in the amount of above-ground biomass developed under both temperature regimes. Under low environmental resources, seedlings developed more below-ground biomass especially in hotter temperature regimes (Figure 5−2B).
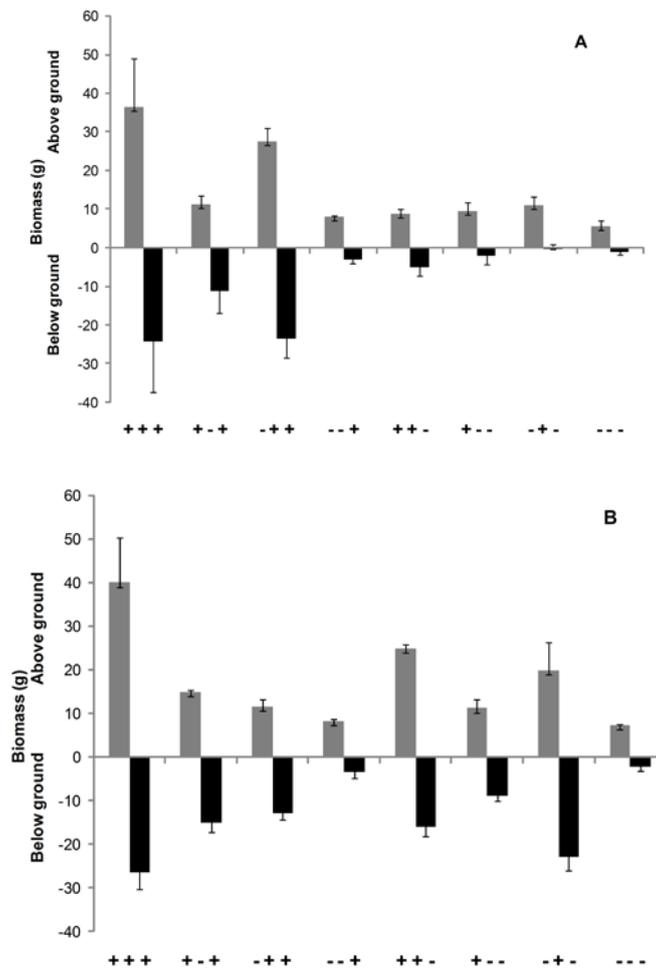
Figure 5−2: Mean above- and below-ground biomass allocation in *Pennisetum setaceum* under A) moderate temperature and B) hotter temperature regimes; A "+" implies additional resources to soil, nutrients and water respectively. For example: +++ means: rich soil, nutrients added and high water content, - - - means: poor soil, no nutrients added and low water content. Error bars indicate 1 Standard Error (1 SE).

5.4.1 Seedling survival

The proportion of seedlings that survived at the end of the experiment varied significantly among treatments. All seedlings that received no water died within a month in both temperature regimes (Figure 5−3 A). More (90%) seedlings survived under high water treatment than those under low water treatments (57%). More seedlings survived under a hot temperature (60%) than those under a moderate temperature regime (39%) (Figure 5−3 B). The type of soil and addition of nutrients did not influence the survival rates of *P. setaceum* seedlings throughout the study period (Figure 5−3 C & D). Many seedlings died during the fifth month (October),

probably as a result of adjusting to the extreme temperature conditions at that time in the greenhouses.

Table 5−4: Analysis of variance (ANOVA) tables comparing average for *P. setaceum* above and below-ground biomass. The experimental treatments: T, temperature regime; S, soil type; N, nutrients; M, moisture regime for the entire experimental period, eight months (June 2007 – Jan 2008). Bold *p* values indicate significant effects and interactions.

Source	df	Below – ground biomass		Above – ground biomass	
		F	p	F	p
T	1	5.216	**0.026**	1.173	0.283
S	1	5.640	**0.021**	9.627	**0.003**
N	1	25.489	**<0.0001**	31.238	**<0.0001**
M	1	13.477	**0.0005**	10.235	**0.002**
T x S	1	0.378	0.541	2.651	0.108
T x N	1	0.618	0.435	0.094	0.760
S x N	1	0.826	0.367	1.438	0.235
T x M	1	7.698	**0.007**	3.934	**0.052**
S x M	1	2.979	0.089	3.889	0.053
N x M	1	2.220	0.141	5.044	**0.028**
T x S x N	1	0.243	0.624	1.574	0.214
T x S x M	1	1.813	0.183	0.736	0.394
T x N x M	1	5.364	**0.024**	4.123	**0.046**
S x N x M	1	0.083	0.774	3.072	0.084
T x S x N x M	1	2.529	0.117	0.208	0.650

5.5   Discussion

Phenotypic plasticity and local adaptability allow many invasive alien species to be highly invasive under variable environmental conditions (Richards *et al*., 2006). *P. setaceum* allocated more resources to root development under hotter temperature regimes (Figure 2B); this could be the plant's strategy to adapt under stressful environments. Williams and Black (1993) reported that under nutrient-rich conditions and high water conditions, *P. setaceum* allocated more biomass to leaves in Hawaii. I also found more above-ground biomass in *P. setaceum* under high environmental resource (nutrient and water) availability. In addition, this study found that under low resource availability *P. setaceum* allocates more resources to root development probably as a strategy to prevail until favourable conditions return.
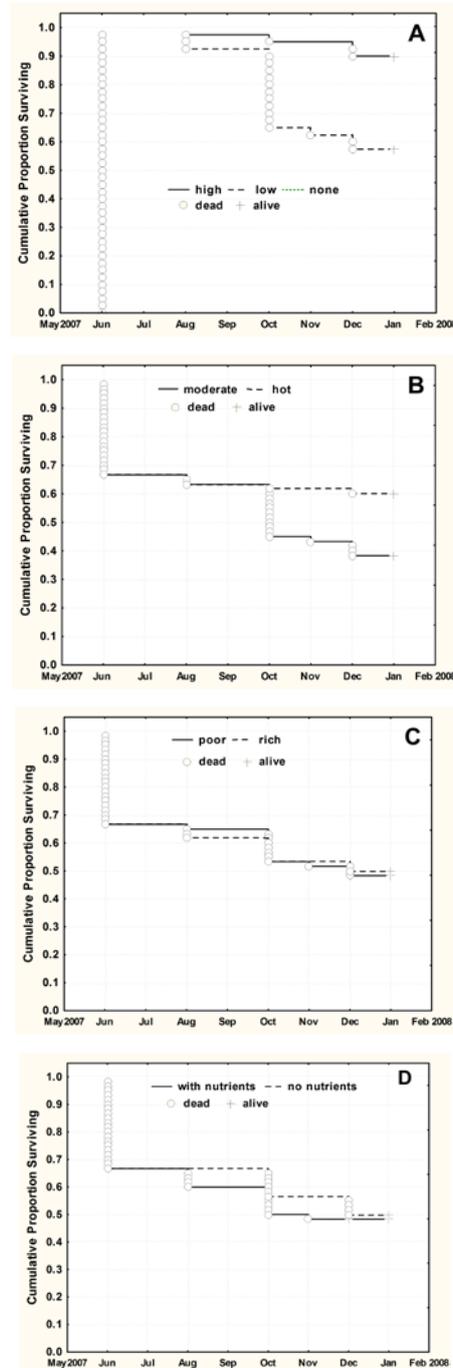
Figure 5−3: The cumulative proportion of surviving *P. setaceum* seedlings under different A) water regimes (no water, low and high water), B) temperature regimes (hot and moderate), C) soil types (nutrient-rich and nutrient-poor), and D) nutrient addition. The plus (+) indicates alive seedlings and the circles (○) indicate dead seedlings.

In desert ecosystems, limited soil moisture availability has been recognized as the likely reason for lower rates of infestation by invasive alien species than in more mesic environments (Rejmánek *et al*. 2004). *P. setaceum* seedlings were unable to

survive in treatments with no water. Increased soil moisture in these dry areas would likely increase the invasibility of vegetation, either as a direct effect or through improved access to mineral nutrients (Dukes and Mooney 1999; Davis *et al.* 2000). Invasive alien grasses also respond positively to increased levels of nitrogen and phosphorus in dry desert regions (Wilson *et al.* 1966; Brooks and Pyke 2001). Nutrient addition increased both the above- and below-ground biomass and overall performance in *P. setaceum* seedlings during the study period.

The amount of water did not affect seedling performance under higher temperatures (Figure 5−1 B). This suggests that once the seedlings have established under these harsh hotter temperatures, they are able to persist even if given little amounts of water. Areas of occurrence with ambient temperatures within the range of those of the hotter greenhouse, which could explain the persistence of *P. setaceum* in hotter arid and semi-arid areas in South Africa, but my results suggest that this may depend on reasonably regular rainfall at seedling stage. This result demonstrates the importance of environmental resources (nutrient and water addition) and their interactions with habitat conditions (e.g. air temperature) in promoting *P. setaceum* growth rates and invasion.

Temperature regime had no effect on plant performance throughout the study period. This result suggests that *P. setaceum* can persist and spread in environments where it is currently absent. This result refutes our initial hypothesis that the plant would perform better under moderate conditions. *P. setaceum* seeds are dispersed by wind and water, and seeds produced in high-environmental resources habitats such as road-river crossings, may be dispersed into low-environmental resource habitats where they could germinate and hold on by allocating resources to root development until favourable habitat conditions prevail.

This study confirms that environmental resource availability (i.e. water and nutrients) improves growth of *P. setaceum* and this may therefore play an important role in management and control of this invasive alien grass species. Identifying and understanding ideal conditions for growth during early stages of this grass are important for its management. Based on these findings, I suggest that managers plan to target seedling removal following precipitation and in areas subject to nutrient enrichment, particularly at road-river crossings where this species performs well (Chapter 3). This could be archived by having teams that can uproot the grass seedlings early after rainfall at identified localities where the grass poses high risks.

CHAPTER 6

VEGETATIVE AND REPRODUCTIVE ADAPTATION OF INVASIVE
PENNISETUM SETACEUM IN SOUTH AFRICA

6.1 Abstract

Biological invasions are a major component of global change with increasing effects on natural ecosystems. Understanding factors that promote invasive alien species is central for their control. Local adaptation individual tolerance of *P. setaceum* was assessed in three different environments in arid and semi-arid parts of South Africa. The growth and reproductive performance of established seedlings of this grass was also examined under common garden experiments in a greenhouse. There was no difference in quantitative traits across the environmental gradient at these sites. Furthermore, growth and reproductive responses in plant characters were not site dependent indicating local adaptation and environmental tolerance rather than plasticity in invasiveness of *P. setaceum*. This study therefore, suggests that local adaptation of both established seedlings plays an important role for the invasion success of *P. setaceum* in South Africa. The results further suggest the overriding effect of disturbance on invasion process over prevailing habitat conditions. This adaptation in reproduction and of *P. setaceum* could contribute to its expansion in distribution and high local abundance and hence increase in invasion risk in South Africa where it has been introduced. Further global changes in South African environments will promote the invasion of this grass.

6.2 Introduction

A better understanding of factors that contribute to invasion success and impact is essential for control of biotic invasion (Pyšek and Richardson 2007). Local adaptation and phenotypic plasticity enable invasive alien plants to cope with heterogeneous environments and contribute to their invasiveness (Sexton *et al.* 2002; Lehmann and Rebele 2005; Sharma and Esler 2008; Ross *et al.* 2009) across environmental gradients (Rejmánek *et al.* 2005; Hulme 2008). Plasticity in plant reproduction and growth rates occurs in response to gradients in disturbance, temperature, water, and nutrients (Dudley 2004) and the ability of a species to survive

and reproduce across a broad range of environmental conditions facilitates its invasive ability (Williams and Black 1993; Ross *et al.* 2009). Understanding the relative growth and reproductive response of an invader to novel environmental conditions may assist in predicting the consequences of invasion (Goergen and Daehler 2001b).

Most studies have focused on invasive plant species that have already had substantial ecological or human impacts, whereas species beginning their spread have received relatively little attention (Culley and Hardiman 2007). The introduced ornamental C4 fountain grass *Pennisetum setaceum* is an emerging invasive alien in southern Africa (Milton 2004; Rahlao *et al.* 2009) and has been declared a weed and invader that must be controlled in South Africa (Henderson 2001). Much has been written about *P. setaceum* ecology and its impacts in Hawaii (Williams and Black 1994; Williams *et al.* 1995; Cabin *et al.* 2002; Goergen and Daehler 2002; Cordell and Sandquist 2008), but less so in California (Poulin *et al.* 2007) and South Africa (Milton *et al.* 1998) where it is moderately invasive (Le Roux *et al.* 2007). Differences in seed production and seed ecology may further explain the invasion success/failure of *P. setaceum*.

