THE COMPETITIVE EFFECT OF VETIVER GRASS ON NATIVE GRASSES AND IMPLICATIONS FOR GRASSLAND REHABILITATION IN SOUTH AFRICA

By

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PREFACE

The research contained in this thesis was completed by the candidate while based in the Discipline of Grassland Science, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg Campus, South Africa. The research was financially supported by National Research Foundation (NRF) and UKZN College bursary.

This thesis is the result of the author's original work except where acknowledged or specifically stated to the contrary in the text. It has not been submitted for any degree or examination at any other university or academic institution.

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DECLARATION: PLAGIARISM

I, Lindokuhle Xolani Dlamini, declare that:

(i) The research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) This dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) This dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

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a) Their words have been re-written but the general information attributed to them has been referenced;

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(v) Where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) This dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

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ABSTRACT

Vetiver grass *(Chrysopogon zizanioides)* is a perennial C_4 grass that originates from central India. This grass is used worldwide for soil (e.g. erosion control) and water conservation (e.g. wetland and river rehabilitation) because it is a fast-growing tufted grass with a dense root system that reaches 3 meters deep forming a wall-like structure that binds soil particles. Vetiver is a very hardy grass, allowing it to withstand environmental hazards such as drought, frost, and floods. The most commonly used cultivars produce infertile seeds or even no seeds, hence it reproduces vegetatively. To date, no study has investigated the competitive ability of vetiver, factors influencing its competitive ability, whether it inhibits germination and establishment of native grasses, and its role in secondary succession of native grasses. The predicted global increase in atmospheric nitrogen deposition and excessive use of agricultural fertilizers will result in changes in soil nutrient status, hence altering the plant competitive trade-offs that drive species coexistence. Introduced plants, for example, are often more adapted to environmental changes and this may lead to invasion through competition with native plants. This study had three aims; 1) to examine the behaviour of vetiver and its association with native grasses in the field; 2) to investigate the effect of established vetiver tufts on native grasses (*E. curvula* and *P. maximum*) seed germination and seedling establishment. Within this aim, the effect of different sowing method on seed germination and establishment, and the effect of vetiver tufts when root competition is excluded was also investigated. Lastly, to investigate the competitive effect of established vetiver tufts and soil nutrient status on mature native grasses (*Eragrostis curvula, Digitaria eriantha*, *Panicum maximum,* and *Hyparrhenia hirta*). The last two aims were investigated using a pot trial. The most important results from the surveyed sites were the marked increase in grass species richness with an increase in distance away from planted vetiver, the abundance of bare ground around planted vetiver, and the presence of the recruited vetiver away from planted vetiver. However, in the pot trial, presence of vetiver tufts facilitated seed germination in both *E. curvula* and *P. maximum*, and seeds sown on the surface had a greater germination percentage compared to other sowing methods. However, vetiver presence inhibited seedling establishment of these grasses, even when the root competition was excluded. Vetiver shade could be retaining soil moisture and hence, creating a favourable environment for the seeds of native grasses to germinate. A combination of vetiver shade, direct root competition, and allelopathy (possibly from oil produced by the roots) could be causing an inhibitory effect on

the establishment of these native grasses. Vetiver tufts exerted a weak competitive effect on all native grass tufts, except for *D. eriantha*, under low nutrient status. Vetiver exerted a facilitative effect on *D. eriantha* under low nutrient status. However, vetiver exerted a strong competitive effect on all native grass species under high nutrient status, except for *P. maximum,* which responded similarly under low and high nutrient conditions. Overall, narrow-leaved grasses (*E. curvula* and *H. hirta*) had a weak competitive ability compared to broad-leaved grasses (*P. maximum* and *Digitaria eriantha*). Therefore, morphological traits are important in competition studies and can predict species that might coexist with vetiver. As soil nitrogen continues to increase globally, this will affect coexistence between native grasses and vetiver, with vetiver gaining competitive advantage over native grass. There is no doubt that vetiver is beneficial for soil and water conservation; however, this study shows that vetiver persists for decades, native grasses fail to successfully recruit in close proximity to vetiver, and vetiver is a strong competitor under both low and high nutrient soils. Irrespective of the predicted increase in soil nutrient status, vetiver is unlikely to be succeeded by the native grasses and therefore, should be used only in heavily degraded sites (e.g. gully erosion) for cover (soil protection) and not for the purpose of retaining or promoting species diversity.

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1 CHAPTER ONE: THE ROLE AND DYNAMICS OF VETIVER GRASS IN REHABILITATION OF GRASSLANDS IN SOUTH AFRICA

1.1 INTRODUCTION

1.1.1 Grasslands in South Africa

Importance and classification

Grasslands are economically and ecologically important ecosystems, and they cover a large proportion of the earth's surface. In South Africa, they constitute approximately 28.4% of the land surface (Tainton, 1999; Fish et al. 2015). They contribute significantly to agriculture, provide numerous ecosystem services (e.g. water), and are rich in biodiversity (Palmer and Ainslie, 2005). Variability in grassland systems is driven mostly by environmental factors and disturbance (i.e. grazing and fire) (Tainton, 1999). Grasslands are managed and maintained through a top-down approach by means of grazing, fire or an interaction between the two (Tainton, 1981a). Milchunas et al. (1988), defined grasslands by categorizing them as either being climatically determined (climatic climax), successional, or agricultural. Climatic climax grasslands have insufficient soil water to support a forest ecosystem but sufficient to maintain the grass layer (Milchunas et al., 1988). Milchunas et al. (1988), suggested that savanna or shrub steppe ecosystems (i.e. ecotone between grassland and forest) with an annual rainfall that is between 250 - 1000mm, are also classified as climatic climax grasslands. Successional or agricultural grasslands are those that result from clearing of forests, hence are maintained by agronomic or other management practices (Acocks, 1988; Milchunas et al., 1988). However, not all fire dependant grasslands are as a result of forests clearing. Some are naturally grasslands but become encroached by woody plants when fire frequency decreases. These grasslands are not at equilibrium with climate and Acocks (1988) termed them "false grasslands" as they require fire to maintain the grassy layer. These grasslands are known as fire climax grasslands, similar to what Milchunas et al. (1988) called successional or agricultural grasslands. The major focus of grassland management is to maintain species diversity and good veld condition. In order to do this, proper management of both fire and grazing is important in grasslands to avoid veld degradation, mostly through soil erosion or species loss (Tainton, 1999).

Degradation

Grasslands are among the most degraded ecosystems globally, because of poor management and a growing human population leading to increased demand for space for development and agricultural practices. Grassland degradation can take many forms, from species shift (i.e. dominance of one species, alien plant invasion, and woody-plant encroachment) to soil erosion. One of the main drivers of such changes in grassland ecosystems is agricultural practices, such as nutrient enrichment and overgrazing (Everson et al., 2007). Changes in soil nutrient status result in changes in grassland species composition, through giving a competitive advantage to species which thrive on nutrient-rich soils or that tolerate nutrient toxicity (Gough et al., 2000). Furthermore, overgrazing, mostly in high altitude fire climax grasslands, results in degradation as a result of soil erosion (Everson et al., 2007). This is because in high rainfall areas there are mostly well-drained, dispersive soils, which are susceptible to erosion (Fey, 2010). Rehabilitation or restoration is important for the maintenance of ecosystem function, provision of ecosystems services, and biodiversity promotion.

Rehabilitation

Grassland rehabilitation aims to facilitate the reestablishment and recovery of ecosystem functions that have been damaged, degraded, or destroyed (Zaloumis and Bond, 2011). Relying on secondary succession processes to naturally rehabilitate rested degraded grasslands is inadequate and does not always work (Zaloumis and Bond, 2011). Rehabilitation in grasslands is slow, difficult, and time consuming, and is required mostly when nutrient-rich top soil has been eroded as a result of soil erosion. The soil seedbank is also lost in the process of erosion, reducing the chance of natural reestablishment of native grasses. This means, rehabilitation efforts shift to the reintroduction of plant propagules (seeds through reseeding, or hydro-seeding, and vegetative propagation-tillers or tufts). Native grasses usually fail to establish in the newly exposed nutrient-poor soil, of which in turn leads to the introduction of fast-growing, soil stabilizing and restoring plants, which are usually alien grasses e.g. Vetiver and Pampas grass (Everson et al., 2007). However, these grasses, depending on their competitive ability and ability to spread, could transform the natural grassland to a monospecific sward.

1.1.2 Vetiver grass

Coexistence with other species

Vetiver (*Chrysopogon zizanioides* (L.) Roberty) is a tufted perennial fast-growing grass from central India with deep root systems that reach approximately 3m deep in a wall-like formation and bind soil particles together (Chōmchalao, 2001; Adigun and Are, 2015). In its native range it forms dense stands and competes strongly with other grasses, because of its unique morphological and physiological features. It is also, an ecological climax, hardy grass enabling it to withstand a variety of environmental conditions (drought, floods, and fires). Information on its ecology is seldom available, particularly in terms of its coexistence with other grasses and competitive strategies. However, its produces oil in its roots which could have allelopathic properties and might inhibit recruitment of other grasses.

Competition

Competition is important in understanding plant coexistence. Competition refers to the negative interference or effects caused by the presence of neighbouring plants, usually through reducing the availability of resources (Eagles, 1972; Fowler, 1986; Casper and Jackson, 1997). Competition plays an important role in structuring grassland and savanna ecosystems. Plants can either compete aboveground for light or belowground for soil resources (water, nutrients, and space), and/or above- and belowground for both, simultaneously (Goldberg, 1996). Numerous studies show that introduced plants are more competitive than the native plants because they acquire resources more efficiently, lack natural enemies, and some produce allelopathic chemicals which inhibit growth of native plants (Alpert et al., 2000; Bakker and Wilson, 2001; Milton, 2004). These attributes could promote the dominance of introduced plants, such as Vetiver, over the native plants. This change in species composition will alter the overall diversity of the grassland or savanna ecosystem. Understanding the ecology, mostly the competitive ability of grasses used for rehabilitation of degraded grasslands is important for the formulation and adaptation of better rehabilitation strategies.

Application

Irrespective of the limited knowledge of its ecology, vetiver's unique morphological and physiological features deem it usefull for soil and water conservation. This grass has been used successfully for decades, for rehabilitation of eroded soils, phytoremediation (as it roots can absorb toxic heavy metals/chemicals), wetland rehabilitation, slope stabilization, and soil conservation, in India and worldwide. The oil from its roots is used in the cosmetic and pharmaceutical industries as it has antifungal and anti-microbial properties. These applications have popularized the use of this grass, but in South Africa, it is mainly used for soil erosion control, rehabilitating mine waste, roadside slope stabilization, and waste water treatment (George et al., 2001; Truong and Loch, 2004; Mulder and Brent, 2006).

This review aims to give a theoretical background to the problem statement and study questions, by linking background information on vetiver grass to competition, seed germination, seedling establishment, and grassland management.

1.2 VETIVER GRASS (CHRYSOPOGON ZIZANIOIDES (L.) ROBERTY)

1.2.1 Growth and behaviour of vetiver grass

Different grasses with different growth forms require different environmental and climatic conditions for germination, establishment, and maturity. Growth form is of ecological significance as it can provide important information about the life history of the grass. Vetiver grass growth is highly dependent on its root system and vegetative reproduction because it produces infertile seeds (Dalton et al., 1996). The reason for this infertility is unknown (Council, 1993). Most researchers have speculated that perhaps the plants are “sterile” or conditions for germination are seldom present. However, there are two varieties of vetiver grass which have the same botanical name (Council, 1993). The “colonizer” wild variety from North India, and the “sunshine” commercially propagated variety from south or central India. The “colonizer” is an aggressive grass capable of spreading, and Council (1993) stated that, if this variety is mistakenly used for soil stabilization, it could become a weed. The sunshine variety was believed to be seedless, with only vegetative reproduction but it has been observed to produce infertile seeds. The question of why would it invest its resources producing infertile seeds, remains unanswered. For this reason the ‘sunshine’ variety is said to not spread.

It is not easy to differentiate between these two varieties, particularly when there are no flowers. Researchers have relied on morphological and physiological characteristics to differentiate between these two varieties. The commercially propagated variety is said to have a thicker stem, roots with less branching, and wider leaves (1.1cm on average) than the wild variety but these characteristics may be too simple to be truly diagnostic (Council, 1993). Furthermore, the commercially propagated variety produces more root biomass and hence more oil (Council, 1993). Initially, vetiver was utilized for its oil and therefore, domestication could have been aimed at producing greater oil yields, not at inhibiting sexual reproduction. This is further evidenced by the fact that utilization of oil was initiated in India, the country of origin, so negating the need for a sterile cultivar. Therefore, vetiver grass having infertile or sterile seeds could have been a by-product of breeding for maximum oil production. Both the commercially propagated, which have many cultivars, and the wild variety are dominant in the tropical and subtropical plains throughout northern India. Both these grasses, particularly the wild variety, prefer low-lying, damp (i.e. swamps and bogs) sites or even river margins (Council, 1993; Dalton et al., 1996).

Adams et al. (2003) suggest that the origin of a non-seeding variety is unknown. However, because there is still a wild vetiver (found in the northern part of India), researchers have begun to use DNA fingerprinting to understand differences between wild vetiver and all other known cultivars. Adams and Dafforn (1997) found that 86 % of 121 plants sampled originated from a single clone (no variation in genetic material). Furthermore, Adams et al. (1998) examined the vetiver wild variety, cultivars, and related genera (*Sorghum* and *Chrysopogon*) using DNA fingerprinting, which led to Veldkamp (1999) combining DNA fingerprinting and morphological data to show that species under *Vetiveria* actually fall under *Chrysopogon*. Therefore, *Vetiveria zizanioides* (L.) Nash. was changed to *Chrysopogon zizanioides* (L.) Roberty (Veldkamp, 1999; Adams and Center, 2000). An important finding of this work was that the genetic material revealed no substantial differences between the wild and commercially propagated vetiver. The only differences relate to reproduction, root biomass and oil production (Adams and Dafforn, 1997; Adams et al., 1998; Adams et al., 2003).

Vetiver grass development is affected by daily temperature, soil moisture, and soil texture (Wang, 2000; Nix et al., 2006). As it is a tropical grass it is adapted to high rainfall and extremely warm conditions with deep soils, resulting in the extensive root systems that make it useful for soil stabilization. Subfreezing conditions have been documented to significantly reduce vetiver grass growth (Nix et al., 2006). For example, in China from Hainan Island (10^{o}N latitude) to Tianjing (39^{o}N latitude)), when vetiver grass was grown in areas with a mean temperature of -4^{0}C with the minimum temperature reaching -22^{0}C, the grass showed a slow growth of about 0.5cm daily (Xu, 2002). Cheng et al. (1994) showed that vetiver started to grow well when mean temperatures reached 10-15^{o}C, the fast growth seen between 20 and 30^{o}C or higher with a daily growth of 2-3 cm in height. Many studies supported these findings, suggesting that at higher temperatures, vetiver grass started tillering and flowering (Xia et al., 1998; Huang, 1999; Xu, 2002). However, when temperatures reach 40^{o}C or above, the growth slowed (0.5cm height increase daily) (Xia et al., 1998), suggesting that both very low and high temperatures negatively affect the growth of this grass. Temperature fluctuations have not been reported to cause mortality in vetiver.

Huang, (1999) noted that vetiver grass height and biomass is more dependent on soil fertility rather than temperature. For example, vetiver grass grew up to 3 m in a fertile loam soil in China compared to a white sandy soil where the grass only grew up to 1m over the growing season with similar temperatures (Huang, 1999). Fertile soils do promote growth and survival of vetiver grass. Studies have shown that vetiver grass growth and leaf quality is mostly influenced by soil phosphorus availability (Huang, 1999; Xu, 2002; Wagner et al., 2003). Soils with limited phosphorus availability result in a slow growth or sometimes mortality in vetiver grass. In contrast, vetiver grass has shown enhanced growth under high levels of soil nitrogen and phosphorus

Vetiver can grow in a variety of environmental conditions (e.g. arid to semi-arid to high humid regions), however, even though it can tolerate drought and salinity, it prefers nutrient-rich and high rainfall areas (Truong et al., 1999; Maffei, 2003). A study in China showed that vetiver grows better than the well-known drought-tolerant grass, *Paspalum notatum* during drought (Xu, 2002). Edelstein et al. (2009) suggested that salinity levels between 3 and 6 deciSiemens per metre (**dS/m**) do not cause significant reduction in growth and mortality in vetiver grass. However, salinity levels above 6dS/m caused extensive reduction in yield, leaf and root quality and even increased tuft mortality (Xu, 2002; Edelstein et al., 2009). This, therefore, is one of the main reasons why vetiver performs poorly in arid regions. In contrast, vetiver grass grows well in wetlands and swamp areas. The grass can even grow in soilless water, when only the leaves are not covered by water (Xu, 1998, 2002). However, vetiver cannot stand long-term waterlogging; for example, Xu (2002) showed that it does not survive when water levels are higher than the base of the tillers during the growing season.

1.2.2 Effect of disturbances on vetiver grass

Grass behaviour cannot be extensively understood without considering the effect of disturbance. Disturbance can be either natural or anthropogenic through grassland management. The two main grassland disturbances utilized in management are fire and grazing. These two disturbances are important in the understanding of grassland ecosystems as they are key factors that influence grassland composition and maintain the dominant grass layer (Tainton, 1981a; Tainton, 1981b, 1999). These two factors either promote or reduce plant diversity by means of promoting the dominance of disturbance-tolerant, grazing resistant, and unpalatable grasses (Tainton, 1981b). For these reasons, it is important to consider how vetiver responds to management through fire and grazing.

Vetiver grass invests extensively in its root system and is said to be highly dependent on roots for regrowth, survival and spreading (Council, 1993; Truong, 2000b; Xu, 2002). Fire does not affect the root systems, therefore, vetiver grass is assumed to be tolerant to both hot and cool fires (Council, 1993). Furthermore, vetiver stays green even in the dormant season which could affect its flammability, and thus fire behaviour. However, no specific study has addressed how vetiver responds to fire. The evidence that exists is anecdotal from small-scale farmers and projects (Xu, 1998, 2002). As such, no scientific experiments, to the best of my knowledge, have been done to evaluate the response and regrowth of vetiver after fire. Furthermore, not much is known about how vetiver responds to fire intensity and frequency. However, considering vetiver grass morphology and growth, it would be feasible to speculate that vetiver could withstand fires because of its low flammability resulting from staying green even in the dormant season. Fire also could result in the regrowth of those few tillers and leaves that were dormant in the time of fire (Council, 1993).

Growth and survival of palatable plants are the two factors most frequently affected by grazing, although trampling also influences germination and establishment through compacting or breaking up compacted soil. However, the outcome of trampling is mostly dependent on the soil physical properties. Vetiver grass has been observed being eaten by most livestock, which suggests that it is relatively palatable when still young and not very fibrous (Council, 1993).

Testing the effect of grazing on a plant is usually done through simulated herbivory (e.g. clipping). Experiments in Guangdong province in the 1950s showed that when vetiver with a height of 150 cm was pruned to approximately 30 cm height, it produced on average 18.6 more tillers in 40 days compared to the uncut plants (Xu, 2002). Xia (1995) suggested that clipping twice annually, early in the year (February or March) and later (August or September) accelerates tillering. However, because vetiver has strong fibrous leaves, it is safe to suggest that, when mature, it is a highly unpalatable grass; hence, it is unlikely that grazing will affect the growth and survival of vetiver.

Vetiver is more fibrous and has sharp edges in resource-poor regions or cold areas (Xu, 2002). Therefore, vetiver grass could only be eaten when it is young and when preferred grasses are limited (Xu, 2002). This could result in its dominance in areas with unmanaged grazing (selective grazed patches) or overgrazing. Integration of fire might increase the likelihood of grazing as the regrowth might be palatable. However, to my knowledge, no studies have looked closely at the palatability and digestibility of vetiver grass at different growth levels.

1.2.3 Vetiver grass uses

Environmental degradation has become a major problem worldwide, more specifically in developing countries such as South Africa. Land degradation includes, but is not limited to, species loss (decreasing diversity and richness), soil loss (erosion and pollution of arable soil), water pollution and water reduction/loss (through changes in catchment vegetation - domination of alien trees which uses more water e.g. eucalyptus species) (Bojö, 1996; Faria et al., 2015). Drought, flooding and other environmental hazards which are as a result of climate change are contributing extensively to land degradation (Bojö, 1996; Faria et al., 2015). These hazards or climate change at large, are believed to be accelerated by changes in land use which are caused by the human population growing exponentially (Faria et al., 2015). The growing demands for food (hence, increase in industrial agriculture- extensive use of fertilizer) and energy (growing demand for oil, coal and gas extraction, hence increase in carbon dioxide (CO_2) in the atmosphere) are a by-product of human population growth (Change, 2001; Guillebaud and Hayes, 2008). The collective effect of changes in land use on soils are; 1) ecosystem eutrophication through nitrogen deposition, and 2) soil contamination through heavy metals deposition [e.g. Zinc (Zn), lead (Pb), and Cadmium (Cd)] from mines (O'Rourke et al., 2016). This then affects the aboveground vegetation, soil microbes, and water health.

Soil contamination degrades ecosystem health, affecting human lives indirectly through the loss of agricultural lands and water pollution, and directly through public health, as many pollutants are linked or associated with cancer and neurological disorders (O'Rourke et al., 2016), and reduced agricultural productivity, through the loss of nutrient-rich topsoil and thus the reduction in arable land (Fey, 2010). Therefore, the unique structure and tolerance of vetiver grass to different disturbances, environmental catastrophes, and soil conditions, popularized its use for environmental protection and rehabilitation (i.e. soil and water conservation). In 1956 John Greenfield used vetiver grass to plant contours on eroded hillsides in Fiji (Council, 1993). This intervention slowed run-off, retained nutrient-rich topsoil, and enabled him to plant sugarcane successfully between the vetiver contours. This initiated research into vetiver grass application in erosion control, agriculture, wastewater treatment, and phytoremediation. The widespread application of vetiver grass known as vetiver grass technology (VGT) was initiated in India by the World Bank for soil and water conservation around the 1980s (Truong et al., 1999; Truong, 2000a; Greenfield, 2002).

This research funded by the World Bank and conducted for several decades has demonstrated that vetiver grass technology is an effective, safe and low-cost natural method of environmental protection (Council, 1993; Adigun and Are, 2015). For this reason, vetiver grass has been used successfully for soil protection and rehabilitation of rill and gully erosion (Cao et al., 2015). It has been shown to successfully reduce soil loss up to 100% through binding the soil with roots and creating a new root level on a culm depending on the new soil level (see Figure. 1.1). In addition, it can increase water conservation up to 60% (Dalton et al., 1996; Xu, 2002; Cao et al., 2015). The ability of vetiver to absorb toxic chemicals and heavy metals effectively has also led to its use as a phytoremediation plant (Truong et al., 1999). Vetiver has been used successfully all over the world for rehabilitating abandoned mine sites and it has proven effective in restoring and maintaining soil health on those sites (Truong et al., 1999). Furthermore, vetiver has recently been used as a floating island in contaminated or nutrient-rich dams to absorb excess nutrients and contaminants, cleaning the water and restoring ecosystem function (Truong, 2000a;

Truong, 2000b; Truong et al., 2001). Vetiver also has been used successfully in wastewater treatment (phytoremediation) and in rehabilitating landfill sites (Truong et al., 2001).

Recent studies have also shown that vetiver grass can be used as an anti-pest or insect trap species to improve agricultural productivity, through drawing insect pests away from crops (Shengluan and Jiayou, 1998). Vetiver grass has been reported to be eaten by most herbivorous insects, mostly termites (Shengluan and Jiayou, 1998). However, most studies, both observational and experimental, indicate that vetiver does not die as a result of herbivory (Shengluan and Jiayou, 1998; Van den Berg et al., 2003). The highest recorded damage caused by termites on the stem is 39% (Shangwen, 1999; Zhu et al., 2001). Van den Berg et al. (2003) conducted a two-choice greenhouse and laboratory study to understand whether vetiver grass is preferred by female *Chilo partellus,* a problematic moth in maize farming, and whether vetiver can be used as a pest control plant. They used maize, vetiver, and napier grass (*Pennisetum purpureum*), a grass that is widely used in Africa as a trap crop for stem borers. They showed that vetiver grass was highly preferred for oviposition; however, larval survival on vetiver grass was extremely low, significantly lower than on the napier grass (Van den Berg et al., 2003). Therefore, their study supported the notion that vetiver grass could be used as a trap plant for insect pest control, as it attracts the insects away from the crops and reduces their survival. For this reason, vetiver has great application in agriculture and mostly in subsistence farming.

In windy areas, vetiver has been used as a windbreak for crops (e.g. maize) mostly by small-scale farmers (Shengluan and Jiayou, 1998). This is done by planting vetiver in contours and the crop plant between those contours. Under these circumstances not only does vetiver reduce soil erosion but increases agricultural productivity by reducing wind damage (Shengluan and Jiayou, 1998; Everson et al., 2007). The space between vetiver contours and the space between vetiver tufts planted in rows is dependent on the topography and the purpose of planting vetiver (Greenfield, 2002; Everson et al., 2007). Spaces between contours in the agricultural fields are generally wider than those of slope stabilization (e.g. roadside) or soil erosion control (i.e. sheet, rill or galleys) (Greenfield, 2002; Maffei, 2003). Generally, for soil erosion control, tufts are planted 15cm to 30cm apart; however, between vetiver contours, the landscape, and the purpose are usually the key determinants of spacing, with most scholars advocating two meters (Council, 1993; Greenfield, 2002; Maffei, 2003; Everson et al., 2007).

Aside from rehabilitation, remediation, and agriculture, the commercial uses of vetiver grass mainly pertain to the extraction of vetiver oil through distillation of the roots. Vetiver oil has extensive applications in the cosmetic industry (e.g. soaps, deodorants and refreshing sprays) and is also used as an anti-microbial and anti-fungal agent in the pharmaceutical industry (Chomchalow, 2001). Furthermore, vetiver is also used in the manufacturing of handy-crafts, thatching of houses, and organic compost production.