In this paper, the reproductive and vegetative performance of *P. setaceum* at three contrasting biome environments in South Africa was tested. The study specifically explored the following questions: 1) what is the relative reproductive and vegetative performance of *P. setaceum* over three sites covering current distribution range of the species in South Africa? 2) what is the effect of different disturbance types on reproductive and vegetative performance in these environments? and 3) what is the relative response of established seedlings from different environments to watering and nutrient addition?

6.3   Methods

6.3.1   Study sites

Three environmentally distinct sites (Karoo National Park – 32°17'44.59"S, 22°33'46.71"E, De Beers Mine dumps in Kimberley – 28°44'17.90"S, 24°47'08.75"E and PPC Mine dumps near Piketberg – 32°55'49.09"S, 18°45'36.22"E) were selected in arid and semi-arid parts of South Africa in the current distribution range of *P. setaceum*. See Chapter 4 for full descriptions of the sites. The altitudinal gradient represented by these three sites ranges from 190 (Piketberg) – 1242 m.a.s.l.

(Kimberley). Precipitation patterns are highly variable between these sites, but follow the same temperature patterns from month to month throughout the year (Figure 6–1A and B).

6.3.1 Reproductive effort and potential

At each of the three sites, 50 plants were selected along a 100 m transect. For each plant, basal diameter, plant height and number of inflorescences were recorded. Five inflorescences were collected from half of these (N = 25) to determine seed production. The surveys and seed collection took place during January 2006 to December 2008 after the end of the rainfall season to ensure that sampling adequately covered the period of peak inflorescence production. Fifty mature and viable seeds per site were germinated to determine germination rates on a common soil type from Kirstenbosch (see Rahlao *et al.* 2009 and Chapter 5 for Kirstenbosch soil characteristics). The total number of seeds per inflorescence was estimated from counts of the total number of spikelets per inflorescence. The total number of seeds per plant was estimated by multiplying the average number of seeds per inflorescence by the average number of inflorescences per plant for each site.
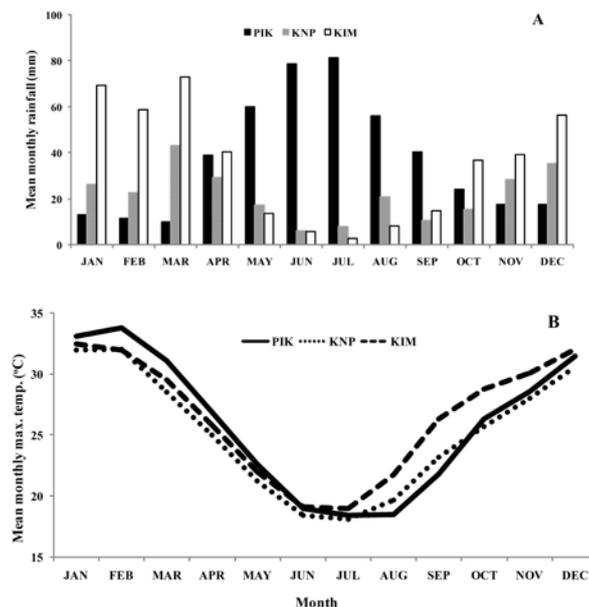
Figure 6−1: Mean monthly precipitation (A) and mean monthly maximum temperatures (B) for Piketberg (PIK), Karoo National Park (KNP) and Kimberley (KIM) from 1990 – 2008. Most of the precipitation falls in winter at Piketberg (average total annual rainfall is 447 mm) while Kimberley (419 mm) receives most of its rainfall in summer, mostly in March. By contrast, Karoo National Park (259 mm) is more arid and has a mixed season rainfall pattern.

See Chapter 2 for further site descriptions. All data were provided by the South African Weather Bureau, unpublished weather data from 1990 to 2008.

6.3.1   Greenhouse experimental design

Greenhouse experiments were conducted to determine the effect of water and nutrient addition on seedling growth rates and reproductive potential (flower and seed production) for all sites. A subset of germinated seedlings (2 – 3 leaves or about 5 cm tall), was then transplanted into pots to investigate their growth rates for different sites in a common soil type (Kirstenbosch soil) in a greenhouse. A factorial design was employed for the experiment with two levels of moisture and two levels of nutrients with five replicates each. High-moisture treatments received 150 mL of water every other day (450 mL per week), while low-water treatments received 150 mL per week. Plants in the high-nutrient treatments received fertilizer (in aqueous form) once a month with one watering cycle while those in the low-nutrient treatment received no added nutrients. The locations of pots on the greenhouse benches were moved randomly every two weeks to reduce position effects. For each treatment, the mean number of inflorescences per plant and mean number of seed per inflorescence were used as indices of reproductive output.

At the end of experiment when most plants had flowered, after eight months, roots and leaves were harvested and washed, separated and then oven-dried for at least 48 hours at 60°C. Dried roots and leaves were weighed separately to determine biomass allocation for each individual.

6.3.2   Data analysis

A repeated measures analysis of variance (ANOVA) was used to evaluate differences between site, water and nutrient treatments (treatment factors), among sampling dates (date factor) and the interaction between treatments and date for basal diameter, number of leaves, height and number of inflorescences for the greenhouse experiments. One-way ANOVA was used to compare both vegetative and reproductive outputs between sites. All the statistical analyses were performed using Statistica 8 (Statsoft 2007).

6.4   Results

6.4.1   Field reproductive effort

Plants from different sites did not differ from each other for the reproductive aspects measured (Figure 6−2A:D).   Although plants in Kimberley were larger (F $_{(2,\ 147)}$ =6.0183, p = 0.003) than those from other areas, there was no difference in the number of seeds produced per plant (F $_{(2,\ 147)}$ = 2.4468, p = 0.09).   Seeds from Piketberg yielded higher germination percentages (F $_{(2,\ 12)}$ = 11.27, p = 0.002) than those from Kimberley and Karoo National Park (Figure 6–2E).
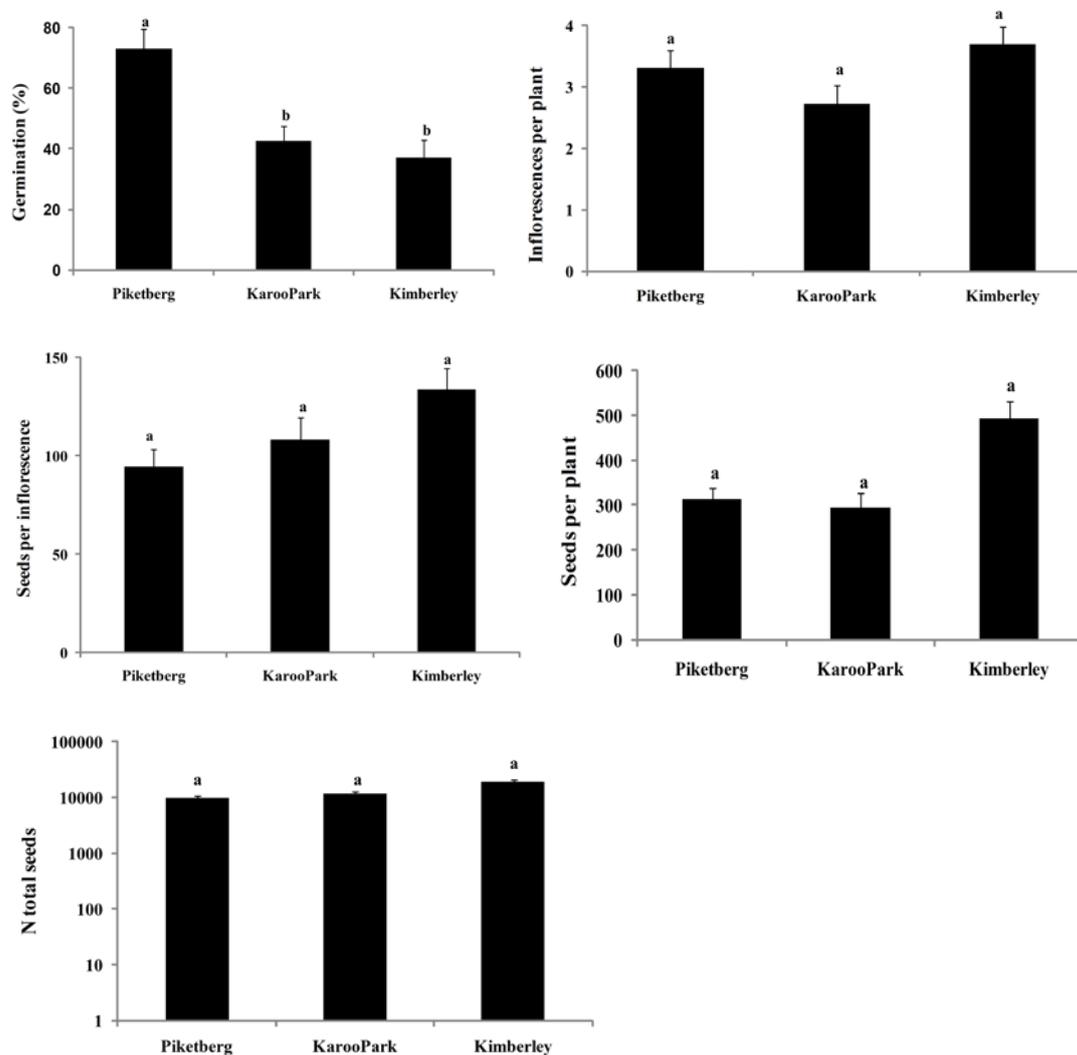
Figure 6−2: Means (+SE) of *P. setaceum* seeds per inflorescence, inflorescences per plant, seeds per plant, total number of seeds and percentage of seeds germinated per site (Piketberg, Karoo National Park and Kimberley).

6.4.1 Response to nutrient and water addition

In the greenhouse, seedlings with added nutrients and high-moisture began flowering in their third month. These seedlings were consistently larger than those under low-moisture and no-nutrient treatments (Table 6–1). There was a positive linear relationship between plant basal diameter and the height ($r = 0.44$, $p = 0.02$) and number of inflorescences per plant ($r = 0.58$, $p < 0.0001$), therefore, only basal diameter results are presented for clarity below. The effect of added nutrients and high-water treatment on seedling growth rates did not differ between seedlings of different origins throughout the study period (Table 6–1). Additional nutrients had a larger impact on seedling growth rates than did additional water (both high and low).

Table 6−1: Repeated measures analysis of variance (ANOVA) for the growth performance (basal diameter) of transplanted *P. setaceum* across the environmental gradient and interactions with addition of water and nutrients.

Effect	SS	df	MS	F	P	Significance level
(1) Site	6.8	2	3.4	2.1	0.130	NS
(2) Water	16.2	1	16.2	10.1	0.003	**
(3) Nutrients	254.1	1	254.1	159.0	<0.001	***
Site x Water	1.8	2	0.9	0.6	0.580	NS
Site x Nutrients	6.2	2	3.1	1.9	0.155	NS
Water x Nutrients	33.7	1	33.7	21.1	<0.001	***
Site x Water x Nutrients	2.5	2	1.3	0.8	0.461	NS
Error	76.7	48	1.6			
(4) Time	213.0	5	42.6	145.9	<0.001	***
Time x Site	4.7	10	0.5	1.6	0.102	NS
Time x Water	21.3	5	4.3	14.6	<0.001	***
Time x Nutrients	129.7	5	25.9	88.8	<0.001	***
Time x Site x Water	1.4	10	0.1	0.5	0.898	NS
Time x Site x Nutrients	4.1	10	0.4	1.4	0.183	NS
Time x Water x Nutrients	31.2	5	6.2	21.4	<0.001	***
4 x 1 x 2 x 3	2.8	10	0.3	1.0	0.475	NS
Error	70.1	240	0.3			

SS = sum of squares, df = degrees of freedom MS = Mean of squares, NS = Not significant, **p<0.001, ***p<0.0001

6.4.1 Greenhouse reproductive output

Only seedlings that received added nutrients and high moisture produced inflorescences within the study period, and there was no difference for the different sites ($F_{(2, 20)} = 1.24$, $p = 0.328$). Nutrient addition increased the above-ground biomass for all treatments, regardless of water content (Table 6−2). The origin of seeds did not affect seedling biomass allocation. Under low environmental resources

of low moisture water and no-nutrients, seedlings had higher below-ground than above-ground biomass (Figure 6−3).

Table 6−2: Analysis of variance (ANOVA) results of water and nutrient treatments, site of origin, and their interaction for aboveground vegetative biomass and belowground biomass in the greenhouse and seeds per inflorescence, total number of seeds for *P. setaceum*. Significance levels (p) are those before Bonferroni correction.