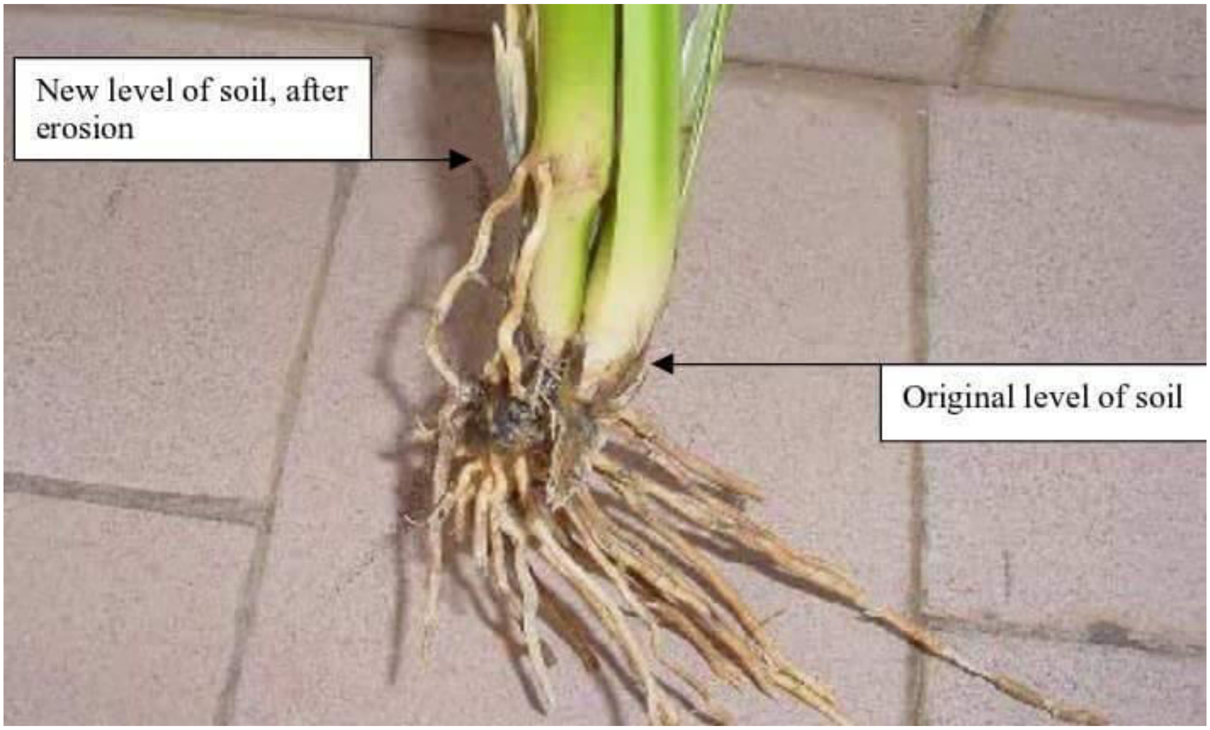

Figure 1.1: New root level formation on vetiver grass culm because of sedimentation (The Vetiver Network International, 2017).

1.2.4 Competition and nutrient addition

Being an ecological climax species, vetiver can outlive its neighbours even other climax species, mostly in relatively nutrient-poor soils (Council, 1993). The question as to whether vetiver affects adjacent plants has not been addressed scientifically. The answers obtained through observations by farmers and researchers show uncertainty and a lack of knowledge about the ecology of this grass. For example, Council, (1993) stated that in theory, vetiver should compete with adjacent plants for water and nutrients. However, no study has examined this.

Furthermore, an edge effect has been reported by farmers, where vetiver limits growth and reduces the productivity of the nearest crop plants; however, not all crops have been reported to experience this effect. This could mean that vetiver does not affect all crops or that farmers do not report the effect but is apparent that there is some effect caused by vetiver grass on neighbouring plants.

Vetiver grass does well in high rainfall areas and nutrient-rich soils. However, no study has shown how vetiver competes with other grasses, and if competition differs under different environmental conditions. Therefore, noting that phosphorus is a key limiting resource and that the addition of phosphorus increases productivity, one could expect increased competitive ability following fertilization.

1.3 COMPETITION

1.3.1 Role of competition in grasslands

Importance of competition

Grasslands are maintained mostly through a top-down effect where perturbations (outside influence, i.e. disturbance such a fire and grazing) are of significance and control the ecosystem stability. There is agreement among ecologists with regard to the importance of perturbations, mostly because of their effect on plant interactions (Kirkman, 1988; Robinson and Rorison, 1988; Tainton, 1999). While ecologists agree that competition is important in structuring grasslands there is uncertainty regarding whether competition promotes or reduces species richness and diversity.

The definition of competition has been a subject of discussion among ecologists for decades. However, because the experimental design used to study competition is fairly standard, a general definition could be created. The basic experimental design involves a target species growing in the presence or absence of neighbouring species, with the manipulation of limiting resources (Goldberg, 1996; Cahill, 1999, 2002). Wall and Begon (1985) offered a simplified definition of interspecific competition, suggesting that competition is “an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of the competing individuals concerned”. As this definition is fairly broad, one can extract a definition that suits the objectives of the study. Hence, here we define competition as a negative interference, being either direct or indirect suppression of one plant by another through resource utilization differences (Fowler, 1986). This is seen when one plants' ability or utilization of resources decreases or influences the growth, fecundity, and survival of a neighbouring plant (Casper and Jackson, 1997). Competition is measured using functional traits such as plant height, shoot/leaf production, biomass, and tillering. However, the most effective measure is biomass (both above and below ground) because it has been shown to give conclusive results (Peltzer et al., 1998) that are useful in explaining the effect of competition in structuring plant communities (Tedder et al., 2012).

Interspecific competition among ecologically similar species is suggested to be a major driver of plant community structure (Wall and Begon, 1985). Studies have shown that interspecific competition could drive certain species to local extinction or could promote diversity (Hardin, 1960; Wall and Begon, 1985). For example, in a 12 year field trial, Fynn et al. (2009) showed that grasses differ in their ability to resist invasion by other grasses, and that plant functional traits can be used to predict species invasion and invasibility in restored grasslands. Therefore, they suggested that restoration of diverse grasslands should use grasses with short stature, low leaf mass, slow growth, few tillers, and high specific leaf area which may facilitate succession by other native species, thereby increasing species richness (Fynn et al., 2009). This is because such grasses had weak competitive effects as predicted by their traits. Interspecific competition, therefore, can work to maintain species diversity in grasslands. However, the grasses must be able to coexist spatially and temporally within the confines of limiting resources.

Competition theories

Plant species coexistence has been the subject of controversial debate among ecologists for decades. Therefore, there have been many theories proposed to explain how different species with similar ecological requirements could coexist (Grime, 1977; Tilman, 1980; Thompson, 1987; Craine, 2005). These theories differ in their objectives but all of them aim to further our understanding of plant community structure. They each try to understand different topics, ranging from the importance of competition and the role of competition in plant community structure (i.e. Grime, 1977 and Tilman, 1980) to invasive plants (i.e. enemy escape theories and novel weapons hypothesis) (Keane and Crawley, 2002; Wolfe, 2002; Colautti et al., 2004).

Grime and Tilman

Grime (1977) elucidating on his theory, suggested that there are two external factors limiting plant biomass. The first one is stress, defined as 'conditions that restrict production e.g. shortages of light, water, or mineral nutrients and suboptimal temperatures" (Grime, 1977), which relates directly to competition because competition is dependent on the availability of resources. The second one is disturbance, defined as "the partial or total destruction of plant biomass" (Grime, 1977), e.g. fire, herbivory, pathogens, wind damage, frost, desiccation, soil erosion, and anthropogenic actives (i.e. mowing, ploughing, and trampling). Grime used the interaction between these two external factors to suggest that there are three possible combinations of stress and disturbance, which result in three plant strategies (Campbell et al., 1991b; Campbell and Grime, 1992). These strategies are 1) competitive plants, which dominate in low stress, resource rich environments with low disturbance, 2) stress-tolerant plants, dominant under high stress resource poor conditions with low disturbance, and 3) ruderal plants, which thrive in low stress resource rich environments with high disturbance (Grime, 1977; Grace, 1991). This theory will be referred in short as the CSR theory.

In short, Grime's CSR theory suggests that species with the maximum capacity for resource capture, thus having the highest growth rate will be superior competitors (Grime, 1977). Therefore, competition is more apparent in resource-rich environments than in resource-poor environments. For example, Mahmoud and Grime (1976) conducted a study focusing on the competitive ability of three grasses under low nitrogen (resource-poor environment) and high nitrogen (resource-rich environment) conditions. The grass species were *Festuca ovina* (dominant in unproductive regions), *Agrostis tenius* (dominant in intermediate-fertility regions) and *Arrhenatherum elatius* (dominant in productive regions). Overall, they showed that competition decreases in importance as resources availability decreases (Mahmoud and Grime, 1976). This was shown through the complete elimination of one species in each pair and the order of competitive ability (*Arrhenatherum elatius> Agrostis tenuis> Festuca ovina)* showing that grasses adapted to productive regions are more competitive than the ones adapted to resource-poor environments (Mahmoud and Grime, 1976). Many studies have shown that fertilization causes decline in species diversity, which is in support of this theory (Campbell et al., 1991b; Campbell and Grime, 1992; Rajaniemi, 2002).

In contrast to Grime's CSR theory, David Tilman's R* model of differential resource utilisation suggests that species with a lower minimum resource requirement (R*), the point at which population decline or loss equals population growth, will be superior competitors (Tilman, 1980, 1985; Tilman, 1987; Begon et al., 1990). This suggests that plant species with a low R* are more competitive in resource poor-environments. To explain how coexistence in plants takes place in his theory, the use of illustrations is required (see Fig. 1.2 below). The basis of this model is the zero net growth isocline (ZNGI), which is defined in simple terms by Begon et al. (1990) as "the boundary between the resource combinations which allow the species to survive and reproduce, and the resource combinations which do not". However, for this theory to predict the outcome of two competing species, consumption vectors (C_A and C_B, in Fig.1.2) should be included. Therefore, where resource 1 (R1) is limiting, species A dominates, but where resource 2 (R2) is limiting, species B dominates. Furthermore, above where the consumption vectors cross, the two species coexist. The consumption vectors indicate resource consumption of each species. If both species consume more of the resource that limits their own growth, the two will exhibit a stable coexistence, but when these species consume more of the resource that limits the other species, coexistence is not possible (i.e. if the consumption vectors are switched in Fig. 1.2) (Tilman, 1985; Grace, 1991).

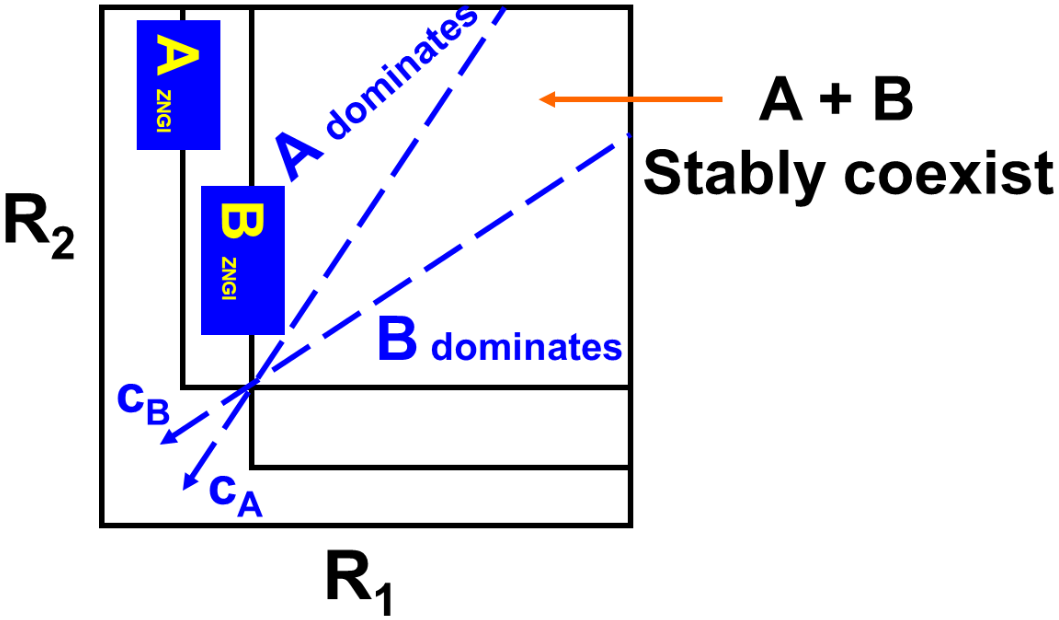

Figure 1.2: Tilman's differentiation resource utilization model (R*) modified from Begon et al. (1990), with A ZNGI and B ZNGI representing isoclines (ZNGI) of species A and B, R1 and R2 representing resources, and CA and CB representing consumption vectors of species A and B.

Tilman suggested that species differ in their ability to compete for limited resources, thus for two species to coexist, they must be differentiated on the basis of their individual abilities to compete for different limiting resources (Grace, 1991). This is one of many assumptions underlying Tilman's ratio model, which has raised controversial debate among ecologists. Thompson (1987) argues with substantive evidence, using the five assumptions of Tilman's theory that Tilman's work "opens up arguments about the nature of competition (above and below ground and at low and high resource levels) and the evolution of life histories in response to stress, which I had hoped had been settled 10 years ago,". However, Tilman (1987) suggested that Thompson (1987) was in support of Grime's idea and misunderstood some of the predictions of his theory. He suggested that his theory is supported by both field trials and pairwise competition experiments, which has shown that the relative abundances of plant species change with changes in the availability of limited resources, which is in line with his theory (Tilman, 1987).

Ward (2010), using water and nitrogen as limiting resources controlling the competition between acacia trees and grasses, showed that Tilman's model can be used to understand the effect of climate change on bush encroachment. He suggested that acacia trees (woody C_3 plants) fix nitrogen, hence, they have a low R^* for nitrogen (Ward, 2010). Contrastingly, grasses can easily access water from the upper soil layer; hence, they have a lower R^* for water (Ward, 2010). Therefore, he showed, using Tilman's model and a field experiment, that increases in water availability will favour acacia trees and that increases in nitrogen availability will favour grasses (i.e. Fig 1.2) (Kraaij and Ward, 2006). He suggested that the resource ratio model is likely to be used as a predictor model once atmospheric CO_2 is about 450 ppm, which will result in a shift from the higher net photosynthetic rate of C4 plants to C3 plants (Ward, 2010).

Both Grime and Tilman's theories are fundamental to our understanding of plant community structure and how competition plays a role in ecosystem function. Given that these two scholars differ in the way they define competition the comparison of these two theories has proven difficult (Grace, 1990; Grace, 1991). However, Austin (1986) conducted a broad comparison and suggested that both Grime and Tilman agree that soil nutrient levels, light, and disturbance are important factors and hold the answers to understanding plant community structure. Grace (1990) pointed out that a limitation of both theories is that they fail to distinguish between adaptation to resource levels and adaptation to non-resource conditions (i.e. soil salinity). Additionally, Craine (2005) commented that these two theories attempt to unify the disparate theories regarding plant community structure, and the role the environment plays in the assembly of these communities. Natural plant communities are inherently complex and dynamic, which is why it has proven difficult to have one unified theory (Austin, 1986; Craine, 2005). Therefore, these two theories both have important ideas about how some species might dominate in a habitat and their response when resource availability changes.

***Plant invasions and theories*?**

Grimes and Tilman's theories did not specifically address why introduced (alien) plants dominate in new regions. However, their theories can be used to understand plant invasion, by closely linking them to “niche opportunity “ (Shea and Chesson, 2002). Niche opportunity is defined by Shea and Chesson (2002) as “the conditions that promote invasions in terms of resources, natural enemies, the physical environment, interactions between these factors, and the manner in which they vary in time and space”. This forms the basis of the enemy release hypothesis (ERH) which states that plant species, upon introduction to a new region, experience a reduced suppression by herbivores (mostly insects) and other natural enemies (e.g. competitors, pathogens), which results in a rapid increase in their distribution and abundance (Keane and Crawley, 2002; Wolfe, 2002; Colautti et al., 2004). Even though the focus of this theory is on pathogens and insect herbivores, for this study, we focus more on competition as the natural enemy. Therefore, differences in competitive ability between introduced and native plants may help us understand the notion of plant invasion (Bakker and Wilson, 2001).

The ERH is underpinned by the assumption that a plant species in its native range experiences suppression from combined enemies (i.e. competitors, pathogens and herbivores). Competition with other plant species for resources, while experiencing suppression from both specialist and generalist herbivores, results in the plant investing resources into survival, defense or/and regrowth rather than on maximising reproductive output (Bakker and Wilson, 2001; Wolfe, 2002; Bakker et al., 2003). However, the new habitat might lack all or some of the aforementioned factors which allow the plant to reallocate available resources to rapid growth resulting in invasion. The assumptions of the ERH are mostly related to insect herbivores and specialist enemies, which are not the focus of this study. However, another hypothesis which focuses more on competition is the "evolution of increased competitive ability hypothesis" (Blossey and Notzold, 1995). This hypothesis states that, a historically introduced plant could relocate resources previously used for defence to increase its competitive ability, because of release from natural enemies (Blossey and Notzold, 1995; Blossey and Kamil, 1996). This incorporates both competitive ability and time, suggesting that shifts in resource allocation take time and which explains why some invasive species take time to show signs of invasion. This hypothesis is supported by the minimum residence time (time since first record or introduction of an alien species) which has been shown to explain patterns and plant invasion dynamics (Castro et al., 2005; Visser et al., 2016). For example, in South Africa Visser et al. (2016) showed that non-invasive alien grasses had a shorter resident time compared to naturalized or invasive grasses.

Callaway and Ridenour (2004) pointed out that theories on alien plant invasion are focused on enemies and they neglect exotic plant behaviour which includes biochemical responses. They proposed an additional hypothesis, "the novel weapons hypothesis" which states that exotic plants could be invasive through exuding biochemicals which are highly inhibitory (allelopathic) to plants and/or soil microbes in the new habitat, but relatively ineffective to communities in its native region (Callaway and Ridenour, 2004). Many invasive plants produce these allelopathic chemicals. Vetiver is one such species, producing oil from its roots which has been shown to inhibit germination and even growth of some weed species (Mao et al., 2004; Mao et al., 2006). Allelopathic chemicals have been shown to alter the competitive between species through excluding neighbouring species, thus facilitating invasion.

Plant succession and erosion control

Plant succession is the progressive development of vegetation over time, through a series of different plant communities or groupings in a region (Clements, 1916; Tainton, 1999). It could be seen as a continual plant invasion because it occurs with and/or without anthropogenic interference. The only difference between invasion and succession is that succession has a direction and vegetation changes in a predictable manner over time, while invasion does not. There are two types of plant succession, primary and secondary succession (Clements, 1916;

Clements, 1928; Tainton, 1999). Primary succession is initiated in an environment which previously did not support vegetation (e.g. recently exposed bare ground or rock) (Tainton, 1999). Plants which can decompose rocks and which survive under extreme environmental and climatic conditions, such as lichens, are usually the first colonizers (pioneer species) (Clements, 1928; Tainton, 1999). Secondary succession links well with the subject of this study. It is initiated after disturbance, which resulted in the destruction of plant communities which were at equilibrium (Clements, 1928; Tainton, 1999).

Soil erosion involves soil and vegetation removal; thus, restoration or rehabilitation of eroded areas is expected to take place via plant succession. Because soil erosion in grasslands results from poor management (e.g. overgrazing) coupled with intense rainfall, the top nutrient-rich soil has generally been lost (Tainton, 1999). Therefore, rehabilitation or restoration requires the introduction of plants (i.e. grasses) that can grow in low nutrient soils. Similar to plant succession, those grasses should hold and modify the soil to allow native grasses to colonize. In a humid environment, early succession usually starts with broad-leaved weeds and annual grasses (Clements, 1928; Tainton, 1999), for example, *Setaria pallide-fusca*, *Digitaria sanguinalis* and *Panicum laevifolium* (Tainton, 1999). Later communities are often dominated by perennial grasses. For example, *Eragrostis* and *Sporobolus* species, which are followed by *Hyparrhenia* species. Such succession is usually rapid because the initial conditions are usually suited to plant growth (Clements, 1928; Tainton, 1999). Restoration is highly dependent on inter and intra-specific competition (Clements, 1928; Tilman, 1985; Tainton, 1999). The rehabilitation process of eroded sites does not usually follow traditional successional pathways because species like vetiver grass (also long rooted broad-leaved grass) are usually introduced to quickly stabilize the soil. The effect of these introduced species on plant succession and colonization by native species is not fully understood.

Grass on grass competition

Understanding plant succession in grassland ecosystems requires the understanding of grass on grass interaction and the interplay of inter and intra-specific competition. Sometimes, for different species growing together to coexist, they must escape direct competition by utilizing different resources or drawing resources from different soil depths (Tainton, 1999). For example, deep-rooted plants could extract nutrients and water from lower soil horizons allowing shallow-rooted plants to extract soil resources from the top horizon (Clements, 1928; Tilman, 1994; Tainton, 1999). Furthermore, winter growing plants can associate with summer growing plants because they demand resources at different times (Tainton, 1999). However, direct competition is usually observed in grassland ecosystems and usually leads to the domination of some species over others.

Interspecific competition in grasslands could regulate the abundance and diversity of coexisting grass species (Silletti et al., 2004). For example, Silletti et al. (2004) investigated the interplay of competition in the tall grass prairie by examining interspecific competition between *Andropogon gerardii* Vitman (dominant species) and *Sorghastrum nutans* L. Nash (codominant species), and the effect of fertilization. They showed that there was asymmetric competition favouring *A. gerardii*; however, *S. nutans* growth was boosted by fertilization with no significant impact on *A. gerardii* (Silletti et al., 2004). Their results are consistent with the dominance of *A. gerardii* in grass prairies, while the ability of *S. nutans* to perform well under nutrient rich soils could be a mechanism to avoid competitive exclusion (Silletti et al., 2004). However, intraspecific competition has been seen to favour species diversity (Tainton, 1999). Intraspecific competition weakens one species' competitive ability and in so doing allows other grasses to coexist with it. Both inter- and intra-specific competition are important in maintaining grassland ecosystems.

Grass on grass competition differs also between grass growth stages. For example, mature grass plant and seedling interactions have been said to be both facilitative and competitive (Aguiar et al., 1992; Tedder et al., 2011). Aguiar et al. (1992) showed that when water is not limited in the soil layer, a seedling growing near adult grass tufts suffers some reduction in biomass. However, during the dry season where water is limited in the soil layer, seedlings growing near adult tufts did not only suffer a reduction in biomass but an increase in mortality (Aguiar et al., 1992). This proves that through competitive interaction, adult grass plants can prevent the establishment of other grass seedlings, thus creating a space of bare ground around them (Aguiar et al., 1992; Tedder et al., 2011). However, some grasses do facilitate seed germination and seedling establishment around them. Many studies have shown that some grasses create a favourable microclimate through shade, making the soil surface damp, for grass seedlings to establish (Foster, 1999; Navarro and Guitian, 2003; Tedder et al., 2011). This is known as the nurse plant theory (Bruno et al., 2003).

Pairwise greenhouse experiments and some field experiments looking at grass on grass competition have shown that different grass species have different competitive abilities in different environments (Mynhardt et al., 1994; Silletti et al., 2004; Suding et al., 2004). Therefore, different grasses are adapted to different environmental conditions, ranging from high rainfall areas and deep soils to dry areas and shallow soils. For example, Tedder et al. (2011) showed that grass biomass of *Themeda triandra* and *Panicum maximum*, increases with increasing soil depth, and thus increasing soil fertility, suggesting an increase in aboveground competition, as per Grime's theory. However, not all grasses showed this trend; for example, *Eragrostis racemosa* showed no significant difference in biomass between shallow, medium, and deep soils (Tedder et al., 2012). This is because of the physical traits of this grass (being a short grass) and because it is highly adapted to shallow, rocky soils (Van Oudtshoorn, 2012).

Furthermore, different environmental conditions allow for differences in allocation of resources in grass species. Some grasses show massive investment in the aboveground material (high productivity), while others show greater investment in below ground material (Peltzer et al., 1998). Therefore, two grass species growing next to each other may either compete asymmetrically, symmetrically or not compete at all, depending on each species resource acquisition strategies (Weiner, 1990). While grass species differ in their resource acquisition, they also differ in their response to different available resources, either through biomass accumulation or/and tillering patterns (Tedder et al., 2011). However, the presence of a neighbour in any soil type could alter the growth (biomass accumulation and tillering) and resource acquisition of a grass species (Fynn et al., 2005; Fynn et al., 2009).

Competition between alien and native grasses

Alien grasses, like all alien plants, have proven problematic in natural veld. Even though alien grasses are often overlooked, their dominance has been linked to their competitive ability and local disturbance regimes. In grasslands, disturbance and competition have been shown to be correlated. For example, disturbance by means of fire or grazing can open space and reduce competitive interference from native grasses, hence, allowing introduced grasses to germinate, establish and sometimes become invasive (Brooks, 2000; Milton, 2004). Therefore, understanding the interaction between introduced grasses and native grasses is important for grassland restoration and biodiversity maintenance at large.

Studies which focused on alien – native grass competition have shown that introduced grasses are usually more competitive than native grasses, which explains the dominance of alien grasses in some areas (Milton, 2004; Vourlitis and Kroon, 2013). For example, pampas grass (*Cortaderia selloana*) from South America has invaded vast areas of land in South Africa, mostly along river banks. Its superior competitive ability as a tussock grass (up to 3.4m in diameter, and 4m stalk height) allows it to dominate available space impeding the growth of native grasses (Vourlitis and Kroon, 2013). It also produces abundant seeds and has greater water use efficiency than native grasses (Domenech and Vila, 2008). Domenech and Vila, (2008) using pot trials showed that pampas grass reduced the aboveground biomass of *Festuca arundinacea* and *Brachypodium phoenicoides* more when water was limiting, suggesting that competition for water plays a role in its dominance and invasion.

However, most alien-native grass interaction studies have been mostly done using grasses which are already invasive. Few or no studies have investigated recently introduced grasses which have not shown signs of invasiveness or even non-invasive historically introduced grasses. It is, however, clear that grasses with strong competitive ability have a better chance of being invasive in a new region. Furthermore, competition is dependent on available resources and the ability to acquire those resources; hence, differences in resource availability and acquisition will render one species more competitive over another.