Trait	Source/effect	df	MS	F	p
Aboveground biomass	Site	2	195.7	1.20	0.309
	Water	1	1728.0	10.61	**0.002**
	Nutrient	1	6382.1	39.20	**<0.0001**
	Site x Water	2	14.0	0.09	0.918
	Site x Nutrient	2	145.9	0.90	0.415
	Water x Nutrient	1	2024.5	12.44	**0.001**
	Site x Water x Nutrient	2	10.8	0.07	0.936
Belowground biomass	Site	2	88.6	2.20	0.122
	Water	1	404.7	10.05	**0.003**
	Nutrient	1	1549.4	38.49	**<0.0001**
	Site x Water	2	2.1	0.05	0.948
	Site x Nutrient	2	54.4	1.35	0.269
	Water x Nutrient	1	631.8	15.70	**0.0002**
	Site x Water x Nutrient	2	11.4	0.28	0.755

6.5   Discussion

Understanding the pattern of *Pennisetum setaceum* invasion, and how it may be influenced by climate change, requires data on whether rainfall and temperature currently limit its distribution and spread (Poulin *et al.* 2007). To investigate the role of local adaptation in promoting invasion by *P. setaceum* in South Africa, areas with different climatic regimes were strategically chosen, especially rainfall patterns. These sites vary with respect to climate, soil types and disturbance regime and these differences in habitat resources and environmental resources yield different vegetation composition (Mucina and Rutherford 2006).

The results indicate that nutrients may limit *P. setaceum* growth rates, and this suggests a potential for local adaptation. There was little difference in the invasion success (growth performance) of *P. setaceum* between the three sites studied (see Chapter 4). This could be attributed to disturbance overriding the effects of rainfall and temperature, important factors that determine plant distribution and abundance (Stephenson 1990) and productivity (Sala *et al.* 1988; Weltzin *et al.* 2003b). In addition, it could be that *P. setaceum* easily adapts to varying environmental resources and habitat conditions.
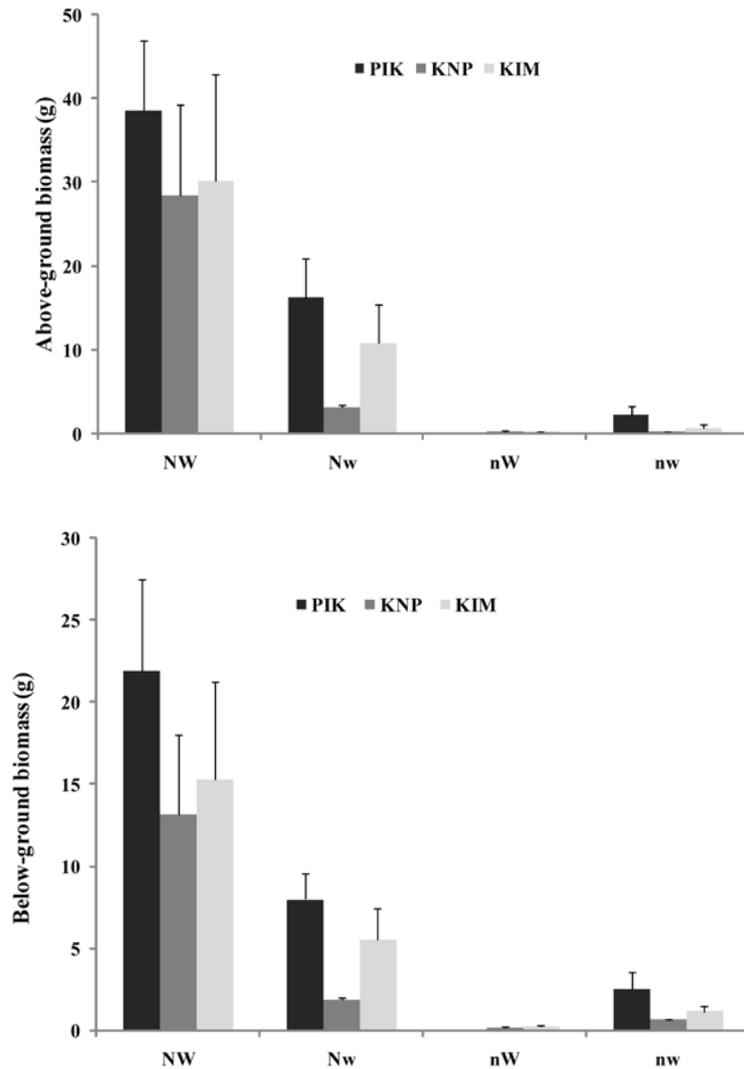
Figure 6−3: Biomass allocation of *P. setaceum* in response to environmental resources of water (high and low) with nutrient addition (yes and no) for the three study sites; NW = nutrient and high-water, Nw = nutrient and low-water, nW = no-nutrient and high-water and nw = no-nutrient and low-water for the three sites: Piketberg (PIK), Karoo National Park (KNP) and Kimberley (KIM). Vertical bars indicate +1 SE.

Broad environmental tolerance promotes the success of alien species in new heterogeneous environment (Williams and Black 1993; Alpert 2006). Local adaptation and phenotypic plasticity are strategies that plants exhibit to cope with new heterogeneous habitats (Joshi *et al.* 2001; Sultan 2001:2004). The performance of *P. setaceum* across these three distinct environments demonstrates its ability to adjust to different conditions prevailing at new locations. This suggests that once seedlings have overcome the critical seedling stage, they are able to grow under hot and arid

environments. *P. setaceum* showed a strong response to extra water availability and nutrient addition, however, and this response was similar for seedlings from different sites. *P. setaceum* seeds can remain viable in the seed bank for six years or more if conditions for germination are not favourable (Tunison 1992). *P. setaceum* seeds germinated within 2 – 5 days if exposed to moderate temperatures with adequate moisture and nutrients (personal observation).

P. setaceum* occurs in a wide range of habitats in parts of the world where it has been introduced (Williams and Black 1993; Williams *et al.* 1995; Joubert and Cunningham 2002). These results reveal that *P. setaceum* possesses a number of traits that promote its invasiveness, including abundant seed production under a wide range of environmental conditions. Lack of differences in vegetative and reproductive responses between sites suggests local adaptation to and/or individual tolerance of varying moisture and nutrient regimes. The results show that *P. setaceum* can survive unfavourable conditions and show increased growth rates in better conditions, a characteristic that would promote its invasion. Seedling recruitment by *P. setaceum* in the greenhouse was more strongly influenced by nutrient addition than water. These findings suggest that occasional wet years may promote *P. setaceum* invasion, especially in areas of high nutrient accumulation such as road-river interchanges. These results emphasize the importance of ecological studies that cover contrasting areas, especially in temperature and disturbance patterns, and are repeated over longer time periods, to develop a better understanding of how habitat conditions and environmental resource regimes affects the invasion dynamics of this grass.

CHAPTER 7

POTENTIAL DISTRIBUTION AND SPREAD OF AN INVASIVE ALIEN GRASS,
PENNISETUM SETACEUM, IN WESTERN SOUTH AFRICA

7.1   Abstract

Predicting the likelihood of invasion success by matching climate data and species current distribution data is important in alien species management. The invasion potential could further be exacerbated by spread in semi-natural areas due to disturbance. Climate matching and probability dynamic spread approaches were used to determine the future potential distribution and potential spread of *Pennisetum setaceum*, respectively. The study has revealed that the invasive alien grass *Pennisetum setaceum* has not reached its full distribution potential under current climatic conditions in South Africa. In general, the climate matching predicts the fynbos, Albany thicket and savanna biomes as high risk areas for invasion by *P. setaceum* under climate change. Removal of standing populations along roadsides especially those near high disturbed areas should be of high priority. Infestations at high disturbance areas such as road/river interchanges should also be targeted, especially in areas of low climatic suitability and spread.

7.2   Introduction

Biological invasions are a major cause of biodiversity loss worldwide (Strayer *et al.* 2006; Ricciardi 2007). Predicting which areas are most susceptible to invasion under climate change scenarios is important in planning, management and control of biological invasions. However, predicting whether a habitat is vulnerable to invasion is especially challenging in natural ecosystems, since the interactions of many species and ecosystem processes are poorly understood (Stohlgren and Schnase 2006). Also, climate change may increasingly affect the potential distributions of species and render other areas vulnerable to invasion (Peterson *et al.* 2003; Thuiller *et al.* 2007). Due to limited management resources, choices must be made about which species to select and where best to focus control and management efforts (Nel *et al.* 2004). Further introductions could be minimized by identifying and modifying the causal factors of invasion (Taylor and Irwin 2004).

Climate and habitat suitability matching for invasive alien species may play important roles in invasion management (Ficetola *et al.* 2007). This requires knowledge of the climatic conditions favourable for the invasive alien species in question (Stohlgren and Schnase 2006). Species distribution models (bioclimatic models) involve species-environment relationships and determine potential future ranges for biological invasions (Guisan and Zimmermann 2000; Rouget *et al.* 2004; Guisan and Thuiller 2005; Thuiller *et al.* 2005). However, other factors such as species' life history traits, disturbance and biotic interactions may override climatic factors (Rejmánek and Richardson 1996; Reichard and Hamilton 1997; Hulme 2003).

Ornamental horticulture has been identified one of the most important pathways for plant invasions in many areas (Reichard and White 2001; Pimentel *et al.* 2005; Dehnen-Schmutz *et al.* 2007). Plant breeders often select plants for introduction based on the same traits that are associated with invasion potential (Anderson *et al.* 2006). Grasses are one set of plants actively moved by humans around the world for many reasons, so invasions are common (D'Antonio and Vitousek 1992). Grasses therefore provide an important platform to understand the role of humans in determining plant distribution ranges.

The objective of this study was to determine the overall distribution range and invasion risk of *P. setaceum* under climate change in South Africa. This was done by addressing the following four-step process; 1) determine current distribution using all climatic parameters including suitability; 2) determine present suitability using only parameters which were available for different climate change scenarios; 3) generate suitability maps for two climate change scenarios (A2 and B2) derived from the Hadley Centre for Climate Prediction and Research (see details in Thuiller *et al.* 2005), a no change scenario (NR) and the current day climate scenario using all variables (PR) for the years 2000, 2050 and 2100 (Thuiller *et al*. 2005). The suitability maps were then linearly extrapolated for the years in between; 4) linearly extrapolate the suitability maps for the years in between from (2) and (3) as the basis of a dynamic, deterministic and probabilistic spread model to predict the risk of all cells being invaded for the next 100 years.

7.3 Data and models

7.3.1 P. setaceum *data and distribution*

Fountain grass *(Pennisetum setaceum)* is a widely distributed invasive C4 perennial bunchgrass from the North African arid Mediterranean area of the Atlas Mountains and Middle East. Although the grass has a limited natural range along the Saharan and Mediterranean Coast, it invades many natural habitat types and broad altitudinal ranges and occurs under varying rainfall and water conditions (Williams and Black 1994; Joubert and Cunningham 2002) and varying soil types. This grass has been introduced to many parts of the world as an ornamental plant and has been used in mine dump stabilization in South Africa and elsewhere. It has subsequently escaped in many places (Henderson 2001; Williams *et al.* 1995; Milton *et al.* 1998). Potential for the spread of *P. setaceum* throughout South Africa is particularly alarming because of the negative impacts associated with its occurrence in arid areas of South Africa (Rahlao *et al.* 2009).

To estimate the distribution of *P. setaceum* in South Africa, sampling was conducted along selected major roads since this is where *P. setaceum* currently occurs in abundance and roads are easily accessible for sampling. The roads surveyed traversed through all biomes of South Africa. The survey recorded the presence and absence of the grass at sampling sites at 10 km intervals in a 1 km transect and covered the western part of South Africa (Figure 7-1, see also Chapter 3 for more details on the road survey). The geographical coordinates of all transects were captured in a Garmin Version 2.01 GPS.

7.3.2 *Potential current climate suitability*

The modelling approach used to estimate the climatic suitability of *P. setaceum* under current climate conditions uses non-random correlations between species occurrence (as longitude/latitude coordinates) and environmental data (as GIS coverages) to identify those areas of the landscape presenting suitable ecological conditions for the species under both present-day and future climates (Heikkinen *et al.* 2006).
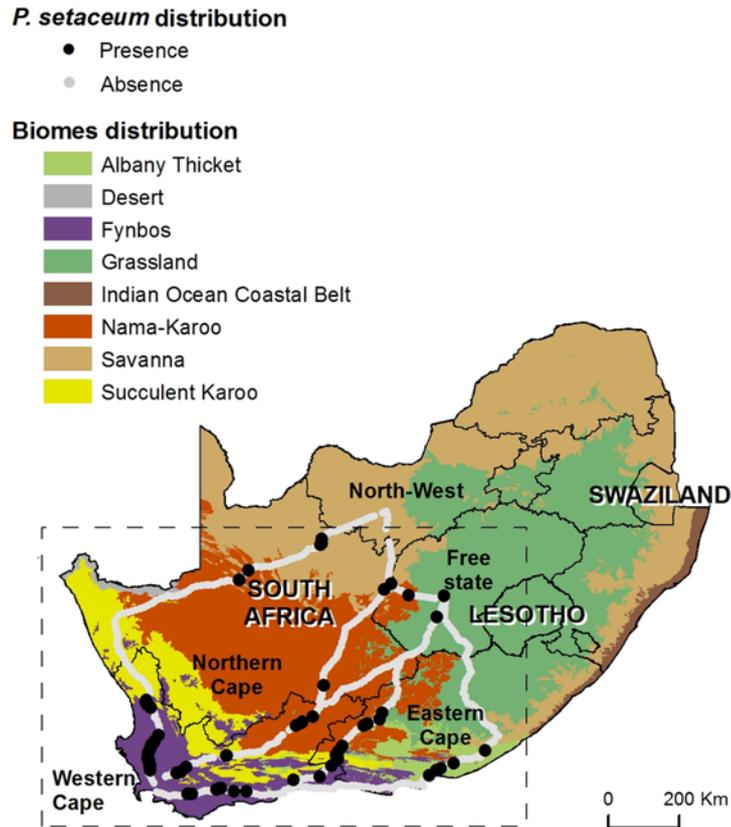
Figure 7-1: Position of sampling sites in South Africa's provinces (black dotted lines) and biomes. The grey line shows the roads sampled in 10km intervals; black dots indicate where the species is present. The dashed box line indicates western South Africa, the focus of both the survey and the model predictions. The different colours indicate major terrestrial biomes from Mucina and Rutherford (2006).

The technique applied to estimate the potential distribution of *P. setaceum* was the generalized boosted model (GBM) method (Friedman 2001), implemented into an R software-based BIOMOD application (Thuiller 2003). Contrary to most classical approaches that produce single parsimonious models, GBM uses an interactive method (the boosting algorithm) to fit a large number of relatively simple regression trees, whose predictions are then combined into one final ensemble prediction (Friedman and Meulman 2003). Regression trees are built by splitting the calibration data repeatedly, according to a simple rule based on a single explanatory variable. At each split, the data are partitioned into two separate groups which are as homogeneous as possible. The heterogeneity of a group is defined with a deviance notion that can be interpreted as the deviance of a multinomial model (Breiman *et al.* 1984). The boosting is used to overcome the inaccuracies of single models (see Araújo and New

2007), and makes it possible to model a complex response surface. For more details or applications in ecology see Ridgeway (1999), Friedman (2001), Elith *et al.* (2006), and Leathwick *et al.* (2006).

Occurrence data derived from the road survey, consisting of 66 presences and 563 absences, were divided randomly into training (70%) and testing (30%) datasets to calibrate and evaluate the performance of models, respectively. Because the prevalence of presence data was lower than absences, the number of absences was reduced to the same number of presences to avoid problems related to differences in prevalence.

The training occurrence data set was combined with available precipitation and temperature data (Schulze *et al.* 2001) on a 1 x 1 minute grid. Climate data included number of frost days (frd), annual potential evapotranspiration (pet), mean annual precipitation (map), precipitation concentration (pc), growing degree days (annual temperature sum above 10°C; gdd10), precipitation seasonality (ps), minimum temperature of the coldest months (mntc), maximum temperature of the warmest months (mxtw), mean annual temperature (mat). The occurrence data set aside from model development (30%) was used to calculate the area under the curve (AUC) of the Receiver Operator Characteristic (ROC), which evaluates model performance independently of the arbitrary threshold of the prediction (Thuiller *et al.* 2006a). Following the scale of Swets (1988), prediction was considered random when it did not differ from 0.5, poor when it was in the range 0.5 – 0.7, and useful when in the range 0.7 – 0.9. Predictive accuracy greater than 0.9 was considered good to excellent (1= perfect). AUC values under 0.5 reflect counter-predictions (omission and commission rates higher than correct prediction). Because of the incomplete sampling in eastern and north-eastern parts of the country, predictions were restricted to western South Africa (Figure 7-1) to avoid the projection of the model into areas outside the range of calibration (Randin *et al.* 2006). Additionally, this helped assure that the range of environmental conditions covered by the road sampling by the road sampling was also representative of the rest of the region. Because of the sensitivity of the model to the input data, ten replicate models were generated varying the original set of occurrences used to calibrate the model. The final predictions were averaged, as well as the influence of the different variables and the performance of the models.

7.3.3 Potential climatic suitability

To evaluate changes in the future climatic suitability of *P. setaceum* under current climate change, the previous exercise was repeated using a reduced set of climatic variables (Table 7−1) which were available for both the present and the future climate scenarios and projected the model into two different scenarios of future climate change for 2050 and 2100. Ten replicate models were then developed based on the current distribution of naturalized individuals of *P. setaceum*, by randomly re-sampling the occurrence data into training (70%) and testing (30%) proportions. Once developed, each set of ten replicate models was also projected onto present-day climatic conditions (to test the performance of the models), and also onto future climates for 2050 and 2100 derived from two different emission scenarios (A2 and B2) of the Hadley Centre for Climate Prediction and Research. The climate change scenario A2 (HadCM3A2) assumes a 1% yr^{-1} CO_2 increase and does not take into account effects of sulphate aerosols while B2 (HadCM3B2) assumes 0.5% yr^{-1} CO_2 increase and incorporates sulphate aerosols forcing. These represent relatively serious and less serious climate change scenarios respectively. Each set of replicate predictions was finally averaged at equal proportions to obtain ensemble predictions for each scenario and time period, resulting in suitability maps for the two climate change scenarios (A2 and B2), no climate change (NC) and, from section 1.3.2 (above), a suitability map based on the present day data (PR). For each of those, projected predictions for 2050 and 2100 were done (for NC and PR the ones for 2050 and 2100 are identical to the ones for 2000).

7.3.4 Dynamic spread model

P. setaceum is known to spread naturally mainly through wind and by cars along roads and downstream along rivers (Jacobi and Warshauer 1992). To determine the role of natural spread on the species' distribution a deterministic, dynamic and probabilistic spread model was developed. In this study, it was assumed for simplicity that the spread rate and dispersal distance of *P. setaceum* is similar everywhere in all directions, although it is acknowledged that this might not be a realistic assumption, given its dispersal along river and road corridors. The dynamic spread model was then used to determine the spread rate and adjusted the suitability away from roads and along rivers to account for disturbances. Four different

scenarios of climatic suitability (A2, B2, NC and PR) were incorporated into the spread model to determine the spread of the species away from the roads. A2 and B2 consider changes in future climatic conditions for the next 100 years under the two different emission scenarios of the Hadley Centre for Climate Prediction and Research (HadCM3), NC is the no climate change scenario that only considers current climatic conditions, and PR is the present distribution based on all data including additionally rainfall seasonality. The first three scenarios of climatic suitability were developed in the previous section, but the last one does not incorporate any prediction assessing the potential climatic suitability of the species. The suitability map is based on presence - absence points along the roads. *P. setaceum* rarely spreads into the areas away from the road even in areas where it occurs. The absence of disturbance away from the roads could be the main reason it is not spreading. Therefore, the absence of disturbance decreases the suitability of the sites away from roadsides. As one does not know by how much suitability is reduced, different reduction scenarios were introduced. To account for this observation, and the fact that all observation points are along roads, suitability away from the roads was reduced by multiplying them with the factor r = 1, 0.5 and 0.25. The suitabilities along perennial rivers were multiplied by 1, 0.75 and 0.625 respectively, representing the half point between 1 and r.

Climatic suitability maps for the climate change scenarios were only available for 2000, 2050 and 2100; therefore the suitability maps for the intermediate years were linearly interpolated in the spread model. The dynamic spread model is based on Roura-Pascual *et al.* 2009. It is a deterministic and probabilistic model, predicting the probability of occupation of the cells based on the suitability maps and parameters determining spread, extinction and colonisation rate. Using a time step of one year, the transition rate of the occupancy probability is:

$$
\begin{aligned}
P_{i,j}\left(t+1\right) &= \left(1 - e_{i,j}\right) P_{i,j}\left(t\right) \\
&+ \frac{c_{i,j}}{\left(2z+1\right)^2 - 1} \cdot \left(1 - P_{i,j}\left(t\right)\right) \left(\left(\sum_{x=i-z}^{i+z}\sum_{y=j-z}^{j+z} P_{x,y}\left(t\right)\right) - P_{i,j}\left(t\right)\right) P_{i,j}\left(t\right)
\end{aligned}
$$

where is the probability, that the cell (i, j) is occupied at time t, $e_{i,j}$ is the extinction rate and $c_{i,j}$ the colonisation rate. As in Roura-Pascual *et al.* 2009, I chose $c_{i,j} = 1\text{-exp}$ $(-5Q_{i,j})$ and $c_{i,j} = \exp(-5Q_{i,j})$ with $Q_{i,j}$ being the suitability of the cell, as described by the different suitability maps. Based on observations in the field, the dispersal distance z was set to one cell, which approximates 1.6km, which is the observed

distance of *P. setaceum* dispersal by wind (personal observation). The model was evaluated for the three different climate change scenarios (A2, B2, NC) and the present day suitability map (PR) for the time period of 100 years (2000 to 2100).

7.3.5 Analysis of dynamic model

The climate suitability maps and reduction scenarios were used due to missing measures of disturbance to obtain suitability maps which include disturbances based on roads and rivers. To obtain an indication of the impact of the reduction factor, five different reduction factors were used for obtaining the suitability maps from the climate suitability maps: 1, 0.5, 0.25, 0.125 and 0.0625 and the results were compared. In addition, to make the comparison of the temporal change for each year, the number of occupied cells was compiled by classifying cells larger than a given threshold as occupied and counting those. The percentage change in suitability and occupancy was compared between these reduction scenarios per biome. The spread of the species was then determined by the ratios of the number of occupied cells for the 0.05 threshold under different climate change scenarios. This was done by dividing the number of cells occupied (>threshold) in the scenarios in which the climatic suitability was reduced away from the roads by the scenario with the original suitability.

7.4   Results

7.4.1 Potential current climate suitability

The model used for predicting the current climatic suitability of *P. setaceum* in western South Africa had a mean AUC of 0.74 (Table 7−1, Model 1), which indicates that the model provides useful estimates of the species current distribution. The most influential (> 15%) variables were four: number of frost days (*frd*), annual potential evapotranspiration (*pet*), mean annual precipitation (*map*) and precipitation concentration (*pc*).

Table 7−1: Relative influence of variables used in the different models to predict the climatic suitability of *Pennisetum setaceum* for current and future climates. Environmental variables

correspond to: *frd* = frost days; *pet* = annual potential evapotranspiration; *map* = mean annual precipitation; *pc* = precipitation concentration; *gdd10* = growing degree days (annual temperature sum above 10˚C); *ps* = precipitation seasonality; *mntc* = minimum temperature of the coldest months; *mxtw* = maximum temperature of the warmest months; *mat* = mean annual temperature.

Model 1 (AUC = 0.74)		Model 2 (AUC = 0.78)	
Variables	Relative influence (%)	Variables	Relative influence (%)
pet	20.59	*pet*	32.52
map	19.06	*map*	27.97
gdd10	9.66	*gdd10*	24.21
mntc	4.02	*mntc*	15.11
frd	21.61		
pc	15.58		
ps	5.68		
mxtw	3.57		
mat	0.22		

Predictions for entire South Africa as a whole suggest higher suitability (18.68%) of *P. setaceum* in the savanna biome (Figure 7−2), followed by succulent-karoo (4.09%) and fynbos (3.29%). Relative to biome size, the Albany thicket is the most suitable (90.75%) followed by succulent karoo (58.24%) and savanna (57.94%) respectively (Table 7−**2**). Despite high sampling (0.54%) and current high invasion (20%), the fynbos biome has relatively lower suitability (46.97%) for *P. setaceum*. The desert (0.12%) and grassland (3.53) biomes are the least suitable for *P. setaceum* (Table 7−**2**).
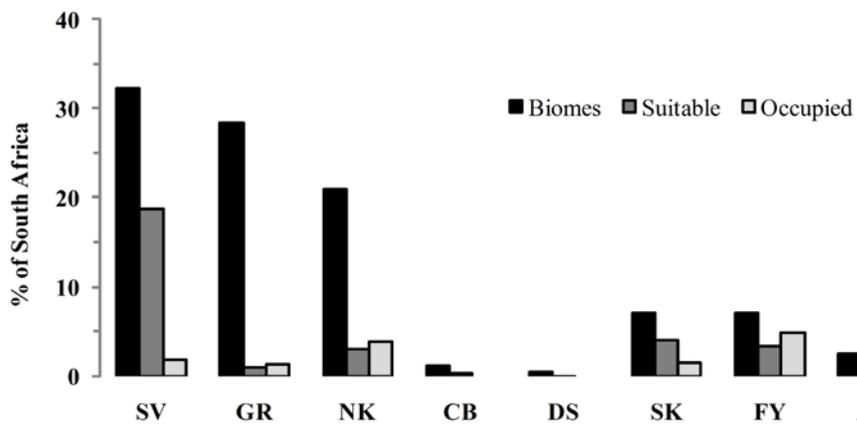
Figure 7−2: The percentage of South Africa as occupied by each biome, the area predicted to be suitable for (climate matching), and predicted to be occupied by (dynamic spread model) *Pennisetum setaceum* per biome size under current climatic conditions. Biomes: SV = savanna; GR = grassland; NK = Nama karoo; CB = Indian Ocean coastal belt; DS = desert; SK = succulent karoo; FY = fynbos; AT = Albany thicket. Cells are classified as "suitable" if the suitability value is larger than a threshold suitability value (the value above which 95% of individuals occur). The threshold for current climate conditions (no climate change) is 0.45.