Above- and Belowground competition

Plants (especially grasses) show differences in their competitive ability above ground (for light) and belowground (for soil nutrients). Goldberg's definition of belowground competition is the most extensively used because it integrates both plant behaviour (response and effect) and resource utility (Goldberg, 1990; Casper and Jackson, 1997). In grasses, belowground competition takes place when the neighbouring grasses or swards suppresses the growth, survival, or reproduction of the other grasses through depletion of available soil resources (Casper and Jackson, 1997). Therefore, belowground competition is correlated with factors such as root surface area, root density, and plasticity in roots or enzymic function involved in the nutrient uptake (Wilson, 1993). Root plasticity is defined as the ability of the root system to facilitate growth through changing its morphology under varying soil conditions to moderate the effect of stress and maintain greater plant productivity (Campbell et al., 1991a; Derner and Briske, 1999; Suralta et al., 2016).

There are many resources in the soil which are important for plant growth, which explains why much of the competition in plants occur underground. For this reason, quantifying belowground competition has been complex and two different approaches have been proposed; a physiological approach and, population and community ecology approach. Physiologically based studies focus on measuring nutrient uptake, without looking at plant performance, while population and community-based studies focus on plant performance (response and effect) (Casper and Jackson, 1997). Both these approaches are important in understanding plant competition belowground; however, experimental designs which incorporate both have proven difficult (Casper and Jackson, 1997).

Physiological studies have found three mechanisms by which soil nutrients reach the root surface of plants. Firstly, root interception, where roots grow and capture nutrients as they grow. This accounts for less than 10% of the total nutrient gain in plants (Casper and Jackson, 1997; Casper et al., 2003). Secondly, mass flow which is dependent on the amount of water and dissolved nutrients in the soil solution and is driven by plant transpiration. This is essential for nitrate (nitrogen) and water uptake in plants (Casper and Jackson, 1997). Lastly, diffusion of nutrients, which happens simultaneously with mass flow; however, is responsible for potassium and phosphorus uptake (Casper and Jackson, 1997). Nutrient diffusion takes place when soil nutrient uptake has exceeded the supply by mass flow, creating a local concentration gradient. There are experimental difficulties when trying to separate mass flow and diffusion of nutrients, because they both supply important nutrients and take place simultaneously (Casper and Jackson, 1997). These three resource acquisition mechanisms are important for understanding plant resource (mostly soil nutrients) competition. However, they are more physiologically based while this study is focusing more on plant performance (response and effect of competition).

With a basic understanding of nutrient acquisition, one can seek to understand the mechanisms of plant response or performance, which are likely to improve or reduce plant competition belowground. One of the traits that affect belowground competition is root density (Casper and Jackson, 1997; Casper et al., 2003). Even though root density has been used as a proxy for measurement of plant belowground competitive ability, some studies have failed to find a correlation between root density and plant competition belowground (Caldwell et al., 1991; Casper and Jackson, 1997). Caldwell et al. (1991) concluded that root abundance alone is sometimes not sufficient to explain relative nutrient uptake in plants. For example, sagebrush steppe species with dense root systems had a low phosphorus uptake, while those with less dense root systems acquired phosphorus better and increased their competitive ability (Caldwell et al., 1991). Therefore, not only the density of roots but root plasticity is important in understanding plant competition belowground.

A grass can take up more space by having denser roots, which might impede the establishment of other grass seedlings (Caldwell et al., 1991; Casper et al., 2003). Root mass (belowground biomass) is useful as a measure of competition because, depending on nutrient availability, grass species show differential investment in belowground structures (Casper et al., 2003; Tedder et al., 2011). Belowground competition is commonly seen to decrease with increasing soil nutrient levels; however, this response is species specific (Casper and Jackson, 1997). This is also the case with other soil resources e.g. water. For example, in arid areas where water is limiting, density-dependent mortality may be intense in seedlings because they lack extensive root systems. Therefore, longer roots in arid regions may be an adaptation to water limitation while in humid environments it may be a strategy that allows the plant to acquire resources from lower levels, avoiding competing with plants that utilize the upper soil horizons.

Additionally, plants with larger root systems are not able to totally monopolize nutrients resources; however, these systems are advantageous, mostly in areas with nutrient-rich patches, in that they can easily locate patches, and hence, be more competitive (Casper and Jackson, 1997; Cahill Jr and Casper, 2000). Belowground competition in grasslands is more variable and more linked to soil resource utilization than in other systems, such as forests (Campbell et al., 1991b). The presence of neighbouring grasses may cause changes in fine-root growth, structure, and distribution, while low soil resource availability may cause changes in soil resource uptake in two or more competing grasses (Cahill, 2003). This is because there are several types of competitive strategies that occur in grassland ecosystems. Firstly, exploitation, which relates to the depletion of a shared soil resource which leads to the suppression of one species or population (Schoener, 1983). Secondly, pre-emptive, where plant species compete for space in areas where it is limiting (Connell, 1983; Goldberg and Barton, 1992). Thirdly, symmetric, where each species or population suppresses the growth of the other species or population equally (Weiner, 1990). Fourthly, asymmetric, which is a one-sided competition where one species or population suppresses other species or populations (Weiner, 1990). And lastly, interference, which is the most difficult to quantify, where the species or population behaves in a manner that reduces the preference and exploration efficiency of other species or populations (Schoener, 1983; Callaway and Ridenour, 2004). Allelopathic behaviour falls under interference competition and plays a major role in belowground competition as it leads to asymmetric competition.

Above- and belowground competition have been shown to be interdependent, because of the shift in resource allocation in plants. Aboveground, competition is strongly related to light and to a limited extent, space. Grime's CSR model states that competition for both light and soil resources increases with an increase in productivity, while Tilman's R* model states that competition shifts from belowground to aboveground with an increase in productivity and changes in species composition (Grime, 1977; Tilman, 1985; Peltzer et al., 1998). Peltzer et al. (1998) investigated these conceptual models in an old, low diversity field with no species turnover. In this field, forty plots were fertilized with different levels of nitrogen annually for five years creating a nutrient gradient. They planted *Agropyron cristatum* along the nutrient gradient with no neighbours, roots of neighbours, and whole neighbouring plants to quantify root and shoot competition. They showed that *A. cristatum* biomass was 22-165% greater where there was no competition compared to when it was competing with roots of neighbours along the soil nutrient gradient, (Peltzer et al., 1998). This suggests that root competition was suppressing growth of *A. cristatum* along a nutrient gradient (Peltzer et al., 1998). Their study, therefore, suggests that the shift from root to shoot competition is not attributed to resource availability (fertilization) or to neighbour biomass along a productivity gradient in an area with low diversity. They concluded that such a conceptual model of plant competition oversimplifies the complex relationship between shoot and root competition in grasslands (Peltzer et al., 1998).

Aboveground competition for light is not as complex as belowground competition. It has been widely shown to be more asymmetric, hence larger plants have a more competitive advantage. For example, a pioneer plant that colonized a region first will gain a more competitive advantage, while in a stable or established grassland, mature plants will have a greater competitive advantage over seedlings through shade (Sala et al., 1996; Tainton, 1999; Silletti et al., 2004). However, some grasses such as *Panicum maximum* show tolerance to shade or sometimes show no negative performance in a shaded environment (Tainton, 1999; Van Oudtshoorn, 2012). By contrast, vetiver grass showed less tolerance to shade and hence, decreased in growth and even displayed increased tuft mortality in a shaded environment (Xia, 1995). Such a response is also strongly related to leaf size with many broad-leaved grasses showing tolerance to shade (Fynn and O'Connor, 2005).

Competitive ability in plants, either above- or belowground is influenced by many factors. For example, competitive ability may be attributed to the season but not soil nutrients. Remison and Snaydon (1978) showed that during the growing season, at the time of inflorescence development, both root growth and nutrient uptake decreased, hence reducing competitive ability of *Holcus lanatus* which was generally more competitive under nutrient poor conditions. The removal of root competition has been shown to increase seedling survival and growth (Aguiar et al., 1992), while the reduction in aboveground biomass through clipping shows no effect (Brown and Archer, 1999; Jurena and Archer, 2003). However, moderate defoliation in an old field which had been ungrazed for 40 years was seen to increase seedling survival and establishment, suggesting a long-term effect of aboveground competition on seedling survival (Remison and Snaydon, 1978; Jurena and Archer, 2003).

Measuring aboveground competition is not difficult because, during harvesting, no material is lost. By contrast, belowground competition when measured using biomass harvests may be inaccurate as fine roots are usually washed out and lost during the extraction process (Goldberg, 1996; Cahill, 2002). The root mass lost (extraction efficiency) during the extraction process has not been fully estimated (Cahill, 2002). The extraction efficiency varies between soil type, root system morphology and researchers (Cahill, 2002). Therefore, studies that separate above- and belowground competition are difficult to perform. Aboveground biomass has been used to give insight into both above- and belowground competition (Cahill, 2002). Furthermore, shoot biomass (i.e. aboveground biomass) has been used as the proxy for the long-term effect of neighbours.

Effect of competition on germination and seedling establishment

The interplay of both above- and belowground competition on seedling establishment has not been discussed fully. Therefore, because the study considers allelopathic behaviour, understanding the mechanism involved and how competition affects not only grass seedlings but also seed germination, is important.

Conditions that allow seed germination are well established; however, different species require different conditions. In general, seed germination requires specific temperature, moisture, and light regimes. However, moisture and warm temperatures are the major requirements for seed germination of most plant species (Ghebrehiwot et al., 2009; Kolb et al., 2016). Different species are adapted to different environmental conditions, where different management occurs (e.g. fire); therefore, seed germination in some species is triggered by such management (e.g. smoke) (Ghebrehiwot et al., 2009). For example, fire-adapted species germinated better in smoke water than in distilled water (control) when incubated under different temperatures (15°C, 20°C, 25°C, 30°C, and 35°C) with temperature also increasing the germination percentage (Ghebrehiwot et al., 2009). As previously stated, plants compete for both light and soil resources (e.g. water); therefore, competition can be expected to influence seed germination. Even though this seems correlated, considering that larger plants can limit light availability reducing temperatures and hence affecting seed germination, field studies show that the evidence relating to the effect of light competition on seed germination is limited (Cideciyan and Malloch, 1982; Kolb et al., 2016). However, there are studies which show that root competition and allelopathy do affect recruitment of grass species (Gallagher and Wagenius, 2016; Kolb et al., 2016). Allelopathy is usually seen in exotic plants and affects native plants because they lack adaptation to that allelopathic chemical, hence reducing germination success (Gentle and Duggin, 1997; Dias et al., 2016).

Aguiar et al. (1992) investigated the effect of plant competition (negative interaction) and facilitation (positive interaction) in the recruitment of the perennial grass species, *Bromus pictus*. The focus was on root competition because it has been documented to affect germination and establishment of native grasses. They showed that seedling survival and establishment was indeed affected by root competition because in areas where root competition was excluded, mortality decreased and growth increased (i.e. number of leaves increased) (Aguiar et al., 1992). Haugland and Fround-Williams (1999) supported their study, by showing that even with the addition of soil nutrients and water, root competition still affected seedling growth and establishment. This may suggest that other factors, such as allelopathy, are causing the observed effect or roots were competing directly for space and not for soil resources (Haugland and Froud-Williams, 1999).

Allelopathy first dominated the field of agriculture as a form of weed control (Dias et al., 2016). The chemicals which inhibit the growth of other species were extracted and used as an herbicide to inhibit germination and growth of weed species (Gentle and Duggin, 1997; Dias et al., 2016). Vetiver grass roots produce oil which is a mixture of various sesquiterpenes (part of phytotoxic agent) and their precursors (Kim et al., 2005; Mao et al., 2006). This oil has many biological uses in the plant as it also contains secondary metabolites which are involved in defence (mostly from insect herbivory), in addition to allowing the plant to be territorial through interference competition (Weyerstahl et al., 1996). Mao et al. (2004) investigated whether vetiver oil has allelopathic properties which may inhibit germination and growth of six weed species. The study showed that vetiver oil inhibited seed germination and seedling growth of five out of six weed species, which led to the conclusion that vetiver oil may indeed be used as a herbicide (Mao et al., 2004). Therefore, vetiver grass could be using such oil as interference competition (allelopathic competition).

However, not only competition affects plant (especially seedling) performance, since the ability of the plant to convert soil resources to biomass, known as water-use-efficiency and/or nutrient-use-efficiency, can be as effective as the competition itself (Casper and Jackson, 1997; Casper et al., 2003). Water-use-efficiency and nutrient-use-efficiency both can affect the relative growth of the plant at different points along a resource gradient (Casper and Jackson, 1997).

1.3.2 Competitive response and effect

Understanding the effects of plant competition on seed germination, seedling and adult grass growth at a species level (e.g. vetiver grass, in this case) or individual level, requires an understanding of their competitive ability (Goldberg and Landa, 1991). Competitive ability is a way to compare and measure individual plant competition in a community or population, which offers an understanding of the short-term and long-term community structure and species composition of that region (Campbell and Grime, 1992). Competitive ability of an individual or species can be examined using two components, competitive response and competitive effect (Goldberg, 1990; Goldberg and Landa, 1991). The ability of a plant to survive, grow and reproduce well in the presence of neighbours is known as competitive response (Goldberg and Fleetwood, 1987; Goldberg and Landa, 1991). While the ability of a plant or neighbours to suppress the survival, growth, and reproduction of the species is known as competitive effect (Goldberg and Fleetwood, 1987; Goldberg and Landa, 1991).

Competitive response can be measured as the change in the biomass (above- or belowground, or both) of the target plant when growing with the neighbours (Goldberg, 1990). Most studies use a small target plant because seedlings are more sensitive to competition and environmental effect than adult plants (Tedder et al., 2011). Competitive response determines which species can persist in a habitat and so can infer the effects on the diversity and productivity at a community level. Thus, species with a strong competitive response can withstand resource shortages imposed on them by neighbouring species and are therefore likely to persist under nutrient-rich conditions (Goldberg and Fleetwood, 1987; Goldberg, 1990). Competitive response is important in grassland research because differences in competitive response among grass species can determine species position within a competitive hierarchy, hence, determining their distribution along a resource gradient, and allowing the prediction of their relative abundance in a community (Grime, 1977; Keddy and Shipley, 1989).

By contrast, competitive effect is measured as per-unit-mass or per-plant reduction in the target plant or species (Goldberg and Fleetwood, 1987; Goldberg, 1990). This focuses more on whether the presence of neighbours results in some negative effect on the target plant or not. Competitive effect measures the effect of neighbours on the target plant, not of one individual plant on the other, therefore, it assumed that neighbours exact an equivalent effect on the target plant without taking into account that the number of neighbouring plants has an effect also (Goldberg and Fleetwood, 1987; Goldberg and Scheiner, 2001). The assumption is grounded in the notion that all plants use similar resources (light, water, and soil nutrients), and these resources occur along a gradient of availability (Goldberg and Landa, 1991). However, such assumptions are still being tested by ecologists. For example, Wedin and Tilman (1993) showed that competitive effect differs in grasses that grow in different successional stages. Late-successional grasses lowered nitrogen availability greater than early-successional grasses, which explains their dominance in matured old field grasslands (Wedin and Tilman, 1993). Furthermore, introduced grasses have been shown to exact a strong competitive effect on native grasses (Bakker and Wilson, 2001; Bakker et al., 2003). Bakker and Wilson (2001) showed that competitive effects have the ability to prevent establishment of native grass seedlings in the *Agropyron*-dominated regions (an exotic grass species in a mixed grassland of southern Saskatchewan, Canada).

It should be noted that grassland ecosystems are maintained through a variety of disturbance factors (e.g. grazing and fire). These disturbances and environmental stresses play a significant role in the competitive ability of species, which could be the reason why they are used to maintain such ecosystems. However, competitive response and effect of neighbouring species under these stresses could either follow Tilman's R* theory or Grime's CSR theory or be an interplay of both. Furthermore, competitive response and effect under such stress, mostly in grasses, has been shown to be species specific (Goldberg and Fleetwood, 1987; Bakker and Wilson, 2001). Therefore, it is important to understand each species' competitive ability (competitive response) against other species (interspecific competition) and with individuals of the same species (intra-specific competitive ability).

1.3.3 Rehabilitation, restoration, and management of grasslands

In South Africa, the largest, most transformed and degraded biome is grassland (Palmer and Ainslie, 2005). Most river catchment areas in South Africa are in grasslands, which indicates how important grasslands are, not only for carbon cycling and fodder production, but for water resources (Van Oudtshoorn, 1999; Palmer and Ainslie, 2005; Everson et al., 2007). Considering that South Africa is a water scarce country, one would assume that grasslands are well-protected and managed ecosystems, however, that is not the case. Out of all African flora, grasses are often overlooked and even the impact of alien grasses on grassland ecosystems is generally overlooked (Milton, 2004). The first peer-reviewed paper focusing on alien grasses in South Africa by Milton (2004), outlined mostly the level of uncertainty regarding alien grasses distribution and the gaps on our understanding of the dynamics of alien grasses in South Africa. After her review, few other studies have expanded on her work. For example, Visser et al. (2017) showed that there are 256 alien grasses in South Africa, of which 122 species have been naturalized, and 37 species have become invasive. The paper offers further evidence of the level of uncertainty specifically in relation to alien grass species distribution, abundance, and impact on the ecosystem. For example, out of the total alien grass species found, 33% of species only had one record of occurrence.

Even though South Africa seems to have fewer alien grasses compared to other regions of the world, South African native grasses are among the most dominant, problematic, and widespread invasive grasses in other parts of the world, proving the existence of a donor-recipient asymmetry. Visser et al. (2016) showed that, even though possible, it is unlikely that such donor-recipient asymmetry is a reflection of bias in sampling method and in introduction dynamics, but could because of two reasons. Firstly, a large proportion of palatable tropical forage grasses are native to Africa, with most occurring in South Africa, hence South Africa is likely to have imported few species from other continents for forage related purposes (Visser et al. 2016). Secondly, South African grasses are adapted to high fire frequencies and as a results, such adaptations give them a competitive advantage (regenerate faster after fire) in other regions, while fire frequency in South Africa is predicted to be limiting the invasion of alien grasses as there are not adapted to such fire regimes (Visser et al. 2017). For example, Visser et al. (2016) showed that the distribution of alien non-invasive grasses was limited to areas with infrequent fire, supporting that notion that fire is limiting the invasion of alien grasses in South Africa. However, species which stay green even during the dormant season (e.g. vetiver, and *Festuca costata*) have the ability to alter fire regimes through reducing fuel bed, and fuel load (McGranahan et al., 2018). International studies have shown that conversion of natural grasslands to those dominated by introduced grasses or even alien invasive grasses poses a threat to grassland ecosystems, through alteration of fire regimes, water and nutrient cycling, and erosion (Humphrey and Schupp, 2004). For example, in North America, *Bromus tectorum* (an alien grass) has dominated hectares of native grassland, altering regeneration structure and the effect of fire (Humphrey and Schupp, 2004). Its seeds germinate faster than those of native grasses and gain a head start after fire, hence gaining a competitive advantage and therefore, impending germination and establishment of native grass seeds (Humphrey and Schupp, 2004).

Even though fire is a widely-used management tool, uncontrolled fires can destroy native perennial grasses' seeds, hence reducing the perennial grass seed bank, which then affects native perennial grass regeneration and establishment (Tainton, 1999; Humphrey and Schupp, 2004). Uncontrolled fires combined with overgrazing could result in grassland degradation or environmental degradation in the form of species loss (domination of unpalatable grasses) and soil erosion. Eroded grasslands, either through rill, sheet or gully erosion, become unable to support productive grasses and have reduced basal cover (Van Oudtshoorn, 2012). Reasons for this loss of productivity are, the removal of topsoil resulting in the exposure of less fertile soil which cannot support grass growth (Everson et al., 2007; Van Oudtshoorn, 2012), and patches of bare soil and sparse grass cover which become unable to effectively capture water resulting in reduced soil moisture, increased evaporation and greater soil temperatures (Everson et al., 2007; Van Oudtshoorn, 2012). Therefore, rehabilitation of such grasslands is sometimes difficult and involves the use of geo-textiles, stone packs and gabions (Everson et al., 2007). Alien grasses which are adapted to harsh environments (e.g. vetiver grass) are usually used to reduce water runoff and to restore the soil so that native grasses can establish (Everson et al., 2007; Van Oudtshoorn, 2012). These alien grasses, used for rehabilitation or slope stabilization (e.g. pampas grass), often outcompete native grasses and sometimes become invasive. Understanding their ecology, mostly in terms of competitive ability (response and effect), could provide information about their invasion potential and ability to allow native grasses to establish, which will then restore the productivity and function of that ecosystem.

Vetiver grass, has been used successfully for decades to rehabilitate eroded sites, abandoned mine sites, to stabilize roadside slopes, and for wastewater treatment. Many claims have been made which relate to the ecology of the grass; however, some of them have been found to be false. For example, the idea that the domesticated vetiver does not flower nor does it produce seeds does not seem to hold, as the presence of flowers and seeds has been reported (Xu, 2002). Therefore, the broad assumption that it will not be invasive raises questions. These questions emphasize the importance of understanding vetiver grass' competitive ability and the interplay of soil nutrients on competitive ability. Therefore, this study will contribute to the understanding of vetiver grass, rehabilitation of eroded sites, and the management of grassland ecosystems through increasing the knowledge of alien grass species' effect on native grass seed germination, seedling establishment, and grass diversity to contribute to regeneration and restoration ecology.

This study aims to addresses the following questions:

1.4 LIST OF QUESTIONS PER CHAPTER

1.4.1 Chapter Two: which native grasses grow in close proximity with vetiver grass?

1. Are native grasses recruiting and coexisting with vetiver in these sites?
2. Which native grasses are present in these rehabilitated sites?
3. How far from the lines of vetiver planted for rehabilitation do these grasses grow?
4. Is vetiver recruiting in areas where it was not originally planted?

1.4.2 Chapter Three: does vetiver allow germination and establishment of native grasses?

1. Do vetiver grass tufts inhibit or facilitate seed germination in native grasses?
2. Is the germination rate of native grasses affected by the seed sowing method?
3. Do vetiver grass tufts inhibit establishment of native grasses?
4. Does the exclusion of direct root interaction decrease the competitive effect exerted on native grass seedlings?
5. Does vetiver root density differ from indigenous grass root density?

For this chapter *Eragrostis curvula* and *Panicum maximum* will be used to represent native grasses, and the details regarding the ecology of these species and those of the following chapter can be found in appendix A.

1.4.3 Chapter Four: effect of vetiver competition and soil nutrients on native grasses.

1. Does vetiver exert a competitive effect on neighbouring native grasses with a strong (*Eragrostis curvula* and *Digitaria eriantha*) and weak (*Panicum maximum* and *Hyparrhenia hirta*) competitive ability?
2. Does vetiver density influence the competitive effect experienced by native grasses?
3. Does soil nutrient addition influence this interaction?

1.5 REFERENCES

Bond, W., Midgley, G., Woodward, F., Hoffman, M., Cowling, R., 2003. What controls South African vegetation—climate or fire? South African Journal of Botany 69, 79-91.

Ellery, W., Scholes, R., Scholes, M., 1995. The distribution of sweetveld and sourveld in South Africa's grassland biome in relation to environmental factors. African Journal of Range & Forage Science 12, 38-45.

Ghedira, K., Goetz, P., 2015. Vétiver: *Vetiveria zizanoides* (L.) Nash (Poaceae). Phytothérapie 13, 193-196.

Hoffmann, W.A., Solbrig, O.T., 2003. The role of topkill in the differential response of savanna woody species to fire. Forest ecology and management 180, 273-286.

Tainton, N.M., Bransby, D., Booysen, P.d.V., 1976. Common veld and pasture grasses of Natal. Shuter & Shooter.

Zacharias, P.J.K., 1990. The seasonal patterns in plant quality in various ecological zones in Natal. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Acocks, J.P.H., 1988. Veld types of South Africa, 2nd ed. Memoirs of the Botanical Survey of South Africa.

Adams, R., Turuspekov, M.Z., Dafforn, M., Veldkamp, J., 1998. DNA fingerprinting reveals clonal nature of *Vetiveria zizanioides* (L.) Nash, Gramineae and sources of potential new germplasm. Molecular Ecology 7, 813-818.

Adams, R.P., Center, P.B., 2000. DNA analysis of the genetic diversity of vetiver and future selections for use in erosion control, Second International Conference on Vetiver-ICV2, Thailand.

Adams, R.P., Dafforn, M., 1997. DNA fingerprints (RAPDs) of the pantropical grass vetiver, *Vetiveria zizanioides* (L.) Nash (Gramineae), reveal a single clone,“Sunshine”, is widely utilized for erosion control. Vetiver Newsletter 18, 27-33.

Adams, R.P., Pandey, R.N., Dafforn, M.R., James, S.A., 2003. Vetiver DNA-fingerprinted cultivars: effects of environment on growth, oil yields and composition. Journal of Essential Oil Research 15, 363-371.

Adigun, M., Are, K., 2015. Comparatives effectiveness of two vetiveria grasses species *Chrysopogon zizanioides* and *Chrysopogon nigritana* for the remediation of soils contaminated with heavy metals. American Journal of Experimental Agriculture 8, 361-366.

Aguiar, M., Soriano, A., Sala, O., 1992. Competition and facilitation in the recruitment of seedlings in Patagonian steppe. Functional Ecology 6, 66-70.

Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in plant ecology, evolution and systematics 3, 52-66.

Austin, M., 1986. The theoretical basis of vegetation science. Trends in Ecology & Evolution 1, 161-164.

Bakker, J., Wilson, S., 2001. Competitive abilities of introduced and native grasses. Plant Ecology 157, 119-127.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G., Waddington, J., 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications 13, 137-153.

Begon, M., Townsend, C., Harper, J., 1990. Ecology: Individuals, Populations and Communities, Second Edition ed. Blackwell Science Inc, Massachusetts, USA.

Blossey, B., Kamil, J., 1996. What determines the increased competitive ability of invasive non-indigenous plants, Proceedings of the IX international symposium on the biological control of weeds. University of Cape Town, Stellenbosch, 3-9.

Blossey, B., Notzold, R., 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83, 887-889.

Bojö, J., 1996. The costs of land degradation in Sub-Saharan Africa. Ecological economics 16, 161-173.

Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. The American Midland Naturalist 144, 92-108.

Brown, J.R., Archer, S., 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. Ecology 80, 2385-2396.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18, 119-125.

Cahill Jr, J.F., Casper, B.B., 2000. Investigating the relationship between neighbor root biomass and belowground competition: field evidence for symmetric competition belowground. Oikos 90, 311-320.

Cahill, J.F., 1999. Fertilization effects on interactions between above-and belowground competition in an old field. Ecology 80, 466-480.

Cahill, J.F., 2002. What evidence is necessary in studies which separate root and shoot competition along productivity gradients? Journal of Ecology 90, 201-205.

Cahill, J.F., 2003. Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. Journal of Ecology 91, 532-540.

Caldwell, M.M., Manwaring, J., Durham, S., 1991. The microscale distribution of neighbouring plant roots in fertile soil microsites. Functional Ecology, 765-772.

Callaway, R.M., Ridenour, W.M., 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2, 436-443.

Campbell, B., Grime, J., Mackey, J., 1991a. A trade-off between scale and precision in resource foraging. Oecologia 87, 532-538.

Campbell, B., Grime, J., Mackey, J., Jalili, A., 1991b. The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. Functional Ecology 5, 241-253.

Campbell, B.D., Grime, J.P., 1992. An experimental test of plant strategy theory. Ecology 73, 15-29.

Cao, L., Zhang, Y., Lu, H., Yuan, J., Zhu, Y., Liang, Y., 2015. Grass hedge effects on controlling soil loss from concentrated flow: A case study in the red soil region of China. Soil and Tillage Research 148, 97-105.

Casper, B.B., Jackson, R.B., 1997. Plant competition underground. Annual Review of Ecology and Systematics 28, 545-570.

Casper, B.B., Schenk, H.J., Jackson, R.B., 2003. Defining a plant's belowground zone of influence. Ecology 84, 2313-2321.

Castro, S. A., Figueroa, J. A., Muñoz-Schick, M., Jaksic, F. M., 2005. Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. Diversity and Distributions 11, 183-191.

Change, I.P.O.C., 2001. Climate change 2007: impacts, adaptation and vulnerability. Genebra, Suíça.

Cheng,K.,Hu,G.Q., Rao,H.M., Xu, L.H.,and Wu, H.Q., 1994 Ecological effects of planting vetiver grass in citrus groves on slopping red soil fields. Acta Ecologica sinice 14, 21-25.

Chōmchalao, N., 2001. Utilization of vetiver as medicinal and aromatic plants. Office of the Royal Development Projects Board.

Cideciyan, M.A., Malloch, A.J., 1982. Effects of seed size on the germination, growth and competitive ability of *Rumex crispus* and *Rumex obtusifolius*. The Journal of Ecology 70, 227-232.

Clements, F.E., 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington.

Clements, F.E., 1928. Plant succession and indicators. Hafner Press; New York,; Collier Macmillan Publishers; London.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A., MacIsaac, H.J., 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7, 721-733.

Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist 122, 661-696.

Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

Craine, J.M., 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of Ecology 93, 1041-1052.

Dalton, P., Smith, R., Truong, P., 1996. Vetiver grass hedges for erosion control on a cropped flood plain: hedge hydraulics. Agricultural Water Management 31, 91-104.

Derner, J.D., Briske, D.D., 1999. Does a tradeoff exist between morphological and physiological root plasticity? A comparison of grass growth forms. Acta Oecologica 20, 519-526.

Dias, L., Pereira, I.P., Dias, A.S., 2016. Allelopathy, seed germination, weed control and bioassay methods. Allelopathy Journal 37, 31-40.

Domenech, R., Vila, M., 2008. Response of the invader *Cortaderia selloana* and two coexisting natives to competition and water stress. Biological Invasions 10, 903-912.

Eagles, C., 1972. Competition for light and nutrients between natural populations of *Dactylis glomerata*. Journal of Applied Ecology, 141-151.

Edelstein, M., Plaut, Z., Dudai, N., Ben-Hur, M., 2009. Vetiver (*Vetiveria zizanioides*) responses to fertilization and salinity under irrigation conditions. Journal of Environmental Management 91, 215-221.

Everson, T.M., Everson, C.S., Zuma, K., 2007. Community based research on the influence of rehabilitation techniques on the management of degraded catchments. Water Research Commission.

Faria, A.P., Fernandes, G.W., França, M.G.C., 2015. Predicting the impact of increasing carbon dioxide concentration and temperature on seed germination and seedling establishment of African grasses in Brazilian Cerrado. Austral Ecology 40, 962-973.

Fey, M., 2010. Soils of South Africa. Cambridge University Press.

Fish, L., Mashau, A. C., Moeaha, M. J., Nembudani, M.T., 2015. Identification guide to southern African grasses. An identification manual with keys, descriptions and distributions. Strelitzia 36. South African National Biodiversity Institute, South Africa.

Foster, B.L., 1999. Establishment, competition and the distribution of native grasses among Michigan old-fields. Journal of Ecology 87, 476-489.

Fowler, N., 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17, 89-110.

Fynn, R., Morris, C., Kirkman, K., 2005. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. Journal of Ecology 93, 384-394.

Fynn, R.W., O'Connor, T.G., 2005. Determinants of community organization of a South African mesic grassland. Journal of Vegetation Science 16, 93-102.

Fynn, R.W., Wragg, P., Morris, C., Kirkman, K., Naiken, J., 2009. Vegetative traits predict grass species' invasiveness and the invasibility of restored grassland. African Journal of Range & Forage Science 26, 59-68.

Gallagher, M.K., Wagenius, S., 2016. Seed source impacts germination and early establishment of dominant grasses in prairie restorations. Journal of Applied Ecology 53, 251-263.

Gentle, C., Duggin, J., 1997. Allelopathy as a competitive strategy in persistent thickets of *Lantana camara* L. in three Australian forest communities. Plant Ecology 132, 85-95.

George, J., Laing, M., Drewes, S., 2001. Phytochemical research in South Africa. South African Journal of Science 97, 93-105.

Ghebrehiwot, H.M., Kulkarni, M.G., Kirkman, K.P., Van Staden, J., 2009. Smoke solutions and temperature influence the germination and seedling growth of South African mesic grassland species. Rangeland Ecology & Management 62, 572-578.

Goldberg, D.E., 1990. Components of resource competition in plant communities. Perspectives on Plant Competition, 27-49.

Goldberg, D.E., 1996. Competitive ability: definitions, contingency and correlated traits. Philosophical Transactions of the Royal Society of London B: Biological Sciences 351, 1377-1385.

Goldberg, D.E., Barton, A.M., 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. The American Naturalist 139, 771-801.

Goldberg, D.E., Fleetwood, L., 1987. Competitive effect and response in four annual plants. The Journal of Ecology 75, 1131-1143.

Goldberg, D.E., Landa, K., 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. The Journal of Ecology 79, 1013-1030.

Goldberg, D.E., Scheiner, S.M., 2001. ANOVA and ANCOVA: field competition experiments. Design and analysis of ecological experiments 2, 69-93.

Gough, L., Osenberg, C.W., Gross, K.L., Collins, S.L., 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos 89, 428-439.

Grace, J., 1991. A clarification of the debate between Grime and Tilman. Functional Ecology 5, 583-587.

Grace, J.B., 1990. On the relationship between plant traits and competitive ability. Perspectives on Plant Competition, 51-65.

Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth. Infinity Publishing.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111, 1169-1194.

Guillebaud, J., Hayes, P., 2008. Population growth and climate change. British Medical Journal Publishing Group.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292-1297.

Haugland, E., Froud-Williams, R.J., 1999. Improving grasslands: the influence of soil moisture and nitrogen fertilization on the establishment of seedlings. Journal of Applied Ecology 36, 263-270.

Huang, X., 1999. Introduction of vetiver grass in Huangshan area, Annual Report. China Vetiver Development Foundation, Nanjing.

Humphrey, L.D., Schupp, E.W., 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. Journal of Arid Environments 58, 405-422.

Jurena, P., Archer, S., 2003. Woody plant establishment and spatial heterogeneity in grasslands. Ecology 84, 907-919.

Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17, 164-170.

Keddy, P.A., Shipley, B., 1989. Competitive hierarchies in herbaceous plant communities. Oikos, 234-241.

Kim, H.-J., Chen, F., Wang, X., Chung, H.Y., Jin, Z., 2005. Evaluation of antioxidant activity of vetiver (*Vetiveria zizanioides* L.) oil and identification of its antioxidant constituents. Journal of Agricultural and Food Chemistry 53, 7691-7695.

Kirkman, K.P., 1988. Factors affecting the seasonal variation of veld quality in South Africa. Unpublished Master's Thesis, University of KwaZulu-Natal, South Africa.

Kolb, R.M., Pilon, N.A.L., Durigan, G., 2016. Factors influencing seed germination in Cerrado grasses. Acta Botanica Brasílica 30, 87-92.

Kraaij, T., Ward, D., 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. Plant Ecology 186, 235-246.

Maffei, M., 2003. *Vetiveria*: the genus *Vetiveria*. CRC Press.

Mahmoud, A., Grime, J., 1976. An analysis of competitive ability in three perennial grasses. New Phytologist 77, 431-435.

Mao, L., Henderson, G., Bourgeois, W.J., Vaughn, J.A., Laine, R.A., 2006. Vetiver oil and nootkatone effects on the growth of pea and citrus. Industrial Crops and Products 23, 327-332.

Mao, L., Henderson, G., Laine, R.A., 2004. Germination of various weed species in response to vetiver oil and nootkatone 1. Weed Technology 18, 263-267.

McGranahan, D. A., Archibald, S., Kirkman, K. P., and O'Connor, T. G., 2018. A native C 3 grass alters fuels and fire spread in montane grassland of South Africa. Plant Ecology, 1-12.

Milchunas, D., Sala, O., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132, 87-106.

Milton, S.J., 2004. Grasses as invasive alien plants in South Africa: working for water. South African Journal of Science 100, 69-75.

Mulder, J., Brent, A.C., 2006. Selection of sustainable rural agriculture projects in South Africa: Case studies in the LandCare programme. Journal of Sustainable Agriculture 28, 55-84.

Mynhardt, J.E., Van Rooyen, M., Theron, G., 1994. Competitive ability of two grass species: *Anthephora pubescens* and *Eragrostis curvula*. 1. Yield and biomass allocation. South African Journal of Botany 60, 261-268.

Navarro, L., Guitian, J., 2003. Seed germination and seedling survival of two threatened endemic species of the northwest Iberian Peninsula. Biological Conservation 109, 313-320.

Nix, K.E., Henderson, G., Zhu, B.C., Laine, R.A., 2006. Evaluation of vetiver grass root growth, oil distribution, and repellency against formosan subterranean termites. HortScience 41, 167-171.

O'Rourke, S., Minasny, B., Holden, N., McBratney, A., 2016. Synergistic use of Vis-NIR, MIR, and XRF spectroscopy for the determination of soil geochemistry. Soil Science Society of America Journal 80, 888-899.

Palmer, A.R., Ainslie, A.M., 2005. Grasslands of South Africa. Grasslands of the World 34, 77.

Peltzer, D.A., Wilson, S.D., Gerry, A.K., 1998. Competition intensity along a productivity gradient in a low-diversity grassland. The American Naturalist 151, 465-476.

Rajaniemi, T.K., 2002. Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. Journal of Ecology 90, 316-324.

Remison, S.U., Snaydon, R.W., 1978. Yield, seasonal-changes in root competitive ability and competition for nutrients among grass species. Journal of Agricultural Science, The 90, 115-124.

Robinson, D., Rorison, I., 1988. Plasticity in grass species in relation to nitrogen supply. Functional Ecology 2, 249-257.

Sala, O., Lauenroth, W., McNaughton, S., Rusch, G., Zhang, X., 1996. 6 Biodiversity and Ecosystem Functioning in Grasslands.

Schoener, T.W., 1983. Field experiments on interspecific competition. The American Naturalist 122, 240-285.

Shangwen, C., 1999. Insects on vetiver hedges. The Vetiver Newsletter 23, 17-18.

Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17, 170-176.

Shengluan, L., Jiayou, Z., 1998. Contribution of vetiver grass to sustainable agricultural development in the hilly red soil region In: Xu Liyu (ed) Vetiver Research and Development. 132-137. China Agriculture Scientech Press, Beijing.

Silletti, A.M., Knapp, A.K., Blair, J.M., 2004. Competition and coexistence in grassland codominants: responses to neighbour removal and resource availability. Canadian Journal of Botany 82, 450-460.

Suding, K.N., LeJeune, K.D., Seastedt, T.R., 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. Oecologia 141, 526-535.

Suralta, R.R., Kano-Nakata, M., Niones, J.M., Inukai, Y., Kameoka, E., Tran, T.T., Menge, D., Mitsuya, S., Yamauchi, A., 2016. Root plasticity for maintenance of productivity under abiotic stressed soil environments in rice: Progress and prospects. Field Crops Research 220, 57-66.

Tainton, N., 1981a. ecology of the main grazing lands of South Africa. Veld and pasture management in South Africa.

Tainton, N.M., 1981b. Veld and pasture management in South Africa. Shuter & Shooter; University of Natal Press.

Tainton, N.M., 1999. Veld Management in South Africa. University of Natal press.

Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2011. Grass-on-grass competition along a catenal gradient in mesic grassland, South Africa. African Journal of Range & Forage Science 28, 79-85.

Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2012. Do soil nutrients mediate competition between grasses and Acacia saplings? Grassland Science 58, 238-245.

The Vetiver Network International, 2017. 20 JUNE The Vetiver Network International, 2017, http://vetiver.org/.

Thompson, K., 1987. The resource ratio hypothesis and the meaning of competition. Functional Ecology 1, 297-303.

Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation. The American Naturalist 116, 362-393.

Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist 125, 827-852.

Tilman, D., 1987. On the meaning of competition and the mechanisms of competitive superiority. Functional Ecology 1, 304-315.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2-16.

Truong, P., 2000a. Application of the vetiver system for phytoremediation of mercury pollution in the Lake and Yolo Counties, Northern California. Proceedings of pollution solutions, 1-13.

Truong, P., 2000b. The global impact of vetiver grass technology on the environment. Proceedings of the Second International Conference on Vetiver, 48-61.

Truong, P., Chomchalow, N., Vessabutr, S., 1999. Vetiver grass technology for mine rehabilitation. Pacific Rim Vetiver Network Technology 2, 1-19.

Truong, P., Hart, B., Chomchalow, N., Sombatpanit, S., 2001. Vetiver system for wastewater treatment. Office of the Royal Development Projects Board.

Truong, P., Loch, R., 2004. Vetiver system for erosion and sediment control. Proceeding of 13th international soil conservation organization conference, 1-6.

Van den Berg, J., Midega, C., Wadhams, L., Khan, Z., 2003. Can Vetiver grass be used to manage insect pests on crops? Proceedings of the Third International Conference on Vetiver and Exhibition, 254-264.

Van Oudtshoorn, F.v., 1999. Guide to grasses of Southern Africa. Briza Publications.

Van Oudtshoorn, F.v., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza Publications.

Veldkamp, J., 1999. A revision of *Chrysopogon* Trin. including *Vetiveria* Bory (Poaceae) in Thailand and Malesia with notes on some other species from Africa and Australia. Austrobaileya 5, 503-533.

Visser, V., Wilson, J. R., Canavan, K., Canavan, S., Fish, L., Maitre, D. L., Kumschick, S., 2017. Grasses as invasive plants in South Africa revisited: Patterns, pathways and management. Bothalia-African Biodiversity & Conservation 47, 1-29.

Visser, V., Wilson, J. R., Fish, L., Brown, C., Cook, G. D., Richardson, D. M., 2016. Much more give than take: South Africa as a major donor but infrequent recipient of invasive non-native grasses. Global Ecology and Biogeography, 25, 679-692.

Vourlitis, G.L., Kroon, J.L., 2013. Growth and resource use of the invasive grass, pampasgrass (*Cortaderia selloana*), in response to nitrogen and water availability. Weed Science 61, 117-125.

Wagner, S., Truong, P., Vieritz, A., Smeal, C., 2003. Response of vetiver grass to extreme nitrogen and phosphorus supply. Proceedings of the Third International Conference on Vetiver and Exhibition, Guangzhou, China.

Wall, R., Begon, M., 1985. Competition and fitness. Oikos, 356-360.

Wang, Y.-W., 2000. The root extension rate of vetiver under different temperature treatments. Proceedings of the Second International Conference on Vetiver. http://www.vetiver.org/TAI_temp.pdf.

Ward, D., 2010. A resource ratio model of the effects of changes in CO2 on woody plant invasion. Plant Ecology 209, 147-152.

Wedin, D., Tilman, D., 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecological Monographs 63, 199-229.

Weiner, J., 1990. Asymmetric competition in plant populations. Trends in Ecology & Evolution 5, 360-364.

Weyerstahl, P., Marschall, H., Splittgerber, U., Wolf, D., 1996. New sesquiterpene ethers from Vetiver oil. Liebigs Annalen 1996, 1195-1199.

Wilson, S.D., 1993. Belowground competition in forest and prairie. Oikos 68, 146-150.

Wolfe, L.M., 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis. The American Naturalist 160, 705-711.

Xia, H., 1995. Effect of shading and cutting on the growth of vetiver. Vetiver Grass for Soil and Water Conservation, 178-179.

Xia, H., Ao, H., He, D., 1998. The effect of environmental factors on the growth of vetiver growth. Vetiver Research and Development, 39-44.

Xu, L., 1998. Vetiver research and development, Proceedings of International Vetiver Workshop, Fuzhou, China. Agricultural Science and Technology Press of China, Beijing.

Xu, L., 2002. Vetiver research and development: A decade experience from China, Proceedings: The Second International Vetiver Conference, ORDPB, Bangkok, 311-322.

Zaloumis, N. P., and Bond, W. J. 2011. Grassland restoration after afforestation: No direction home?. Austral Ecology 36, 357-366.

Zhu, B.C., Henderson, G., Chen, F., Maistrello, L., Laine, R.A., 2001. Nootkatone is a repellent for Formosan subterranean termite (*Coptotermes formosanus*). Journal of Chemical Ecology 27, 523-531.

2 CHAPTER TWO: WHICH NATIVE GRASSES GROW IN CLOSE PROXIMITY WITH VETIVER GRASS?

2.1 ABSTRACT

Soil erosion has become a major problem affecting agricultural and rangeland productivity, especially in developing countries. To combat this problem, a fast-growing, densely rooted, and drought resistant grass called vetiver (*Chrysopogon zizanioides*) has been widely used, mostly in developing countries. Its use is grounded in two claims, firstly that it does not compete with neighbouring plants, and secondly, that it does not spread as it produces non-viable seeds. However, no study has evaluated areas rehabilitated using vetiver to verify these claims. The contiguous quadrat method was used to survey six sites rehabilitated using vetiver with the aim to determine how far native grasses grow from planted vetiver and the extent of plant succession in these rehabilitated sites. The most important results of this study were the marked increase in grass species richness with an increase in distance away from planted vetiver, the abundance of bare ground around planted vetiver, and the presence of the recruiting vetiver grass away from planted vetiver. The presence of bare ground could either indicate a strong competitive ability of vetiver, and/or an allelophatic effect (possibly from the oil produced by the roots), hence challenging the first claim. The second claim is challenged by the presence of recruiting vetiver, indicating signs of spreading. These sites were dominated by unpalatable subclimax species e.g. *Aristida bipartite*, climax species e.g. *Hyparrhenia hirta*, and only one unpalatable pioneer grass i.e. *Aristida congesta* subsp *barbicollis* occurring only in one site. The marked dominance of increaser grasses was as a result of overgrazing because the area surveyed is a communal rangeland with poorly controlled grazing. There is no doubt that vetiver is beneficial for soil conservation; however, this study shows that vetiver persists for decades with no sign of being succeeded by native grasses, and native grasses do not grow in close proximity to vetiver.

2.2 INTRODUCTION

Rangeland degradation in the form of soil erosion has become a worldwide problem, especially in developing countries (Tainton, 1999; O'Rourke et al., 2016). For decades, research has focused on understanding the causes of soil erosion, mapping erosion over time, and implementing environmentally sound ways to combat soil erosion (Boardman and Poesen, 2006; Morgan, 2009). Even though soil erosion is a natural process, it is accelerated by factors such as clearing of vegetation, overgrazing, and soil tillage, which are directly linked to human activities

(Morgan, 2009). Grasses have been shown to effectively stabilize the soil, increase water infiltration and reduce surface runoff, hence preventing or reducing the occurrence of soil erosion (Council, 1993; Everson et al., 2007). However, poor management of rangelands, such as overgrazing, exposes the topsoil making it susceptible to sheet or rill erosion during rainfall events (Boardman and Poesen, 2006; Everson et al., 2007). Soil erosion removes the nutrient-rich topsoil, exposing the nutrient-poor subsoil which prevents re-establishment of native grasses. Through top soil removal, the soil seed bank is also lost, further reducing the likelihood of reestablishment (Zhang et al., 2001; DeFalco et al., 2009). Therefore, attempts to rehabilitate these degraded areas require the re-introduction of native species by means of seeds or tufts to regain the lost vegetation (Everson et al., 2007). However, not all plant species can grow in these nutrient poor conditions. Fast growing grass species that can tolerate low nutrient soils and harsh environmental conditions have been seen as a practical solution to combat soil erosion (Council, 1993). These grasses stabilise the soil and help to capture topsoil runoff with the view to allowing recolonization of the more sensitive native species. Many indigenous species do not grow in these nutrient-poor eroded soils and so some exotic species have been propagated for this purpose.

Vetiver (*Chrysopogon zizanioides* (L.) Roberty) is an exotic grass originating in India which has been extensively used for controlling soil erosion (Chen et al., 1993; Grimshaw, 1993). It is a fast-growing grass with an extensive root system that extends down to 4m, binding soil particles together. Vetiver grass tolerates many harsh environmental conditions, such as drought, floods, nutrient poor soil, and salinity and it is resistant to fires (Chen et al., 1993; Grimshaw, 1993; Edelstein et al., 2009). A number of claims have been made by promoters of vetiver grass (The Vetiver Network International, 2017) relating to its competitive ability and coexistence with other species, which have been used to support and popularize the use of this grass. The first claim is, vetiver grass does not compete with adjacent crops (Council, 1993; Vieritz et al., 2003). This means that, after vetiver has established, it should trap the top soil and restore the nutrient status to allow for establishment of native grasses. However, the evidence that exists for such claims is from crop plants only, not naturally occurring grasses (Council, 1993; Vieritz et al., 2003). For example, compared with other vegetative barriers (*Leucaena leucocephala*, *Cymbopogon flexuosus*, and *Chrysopogon martini*), vetiver grass resulted in a 25.5% greater yield in seed cotton (*Gossypium hirsutum*) compared to the control, 24% more compared to *L. leucocephala*, 15% more compared to *Cymbopogon flexuosus*, and 11% more compared to *Chrysopogon martini* (Vieritz et al., 2003). It is therefore, assumed that even in rangelands, indigenous grasses will coexist with vetiver and that vetiver will enhance their recruitment process. The second claim is, vetiver grass does not spread because it produces non-viable seeds, and has no stolons or rhizomes (Council, 1993). However, no study has properly evaluated the validity of these claims in rangelands. In rangelands, rehabilitation does not only involve reestablishing aboveground cover and preventing soil erosion, it also involves promoting species diversity and retaining naturally occurring species to promote rangeland productivity.

This study aimed to evaluate areas rehabilitated using vetiver grass to determine which species grow in close proximity to vetiver grass. The three following questions were addressed in this study:

1. Are native grasses recruiting and coexisting with vetiver in these sites?
2. Which native grasses are present in these rehabilitated sites?
3. How far from the lines of vetiver planted for rehabilitation do these grasses grow?
4. Is vetiver recruiting in areas where it was not originally planted?

There is so much uncertainty and anecdotal evidence relating to other species' association with vetiver; therefore, this study is exploratory in that regard.

2.3 MATERIALS AND METHODS

2.3.1 Study site

The study was conducted in the Okhombe valley, located at the foot of the Northern Drakensberg Mountains, Bergville, KwaZulu-Natal, South Africa. The Okhombe valley is a communal rangeland which receives a mean annual rainfall of 800 – 1000 mm, with about 82% of the rainfall received during summer (Mansour et al., 2012). The mean altitude of this area ranges from 1200 to 3350 m, with a mean monthly minimum temperature of 11.5^{o}C to 16^{o}C in summer (October to March) and below 5^{o}C in winter (June to July), with frost and snow occurring almost every year (Temme, 2008; Mansour et al., 2012). The area has a mixed geology, ranging from mudstone and sandstone to ampholite, basalt, and tillite with increasing altitude (Mansour et al., 2012). The mixed geology, rainfall, and topography give rise to mostly oxidic, well-drained soils with Griffin, Hutton (Oxisol) and Clovelly (Alfisol) on the slopes, and shallower soils, such as Mispah on top of the catena (Mansour et al., 2012).

The grazing camps are situated on top of the ridges surrounding the settlements in the bottom of the valley (Fig. 2.1). This presents a management problem because livestock have to move up to the grazing camps every morning and down to the settlements at night. This movement creates paths on the slopes which then get easily eroded during intense rainfall periods. As a result, these soils have become heavily eroded and so rehabilitation programmes have been initiated. Vetiver grass was planted as one of the techniques employed for a programme that aimed at rehabilitation and management of degraded catchments, funded by the Department of Environmental Affairs, and run by staff from the University of KwaZulu-Natal. This programme trained local people in the basic causes and effects of soil erosion, the importance of rehabilitation, ways to rehabilitate eroded sites (e.g. how to plant vetiver), and formed the Okhombe Monitoring Group. This programme aimed to empower the community and utilize simple techniques, such as vetiver planting, and stone packs, to rehabilitate degraded catchments (see Everson et al. 2007 for more detail).

The area is primary grassland, classified as upland moist grassland (Mucina and Rutherford, 2006). The most dominant grasses in the region are *Hyparrhenia* species, *Eragrostis* species, *Aristida* species, *Themeda triandra, Digitaria* species, *Panicum* species, *Cymbopogon* species, *Monocymbium ceresiiforme*, *Sporobolus* species, and *Miscanthus capense* (O'Connor and Bredenkamp, 1997; Mansour et al., 2012). The area has a long history of research and collaboration with the University of KwaZulu-Natal as it is a catchment for the Tugela River, and therefore, a number of different rehabilitation and management programmes have been run over the last two decades commencing in about 1992. For this work, six sites where vetiver grass has been used to rehabilitate eroded areas were identified. These sites were rehabilitated between 1992 and 2015.