Table 7−2: The number of cells for each biome indicating the size of the biomes, sampled and invaded cells by *P. setaceum* during the field survey, the predicted suitability and occupancy percentage under current climatic conditions and biome size as predicted by climate matching and dynamic spread models respectively in South Africa.

Biome	Biome size	Number of cells		Percent (%)			
		Sampled	Invaded	Sampled	Invaded	Suitable	Occupied
Savanna	136014	73	5	0.05	6.85	57.94	5.78
Grassland	119810	87	2	0.07	2.30	3.53	4.65
Nama karoo	88185	216	12	0.24	5.55	14.35	18.81
Coastal belt	5249	0	0	0.00	0.00	23.47	0.00
Desert	2404	2	0	0.08	0.00	0.12	0.00
Succulent karoo	29657	49	6	0.17	12.24	58.24	21.37
Fynbos	29588	160	32	0.54	20.00	46.97	70.96
Albany thicket	10970	30	8	0.27	26.67	90.74	51.63
All	421877	617	65	0.15	10.53	32.72	14.94

7.4.2 Potential future climate suitability of P. setaceum *under climate change*

All variables had a relatively high importance in the calibration of the model, but the most influential (> 24%) ones were: annual potential evapotranspiration (*pet*), mean annual precipitation (*map*) and the growing degree days (*gdd10*). The areas predicted by this model as climatically suitable for the species considering the current climate (Figure 7−3, NC) are similar to those predicted by the climate matching model using a broader number of climatic variables (Figure 7−3, PR). However, the model predicts a lower climatic suitability at the north-western coast and some inland areas.

Climatic suitability

0.2- 0.3   0.9 - 1
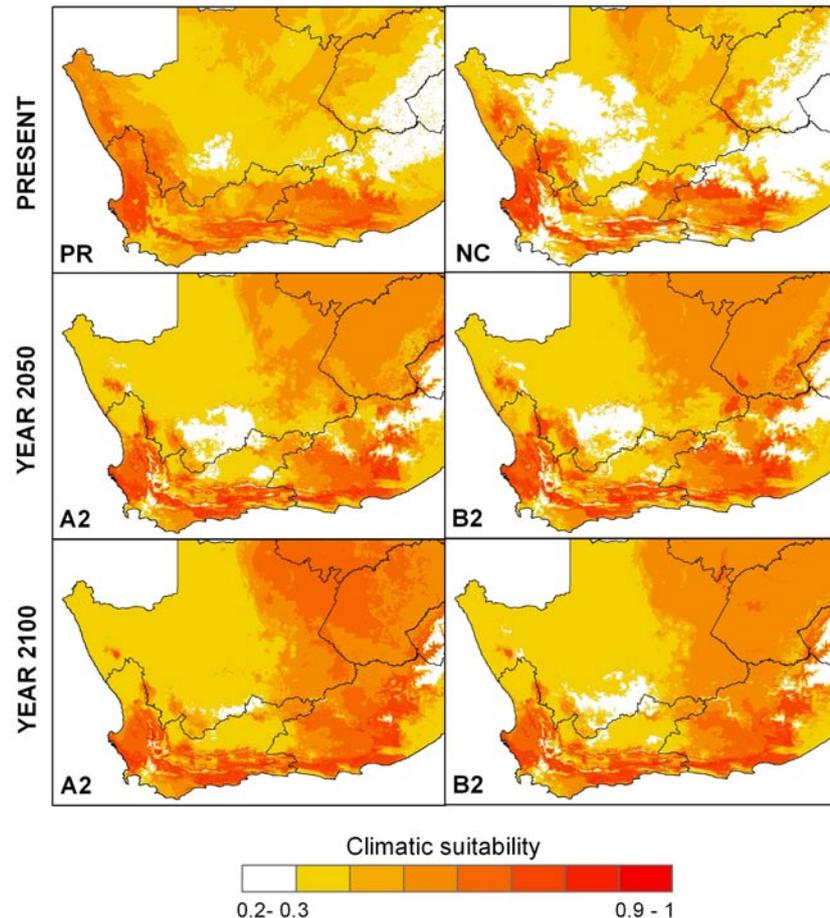
Figure 7−3: Predicted climatic suitability of *Pennisetum setaceum* under current climatic conditions and the two climatic scenarios of climate change (A2 and B2) for years 2050 and 2100 generated using boosted regression trees. The first row indicates the predicted distribution for present climates using all climatic variables (PR, on the left), and the predicted distribution for the present climate using only a subset of the climatic variables (NC, right). NC is the model that has been used to predict future climate scenarios (last two rows). This model has been calibrated using a subset of variables used in the model presented in Figure 7-1 due to data limitations.

In terms of future scenarios of climate change, predictions suggest a similar increase in the areas suitable for the species under both A2 and B2 scenarios (Figure 7−3). While areas along the north-western coast are predicted to become less suitable for *P. setaceum* in the future, most of the areas in the Western Cape will remain quite stable and central-eastern part of this study area will progressively become more suitable. In general, the model predictions under A2 and B2 scenarios suggest that the fynbos, savanna and Albany thicket will remain the most suitable biomes in both 2050 and 2100 climates. Arid areas of the Nama- and succulent karoo biomes in both 2050

and 2100 are however, predicted to become less suitable (Figure 7−3). The succulent karoo in particular, has a declining suitability for *P. setaceum* (Figure 7−4).
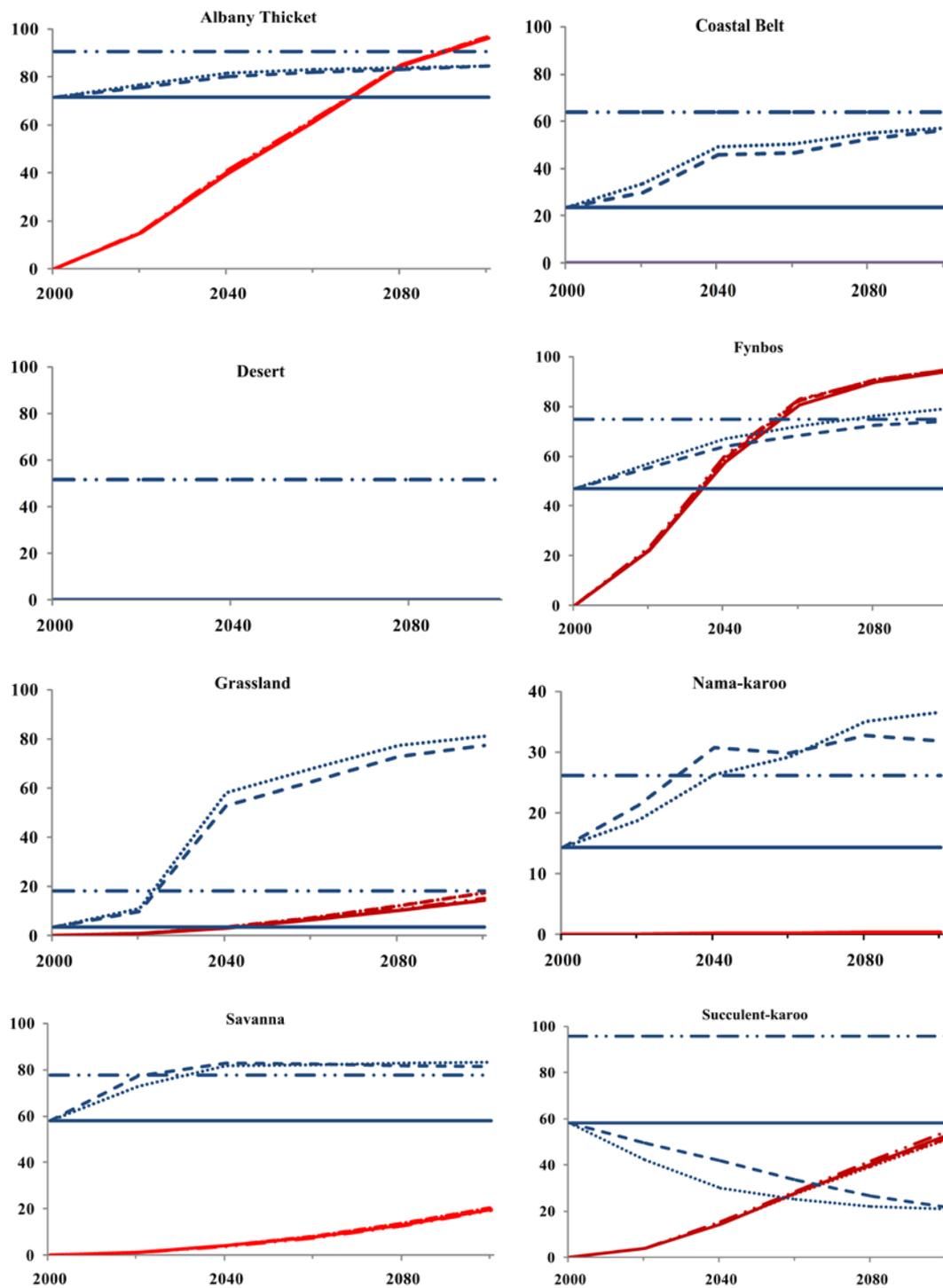
Figure 7−4: The percentage of cells per biome suitable for *Pennisetum setaceum* (blue lines) and invaded as predicted by the dynamic probabilistic spread model (red lines) in different biomes. Solid lines indicate no climate change (N), dotted and dashed lines indicate two

climate-change scenarios, A2 and B2, respectively and dotted with dashed lines indicate the current climatic conditions (PR) with all climatic variables including rainfall seasonality. The x- and y-axes represent the percentage of cells per biome and years respectively for all the graphs. Suitability thresholds are 0.45 for A2, B2 and 0.41 for NC.

7.4.3 Potential spread under different suitability reduction scenarios

In order to account for lack of disturbance regimes, suitability reduction scenarios were introduced to estimate the effect of reduced disturbance away from roads on *P. setaceum* spread. The result was a reduced probability of *P. setaceum* performance with distance from road verges (Table 7−3). The dynamic spread model predicted low probability of occupancy (spread) by *P. setaceum* in biomes of low climatic suitability under no reduction scenario (100% suitability) in 2050 and 2100, notably, the savanna and grassland biomes, despite high habitat suitability due to climate change. The succulent karoo on the other hand exhibits increasing probability of spread away from roadsides despite a declining suitability (Figure 7−4). The fynbos and Albany thicket biomes with high predicted habitat suitability have high probability of spread away from roadsides.

7.5   Discussion

Predicting the likelihood for invasion success by matching climate data and species current distribution data is important in alien species management (Kolar and Lodge 2001; Ficetola *et al*. 2007). Climate change interacts with other existing stressors to affect the distribution, spread, abundance, and impact of invasive species (Gritti *et al*. 2006). In this study a climate matching modelling approach was used to determine the potential distribution of *P. setaceum* in South Africa under current and future climates.

Table 7−3: Predicted change in the number of cells occupied by *Pennisetum setaceum* under different climate change and habitat suitability reduction scenarios for 2050 and 2100. The proportion of reduction in spread of the species was determined by the difference in the number of occupied cells in the scenarios in which the suitability was reduced away from the roads from the scenario with the original maximum suitability (100%). Climate-change scenarios: A2 (temperature rise by 2.8ºC in 2080), B2 (temperature rise by 2.1ºC in 2080), NC (no climate-change); PR (current climate using all the available climate change variables

including rainfall seasonality) and suitability reduction scenarios away from the roads (50%, 25% and 3.125%).