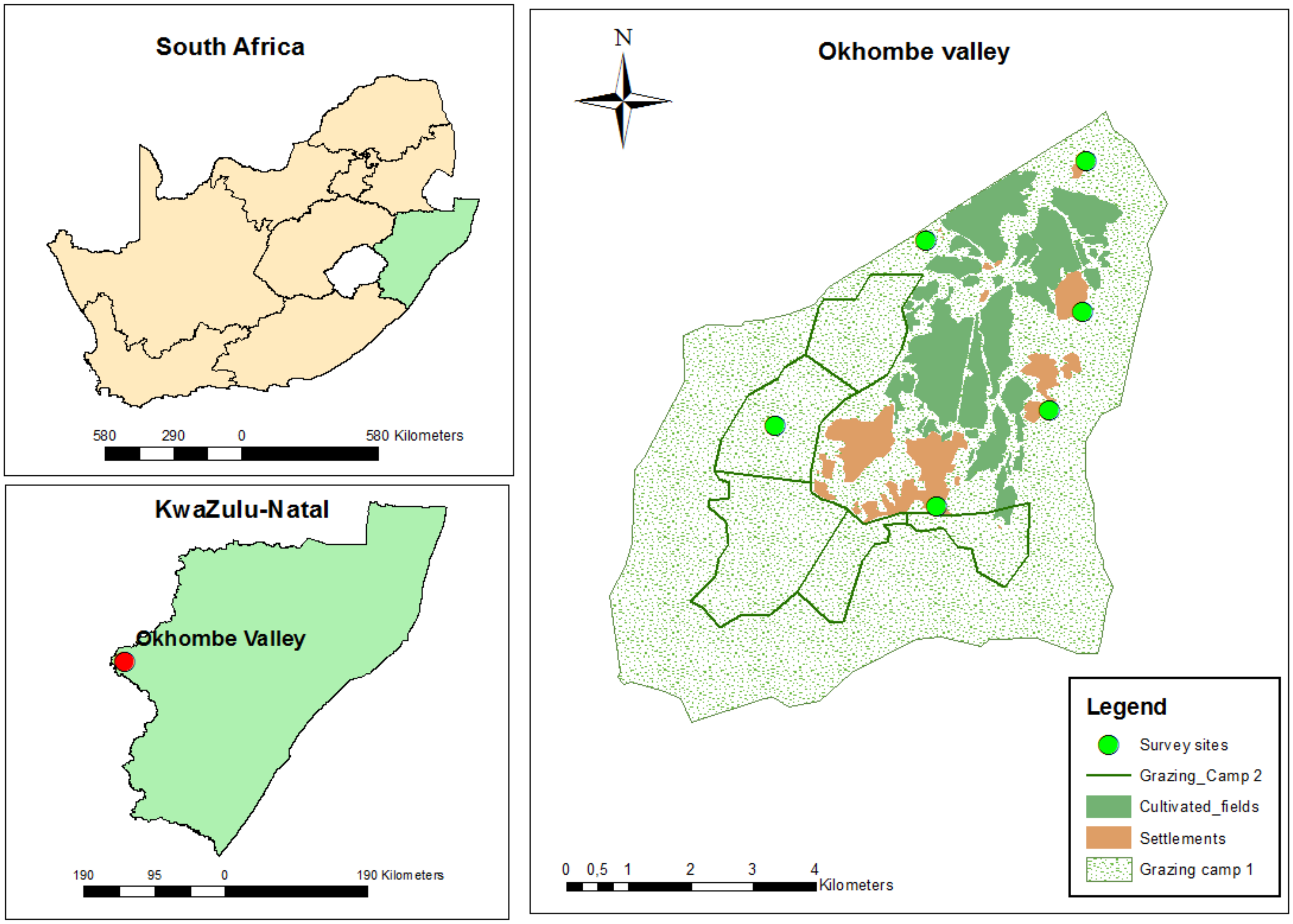

Figure 2.1: The Okhombe Valley in KwaZulu-Natal showing the location and the six survey sites and the different forms of land use in the region (Mansour et al., 2012).

2.3.2 **Data collection**

The contiguous quadrat method was used when recording species composition and cover data. All species in each quadrat were identified and their aerial cover was estimated. Starting at the edge of the planted vetiver grass row, a 0.5m x 0.5m quadrat was placed and then turned over six times to cover a distance of 3m. This was replicated four times per sites. GPS coordinates were also recorded at all sites.

2.3.3 Statistical analysis

The quadrat data were used to calculate species richness and species abundance. The residuals for species richness were normally distributed; therefore, the relationship between species richness and distance from vetiver grass was analysed using linear regression in SPSS software version 24 (IBM Inc).

Given the rapid species turnover within the dataset, a unimodal method, correspondence analysis (CA), was used for the ordination of species composition and abundance (species cover), assessing which species are associated with vetiver grass in relation to years since rehabilitation and distance from planted vetiver grass rows. Distance from planted vetiver rows and years since rehabilitation were overlaid as environmental variables. The CA was performed using Canoco, and the ordination graph drawn using CanoDraw (Ter Braak and Smilauer, 1997).

2.4 RESULTS

Overall, a total of ten grass species, one *Helichrysum* species, and one sedge were found within 3m of vetiver planted in rows (Table 1). *Aristida bipartita, Sporobolus africanus, Eragrostis plana, Eragrostis curvula, and Paspalum notatum* were present in all sites, while *Hyparrhenia hirta* and *Cymbopogon caesius* were present in most sites except the site that was rehabilitated in 1992 (Table 2.1). *Aristida congesta,* and *Helichrysum* species were present in sites rehabilitated in 1992, while *Chloris gayana,* and sedges were found in sites rehabilitated in 2011 and 2002, respectively (Table 2.1). Surprisingly, there were two sites (2002 and 2011) that had vetiver grass recruiting where it was not originally planted (Table 2.1). Species richness significantly increased with increasing distance from planted vetiver grass rows (R^2=0.4606; p<0.0001; Figure. 2.2; Table 2.2). However, an increase in variability in species richness moving away from the planted vetiver grass rows was evidenced (Fig. 2.2).

Table 2.1: Species found in areas rehabilitated using vetiver grass in different years, and their successional and ecological status. Two sites were rehabilitated in 2002 while other sites were

rehabilitated in different years. In the table below, (**x**) indicates that the species was present, and (**-**) indicate absence at that site

Species	**Years since rehabilitation**					**Successional and ecological status (Van Oudtshoorn, 2012)**
	1992	**2002**	**2007**	**2011**	**2015**	
Aristida bipartita	x	x	x	x	x	Subclimax – Increasor II
Aristida congesta	x	-	-	-	-	Pioneer – Increasor II
Chloris gayana	-	-	-	x	-	Subclimax – Decreasor
Cymbopogon caesius	-	x	x	-	x	Climax – Increasor I
Eragrostis curvula	x	x	x	x	x	Sub/Climax – Increasor II
Eragrostis plana	x	x	x	x	x	Subclimax – Increasor II
Helichrysum species	x	-	-	-	-	N/A
Hyparrhenia hirta	-	x	x	x	x	Sub/Climax – Increasor I
Melinis nerviglumis	-	-	x	-	-	Climax – Increasor I
Paspalum notatum	x	x	x	x	x	Exotic grass – Invasive
Sedge	-	x	-	-	-	N/A
Sporobolus africanus	x	x	x	x	x	Subclimax – Increasor III
Vetiver grass recruit	-	x	-	x	-	Exotic/Climax-Invasive

Table 2.2: Analysis of variance for a linear regression of species richness against distance from planted vetiver grass rows (m) in all sites rehabilitated using vetiver grass in Okhombe Valley, Bergville, KwaZulu-Natal

	DF	**SS**	**MS**	**F**	**P**
Regression	1	52.8595	52.8595	29.0388	**<0.0001**
Residual	34	61.8905	1.8203		
Total	35	114.7500	3.2786		

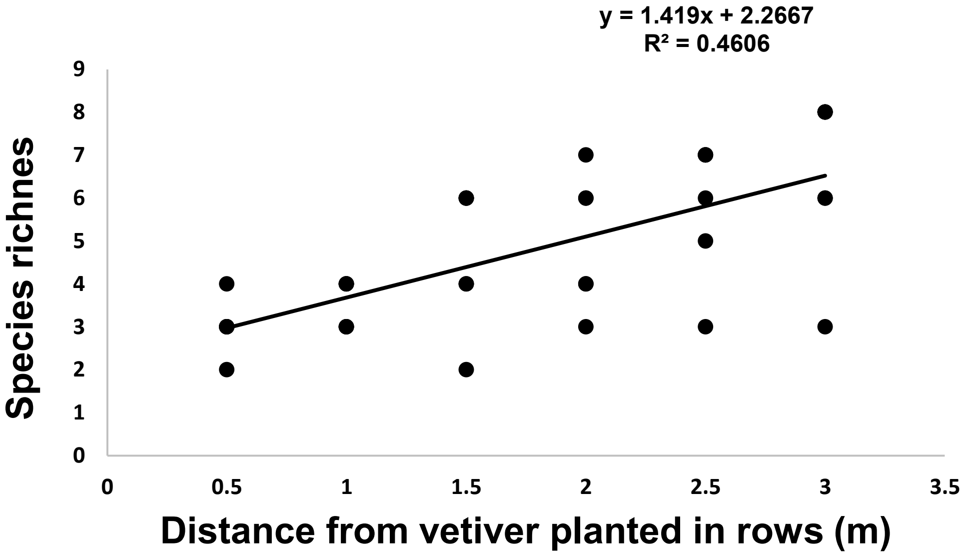

Figure 2.2: Relationship between species richness and distance from vetiver grass in areas rehabilitated using vetiver grass between 1992 and 2015 in the Okhombe Valley, Bergville, KwaZulu-Natal.

The correspondence analysis revealed that distance from planted vetiver explained more variation than years since rehabilitation, in species distribution of these rehabilitated sites (Fig.2.3). The secondary axis explained more variation in species and environment relation than the primary axis (CA2; Fig. 2.3). Distance from vetiver was more strongly associated with the secondary axis than time since rehabilitation (CA2; Fig. 2.3). The main variation shown by the correspondence analysis was along the primary axis and neither time nor distance from planted vetiver explains it (CA1; Fig. 2.3). This variation may be due to the species recruiting into the rehabilitated sites from the surrounding grasssland. *Sporobolus africanus, Chloris gayana, Paspalum notatum,* and sedges were dominant or growing several centimetres (50-100 cm) away from vetiver planted in rows (Fig. 2.3). There was also evidence of vetiver recruiting within the same range (Fig. 2.3). However, areas around vetiver rows were dominated by bare soil. *Aristida bipartita, Melinis nerviglumis, Cymbopogon caesius, Hyparrhenia hirta, Eragrostis curvula,* and *Eragrostis plana* started appearing when moving away from vetiver planted in rows (100-250cm). *Aristida congesta* was the only species that dominated areas furthest from vetiver planted in rows (250-300cm) (Fig.2.3).

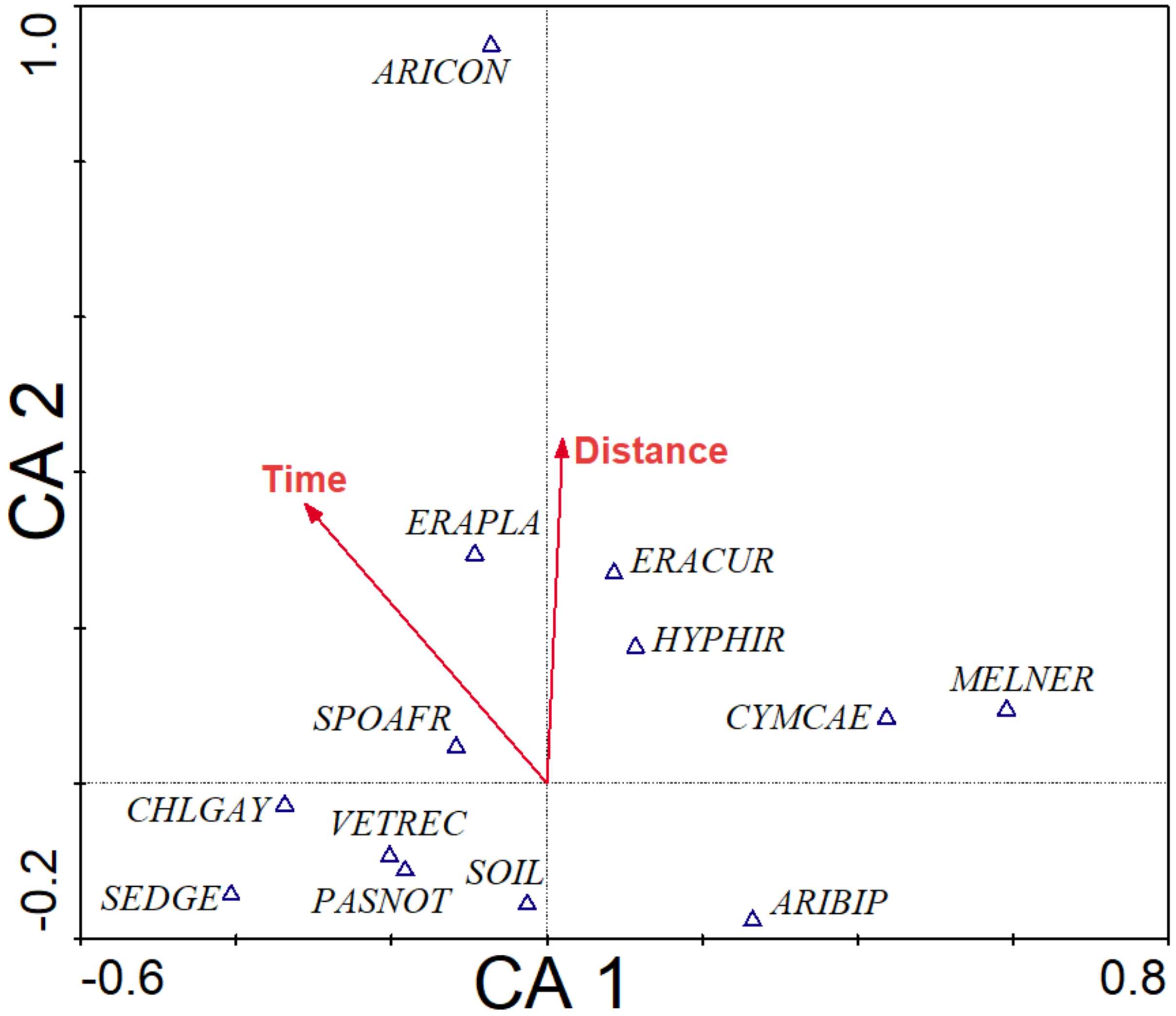

Figure 2.3: Correspondence analysis (CA) ordination of species composition and their basal cover from sites rehabilitated using vetiver grass in different years (i.e. time) correlated with distance from planted vetiver grass (i.e. distance), at Okhombe valley, Bergville, KwaZulu-Natal, South Africa. The eigenvalues for species and species-environment relation of the primary (CA1) and secondary axes (CA2) are 0.572 and 0.492, and 0.312 and 0.571, respectively. The primary and secondary axes accounted for 16% and 13% of the variation in species data, and 19.5% and 56% of the variation in species and environment relations, respectively. Full names of the abbreviations for species are provided in Appendix 2.1.

2.5 DISCUSSION

The most consequential results of this study were the marked increase in grass species richness with an increase in distance away from the planted vetiver, the abundance of bare ground around the planted vetiver, and the presence of the recruiting vetiver grass away from the planted vetiver. Native grasses, therefore, appear to fail to recruit in close proximity with vetiver, with only a few species managing to successfully recruit half a meter to a meter away from planted vetiver. The surveyed sites were in a communal rangeland with continuous grazing (Everson et al., 2007; Mansour et al., 2012). The grass community in these sites, therefore, reflects both the effect of selective grazing and/or overgrazing, and the extent of secondary succession as influenced by planting of vetiver (Mansour et al., 2012). The general secondary successional pattern in grasslands usually follows this order, pioneer grasses — subclimax grasses — climax grasses (Tainton, 1981, 1999; Van Oudtshoorn, 2012). The pioneers, being annual grasses which allocate more resources to seed production and have effective seed dispersal strategies, a trade-off between leaf production and seed production, giving them a relatively low grazing potential (Van Oudtshoorn, 2012). Subclimax grasses are more densely tufted and produce more leaf material than annual pioneer grasses (Meredith, 1955; Van Oudtshoorn, 2012). These grasses offer more soil protection, there are much denser and better at resource capture e.g. light and nutrients (Meredith, 1955; Tainton, 1999). They outcompete pioneer grasses and dominate either in areas with moderate rainfall and low soil nutrient status or moderate soil nutrient status and low rainfall (Tainton, 1999). The grazing potential of most subclimax grasses range from poor to relatively good (Van Oudtshoorn, 2012). Lastly, climax grasses are strongly perennial and tufted which vary greatly in their environmental requirements but grow in normal, optimal conditions that support long-term survival (Van Oudtshoorn, 2012). These grasses also vary greatly in their grazing potential, with very unpalatable grasses e.g. *Aristida junciformis*, and very palatable grasses e.g. *Themeda triandra* (Tainton, 1999; Van Oudtshoorn, 2012).

Selective grazing resulting from a continuous grazing regime could result in the dominance of unpalatable grasses, which may include unpalatable pioneer, subclimax, and climax grasses (Tainton, 1999). As grazers select for palatable grasses, less palatable grasses gain competitive ability and reproduce successfully, hence dominating the sward (Tainton et al., 1980; Tainton, 1999). Grazing in these rehabilitating sites acts as a second disturbance (Cramer et al., 2008) which could, therefore, potentially alter the general successional pattern, resulting in vegetation that is a mixture of unpalatable subclimax and climax species, and even some strong competitive pioneer species (Tainton, 1999; Cramer et al., 2008). This is evidenced in this study as the surveyed plots were dominated by unpalatable subclimax species e.g. *Aristida bipartita, Sporobolus africanus,* and climax species e.g. *Hyparrhenia hirta* and *Cymbopogon caesius*, with only one unpalatable pioneer grass i.e. *Aristida congesta* subsp *barbicollis* occurring only in one site. The only palatable grass i.e. *Chloris gayana* occurred only in one site and was not a dominant species. This grass reproduces by both seeds and vegetatively- through a creeping stolon. It adopts several seed dispersal strategies, namely wind, water, and animal agents (Meredith, 1955). Therefore, this grass could have established from seeds which were either attached to livestock skin, collected from palatable climax patches dominated by *Chloris gayana* in the surrounding areas, or/and wind-dispersed seeds. There are previous studies in this village which used hyperspectral remotely sensed data to discriminate patches dominated by palatable climax grasses (e.g. *Themeda triandra*) to those dominated by less palatable climax grass (e.g. *Hyparrhenia hirta*) as a management approach (Mansour et al., 2012; Mansour et al., 2016). They showed that it is possible to discriminate between these patches using remotely sensed data and that there are still patches dominated by palatable climax species in these continuously grazed grasslands (Mansour et al., 2012; Mansour et al., 2016). This, therefore, means that these patches could have been the source for *Chloris gayana* seeds. However, it is fair to assume that some surveyed sites did not have patches dominated by palatable species near them, hence why only one out of the six surveyed sites had *Chloris gayana* out of the six surveyed sites. *Chloris gayana* seeds have a relatively good germination potential, thus explaining the recruitment success, and it is usually a preferred grass for reseeding, mostly with the aim to stabilize the soil (Meredith, 1955; Van Oudtshoorn, 2012).

These rehabilitated rangelands can be classified as unpalatable climax grassland, as they were dominated by more climax species than subclimax species. The subclimax species occurred relatively close to the planted vetiver compared to the climax species. However, there was no clear relationship between successional stages and years since rehabilitation. These findings are relatively similar to those reported by studies of plant succession in old-fields or abandoned agricultural fields (Bonet, 2004; Bonet and Pausas, 2004). For example, Bonet (2004) in a vegetation change study examining a 60 year old abandoned agricultural field, showed that there was a nonlinear relationship between years since abandonment and plant successional status, and rather there was a clear coexistence of different plant functional groups. The progress of plant succession and species turnover is dependent on many factors e.g. seed dispersal, soil and climatic conditions, and availability of a seed bank in that rehabilitating area(Tainton, 1999; Bonet, 2004). The soil and climatic factors determine which species can recruit; however, if there are no dispersed seeds or no buried seeds (seed bank) of native plants, such species will not recruit in that area (Tainton, 1999). For example, climax grass species usually have a poor seed dispersal ability; therefore, their recruitment is usually dependent on an existing seed bank, although they can only recruit when the soil and climatic conditions are favourable (Tainton, 1999). Soil erosion usually removes the topsoil and hence the seed bank, therefore, grass species which have poor dispersal abilities are unlikely to be found in these sites, unless the sites are reseeded (Tainton, 1999). Therefore, a combined effect of planted vetiver (possibly competition), grazing, and lack of dispersed and buried seeds could determine the community structure of these previously eroded sites.

This study showed a relatively clear progressive succession moving away from planted vetiver, i.e. a clear turnover of subclimax to climax species accompanied by an increased species richness. The ecological and successional status of these plant communities can be related to specific species responses to defoliation (i.e. grazing) or the decreaser-increaser concept described by Foran et al (1978) and modified by Tainton et al (1980). Decreaser species are grasses which dominate in good veld, but decreases in abundance with poor management i.e. overgrazing or undergrazing (Foran et al., 1978). These grasses are palatable subclimax and climax grasses, which are usually preferred by grazing animals (Van Oudtshoorn, 2012). Increaser I species are grasses which dominate in undergrazed or underutilized veld (Foran et al., 1978). These are usually robust climax, unpalatable species which usually grow well without any form of defoliation (Van Oudtshoorn, 2012). Increaser II species are subclimax and pioneer grass species which dominate in overgrazed veld (Foran et al., 1978). These species are a mixture of palatable and less palatable grasses, and are usually associated with low rainfall areas, but can be found in high rainfall areas which are overgrazed and have nutrient-poor soils (Van Oudtshoorn, 2012). Increaser III species are climax grass species which dominate in selectively grazed veld (Tainton et al., 1980). These are usually very unpalatable robust tufted perennials, which are strong competitors and increase when climax palatable grasses are weakened by being overgrazed (Tainton et al., 1980; Van Oudtshoorn, 2012).

The species dominating in all sites were mostly increaser II (i.e. *Aristida bipartita, Eragrostis plana, Eragrostis curvula*) and increaser III (i.e. *Sporobolus africanus*), and one invasive (i.e. *Paspalum notatum*) species (Van Oudtshoorn, 2012). This is a clear indication of the effect of grazing on the succession status and community structure of these rehabilitating sites. *Paspalum notatum* was sown concurrently with vetiver, as part of the rehabilitation programme (Everson et al., 2007). This grass is an alien grass from Mexico, the Caribbean, and South America, tolerant to drought, increases in abundance when grazed because of its deep roots and strong creeping rhizomes, and this is thus useful for soil erosion control (Van Oudtshoorn, 2012). However, even this creeping strong competitive grass could not cover the bare ground around vetiver (Van Oudtshoorn, 2012), suggesting that either the competitive ability of vetiver and/or allelopathy from oil produced in the roots is inhibiting the recruitment of other grasses near vetiver (Van den Berg et al., 2003). This therefore, challenges the two claims made about vetiver competitive ability and coexistence with other grasses. These claims are 1) vetiver does not compete with adjacent crops, and 2) vetiver does not spread because it produces non-viable seeds, and has no stolon or rhizomes (Vieritz et al., 2003). For these claims to hold, other grasses should coexist well with vetiver, and there should be no signs of vetiver recruiting outside of the planted areas. Unfortunately, the presence of bare ground around the vetiver plants and the evidence of vetiver recruiting, where it was not planted, strongly challenges the validity of these claims.

Council (1993) reported that there are few incidences where vetiver was reported to have recruited, showing signs of spreading, although this was anecdotal evidence from interviews with the farmers. Whether vetiver recruited using suckers developed from roots or if the environment became favourable to allow a few seeds to be produced and to germinate, is not known. These surveyed sites need to be monitored regularly to understand whether or not the recruitment is accidental through the washing away of few vetiver reproductive roots to a nearby location, or whether these are initial signs of vetiver spreading. However, it is clear that it did recruit, even though only a few tufts were seen, suggesting that even through recruiting, probably, there are still unknown inhibitory factors that inhibit recruitment and spreading of this grass. Vetiver grass is very dependent on its belowground material for reproduction, thus clipped upper surface roots alone can give rise to new plants (Greenfield, 2002).

From this study and the published literature, there are many unanswered questions relating to: 1) vetiver reproductive potential, seed germination and the extent of vegetative reproduction; 2) the effect of established vetiver on seed germination and seedling establishment of indigenous species and; 3) the competitive interaction between established vetiver and mature native grass tufts. These questions will help develop a better understanding of vetiver ecology and, particularly questions 2 and 3 will help to understand what causes the bare areas around planted vetiver. In addition, all these questions are important to understand the potential of vetiver becoming invasive. From this study, it is clear that the previously mentioned two claims about vetiver do not hold and have to be revisited. While there is no doubt that the use of vetiver is beneficial for soil and water conservation and allows (to a limited extent) progressive vegetation succession, the availability of bare ground around planted vetiver could indicate that vetiver is a territorial grass. Vegetative regeneration by means of tillering adopted by vetiver is an extremely slow process (Tainton, 1999; Greenfield, 2002). For this reason, vetiver is unlikely to become a problem but can become a permanent feature in rehabilitated areas, reducing forage availability. Even though these rehabilitated sites showed progress in terms of plant succession and increases in species richness within 3m of planted vetiver, suggesting that vetiver does help retain topsoil allowing other grasses to grow, this study shows that native grasses do not grow in particularly close proximity to vetiver, supporting the notion that it may develop permanent monotypic patches.

2.6 REFERENCES

Boardman, J., Poesen, J., 2006. Soil erosion in Europe: major processes, causes and consequences, in: Boardman, J., Poesen, J. (Eds.), Soil Erosion in Europe. Wiley., Chichester, pp. 477-487.

Bonet, A., 2004. Secondary succession of semi-arid Mediterranean old-fields in south-eastern Spain: insights for conservation and restoration of degraded lands. Journal of Arid Environments 56, 213-233.

Bonet, A., Pausas, J.G., 2004. Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. Plant Ecology 174, 257-270.

Chen, K., Hu, G., Rao, H., Xu, L., Hu, H., 1993. Ecological effects of planting vetiver grass in citrus groves in sloping red soil fields. Acta Ecologica Sinica 14, 249-254.

Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology & Evolution 23, 104-112.

DeFalco, L., Esque, T., Kane, J., Nicklas, M., 2009. Seed banks in a degraded desert shrubland: influence of soil surface condition and harvester ant activity on seed abundance. Journal of Arid Environments 73, 885-893.

Edelstein, M., Plaut, Z., Dudai, N., Ben-Hur, M., 2009. Vetiver (*Vetiveria zizanioides*) responses to fertilization and salinity under irrigation conditions. Journal of Environmental Management 91, 215-221.