Climate change scenario	Year	Suitability reduction scenarios					
		100%	50%	25%	12.5%	6.25%	3.125%
A2	2050	65168	0.66	0.22	0.08	0.04	0.03
	2100	143101	0.71	0.26	0.09	0.04	0.03
B2	2050	65275	0.66	0.22	0.08	0.04	0.03
	2100	143130	0.71	0.24	0.09	0.04	0.03
NC	2050	63019	0.60	0.20	0.07	0.04	0.03
	2100	136566	0.62	0.19	0.06	0.03	0.02
PR	2050	65387	0.65	0.21	0.07	0.04	0.03
	2100	139562	0.67	0.21	0.07	0.04	0.03

7.5.1 Current P. setaceum *potential distribution in South Africa*

The initial survey has shown that only around 10 % of South Africa is invaded by *P. setaceum* (

Table 7−**2**). This suggests that the species has not reached its full distribution range, given that the areas predicted as suitable for the species under current climates are considerably bigger, nearly 33%. The variables used for the climate matching model have been able to predict the current climatic suitability of the species in South Africa (Table 7−1). Despite high sampling levels in the Nama karoo, that biome is less invaded (6%) and shows relatively low suitability (about 14%) to invasion. The desert and the Indian coastal belt biomes show the least suitability under current climatic conditions although the low suitability increases with climate change in the coastal belt.

7.5.2 Impact of climate change on P. setaceum *potential distribution*

Climate change affects ecosystems in many ways, including through shifts in species geographic ranges (Thuiller *et al*. 2007). The climate matching model has predicted an increase due to climate change in the area suitable for *P. setaceum* in most biomes,

notably savanna and Albany thicket (Figure 7−4). However, there is more than a 36% decline under climate change in the area projected as suitable in the succulent karoo biome. The grassland biome has a low suitability for *P. setaceum* under current climatic conditions, but the suitability increases to 81% in 2100 under predicted climate change. The fynbos biome has a currently higher invasion (nearly 47%) and this area is projected to increase due to climate change (to 79% in 2100). This result is not surprising as the grass originates from the Mediterranean region of North Africa (Williams *et al.* 1995; Williams and Baruch 2000). However, unlike other C4 perennial grasses such as *Themeda triandra*, it is better adapted to winter rainfall regions. The Albany Thicket currently has high suitability for *P. setaceum* and this remains stable until 2100 under climate change (Figure 7−4). In general, the climate matching predicts that fynbos, Albany thicket and savanna biomes are high risk areas for invasion by *P. setaceum* under climate change. The succulent and Nama karoo biomes are predicted as low risk areas. This may be because *P. setaceum* performance appears to be controlled largely by soil moisture in South Africa (Rahlao *et al*. 2009; chapter 5). These results suggest that the grass will be confined to areas with higher annual rainfall for growth.

Other factors other climate could play a role, hence the low suitability in areas where the survey (Figure 7-1) found *P. setaceum*. These factors could include disturbance, especially along roads where *P. setaceum* could establish despite predicted low suitability. This could also be due to the limited number of *P. setaceum* occurrence data points there.

7.5.3 Spread of P. setaceum *away from roadsides*

Models that predict alien species distributions based on the climate in native and potential introduced ranges are essential for species' future spread predictions (Pattison and Mack 2008). Due to lack of disturbances measure away from roadsides where *P. setaceum* occurs, suitability reduction scenarios were introduced. The probabilistic dynamic spread model predictions are based on the climate matching model. The limited number of occurrences along roads could affect precision in this model. The model assumed natural dispersal by wind away from roadsides. However, other factors such as vehicles and water down rivers can disperse *P. setaceum* seeds (see Appendix).

The dynamic spread model predicted high probability of spread in areas of low climatic suitability (Figure 7−4). This result suggests that other factors (not climate), such as disturbance play a major role in *P. setaceum* distribution. Disturbance is crucial in facilitating growth and hence in promoting ecosystem invasion (Brooks *et al.* 2004). These results suggest that *P. setaceum* can spread away from roadsides into semi-natural areas. This suggests that if not controlled and managed, *P. setaceum* would spread to areas where it is presently absent. The dynamic spread model results could suggest that increased disturbance regimes away from roadsides will promote the spread of this grass, and that this may be exacerbated by climatic suitability. Disturbances such as mining operations, overgrazing and road cuttings, especially away from roadsides, are all likely to promote *P. setaceum* performance. These disturbed areas provide suitable habitats that could increase propagule pressure and hence increase invasion risk. Control of *P. setaceum* at roadsides and disturbed areas should be of high priority to prevent further spread.

A number of factors could affect the reliability of climate-matching models and hence the conclusions need to be treated with some caution. Since suitability predicted by these models is based on the distribution of *P. setaceum*, the predicted suitability could be an underestimate as the species may still be spreading, and thus not be in equilibrium with the environment. The sample size of 10% presences (

Table 7−**2**) could also have affected both models' predictive performances (Peterson *et al.* 2003; Araújo *et al.* 2005b; Heikkinen *et al.* 2006). The selection of climatic variables depended on the availability of those parameters both for present and future. Only a subset of variables was used (Table 7−1) in the final climate-matching model to determine suitability and some important climate variables such as rainfall seasonality were only available for current distribution predictions. Also, the reduced number of presences was used to match the number of absences. The performance of the model will improve in the future when more occurrence data are available.

Furthermore, many factors other than climate may influence the performance and subsequent invasion by invasive alien species (Thuiller *et al.* 2006b). These factors include propagule pressure, habitat conditions, environmental resources and their interactions, and disturbance (Kolar and Lodge 2001; Lockwood *et al.* 2005; Hierro *et al.* 2006). Species traits could also have an effect on the performance and reliability of bioclimatic models (Poyry *et al.* 2008).

The type of probabilistic dynamic spread modelling approach used does not incorporate management scenarios for the better understanding of different control efforts. However, it does provide an indication of rates of spread into areas away from roadsides following disturbance. These limitations need to be considered when evaluating model predictions, especially when projected to future climates. Models projected to future climates need to be regarded with caution, since there are numerous uncertainties associated with these modelling practices (Heikkinen *et al*. 2006). Despite all these caveats, the utility of climate-matching approaches is in their ability to provide a coarse estimate of the climatic suitability of species.

7.6   Conclusions

Despite some uncertainties in the model parameters, the study has been able to predict the potential distribution and spread of *P. setaceum* under different climate change scenarios in South Africa. The invasion potential of the grass will further be increased by changing climate. Should the species spread from where it currently occurs along roads, rivers and mine dumps, its growth is unlikely to be limited only by climate. In order to mitigate the potential economic and ecological impacts of *P. setaceum* on vulnerable ecosystems in South Africa, management and control efforts should focus on reducing propagules especially at these high risk areas identified by both models. Removal of standing populations along roadsides, especially those near highly disturbed areas, should be of high priority. This will assist in reducing the rate at which it could disperse to uninvaded sites. Infestations in areas of high disturbance, such as road/river interchanges, should also be targeted in areas of lower climatic suitability. This observation stresses the importance of implementing an early detection and eradication plan for this species within areas with the potential for further spread.

CHAPTER 8

EFFECTS OF INVASION OF FIRE-FREE ARID SHRUBLANDS BY A FIRE-PROMOTING INVASIVE ALIEN GRASS (*PENNISETUM SETACEUM*) IN SOUTH AFRICA

8.1 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*. Ten plots (5 x 10 m) separated by 2.5 m were established, 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). Plant species and their cover before and after burning on each of the plots were recorded. 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. The 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.

8.2 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 and Tunison 1992; Mack and D'Antonio 1998; Rossiter *et al.* 2003; Brooks *et al.* 2004). Grasses have been easily moved around the world, and many are now common invaders that cause irreversible alterations to fire regimes in many ecosystems (D'Antonio and 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).

Invasive alien 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 and Dean 1998; Milton *et al.* 1998; Bromilow 2001; Joubert and 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 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 recolonise 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 and Hanrahan 1993), droughts (Milton *et al.* 1995) and grazing (Todd and 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 and 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. This paper reports 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.

8.3   Methods

8.3.1   Study area

The study was undertaken at the 100 ha Tierberg Karoo Research Centre ($33^0$09'S, $22^0$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. 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/yr); 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 (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.

8.3.2   Experimental design

Ten plots of 5 x 10 m separated by 2.5 m buffer zones in natural vegetation were established. 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 and the other half with 10 tons/ha. 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, and that grass fuel loads seldom exceed 12 tons/ha. Five to ten tons/ ha were added 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 m to 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.

8.3.3 *Vegetation sampling*

Prior to burning, herbaceous canopy cover was measured for each treatment plot (Figure 8−1A). These surveys were done 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, five meters 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 m² plot for each survey period.

8.3.1 *Experimental fires*

Tufts of *P. setaceum* were placed systematically within interspaces in an upright position propped up against the karoo shrubs (Figure 8−1B). This increased the total fuel load (including natural vegetation) to 8 and 13 tons/ha 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 hr 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 (Figure 8−1C). 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), H is heat yield (J/g), w the mass of fuel combusted (g/m) and r the rate of spread of the fire front (m/s) (Byram 1959). As almost all of the grass fuels and other plant material were consumed in the experimental burns, the pre-fire grass plus the estimate for standing air-dry biomass mass, 3.27 tons/ha (Milton 1990) were used as equivalent to fuel consumed.
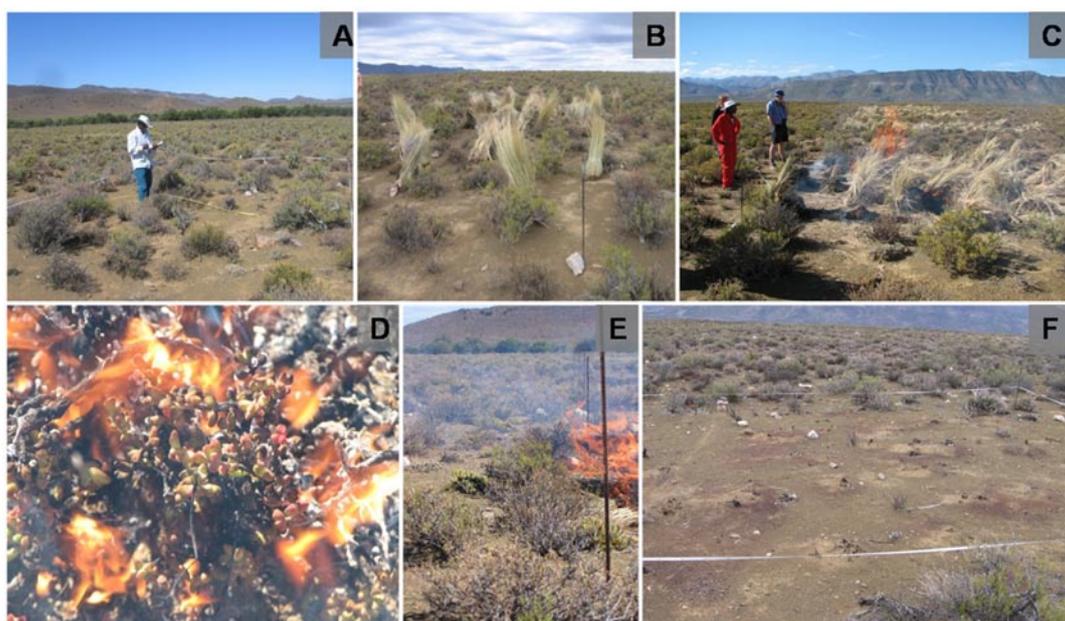
Figure 8−1: A) The pre-burn vegetation survey, B) mature tussocks of *Pennisetum setaceum* were harvested along roadsides in and near the town of Prince Albert and to simulate invasion of *P. setaceum*, tufts were placed among the karoo shrubs at a loading of 5 t/ha and 10 t/ha next to the karoo shrubs. 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, e.g. *Gazania krebsiana* and dwarf shrubs, e.g. *Tripteris sinuata* resprouted.

Nomenclature follows Germishizen and Meyer (2003).

8.3.2 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 and 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 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 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.

8.4 Results

8.4.1 Fire characteristics

The heat yield (corrected for incomplete combustion) of *P. setaceum* was 15765 J/g. The fuel moisture contents were consistently low (<1%) across all samples (Table 8−1). The mean rate of fire spread was also low (0.034 m/s) and did not differ (t = -0.913, df = 8, $p = 0.39$) between low and high fuel loads. Fireline intensity (kW/m) was significantly higher (t = - 2.725, df = 8, $p = 0.026$) in high fuel loads than in low fuel loads (mean, 894 and 427 kW/m 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 (Figure 8−1D) and the fire did not burn beyond the plots into the surrounding natural shrubland vegetation where fuel was not added (Figure 8−1E).