Everson, T.M., Everson, C.S., Zuma, K., 2007. Community based research on the influence of rehabilitation techniques on the management of degraded catchments. Water Research Commission.

Foran, B., Tainton, N., Booysen, P.d.V., 1978. The development of a method for assessing veld condition in three grassveld types in Natal. Proceedings of the Annual Congresses of the Grassland Society of Southern Africa 13, 27-33.

Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth. Infinity Publishing.

Grimshaw, R.G., 1993. The role of vetiver grass in sustaining agricultural productivity. Asia Technical Department. The World Bank, Washington DC USA.

Mansour, K., Mutanga, O., Adam, E., Abdel-Rahman, E.M., 2016. Multispectral remote sensing for mapping grassland degradation using the key indicators of grass species and edaphic factors. Geocarto International 31, 477-491.

Mansour, K., Mutanga, O., Everson, T., Adam, E., 2012. Discriminating indicator grass species for rangeland degradation assessment using hyperspectral data resampled to AISA Eagle resolution. ISPRS Journal of Photogrammetry and Remote Sensing 70, 56-65.

Meredith, D., 1955. The grasses and pastures of South Africa. The grasses and pastures of South Africa.

Morgan, R.P.C., 2009. Soil erosion and conservation. John Wiley & Sons.

Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute.

O'Connor, T.G., Bredenkamp, G.J., 1997. Grassland. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press, Cambridge, 215–257.

O'Rourke, S., Minasny, B., Holden, N., McBratney, A., 2016. Synergistic use of Vis-NIR, MIR, and XRF spectroscopy for the determination of soil geochemistry. Soil Science Society of America Journal 80, 888-899.

Tainton, N., Edwards, P., Mentis, M., 1980. A revised method for assessing veld condition. Proceedings of the Annual Congresses of the Grassland Society of Southern Africa 15, 37-42.

Tainton, N.M., 1981. Veld and pasture management in South Africa. Shuter & Shooter; University of Natal Press.

Tainton, N.M., 1999. Veld Management in South Africa. University of Natal press.

Temme, A., 2008. Understanding Landscape Dynamics over Thousand Years: Combining Field and Model Work: With Case Study in the Drakensberg Foothill. KwaZulu-Natal, South Africa.

Ter Braak, C., Smilauer, P., 1997. Canoco for Windows, Biometrics. Plant Research International, Wageningen, The Netherlands.

The Vetiver Network International, 2017. 20 June, The Vetiver Network International, 2017, http://vetiver.org/.

Van den Berg, J., Midega, C., Wadhams, L., Khan, Z., 2003. Can Vetiver grass be used to manage insect pests on crops? Proceedings of the Third International Conference on Vetiver and Exhibition (ed. by RG Grimshaw), 254–264.

Van Oudtshoorn, F.v., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza Publications.

Vieritz, A., Truong, P., Gardner, T., Smeal, C., 2003. Modelling Monto vetiver growth and nutrient uptake for effluent irrigation schemes. Proceedings of the Third International Conference on Vetiver and Exhibition, 254-264.

Zhang, Z., Shu, W., Lan, C., Wong, M., 2001. Soil seed bank as an input of seed source in revegetation of lead/zinc mine tailings. Restoration Ecology 9, 378-385.

3 CHAPTER 3: DOES VETIVER ALLOW GERMINATION AND ESTABLISHMENT OF NATIVE GRASSES?

3.1 ABSTRACT

Vetiver grass (*Chrysopogon zizanioides* (L.) Roberty) is a tufted perennial grass from India, used worldwide for rehabilitating eroded rangelands and for other soil and water conservation practices. Morphological features e.g. dense extensive root system (4m deep), and the claim that it allows recruitment of other grasses around it has popularized the use of this grass. However, this claim has not been extensively examined. The effect of vetiver tufts and sowing method on seed germination and seedling establishment of *Eragrostis curvula* and *Panicum maximum* was examined using pot trials. One hundred seeds of each species were planted alone, around one vetiver tuft and between two vetiver tufts planted fifteen centimeters apart. These native grass seeds were sown on the soil surface, buried, and mixed with a water retention gel. Native grass seedling response when root interaction was excluded using a 42-micron nitex mesh was also investigated as a follow-up pot trial. The root profile picture taken from cutting the soil-root material of vetiver and *E. curvula* was analyzed using NIS-Element BR software to quantify the amount of space available around each species for other species to colonize.Vetiver tufts facilitated seed germination in both *E. curvula* and *P. maximum*, and seeds sown on the soil surface had a greater germination percentage compared to other sowing methods. However, vetiver tufts inhibited seedling establishment of these grasses, even when the root competition was excluded. Vetiver had less root space available for other species to colonize compared to *E. curvula*, which suggests that dense roots of vetiver could be causing direct root competition for space and thus, inhibiting establishment of native grasses. Shading by vetiver could be retaining soil moisture and hence creating a favorable environment for the seeds of native grasses to germinate. A combination of vetiver shade, direct root competition, and allelopathy (possibly from oil produced by the roots) could be causing an inhibitory effect on native grass seedling establishment. These findings, therefore, suggest that it is unlikely that vetiver will allow recruitment of native grasses, which means rehabilitation using vetiver is unlikely to allow succession by native grasses.

3.2 INTRODUCTION

Vetiver (*Chrysopogon zizanioides* (L.) Roberty) is a densely tufted perennial C_4 grass from India possessing unique morphological and physiological features which enable it to be useful in soil and water conservation (Council, 1993; Vieritz et al., 2003). Irrespective of environmental conditions, vetiver establishes faster than most grasses, rapidly extending its dense roots 4m deep into the soil, binding the soil particles together (Vieritz et al., 2003). For example, Greenfield (2002) showed that vetiver grass can reach rooting depths of 3.6m after 8 months of growth. Vetiver produces non-viable seed, hence relying on vegetative reproduction and its large root stocks allow it to survive for decades. Its hardy tufts with broad leaves act as a wind break in agricultural fields (Grimshaw, 1993), attracting stem borer insects to lay their eggs but resulting in larval mortality, and therefore, acting as an insect trap (Shangwen, 1999; Van den Berg et al., 2003). Vetiver has been successfully planted in coastal sand with high salinity (Xia et al., 1998), abandoned mine sites with toxic heavy metals (Truong et al., 1999), landfill sites with toxic anthrosoils, and in contaminated dams with high nitrogen levels (Truong et al., 2001; Wagner et al., 2003). Furthermore, vetiver produces oil in its roots which has been extensively harvested by pharmaceutical companies for its antimicrobial and antifungal properties, and by cosmetics companies for its strong, unique aroma (Weyerstahl et al., 1996; Danh et al., 2010; Chahal et al., 2015). However, vetiver grass has been mostly popularized and used as a cost-effective, natural technology for environmental protection worldwide, among other uses.

For decades, research has focused on the utilization of vetiver grass in soil and water conservation, but less attention has been given to its ecology and behavior (Chōmchalao, 2001; Greenfield, 2002; Xu, 2002). A particularly important aspect of its ecology relates to coexistence with other grass species, and whether it allows recruitment and succession of native grasses. As the grass is being used to rehabilitate degraded rangelands, seed germination and seedling recruitment of native grasses is crucial for a successful rehabilitation. Seed germination is controlled by soil moisture, temperature, and direct sunlight, and surrounding mature grasses can influence these factors (Ammondt and Litton, 2012; Gallagher and Wagenius, 2016). Numerous studies have shown that established grass plants can either facilitate seed germination and seedling establishment by creating a favorable microclimate through shade and moisture retention (Rees and Brown, 1991; Brooker et al., 2008; Tedder et al., 2011), or can be territorial and inhibit seed germination and seeding establishment through direct root competition and/or allelopathy (Schenk et al., 1999).

Territoriality in plants relates to both root spatial segregation and allelopathy (Schenk et al., 1999; Dias et al., 2016). Plants with spatially segregated roots occupy vacant soil volumes and by so doing, they avoid direct root competition from the neighboring plants (Schenk et al., 1999). However, some plants with dense roots and those with creeping stolons or rhizomes can utilize most soil space around them, creating an unfavorable microclimate for recruitment of other grasses (Schenk et al., 1999; Schenk and Jackson, 2002). Allelopathy does not require segregated or clumped roots because it involves the release of allelochemicals which inhibit seed germination and establishment of other grasses (Ghebrehiwot et al., 2014; Dias et al., 2016). These two behaviors are seen as territoriality because they usually result in bare soil around that grass plant (Ghebrehiwot et al., 2014). If these bare soil areas are large, a soil crust could develop, lacking soil moisture and thus further inhibiting seed germination and seedling establishment of native grasses (Morgan, 2009). Vetiver oil has been shown to have allelopathic propitiates that inhibit weed species germination and establishment (Mao et al., 2004). This allelopathic behaviour could also inhibit native grasses germination and establishment; however, no study has addressed this question. Therefore, vetiver research should shift from the application of vetiver in soil and water conservation to questions surrounding its ecology such as, its effect on native grasses germination and seedling recruitment because seedlings are more sensitive to competition than adult plants. Moreover, the focus of rangeland rehabilitation projects has shifted from soil protection alone to promoting species diversity with the aim of improving grassland productively (Bakker et al., 2003).

It is for these reasons that this study was conducted, and aimed to answer the following questions:

1. Do vetiver grass tufts inhibit or facilitate seed germination in native grasses?
2. Is the germination rate of native grasses affected by the seed sowing method?
3. Do vetiver grass tufts inhibit establishment of native grasses?
4. Does the exclusion of direct root interaction decrease the competitive effect exerted on native grass seedlings?

5. Does vetiver root density differ from indigenous grass root density?

An improved understanding of whether vetiver allows recruitment of native grasses, and how to sow native grass seeds to promote successful coexistence with vetiver grass will help to explain the patterns observed in areas already rehabilitated using vetiver. Furthermore, it will help to formulate a practical guide to using vetiver not only for soil erosion control but for promoting grassland productivity.

3.3 MATERIALS AND METHODS

3.3.1 Study area and species

The study was conducted under greenhouse conditions at the NM Tainton Arboretum at the University of KwaZulu-Natal, Pietermaritzburg campus, South Africa, (S 29°37′47″, E 30°24′07″).

Two native grass species, *Eragrostis curvula* and *Panicum maximum* (also known as *Megathyrsus maximus*) were used in this study. These two native grasses were chosen because they have contrasting physical and ecological traits but are both used for rehabilitation. For example, *E. curvula* is a pioneer grass, producing large numbers of small seed with a high germination percentage, while *P. maximum* is a late seral grass, producing fewer, larger seeds with lower viability (Meredith, 1955; Adkins et al., 2000: Fish et al. 2015). *Eragrostis curvula* is a densely tufted perennial grass with an open panicle (6-30cm) and leaves that are crowded at the base, but it is an increaser grass species which is extremely variable with many different forms (Meredith, 1955; Tainton et al., 1976; Van Oudtshoorn, 2012). *P. maximum* is a tufted perennial, shade tolerant grass usually with a creeping rhizome and an open panicle (20-30 cm), and has broad leaves (Meredith, 1955; Tainton et al., 1976; Van Oudtshoorn, 2012). It is a decreaser species grass which is exceedingly variable in height (up 200 cm) and is invasive in other parts of the world (Meredith, 1955; Bogdan, 1977; Van Oudtshoorn, 2012).

In order to maximize germination potential, the seeds of these grasses were bought from a commercial supplier (McDonald’s Seeds, 2 Trek road, Mkondeni, Pietermaritzburg, South Africa).

3.3.2 Experimental design

The study consisted of two trials, a germination and establishment trial, and then a root exclusion trial.

Germination and establishment trial

Using 6L plastic pots filled with commercial potting soil, vetiver tufts of similar size and age were planted one-month prior to the sowing of native grass seeds, to allow them time to establish. Pots with no vetiver grass were used as a control and compared with pots containing one vetiver tuft (low competition), and two vetiver tufts planted 15 cm apart (intense competition). The distance of 15 cm apart simulates the field planting procedure and spacing of vetiver tufts when rehabilitating an eroded site (Dalton et al., 1996).

One hundred seeds of each native grass species were sown per pot. These seeds were laid on the soil surface (unburied), buried (2 cm deep), and mixed with a hydro-seeding gel containing moisture retention polymers. Hydro-seeding is a method of sowing seeds used in rehabilitation projects to attain quicker seed germination and seedling establishment. For the hydro-seeding mixture, 2.5 grams of fluid drilling gel and 100 seeds of either *E. curvula* or *P. maximum* were added into 500ml of water to make a jelly-like mixture (Pill, 1991). This mixture was then applied to the soil surface in the hydro-seeding treatments. The pots were watered every second day. The experiment was a full factorial, completely randomized design with six replicates of each treatment combination and 18 combinations in total.

This trial ran for 4 months (November 2016 to February 2017) and the percentage germinated seeds, seedling survival (%), seedling height (cm), number of leaves per seedling, and number of tillers per seedling were recorded every second week. Aboveground biomass was not harvested in this trial because the number of germinated and surviving seedlings was not uniform, hence this would have been a weak measure of establishment success.

Root exclusion trial

The previous trial was a full competition experiment; however, upon observing seedlings failing to grow to their full size when growing with vetiver, this short-term follow-up trial was started. The trial aimed at understanding whether the exclusion of vetiver root interaction would boost the performance of native grass seedlings. This was a small supporting trial; therefore, it did not have full root interaction (full root interaction vs. none) because it would have given us results which are similar to the previous trial, and therefore, the only control was the native species growing alone. *Panicum maximum* had a slow germination rate and low germination percentage and so was omitted from this follow-up study, with *E. curvula* being the only native grass used. The interaction between the roots of vetiver and those of *E. curvula* was prevented using a 42-micron Nitex mesh (purchased at Meshcape Industries (Pty) Ltd, 30 Nipper Rd, New Germany, South Africa).

Three-week-old *E. curvula* seedlings were planted alone, with one vetiver tuft, and with two vetiver tufts, with the roots of these species carefully separated by pasting the Nitex mesh into the pots to create two, or three chambers using a strong waterproof epoxy (Epidermix 372 purchased at Hayfields Mica Hardware, Pietermaritzburg) (See Fig. 3.1). Five seedlings of *E. curvula* were planted in each pot, and there were six replicates of each treatment. The Nitex mesh prevents direct root interaction but allows chemicals and nutrients to pass through it (Fig 3.1). Therefore, it excludes root competition but allows any allelopathic behavior and shading to be investigated. The experiment had six replicates, laid out in a completely randomized arrangement. Pots were watered every second day and the water that appeared in the tray under the pot was used also to re-water the pots to ensure that any compounds released by the vetiver were not lost.

The trial ran for 4 months (March to June 2017) and seedling height, number of leaves per seedling, and number of tillers per seedling were recorded every second week. The aboveground biomass was harvested at the end of the trial, oven dried for 48 hours at 60^{o}C and then weighed.

Root density analysis

Previous studies have found that measuring root density has proven difficult because fine roots are easily washed out and lost during the root extraction process (Cahill, 2002). For this reason, a different approach was used to quantify how much space is available for other roots to colonize using the plants in the control pots (grasses that were grown alone). Four replicates of representative pots containing one vetiver tuft, two vetiver tufts and mature *E. curvula* growing alone, were selected. The soil and root material was carefully removed from the pot and cut in half, without disturbing the soil, to form a root profile. A photograph of the root profile was taken and analyzed using NIS-Element BR software (Nikon Inc.). The NIS-Element BR software analyzed pixel colour of roots and the soil and by setting the intensity of the colours as a constant (roots coloured blue and soil coloured red with the intensity of both colours standardized to 80%) the total area comprised of by roots (blue) and soil (red) was calculated (Fig.3.2). This data was then used to determine the percentage (%) space taken up by the roots and percentage space available for other roots to colonize.

3.3.3 Statistical analysis

Generalized linear models (GZLM) in SPSS version 24 (IBM Inc. 2016) were used to analyze the data because the data violated the assumptions of the analysis of variance (ANOVA) even when transformed (Quinn and Keough, 2002). A gamma distribution with a log link function was used for scale data such as the mean number of leaves per seedling, mean seedling height (cm), and mean number of tillers per seedling to assess the effect of vetiver presence (full competition) and sowing method in the germination and establishment trial.

However, for count data, in this case the number of germinated seeds, a Poisson distribution was used, with over-dispersion of the data controlled. To assess the effect of competition and sowing method on seedling survival a binomial distribution with a logit link function was used, where survival (number of seedlings that survived) was an event and the number of germinated seeds was a trial. For the survival data, where the generalized linear models were not appropriate, because of a lack of variance (e.g. in *P. maximum* where there was one seed germinated and one seedling survived), a single value was substituted, which made the test more conservative (Kiepiel and Johnson, 2014). Values from a linear scale were back-transformed to obtain marginal means which resulted in asymmetrical standard errors (Kiepiel and Johnson, 2014).

For the root exclusion trial, a linear distribution with an identity link function was used to assess the effect of vetiver presence (competition) on the mean seedling height (cm), mean number of leaves per seedling, mean number of tillers per seedling, and aboveground biomass (g). Furthermore, a linear distribution with an identity link function was used to assess whether there was a significant difference in soil space occupied by roots of *E. curvula*, and one or two vetiver grass tufts. For all these analyses, where the model showed significant differences, sequential Sidak was used to adjust for multiple comparisons ($\alpha = 0.05$).

Figure 3.1: The pot design for the root exclusion trial showing how a 32-micron Nitex mesh was pasted into the pots using a strong waterproof epoxy (**A**) and how *E. curvula* was planted with one (**B**) and between two vetiver tufts (**C**).

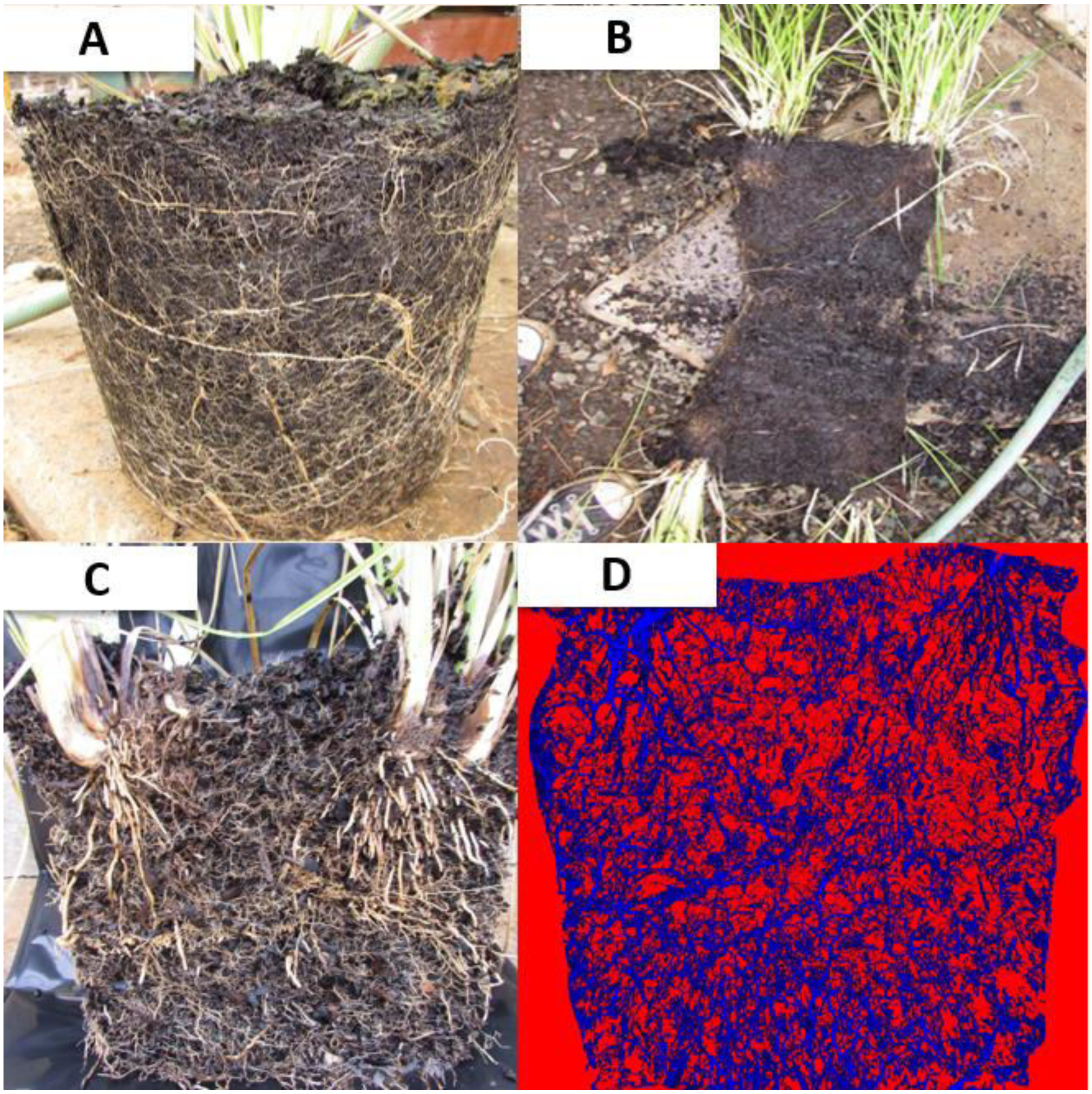

Figure 3.2: The root-soil profile used for analyzing root density and the illustration of the steps involved from the careful removal of roots and soil from the pot (**A**), cutting of a soil profile (**B**), Taking a picture (**C**), and root pixel analysis (**D**).

3.4 RESULTS

3.4.1 Seed germination

Main effects

Eragrostis curvula and *Panicum maximum* differed significantly in their germination percentage (*P* <0.0001) (Table 3.1), with *E. curvula* (39% ± 1.683) having a greater germination percentage than *P. maximum* (2.20% ± 0.279). The presence of vetiver tufts and sowing method significantly affected seed germination overall (*P*<0.0001) (Table 3.1). *Eragrostis curvula* and

P. maximum responded differently to competition (*P*<0.0001) but not to sowing method (*P*= 0.448). The interaction between competition and sowing method had no significant effect on germination overall (*P*= 0.260) or on each species individually (*P*=0.245) (Table 3.1).

Table 3.1: The effect of the presence of vetiver (competition), sowing method, and their interaction using a generalized linear model on seed germination (Poisson distribution) and seedling survival (%) (Binary distribution, events by trials) of two native grass species (*Eragrostis curvula and Panicum maximum*). Significant p-values (p< 0.05) are in bold

Source of variation	Seed germination (%)			Seedling survival (%)		
	χ^2	df	*P*	χ^2	df	*P*
Species (S)	1768.650	1	**<0.0001**	1.368	1	0.227
Competition (C)	31.069	2	**<0.0001**	22.357	2	**0.004**
Sowing method (M)	16.500	2	**<0.0001**	2.899	2	0.772
S*C	16.394	2	**<0.0001**	15.456	2	0.103
S*M	1.606	2	0.448	5.532	2	0.292
C*M	5.282	4	0.260	4.990	4	0.493
S*C*M	5.441	4	0.245	7.709	4	0.240

Effect of competition

Overall the native grasses germinated better in the presence of vetiver tufts compared to the control, but there was no significant difference in percentage germination between one vetiver tuft and two vetiver tufts (Fig.3.3A). Individually, these species showed a similar trend, although, *E. curvula* germination was substantially greater than *P. maximum* with *E. curvula* having a maximum percentage germination of about 45% and a minimum of 30%, compared to 6 % and 1% maximum and minimum germination by *P. maximum,* respectively (Fig.3.3B).

Sowing method

Seeds sown on the soil surface germinated better than those that were buried and those mixed with water retention gel, but there was no significant difference between seeds buried and those mixed with a water retention gel (Fig. 3.4).

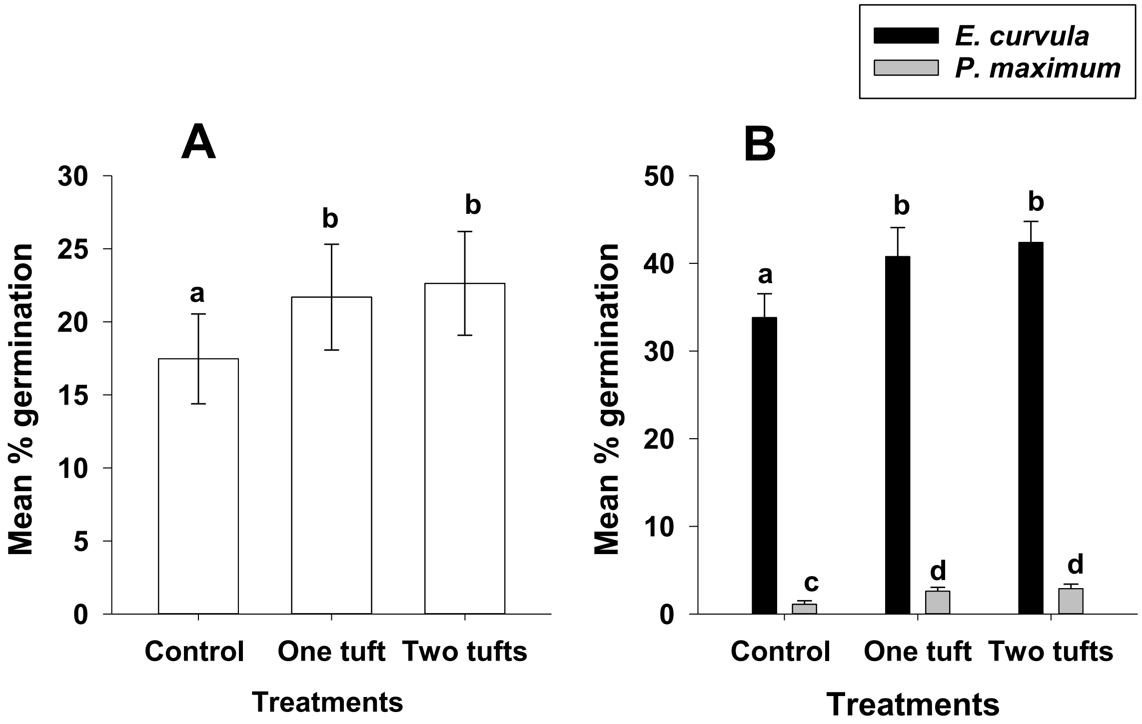

Figure 3.3: Main effect of vetiver on the mean germination percentage (± SE) of *Eragrostis curvula* and *Panicum maximum* overall (**A**), and their effect on each species (**B**). Different letters represent a significant difference between treatments ($p<0.05$).

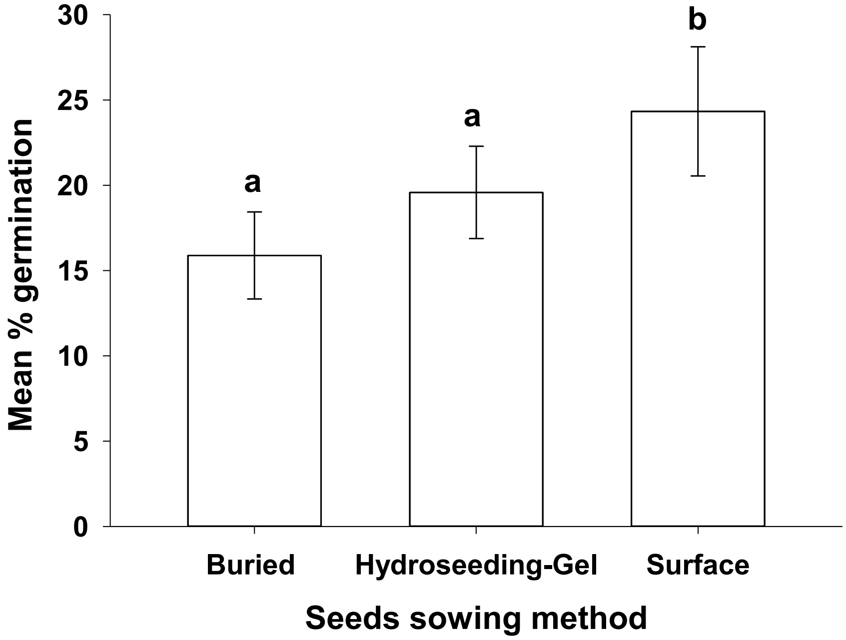

Figure 3.4: Main effect of sowing method on mean germination percentage (± SE) of *Eragrostis curvula* and *Panicum maximum* overall. Different letters represent a significant difference between treatments (p<0.05).

3.4.2 Seedling survival

Main effects

Eragrostis curvula and *P. maximum* did not differ significantly in terms of their seedling survival (*P*=0.227) and overall, competition but not sowing method (*P*=0.772) affected seedling survival (*P*=0.004) (Table 3.1).However, *E. curvula* and *P. maximum* did not differ in their response to both competition (*P*=0.103) and sowing method (*P*=0.292) (Table 3.1). Furthermore, the interaction between competition and sowing method did not affect the seedling survival of these species (*P*=0.240) (Table 3.1).

Effect of competition

Overall, seedlings survived better when growing alone (78.24% ± 3.68) than when growing with two vetiver tufts (72.65% ± 3.30; *P*=0.003), but there was no significant difference in seedling survival between the control and one vetiver tuft (76.23% ± 2.92; *P*=0.111), and between one vetiver tuft and two vetiver tufts (*P*=0.075; Fig. 3.5).

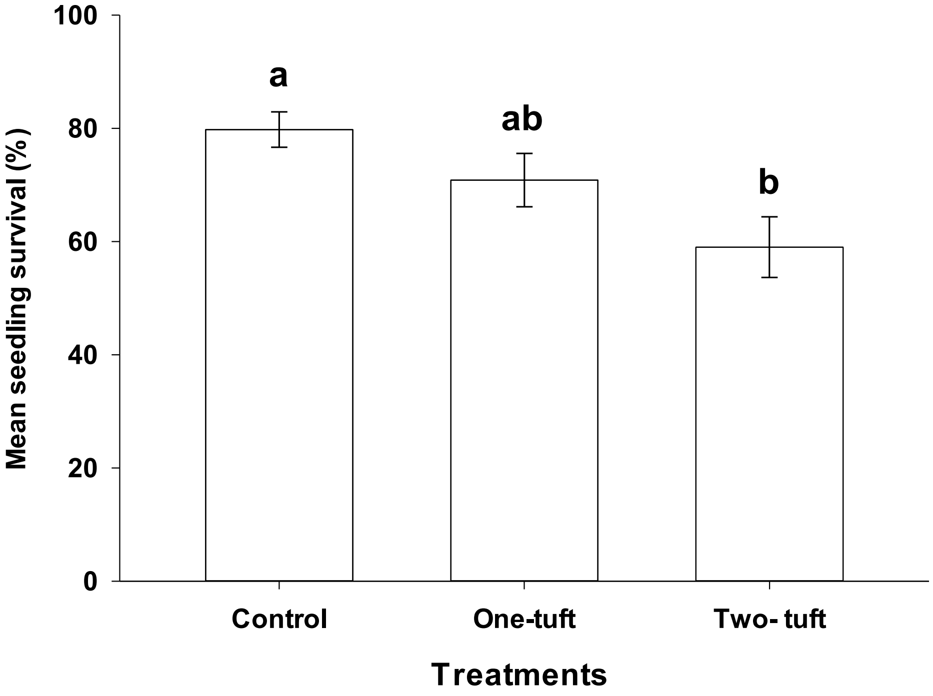

Figure 3.5: Main effect of vetiver on the mean percentage seedling survival (± SE) of *Eragrostis curvula* and *Panicum maximum* overall. Different letters represent a significant difference between treatments (p<0.05).

3.4.3 Growth traits

Eragrostis curvula and *P. maximum* did not differ in terms of seedling height (P=0.180) or number of tillers per seedling (P=0.191), but differed significantly in the number of leaves produced per seedling (P=0.04; Table 3.2), with *E. curvula* producing more leaves per seedling (10.34 ± 0.896) then *P. maximum* (6.15 ± 0.897). Competition affected seedling height (P<0.0001), number of tillers per seedling (P<0.0001), and number of leaves per seedling overall (P<0.0001) (Table 3.2). Full competition exerted by one and two vetiver tufts influenced the growth of native grass negatively (Fig.3.6). Overall, native grasses seedlings grew taller (Fig.3.6A), produced more tillers (Fig.3.6B), and more leaves per seedling (Fig.3.6C) when growing alone (control) compared to when growing with either one or two vetiver tufts. However, there was no significant difference in seedling height (Fig.3.6A), number of tillers (Fig.3.6B), and number of leaves produced per seedling (Fig.3.6C) when experiencing competition from one and two vetiver grass tufts.

Sowing method; however, did not affect seedling height (*P*=0.238), number of tillers per seedling (*P*=0.372), and number of leaves per seedling of both native species (*P*=0.843). *Eragrostis curvula* and *P. maximum* responded differently to competition in terms of seedling height (*P*= 0.007), but not number of tillers per seedling (*P*=0.071), and number of leaves per seedling (*P*=0.539). Seedling height of *P. maximum* was significantly greater than that of *E. curvula* in the control but these species did not differ significantly in their seedling height when growing with one, or two vetiver tufts (Fig. 3.7). Both these species experienced a reduced seedling height when growing with one and two vetiver tufts, but there was no significant difference between one and two tufts (Fig. 3.7). Sowing method, and the interaction between competition and sowing method had no effect on any of the variables measured (Table 3.2).

Table 3.2: The effect of the presence of vetiver (competition), sowing method, and their interaction on seedling height (cm), number of leaves per seedling, and number of tillers per seedling of two native grass species (*Eragrostis curvula* and *Panicum maximum*) using a generalized linear model with a gamma distribution and a log link function. Significant p-values (p< 0.05) are in bold

Source of variation	Seedling height			Number of leaves per seedling			Number of tillers per seedling		
	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*
Species (S)	1.799	1	0.180	8.453	1	**0.04**	1.709	1	0.191
Competition (C)	260.68	2	**<0.0001**	165.51	2	**<0.0001**	205.68	2	**<0.0001**
Sowing method (M)	2.871	2	0.238	0.341	2	0.843	1.976	2	0.372
S*C	9.954	2	**0.007**	1.236	2	0.539	5.302	2	0.071
S*M	0.448	2	0.799	0.687	2	0.709	4.121	2	0.127
C*M	0.715	4	0.949	2.738	4	0.603	0.455	4	0.978
S*C*M	2.951	4	0.566	6.606	4	0.158	0.941	4	0.919

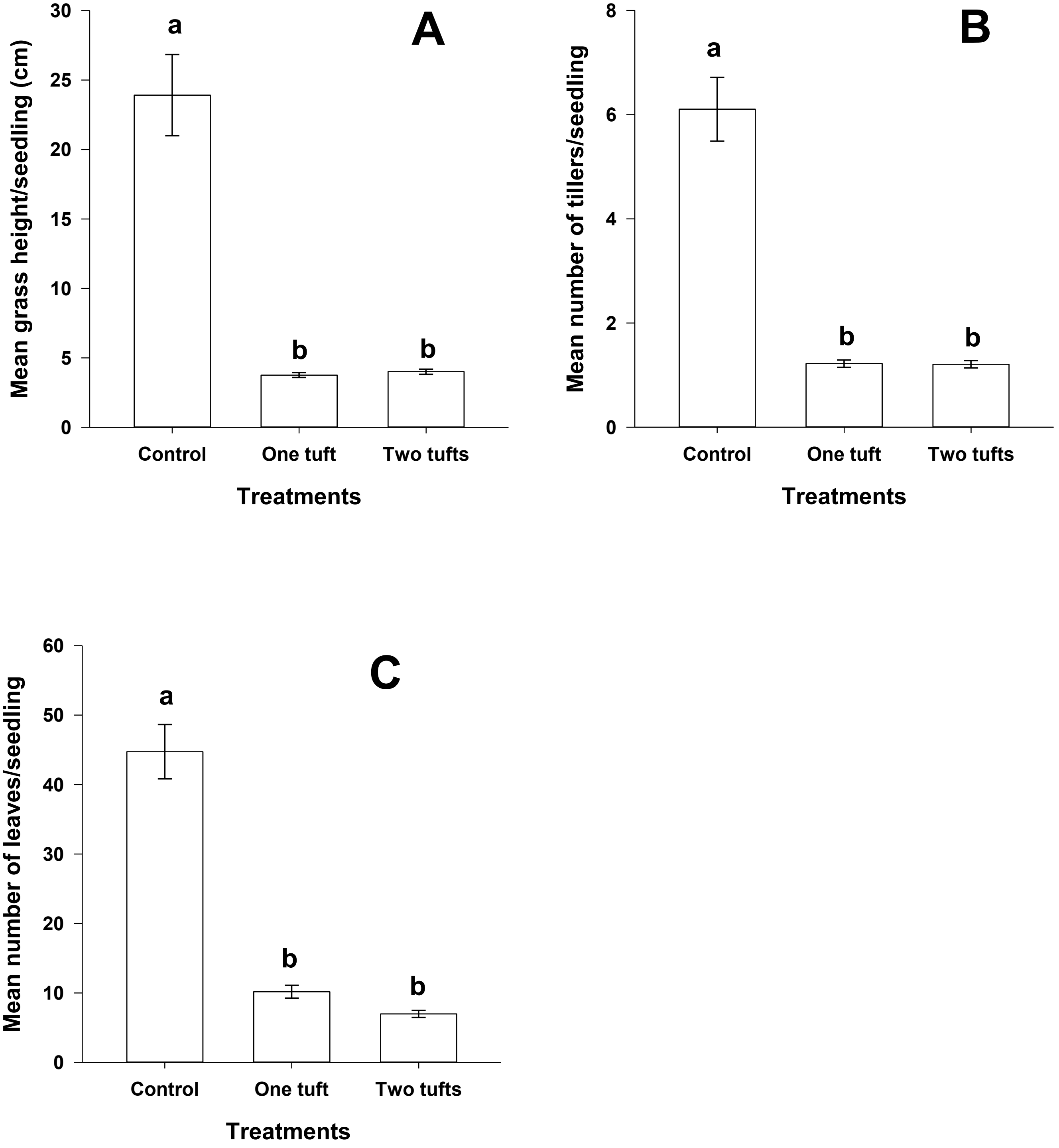

Figure 3.6: Effect of vetiver (full competition) on the mean seedling height (±SE) (**A**), mean number of tillers per seedling (±SE) (**B**), and mean number of leaves per seedling (±SE) (**C**) of both *Eragrostis curvula* and *Panicum maximum* overall. Different letters represent a significant difference between treatments (p<0.05).

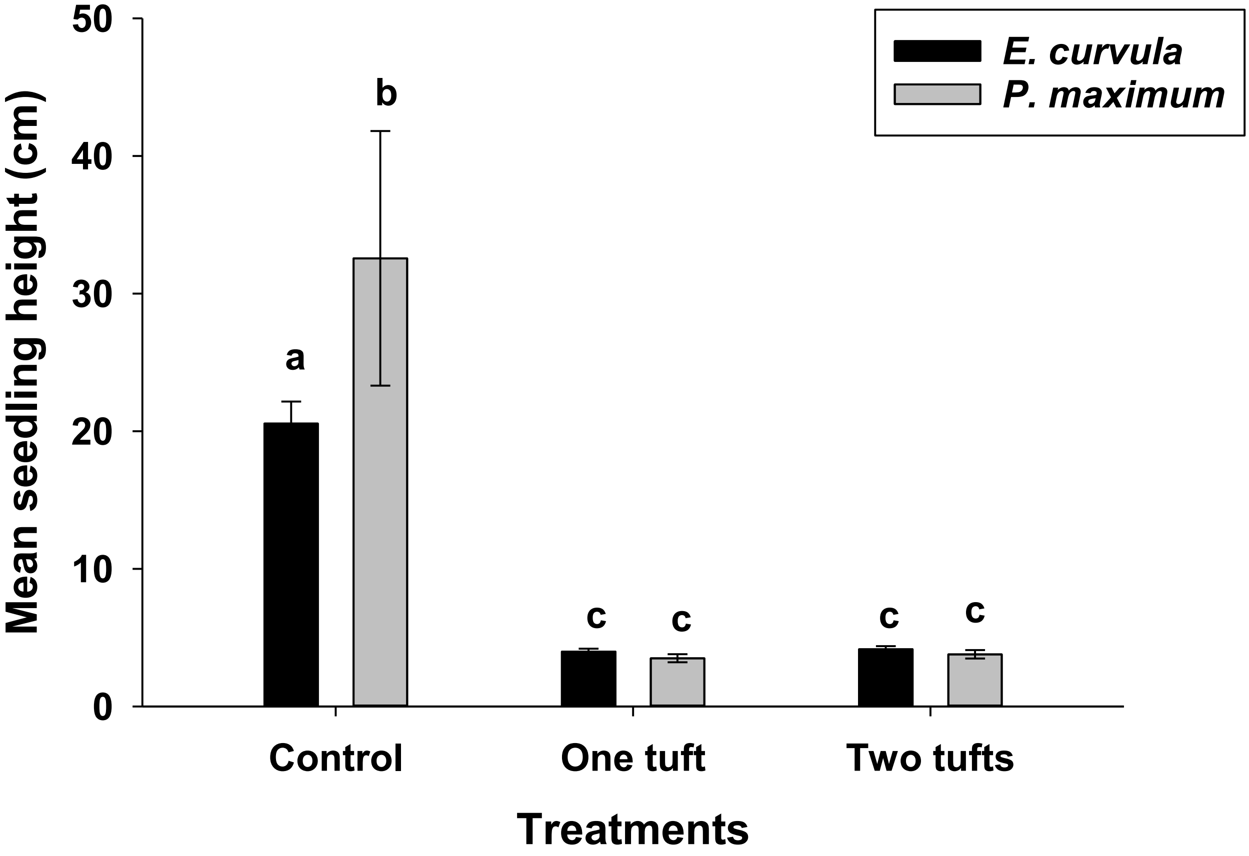

Figure 3.7: Effect of vetiver (full competition) on the mean seedling height (± SE) of the interaction between *Eragrostis curvula* and *Panicum maximum*. Different letters represent a significant difference between treatments (p<0.05).

3.4.4 Roots exclusion trial

Competition caused an increase in percentage germination but a reduction in seedling survival and slowed the growth of native grasses. For that reason, *E. curvula* seedlings were grown in pots with vetiver tufts (roots excluded) to investigate whether roots of vetiver grass were causing this reduction in survival and slow growth of native grasses seedlings, or whether other factors were in play.

Even with vetiver roots excluded, vetiver tufts still had an effect on *E. curvula* seedling growth in terms of aboveground biomass (χ^2=34.252, df=2, *P*< 0.0001), seedling height (χ^2=38.693, df=2, *P*< 0.0001), number of leaves per seedling (χ^2=21.443, df=2, *P*< 0.0001), and number of tillers per seedling (χ^2=39.128, df=2, P< 0.0001). *Eragrostis curvula* tufts still experienced a reduction in growth even with the exclusion of vetiver roots. *Eragrostis curvula* still produced more aboveground biomass (Fig.3.8A), grew taller (Fig.3.8B), produced more tillers per seedling (Fig.3.8C), and more leaves per seedling (Fig.3.8D) when growing alone (control) compared to when growing with one and two vetiver grass tufts. Surprisingly, *E. curvula* also grew better when growing with one vetiver grass tuft (Fig.3.8 A, B, and C) compared to when growing with two vetiver tufts (Fig.3.8A, B, and C), which is contrary to when growing with full competition (vetiver roots present, Figure 3.6 and 3.7).

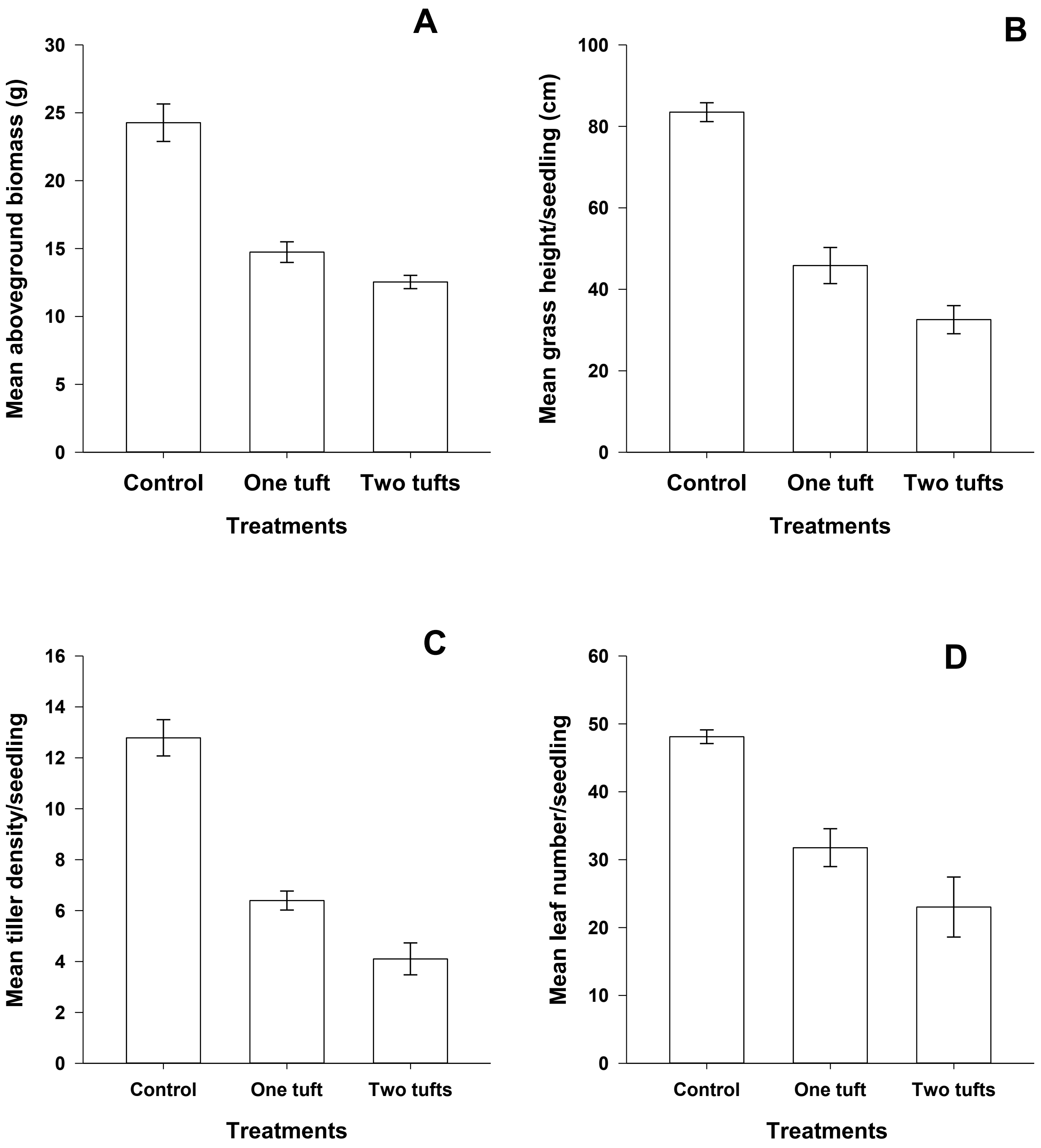

Figure 3.8: Effect of vetiver with root interaction excluded on the mean aboveground biomass (±SE) (**A**), mean seedling height (±SE) (**B**), mean number of tillers per seedling (±SE) (**C**), and mean number of leaves per seedling (±SE) (**D**) of *Eragrostis curvula.*

3.4.5 Roots density analysis

The space available around one and two vetiver tufts was examined and compared it to the space available around *E. curvula* roots to understand whether vetiver root density could also be limiting the growth and survival of native grasses. There was a significant difference in the space available (unoccupied soil space) around vetiver roots compared to *E. curvula* roots (χ^2=28.865, df =2, P<0.001). *Eragrostis curvula* (60.27% ± 4.517) had significantly more soil space unoccupied by roots compared to one (30.913% ± 1.820) and two vetiver tufts (23.87% ± 0.957; Figure 3.9). Furthermore, one vetiver tuft has significantly more soil space unoccupied by roots when compared to two vetiver tufts (Fig.3.9). Therefore, there is limited soil space around vetiver tufts that can allow the establishment of native grasses.

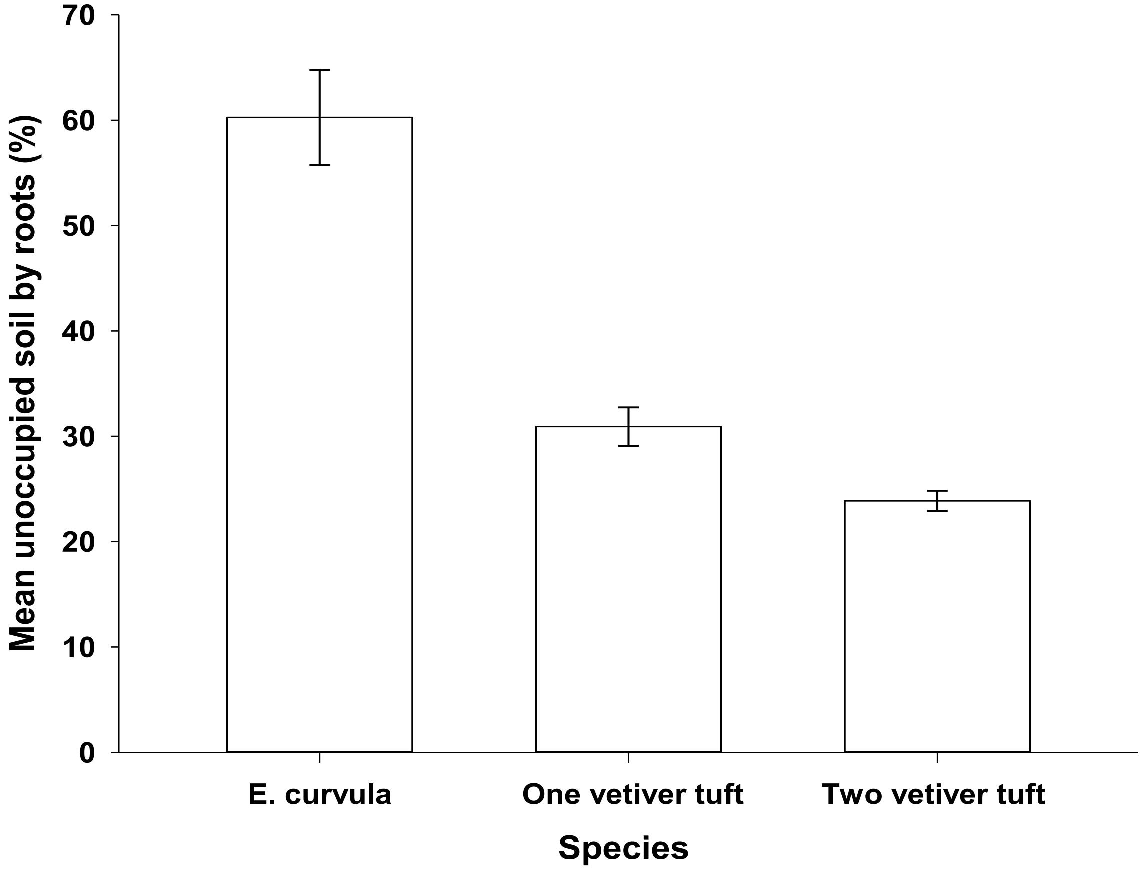

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Figure 3.9: Mean (± SE) soil space unoccupied by the roots of one and two vetiver grass tufts compared to unoccupied space around *Eragrostis curvula*.

3.5 DISCUSSION

In this study, vetiver tufts were used to investigate the effect of established vetiver on seed germination, seedling survival, and seedling establishment of native grasses, with the overall purpose being to test the claim that vetiver acts as a pioneer species enabling recruitment of native grasses. Furthermore, to understand the basic effect of biotic factors on native grasses recruitments. Our findings showed that vetiver tufts facilitated seed germination in native grasses, which partially supports the previous claim that vetiver allow recruitment of native grasses. This is because germination is only the first step towards successful plant recruitment (Lenz and Facelli, 2005). Most studies on seed germination have focused on abiotic factors e.g. soil moisture, temperature, and light (Knipe, 1968; Lindig-Cisneros and Zedler, 2001; Kolb et al., 2016), with few studies testing biotic factors e.g. competition/facilitation and allelopathy from mature established plants (Aguiar et al., 1992). Among the few studies which looked at the effect of mature established plants on seed germination, most have shown a negative effect. For example, Rees and Brown (1991) showed that established plants have a negative effect on seed germination of the annual forb *Sinapis arvensis*, with the effect not caused by seed mortality, but a reduction in germination rate, and reduced recruitment of germinated seeds. However, other studies have given evidence of the existence of nurse plants, i.e. plants that create a favorable environment through shade and moisture retention, resulting in an increased germination percentage/rate and seedling establishment around or beneath them (Fowler, 1986b; Ren et al., 2008). Even though this phenomenon has been studied mostly between trees (nurse plant) and small plants (e.g. forbs and grasses) in arid regions where water is limiting, this notion has been termed the nurse plant theory (Ren et al., 2008). Vetiver ability to facilitate seed germination can, therefore, be explained using this nurse plant theory.