Table 8−1: Fuel and fire behaviour characteristics associated with experimental fires on 5 x 10 m plots in the Nama - succulent karoo interface. 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 1,000 gm^{-2} respectively for the low and high fuel load treatments).

Fuel load	Dry mass (gm^{-2}) (± 1 SE)	Fuel moisture (%) (± 1 SE)	Rate of spread (m/s) (± 1 SE)	Fireline Intensity (kW/m) (± 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)

8.4.2   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, df = 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 *Ruschia 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.

8.4.3   Responses of vegetation to fire

The mass of added fuel load (high or low) did not influence (F = 0.24, df = 20.8, *p* = 0.79) vegetation recovery rates after fire during the study period on burned plots (Table 8−2). 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, due to seasonal dieback of above-ground plant parts. Both the leaf succulent shrubs and non-succulent shrubs remained unchanged on these control plots (Figure 8−3a, b).

The burned plots remained bare for most of the study period after fire (Figure 8−1F) except for cover of the only two resprouting species (*Tripteris sinuata* and *Gazania krebsiana*) that rapidly recovered to pre-burn levels after fire ($p = 0.68$) decreasing over time as dry conditions prevailed (Figure 8−2b). 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 (Figure 8−3c).

Table 8−2: 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	df	MS	F-value	p - value	Significance level
Total cover						
Treatment	106.9	1	106.90	2.17	0.18	NS
Time	3042.5	2	1521.31	66.45	<0.0001	***
Treatment x Time	10.9	2	5.47	0.23	0.79	NS
Resprouting species						
Treatment	4.2	1	4.22	0.15	0.71	NS
Time	114.0	2	57.01	16.38	<0.001	**
Treatment x Time	3.7	2	1.87	0.54	0.59	NS
Succulents						
Treatment	35.3	1	35.33	0.68	0.43	NS
Time	1499.8	2	749.91	141.99	<0.0001	***
Treatment x Time	31.7	2	15.86	3.00	0.078	NS
Non-succulents						
Treatment	16.6	1	16.59	0.62	0.45	NS
Time	4026.5	2	2013.27	230.69	<0.0001	***
Treatment x Time	12.0	2	6.02	0.68	0.52	NS

Herbs

	SS	df	MS	F	p	Sig.
Treatment	30.3	1	30.34	0.16	0.69	NS
Time	416.8	2	208.42	16.82	<0.001	**
Treatment x Time	11.2	2	5.60	0.45	0.64	NS

Resprouting species: *Tripteris sinuata* and *Gazania krebsiana*
SS = sum of squares; MS= Mean square; df = degrees of freedom; Significance: NS = Non significant; *p<0.05; **p<0.001; ***p<0.0001.
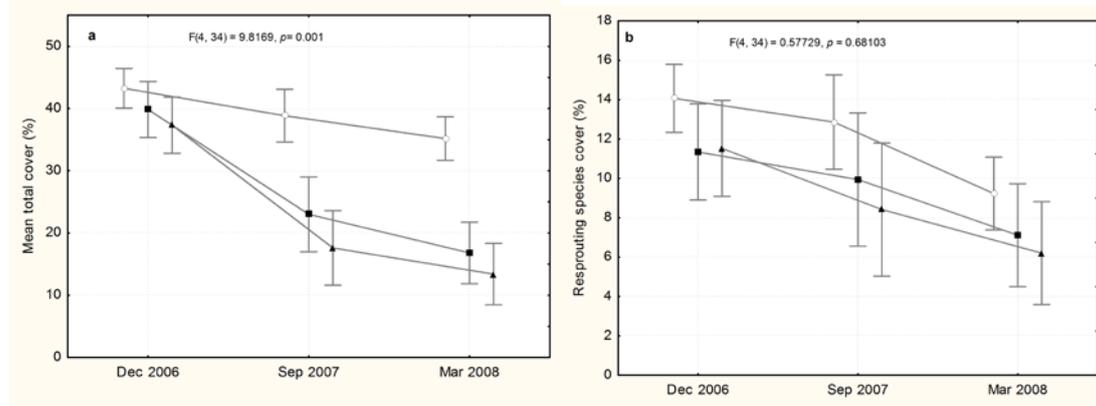
Figure 8−2: Response of a) mean total vegetation cover and b) resprouting species (*Gazania krebsiana* and *Tripteris sinuata*) over time on burned and unburned plots and in the Tierberg Karoo Research Centre before (Dec 2006) and after fire (Sep 2007 and Mar 2008). (○) Control (■) low fuel load (▲) high fuel load. Error bars indicate 95% CI.

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 8−3). 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.

Table 8−3: 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.

| Fire survival category | Treatment | | |
	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
Colonised plot after treatment	1	0	2

8.5 Discussion

8.5.1 Fire characteristics

The heat yield that was found in this study (15 765 J/g) 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.

8.5.2 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 (Figure 8−3c). This could probably be as a result of the hot dry summer, since 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 damaged by the fire. *Tripteris 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 and 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 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 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 runoff and erosion, leading to soil erosion and reduction in effective rainfall (Snyman and van Rensburg 1986).

P. 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 and Cunningham 2002; Milton 2004). If widespread invasion should occur (and no reason is seen why this will not happen), it will almost certainly change the vegetation structure and increase the risk of fire. The results suggest that this will lead to adverse impacts on an ecosystem on which many plant species are ill-equipped to deal with fire.

8.5.3   *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).
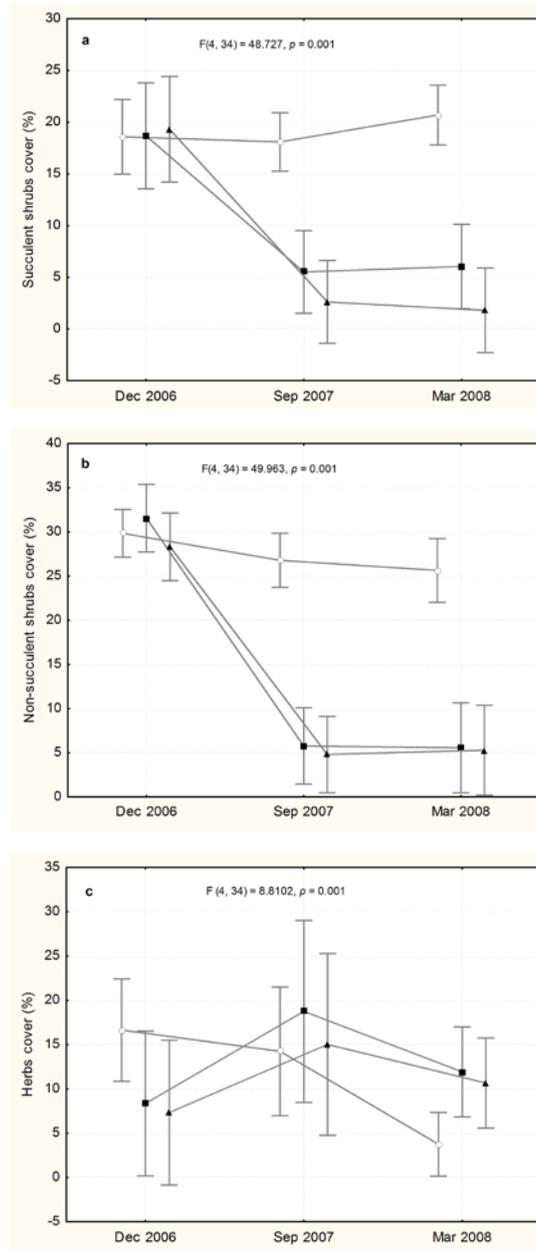
Figure 8−3: Percentage cover change of total cover for three major plant life-forms: (a) leaf succulent, (b) non-succulent shrubs, (c) herbaceous and geophytic species on burned and unburned plots in the Tierberg Karoo Research Station before (December 2006) and after fire (2007 and 2008). Symbols on the graph represent (○) Control (■) low fuel load (▲) high fuel load. Error bars indicate 95% CI.

8.5.4 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). Firstly, reduction of forage species would lead to a decrease in the grazing potential of this area. This study has shown a reduction in total vegetation cover and density of most species except for a few resprouting species during the study period. Secondly, 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. Thirdly, 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 (Milton and Hoffman 1994; Yeaton and Esler 1990) from abiotic stress during seedling stages (Dean and 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.

P. setaceum has been found to threaten biodiversity in other desert regions of the world (Brooks and Esque 2000; Williams and Baruch 2000; Brooks and 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 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.

The 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 postfire weather conditions) following invasion by *P. setaceum* would improve the understanding of potential impacts of this invader on a species-rich succulent desert.

CHAPTER 9

CONCLUSIONS AND RECOMMENDATIONS

9.1   Introduction

This chapter provides an overview of the major results of this study. The discussion of findings follows the conceptual model of invasion process (**Figure 9−1**) and is linked to the relevant chapter where the subject is dealt with in more detail.
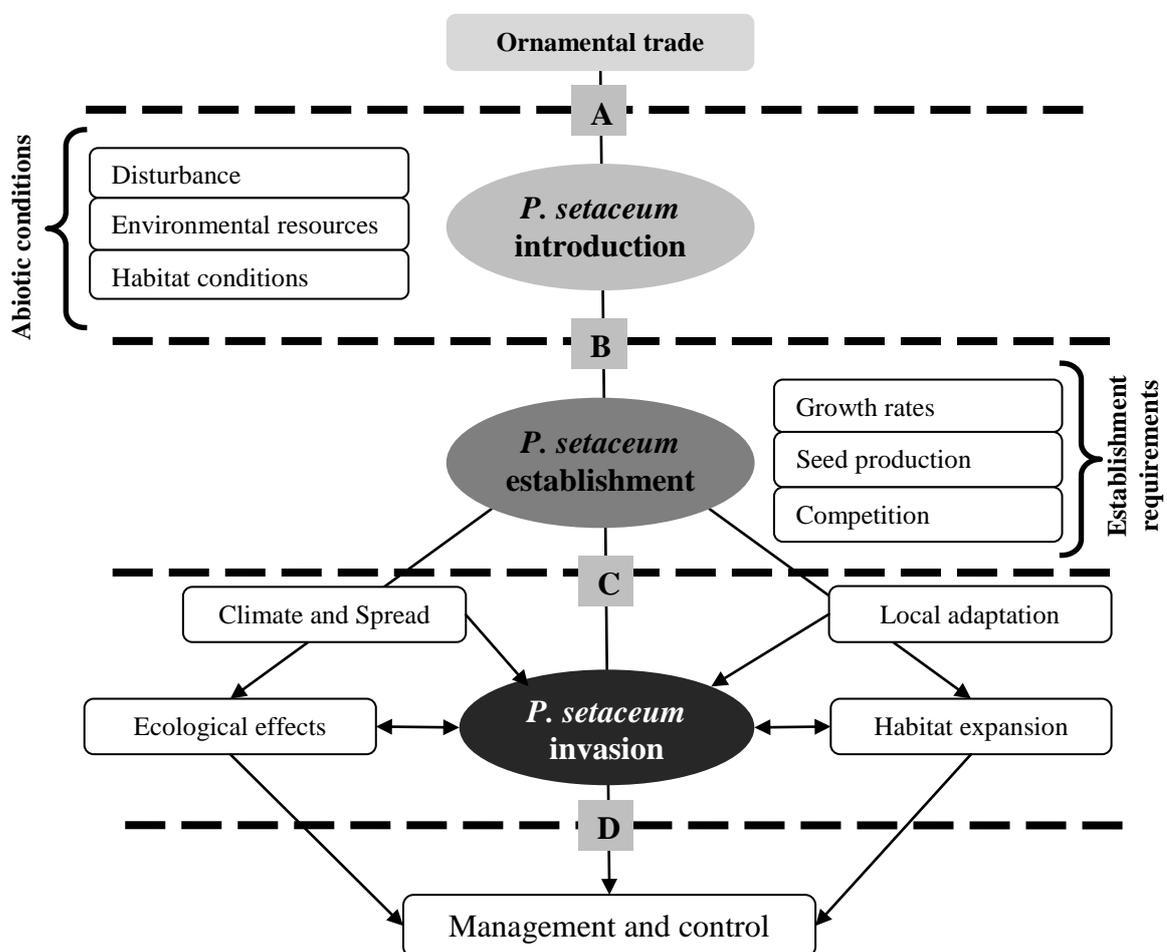
Figure 9−1: Conceptual model of *Pennisetum setaceum* invasion as it filters through various invasion barriers (A – D) on its invasion pathway. The model shows that *P. setaceum* invasiveness is determined by evaluating its biological and ecological characteristics against factors that determine its growth rates, competitive ability, reproduction and dispersal. Global transport and ornamental horticulture have brought the invasive *P. setaceum* into South Africa (A) where it is assisted to reproduce by abiotic conditions such as disturbance (B). The

species high reproductive output and potential as well as high germination and growth rates assist in its performance (C). At this stage, other factors such as climate play an important role in providing suitable conditions for its expansion and hence its ability to affect ecosystem processes and function where it invades. Management and control efforts should focus on these factors to curb the invasion of this grass (D).

9.2 *Pennisetum setaceum* introduction and escape

Pennisetum setaceum was introduced in South Africa as an ornamental plant (Henderson 2001) and probably to rehabilitate mine dumps (personal observation). This study (chapter 3) and other southern African studies (Joubert & Cunningham 2002, Milton 2004) found the grass to occur along roadsides, especially adjacent to settlements. This shows how the species has filtered through the geographic barriers from its place of origin, North Africa, into other areas.

9.3 Growth requirements

In order for an alien species to become invasive, it has to be able to establish and produce self-perpetuating offspring in a new area. At this stage it requires a number of conditions and characteristics for growth. These are discussed in the following sections.

9.3.1 Disturbance

The success of *P. setaceum* across the South African landscapes can, to a large degree, be explained by increased disturbance regimes, particularly the historical production of mine dumps and road infrastructure. The grass was persistently found along disturbed roadsides, and larger plants particularly on the more disturbed road-river interchanges (Chapter 3). Away from roadsides, the presence of *P. setaceum* was more associated with water bodies and disturbances such as the presence of open spaces caused by overgrazing and burning. In many ecosystems, disturbances modify the distribution of resources and may lead to major changes in species composition (Lake and Leishman 2004). In this case, disturbance creates new spaces and increases the availability of resources such as light, water and nutrients for *P. setaceum*.

9.3.2   Environmental resources and habitat conditions

In most instances, *P. setaceum* was found in open, disturbed areas, possibly because it requires full sunlight for growth. The availability of extra nutrients and water on roadsides could explain its prevalence in these areas relative to other parts of the landscape. In Chapter 5, I found that the availability of additional nutrients and water increased the growth rates, seed production of *P. setaceum* irrespective of habitat conditions of air temperature and soil type. This could therefore, explain the prevalence of *P. setaceum* in diverse ecosystems along roadsides and especially its better performance on road-river interchanges. This study has also shown that the *P. setaceum* takes only about 4 – 5 months to reach reproductive maturity under greenhouse conditions with unlimited water and nutrients.

9.3.3   Growth rates

Invasive alien species often grow relatively faster than indigenous species to utilize available resources such as light (Keane and Crowley 2002). In Chapter 4, *P. setaceum* seedlings translocated into the field, grew faster in areas with extra moisture and nutrients and disturbance. Seedlings in Karoo National Park had higher growth rates than those in other areas, seemingly due to extra moisture along a river. Furthermore, seedlings with extra moisture and additional nutrients grow faster and produced flowers and seeds before those with no additional environmental resources (Chapters 5 and 6).

Many invasive alien species are aggressive competitors that out-compete natives for available environmental resources and habitat conditions. In this, *P. setaceum* performed better under less or no competition from native species (Chapter 4). This could explain the prevalence of this grass on disturbed areas where it grows faster and fills the entire area as monospecific stands wherever it occurs.

9.3.4   Seed production and dispersal

Many invasive alien species produce a lot of propagules to ensure high propagule pressure for establishment. This study (Chapter 6) found that *P. setaceum* has a high reproductive output and potential by producing an average of 350 inflorescences per plant under greenhouse conditions. *P. setaceum* reproduces asexually and by seeds following pollination by either fertilized or unfertilized seeds (Simpson & Bashaw,

1969). This ensures that abundant seeds are available to be dispersed further. In some instances where the immature inflorescences are inundated, they form pseudo-viviparous plantlets that could also contribute to spread of this species (Appendix).

Roads and rivers act as conduits for the dispersal of *P. setaceum* seeds away from source populations into semi and natural areas. The seeds were found some distances (300m) from the perceived source populations.

9.4 Drivers of *P. setaceum* invasion

Following introduction, growth and spread of an alien species, additional attributes and conditions are required to result in invasion into natural and semi natural areas. This section deals with adaptations and conditions that promote the invasion of *P. setaceum* into South African ecosystems and feedbacks that the invasion may have on further invasion via changes in ecosystem function.

9.4.1 Local adaptation

P. setaceum can grow in diverse habitats as a result of its phenotypic plasticity (Williams *et al.* 1995; Le Roux *et al.* 2007). This study (Chapter 6) found no plasticity in growth and reproductive traits across varying environmental habitats. Instead, this study found evidence that local adaptation could be the cause for the success of *P. setaceum* in diverse biome environments in South Africa. This adaptation could explain the prevalence of the species throughput the country. These findings suggest that the grass has the potential for further spread and hence habitat expansion.

9.4.2 Effect of climatic change on distribution and spread

Many invasive alien species could benefit from the effects of the global climate change. This could increase the available habitat for growth or facilitate the availability of resources (such as light and water) for growth. In this study (Chapter 7), the suitable habitat was found to be increasing as a result of climate change. The fynbos biome was found to have high habitat suitability and possibility of further spread if disturbance away from the roadsides increases. Furthermore, unlike many C4 grasses that occur in warmer summer rainfall regions, *P. setaceum* is able to invade winter-rainfall rainfall regions. Through rapid production of dead biomass that

increases flammability, the grass has potential to shorten fire cycles, and this change in the prevailing disturbance regime might facilitate its own growth even in less fire-prone ecosystems, as discussed below.

9.5   Ecological effects

Reviews of biological invasions have demonstrated impacts of invasive alien species on ecosystem functions. This could be either by excessively using available resources or adding unusable resources to the system. *P. setaceum* produces large quantities of fine flammable fuels that inevitably promote fire. This, along with the predicted suitability of the grass in semi-arid and arid areas could lead to conversion of much of the Nama karoo landscape to dominance by this grass species and resprouting shrubs (Rahlao *et al*. 2009, and Chapter 8). This study found that *P. setaceum* has the potential of promoting fire that could affect the ecosystem processes and composition in fire-free shrublands of Nama karoo. Furthermore, *P. setaceum* is fire adapted and promotes fire that kills most of the native succulents in the arid and semi-arid areas that are not adapted to fire.

9.6   Control and management

P. setaceum would be difficult to eliminate once the plants have established. Control methods investigated elsewhere include herbicide application and hand pulling (Tunison 1992). None of these has achieved control after a single treatment. Control and management may need to be repeated several times a year and directed to areas that are suitable for its performance, such as at the road-river interchanges. Small infestations of *P. setaceum* can be removed by uprooting and removing and destroying inflorescences particularly following periods of precipitation, a condition that favours rapid growth and high performance of *P. setaceum* (Chapter 5), and at nutrient accumulation sites.

The grass is prevalent on disturbed areas where there is little or no competition. For this reason, re-vegetation of the cleared areas with indigenous plants should happen as soon as the grass is removed to ensure that it does not return to the disturbed area. Small infestations with smaller plants (seedlings) may be hand-pulled and disposed for burning before they flower. Large infestations with mature plants may be chemically controlled. Disposing of the entire plant after removal will

eliminate seeds caught in the leaves at the base of the plant, which can spread after the plant is uprooted. After removing *P. setaceum*, native species could be planted as the alien does not do well under competition (Chapter 4).

This study should assist in developing a predictive framework for invasions, by ecologically similar perennial grasses, and better inform management strategies for early detection and rapid response in areas where habitat suitability and spread have been predicted to be higher.

9.7 Major contributions of this thesis

This study has been the first in southern Africa to use a combination of observation and experimentation to show how a perennial grass overcomes invasion barriers. My work revealed that there is synergy between global changes, particularly climate and land use changes, and invasion of *P. setaceum*. The study has also demonstrated possible arid ecosystem effects resulting from invasion by perennial grass invasions and provides simple guidelines based on this research for the management and control of *P. setaceum* and other perennial grasses in southern Africa. As such, the thesis should make a significant input to our understanding of emerging invasive perennial grasses and the effect of global changes to their proliferation in southern Africa.

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APPENDIX

Evidence for induced pseudo-vivipary in *Pennisetum setaceum* (Fountain grass) invading a dry river, arid karoo, South Africa

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Abstract

We report the development of rootless plantlets in inflorescences of *Pennisetum setaceum* (fountain grass) invasive in the Gamka River in the Karoo National Park, South Africa. The pseudo-vivipary appeared to have been induced by inundation of immature inflorescences when the river flooded. Plantlet production may facilitate the spread of this species in seasonally flooding rivers in arid regions. To the best of our knowledge this is the first record of induced pseudo-vivipary in this grass species.

Keywords: Dispersal; Inundation; Spikelet proliferation; Vegetative reproduction

Fountain grass, *Pennisetum setaceum* (Forssk.) Chiov. a perennial tussock grass native to North Africa, has escaped horticulture to become invasive in many arid and semi-arid areas including parts of Australia (Batianoff and Butler, 2002), Hawaii, Arizona and California in the USA (Williams *et al.*, 1995; Poulin *et al.*, 2005), and Southern Africa (Milton, 2004). In South Africa it is a declared weed (Henderson, 2001).

The species produces large quantities of seeds with feathered glumes. Dispersal is assumed to be mainly by wind, although seeds may also be moved on vehicles and animals (Williams *et al.*, 1995). In addition to producing seed, vegetative reproduction through pseudo-vivipary (or production of plantlets in spikelets) is known for three species within the genus *Pennisetum* (Schmelzer, 1997), but has not been reported for *P. setaceum*.

While carrying out a survey of the distribution of *P. setaceum* as an alien species in the Droërivier, a tributary of the Gamka River in Karoo National Park near Beaufort West (Western Province of South Africa, 32° 18′S, 22° 33′E, 900°m a.s.l.),

we noticed that inflorescences on some of the plants had proliferated, producing plantlets (Figure 1). The distribution of inflorescences with plantlets appeared to be heterogeneous, and mainly confined to the central part of the river bed and the lower parts of the plants. We therefore hypothesised that the pseudo-vivipary may have been induced by submergence of developing inflorescences in water.

The Beaufort West region is semi-arid (mean annual rainfall 227 mm, range 62–515 mm). For this reason, river beds are usually dry, but tend to flash flood following heavy rain. The Gamka River had flowed 8 weeks before our visit, as a result of widespread rains in the region in mid May 2006, but at the time of the survey on 3 July 2006, only a few pools of water remained.

To test our hypothesis that pseudo-vivipary had been induced by submergence, we recorded the presence or absence of plantlet-bearing inflorescences on the first 80 flowering *P. setaceum* plants encountered in the bed of the river, and on the first 80 plants encountered on the adjacent stretch of the alluvial river bank, which was 0.5 to 1.5 m above the level of the river bed. We also measured the height above-ground of each plantlet-bearing tussock encountered. Spikelets were later dissected to examine morphology.

We found that 15 (18%) of the 80 plants surveyed in the river bed had one or more inflorescences that were producing plantlets, whereas pseudo-vivipary was absent among plants growing on the bank of the river. The flowering *P. setaceum* plants in the river bed were 0.8–1.2 m in height and most of the inflorescence culms were in the upper parts of the plant. All 15 inflorescences with plantlets were on the lower parts of the grass tussocks, having a mean height above-ground level of 0.34 m (SD 0.09 m).

Dissection of individual spikelet-bearing plantlets revealed immature anthers in the bases of the spikelets, indicating that the plantlets had developed asexually rather than from unshed seed in the inflorescence. The plantlets had no roots. The position and size of the proliferating inflorescences suggested that they were immature when inundated by the flooding river; supporting our hypothesis that pseudo-vivipary had been induced by inundation of young inflorescences.

Vegetative propagation through pseudo-vivipary (or spikelet proliferation) in grasses (Poaceae) can be caused by genetic factors, injury or unfavourable environmental conditions (Beetle, 1980). The phenomenon is known from over 100

Figure1: Pseudo-vivipary in two *P. setaceum* inflorescences. Plantlets on the left-hand inflorescence are well developed whereas proliferation is in an early stage in the right-hand inflorescence.

species of grasses (Poaceae) worldwide (Beetle, 1980; Vega and Rúgolo de Agrasar, 2006), and has been reported for three species of *Pennisetum* (*P. polystachioin* (L.) Schult., *P. subangustum* (Schum.) Stapf and Hubb., *P. setosum* (Swartz) L. Rich.) by Schmelzer (1997).

As in most other sedges and grasses, the *P. setaceum* plantlets produced by pseudo-vivipary on inflorescences are rootless. However, as this grass species invades canyons and desert drainage lines in the USA (Halvorsen and Guertin, 2003) and South Africa (Milton, 2004), further research is needed to ascertain whether pseudo-viviparous plantlets can establish in moist sites and contribute to the spread or persistence of this invasive plant.

Acknowledgements

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