Many well-studied abiotic factors that affect seed germination can be altered by established neighboring plants e.g. available light through shading (Aguiar et al., 1992). The alteration can produce either a favorable or an unfavorable environment for seed germination. Even though we never measured these factors (soil moisture, temperature, and light), it is obvious that the vetiver grass tufts altered these factors as they triggered seed germination in native grasses. Considering that the two grasses used in the study (i.e. *Eragrostis curvula* and *Panicum maximum*) are relatively shade tolerant grasses, their seeds (especially those of *P. maximum*) could be adapted to germinate in relatively shady, moist areas (Meredith, 1955; Fish et al. 2015). This might explain why the presence of a neighboring plant boosted seed germination. However, because *E. curvula* is more of a pioneer type species which produces small abundant seeds with greater viability compared to *P. maximum*, which is a late seral species producing large fewer seeds with reduced viability (Meredith, 1955), it germinated better than *P. maximum* in all treatments. This also suggests that *E. curvula* has a wider microclimate tolerance for seed germination compared to *P. maximum.* Furthermore, seed size has been shown to also affect germination, with most studies reporting an increase in germination percentage rate with a decrease in seed size (Silvertown, 1981; Gross, 1984; Aldrete and Mexal, 2005), which supports these findings.

Seed sowing method is also one of the factors that affects seed germination, but it is mostly studied using commercially important crops (e.g. maize and sorghum) and trees (e.g. pine trees) (Aldrete and Mexal, 2005). Few studies looked at naturally occurring rangeland grasses (Maun and Lapierre, 1986). This study is among the first to investigate the influence of sowing method in rangeland grasses, and it showed that surface sowed seeds germinate better than buried seeds or seeds mixed with a water retention gel. Several studies have shown that burying seeds reduces germination percentage by increasing seed mortality (Maun and Lapierre, 1986; Harris, 1996; Aldrete and Mexal, 2005). However, this is dependent on sowing depth, with an increase in sowing depth resulting in a decrease in seed germination rate. For example, Maun and Lapierre (1986) showed that seed germination, the rate of emergence of those germinated seeds, and the total emergence of dune species (*Elymus canadensis*, *Cakile edentula*, and *Corispermum hyssopifolium*) decreased with an increase in seed burial depth in sandy soils.

Aldrete and Mexal (2005), using potting soil, also showed a clear decrease in seed germination and seedling emergence of three pine species with an increase in sowing depth. Even though our study did not compare different sowing depths, the differences between surface sowing and buried seeds (2cm) support these examples. However, should water be a liming factor (i.e. arid regions), one should expect better germination of buried seeds and those seeds mixed with a water retention gel compared to surface sown seeds. These sowing methods maintain moisture for longer periods compared to surface sowing (Ren et al., 2008). For this study, watering was done frequently (watered every second day), thus water availability is excluded as a limiting factor, which explains the findings obtained. Harris (1996), studied the effect of sowing depth on seed germination and seedling emergence of *Sorghum bicolor* in semi-arid Botswana. He showed that the soil dried quickly, indicating that even though deeper sowing depth reduced seed germination and emergence, shallow sowing (not surface sowing) retained moisture longer resulting in quicker seedling emergence and did not result in seed mortality (Harris, 1996). Microsites that favours seed germination are those that do not allow seed desiccation (Fenner, 1978). Some studies use mulching or water retention gel to combat quick drying of the top soil which in turn reduces seed germination (Pill, 1991).

Even though vetiver facilitated seed germination, it also reduced the establishment of those germinated seeds resulting in a slow seedling growth and increased seedling mortality. This is contrary to the claim that vetiver promotes reestablishment in native grasses. Numerous studies have demonstrated that established surrounding swards have a negative effect on seedling establishment of either invading species or of the same species (Fenner, 1978; Snaydon and Howe, 1986; Fowler, 1986a). This is because the seedling stage is a critical stage in plant development and requires enough above and belowground resources, hence why seedlings tend to be more sensitive to competition than mature plants. For example, in a field trial, Snaydon and Howe (1986) studied the effect of shoot, root, and full competition exerted by established ryegrass (*Lolium perenne*) on the establishment of *Poa annua*, *P. trivialis*, and *Festuca rubra*. They showed that full competition and root competition affected the seedling establishment of these grasses by reducing the dry weight of seedlings by about sevenfold (Snaydon and Howe, 1986). Their findings suggested that seedlings are more severely affected by belowground competition than aboveground competition as shoot competition had little effect on seedling growth (Snaydon and Howe, 1986). Vetiver has an extensive investment in belowground material, which may explain why seedling growth was substantially reduced by the presence of vetiver.

This study showed similar results to those of Fowler (1986a), Fenner (1978), and Wesson and Wareing (1969). Fowler (1986a) used a field trial to investigate the effect of established grasses on seed germination, seedling establishment, and survival of other grasses. He showed that established grasses had no negative effect on seed germination but rather had a slight positive effect, despite substantially reducing the number of tillers in *Bouteloua rigidiseta* (Fowler, 1986a). Using artificial swards, Fenner (1978) showed that seed germination in ruderals was not negatively affected by established grass swards mostly in short turf treatment. However, seedlings of ruderal species could not establish successfully in these swards (Fenner, 1978). Wesson and Wareing (1969), focused on the effect of grass swards on buried seeds of weed species e.g. *Veronica persica* and *Sinapis arvensis*. They showed that seeds of these plants germinated well within established grass swards but failed to establish (Wesson and Wareing, 1969). This provides further evidence that the microclimate requirements for seeds and seedlings can be different. Seeds require specific abiotic conditions to trigger germination, while seedlings are influenced by both abiotic and biotic factors with competition for resources being the key determinant of seedling survival (Aguiar et al., 1992). In these grass sward conditions, seedling fail to recruit because they have no fully developed shoots and roots which can help them compete effectively for both aboveground and belowground resources with surrounding swards community (Fenner, 1978).

Factors responsible for hindering growth and establishment of native grasses were then investigated in more detail. Vetiver root density was compared to that of *E. curvula* with the aim of understanding how much space is available for other species to utilize around these two species. *Eragrostis curvula* had more space around its roots compared to vetiver, suggesting that there is limited space for the establishment of native grasses around vetiver. Reduced space could result in direct root competition between recruiting seedlings and vetiver roots (Schenk et al., 1999). Numerous studies have shown that when there is enough available soil space, roots tends to avoid direct root competition by foraging in unoccupied soil resource patches (Schenk and Jackson, 2002; Bliss et al., 2002; Hutchings and John, 2003). However, changes in available soil space force direct root competition between mature grasses and seedlings (Schenk et al., 1999), with seedlings experiencing substantial negative effect because of their sensitivity to competition.

Above- and belowground competition interacts simultaneously in a natural ecosystem, but can exert different pressures on recruiting species, with one being more important than the other (Cahill, 1999). For this reason, an additional trial which excluded root competition was conducted. This tried to understand if the exclusion of root competition reduced the negative effect exerted by vetiver on native grass seedlings or if other factors i.e. shade and/or allelopathy were important in explaining the observed results. Seedlings still suffered a substantial decrease in growth even though root competition was excluded, which means either shade or allelopathy or both were responsible for reducing seedling growth. Surprisingly, there was also a difference between one and two vetiver tufts, with two tufts exerting more negative effect than one tuft. This is contrary to what was observed in the trial with no root exclusion (i.e. no difference between one and two tufts). The existence of strong root intraspecific competition between vetiver tufts could explain these findings. Root competition between vetiver tufts could be reducing the interspecific competition exerted by two vetiver tufts to the same level as that of one tuft. Strong intraspecific competition has been suggested to reduce the magnitude of interspecific competition when the density (the number of species per unit areas) of the competing species increases, allowing other species coexistence between those two species (Wedin and Tilman, 1993; Tilman, 1994).

Shade is not expected to be a major limiting factor affecting seedling establishment, as results from the full competition and roots exclusion trials were not similar, even though shade between these trials (i.e. one and two tufts) should have been relatively similar, because vetiver tufts in both trials were of a relatively equal height. However, the amount of oil produced by the roots can be affected by root intraspecific competition because it is closely related to metabolism in roots which is affected by both abiotic and biotic factors (Massardo et al., 2006). Oil production is influenced by soil resource availability also (Adams et al., 2003), hence intraspecific competition could result in a trade-off in resource allocation to either growth and oil production. Therefore, two vetiver tufts can produce a relatively similar amount of oil to that of one vetiver tuft as a result of intraspecific competition between the two vetiver tufts. Vetiver oil has been reported to have allelopathic compounds that negatively affect the seedling establishment of other plants (Mao et al., 2004; Mao et al., 2006). For example, Mao et al. (2004) investigated the effect of vetiver oil on seed germination and seedling growth of six weed species. They showed that vetiver oil inhibited seed germination and seedling establishment in five out of six weed species providing evidence for the existence of an allelopathic behaviour by vetiver grass (Mao et al., 2006). However, this argument does not completely exclude competition for light as a contributing factor, it only suggests that allelopathic effects appears to be major contributing factor to the result found in the root exclusion trial. Furthermore, *P. maximum* is a shade tolerant species, and *E. curvula* is also a moderately shade-tolerant species, meaning they can both grow in a shaded environment. A simple trial separating allelopathy interference, root competition, and shading effect is needed to understand which factor is responsible for the suppression of growth in native grasses.

Surface sowing and the presence of vetiver are beneficial only for seed germination but not for seedling establishment as vetiver reduced the seedling growth and survival of native grasses. The reduction could be caused by one or the combination of these factors: 1) Direct root competition between vetiver roots and seedlings roots; 2) vetiver shade, reducing the photosynthetic activity in native grass seedlings; and 3) possibly an allelopathic effect caused by vetiver oil produced by the roots. Results of this study, therefore, suggest that it is unlikely that vetiver grass will allow recruitment of native grasses, which means rehabilitation using vetiver is unlikely to allow succession by native grasses.

3.6 REFERENCES

Adams, R.P., Pandey, R.N., Dafforn, M.R., James, S.A., 2003. Vetiver DNA-fingerprinted cultivars: effects of environment on growth, oil yields and composition. Journal of Essential Oil Research 15, 363-371.

Adkins, S., Davidson, P., Matthew, L., Navie, S., Wills, D., Taylor, I., Bellairs, S., 2000. Smoke and germination of arable and rangeland weeds. Seed biology: advances and applications. CABI Publishing, New York, 347-359.

Aguiar, M., Soriano, A., Sala, O., 1992. Competition and facilitation in the recruitment of seedlings in Patagonian steppe. Functional Ecology 6, 66-70.

Aldrete, A., Mexal, J., 2005. Sowing depth, media, and seed size interact to influence emergence of three pine species. Tree planters' notes.

Ammondt, S.A., Litton, C.M., 2012. Competition between native Hawaiian plants and the invasive grass *Megathyrsus maximus*: implications of functional diversity for ecological restoration. Restoration Ecology 20, 638-646.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G., Waddington, J., 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications 13, 137-153.

Bliss, K.M., Jones, R.H., Mitchell, R.J., Mou, P.P., 2002. Are competitive interactions influenced by spatial nutrient heterogeneity and root foraging behavior? New Phytologist 154, 409-417.

Bogdan, A., 1977. Tropical pasture and fodder plants. Longman.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M., Anthelme, F., 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96, 18-34.

Cahill, J.F., 1999. Fertilization effects on interactions between above-and belowground competition in an old field. Ecology 80, 466-480.

Cahill, J.F., 2002. What evidence is necessary in studies which separate root and shoot competition along productivity gradients? Journal of Ecology 90, 201-205.

Chahal, K.K., Kaushal, S., Sandhu, A.K., 2015. Chemical composition and biological properties of *Chrysopogon zizanioides* (L.) Roberty syn. *Vetiveria zizanioides* (L.) Nash-A Review. Indian Journal of Natural Products and Resources [Formerly as Natural Product Radiance] 6, 251-260.

Chōmchalao, N., 2001. utilization of vetiver as medicinal and aromatic plants. Office of the Royal Development Projects Board.

Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

Dalton, P., Smith, R., Truong, P., 1996. Vetiver grass hedges for erosion control on a cropped flood plain: hedge hydraulics. Agricultural Water Management 31, 91-104.

Danh, L.T., Truong, P., Mammucari, R., Foster, N., 2010. Extraction of vetiver essential oil by ethanol-modified supercritical carbon dioxide. Chemical Engineering Journal 165, 26-34.

Dias, L., Pereira, I.P., Dias, A.S., 2016. Allelopathy, seed germination, weed control and bioassay methods. Allelopathy Journal 37, 31-40.

Fenner, M., 1978. A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. The Journal of Ecology 66, 953-963.

Fish, L., Mashau, A. C., Moeaha, M. J., Nembudani, M.T., 2015. Identification guide to southern African grasses. An identification manual with keys, descriptions and distributions. Strelitzia 36. South African National Biodiversity Institute, South Africa.

Fowler, N., 1986a. Microsite requirements for germination and establishment of three grass species. American Midland Naturalist 115, 131-145.

Fowler, N., 1986b. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17, 89-110.

Gallagher, M.K., Wagenius, S., 2016. Seed source impacts germination and early establishment of dominant grasses in prairie restorations. Journal of Applied Ecology 53, 251-263.

Ghebrehiwot, H.M., Aremu, A.O., Van Staden, J., 2014. Evaluation of the allelopathic potential of five South African mesic grassland species. Plant Growth Regulation 72, 155-162.

Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth. Infinity Publishing.

Grimshaw, R.G., 1993. The role of vetiver grass in sustaining agricultural productivity. Asia Technical Department. The World Bank, Washington DC USA.

Gross, K.L., 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. The Journal of Ecology 72, 369-387.

Harris, D., 1996. The effects of manure, genotype, seed priming, depth and date of sowing on the emergence and early growth of *Sorghum bicolor* (L.) Moench in semi-arid Botswana. Soil and Tillage Research 40, 73-88.

Hutchings, M., John, E., 2003. Distribution of roots in soil, and root foraging activity, Root ecology. Springer, pp. 33-60.

Kiepiel, I., Johnson, S.D., 2014. Breeding systems in Clivia (*Amaryllidaceae*): late-acting self-incompatibility and its functional consequences. Botanical journal of the Linnean Society 175, 155-168.

Knipe, O., 1968. Effects of moisture stress on germination of alkali *Sacaton, Galleta*, and glue grama. Rangeland Ecology & Management/Journal of Range Management Archives 21, 3-4.

Kolb, R.M., Pilon, N.A.L., Durigan, G., 2016. Factors influencing seed germination in Cerrado grasses. Acta Botanica Brasílica 30, 87-92.

Lenz, T.I., Facelli, J.M., 2005. The role of seed limitation and resource availability in the recruitment of native perennial grasses and exotics in a South Australian grassland. Austral Ecology 30, 684-694.

Lindig-Cisneros, R., Zedler, J., 2001. Effect of light on seed germination in *Phalaris arundinacea* L.(reed canary grass). Plant Ecology 155, 75-78.

Mao, L., Henderson, G., Bourgeois, W.J., Vaughn, J.A., Laine, R.A., 2006. Vetiver oil and nootkatone effects on the growth of pea and citrus. Industrial Crops and Products 23, 327-332.

Mao, L., Henderson, G., Laine, R.A., 2004. Germination of various weed species in response to vetiver oil and nootkatone 1. Weed technology 18, 263-267.

Massardo, D.R., Senatore, F., Alifano, P., Del Giudice, L., Pontieri, P., 2006. Vetiver oil production correlates with early root growth. Biochemical systematics and Ecology 34, 376-382.

Maun, M., Lapierre, J., 1986. Effects of burial by sand on seed germination and seedling emergence of four dune species. American Journal of Botany 73, 450-455.

Meredith, D., 1955. The grasses and pastures of South Africa.

Morgan, R.P.C., 2009. Soil erosion and conservation. John Wiley & Sons.

Pill, W.G., 1991. Advances in fluid drilling. HortTechnology 1, 59-65.

Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press.

Rees, M., Brown, V.K., 1991. The effect of established plants on recruitment in the annual forb *Sinapis arvensis*. Oecologia 87, 58-62.

Ren, H., Yang, L., Liu, N., 2008. Nurse plant theory and its application in ecological restoration in lower subtropics of China. Progress in Natural Science 18, 137-142.

Schenk, H.J., Callaway, R.M., Mahall, B., 1999. Spatial root segregation: are plants territorial? Advances in Ecological Research 28, 145-180.

Schenk, H.J., Jackson, R.B., 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. Journal of Ecology 90, 480-494.

Shangwen, C., 1999. Insects on vetiver hedges. The Vetiver Newsletter 23, 17-18.

Silvertown, J.W., 1981. Seed size, life span, and germination date as coadapted features of plant life history. The American Naturalist 118, 860-864.

Snaydon, R., Howe, C., 1986. Root and shoot competition between established ryegrass and invading grass seedlings. Journal of Applied Ecology 23, 667-674.

Tainton, N.M., Bransby, D., Booysen, P.d.V., 1976. Common veld and pasture grasses of Natal. Shuter & Shooter.

Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2011. Grass-on-grass competition along a catenal gradient in mesic grasseland, South Africa. African Journal of Range & Forage Science 28, 79-85.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2-16.

Truong, P., Chomchalow, N., Vessabutr, S., 1999. Vetiver grass technology for mine rehabilitation. Pacific Rim Vetiver Network Technology 2, 1-19.

Truong, P., Hart, B., Chomchalow, N., Sombatpanit, S., 2001. Vetiver system for wastewater treatment. Office of the Royal Development Projects Board.

Van den Berg, J., Midega, C., Wadhams, L., Khan, Z., 2003. Can Vetiver grass be used to manage insect pests on crops? Proceedings of the Third International Conference on Vetiver and Exhibition (ed. by RG Grimshaw), 254–264.

Van Oudtshoorn, F.V., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza Publications.

Vieritz, A., Truong, P., Gardner, T., Smeal, C., 2003. Modelling Monto vetiver growth and nutrient uptake for effluent irrigation schemes. Proceedings of the Third International Conference on Vetiver and Exhibition, 254-264.

Wagner, S., Truong, P., Vieritz, A., Smeal, C., 2003. Response of vetiver grass to extreme nitrogen and phosphorus supply. Proceedings of the Third International Conference on Vetiver and Exhibition, 100-108.

Wedin, D., Tilman, D., 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecological Monographs 63, 199-229.

Wesson, G., Wareing, P., 1969. The role of light in the germination of naturally occurring populations of buried weed seeds. Journal of Experimental Botany 20, 402-413.

Weyerstahl, P., Marschall, H., Splittgerber, U., Wolf, D., 1996. New sesquiterpene ethers from Vetiver oil. Liebigs Annalen 1996, 1195-1199.

Xia, H., Ao, H., He, D., 1998. The effect of environmental factors on the growth of vetiver growth. Vetiver Research and Development, 39-44.

Xu, L., 2002. Vetiver research and development: A decade experience from China. Proceedings: The Second International Vetiver Conference, ORDPB, Bangkok, 311-322.

4 CHAPTER 4: EFFECT OF VETIVER COMPETITION AND SOIL NUTRIENT STATUS ON NATIVE GRASSES

4.1 ABSTRACT

Vetiver grass (*Chrysopogon zizanioides* (L.) Roberty) is a densely tufted perennial C_4 grass from central India, used worldwide for soil and water conservation. It is a hardy, fast-growing, and densely rooted grass enabling it to withstand most environmental hazards (drought, frost, and floods). Worldwide use of vetiver is grounded in the claims that it does not compete with neighbouring grasses and it is not invasive. Recent studies have demonstrated that nitrogen deposition has dramatically risen after the industrial and agricultural revolution, and is expected to continue rising. Such increase is predicted to alter plant species coexistence, particularly in grasslands, through making limiting resources non-limiting, hence eliminating the competitive trade-off that allows species coexistence. The claims about vetiver's competitive ability were investigated using a pot trial examining the competitive interactions between vetiver and four native grasses (*Eragrostis curvula, Digitaria eriantha*, *Panicum maximum* and *Hyparrhenia hirta*) under different soil nutrient levels. Nutrient addition was achieved using 80% Hoagland's solution (N=172, P=25, K=188mg/L), and the relative interaction index (RII) and the percentage change in yield (Ry) were used as indices to assess the effect of competition and nutrient status on native grasses. Vetiver exerted a weak competitive effect on all native grass tufts, except for *D. eriantha*, under low nutrient status. Vetiver exerted a facilitative effect on *D. eriantha* under low nutrient status. However, vetiver exerted a strong competitive effect on all native grass species under high nutrient status, except for *P. maximum,* which responded similarly under low and high nutrients conditions. Overall, narrow-leaved grasses (*E. curvula* and *H. hirta*) had a weak competitive ability compared to broad-leaved grasses (*P. maximum* and *Digitaria eriantha*). Therefore, morphological traits are important to consider in competition studies and could predict species that might coexist with vetiver. As soil nitrogen continues to increase globally, this will affect coexistence between native grasses and vetiver, with vetiver gaining an increased competitive advantage over native grasses. For this reason the claims that vetiver does not compete with neighbouring grasses need to be reconsidered and care taken when using vetiver for soil and water conservation.

4.2 INTRODUCTION

Vetiver grass (*Chrysopogon zizanioides* (L.) Roberty) is a densely tufted perennial C_4 grass from central India but is found in many tropical regions, including in tropical Africa (Council, 1993; Adigun and Are, 2015). It is a hardy, fast-growing, and densely rooted grass enabling it to withstand most environmental hazards (drought, frost, and floods) and to be useful in soil and water conservation (Dalton et al., 1996; Xu, 2002). Vetiver has been shown to grow successfully in abandoned mine sites with toxic heavy metals (Truong et al., 1999; Roongtanakiat and Chairoj, 2001), coastal sand with high salinity (Xu, 1998; Xia et al., 1998), landfill sites with toxic anthrosoils, and in contaminated dams with high nitrogen levels (Truong et al., 2001). The popularity and the worldwide use of vetiver is underpinned by two largely untested claims, firstly that vetiver grass is noncompetitive with adjacent grasses or crops, and secondly that vetiver is not invasive (Vieritz et al., 2003). Vetiver produces non-viable seeds and has no stolons or rhizomes, so it is propagated vegetatively (Council, 1993). As both these claims relate strongly to vetiver competitive ability it results in the assumption that it can coexist with native grasses.

Competition is a negative interference, being either direct or indirect suppression of one plant by another through differences in resource utilization (Goldberg, 1996). Competition is dependent on resource availability and is one of the key drivers of species diversity in grassland ecosystems (Wedin and Tilman, 1993; Tilman, 1994). For example, competition has been shown to increase in its importance when soil nutrient status increases, with species diversity usually declining as a result of nutrient addition (Grime, 1977; Campbell and Grime, 1992). Furthermore, Tilman suggested that functionally similar species compete more strongly than dissimilar species, and species coexistence occurs when all species in the ecosystem share the same underlying quantitative trade-off that is linked to resource utilization (Tilman, 1980; Wilson and Tilman, 1995). That is, each species in an ecosystem has a lower minimum resource requirement (R*) for a certain available resource which allows it to be more competitive when such a resource is limiting, but has a higher R* for other resources which in turn boost the competitive ability of other species, thus allowing coexistence between these species (Tilman, 1980). However, addition of limiting resources (e.g. nitrogen) make that resource non-limiting, results in the elimination of this competitive trade-off responsible for species coexistence (Tilman, 1994; Harpole et al., 2016). Furthermore, species that are better at absorbing (lower

R*) two or more resources (e.g. water and sunlight) will be better competitors and can outcompete other species, hence altering species coexistence in that ecosystem (Tilman, 1980; Wedin and Tilman, 1993). Introduced plants are generally better at resource acquisition than native plants, hence the interaction between introduced plants and native plants can sometimes favour introduced plants resulting in their invasion (Brooks, 2000; Vilà et al., 2003).

Numerous studies have shown that atmospheric nitrogen deposition has increased the levels of nitrogen in the soil and this is directly linked to the agricultural and industrial revolution (Stevens et al., 2004; Clark and Tilman, 2008; Bobbink et al., 2010). Nitrogen cycling in an ecosystem is derived from three main sources; biological N-fixation, mineralization, and atmospheric deposition, with the two dominant sources being atmospheric deposition, increased by combustion of fossil fuels, and mineralization which is directly linked to emission of NH_3 from the use of fertilizer and manure in agricultural fields (Bobbink et al., 2010). These sources are driven by the human demand for food and energy, which is unlikely to decrease given the current population growth predictions (Tilman and Wedin, 1991). Nitrogen, an essential nutrient for plant growth and nutrient enrichment, as a result of atmospheric nitrogen deposition has been shown to potentially reduce species diversity, with rare species being the most sensitive (Tilman and Wedin, 1991; Stevens et al., 2004; Clark and Tilman, 2008). The mechanisms driving this decline remain unclear, but are strongly linked to plant competition, as increased nitrogen levels alter individual plant physiology (e.g. water and nutrient use efficiency) and biomass allocation patterns (e.g. root to shoot ratio) (Bobbink et al., 2010).

Moreover, atmospheric nitrogen and sulphur deposition have been shown to acidify soil in the long-term, leading to lower soil pH, leaching of cations, and increased levels of toxic metals (e.g. Al) in the soil, mostly in regions with high rainfall (Bobbink et al., 2010). In South Africa, regions with high rainfall are also associated with highly dispersive soils which are susceptible to soil erosion, making these areas a prime target for the use of vetiver (Fey, 2010). Considering that vetiver can tolerate low soil pH, toxic metals, and high nitrogen levels, it is important to understand its competitive ability under these conditions to understand and predict the species shifts that can be expected in areas rehabilitated using vetiver.

An improved understanding of both the competitive effect of vetiver and competitive response of selected native grasses, with both strong and weak competitive ability, and how soil nutrient levels influence these interactions will help predict the potential of vetiver to become invasive and suggest indigenous species that are likely to coexist or even outcompete vetiver. The claims about vetiver competitive ability were investigated using a pot trial by examining the competitive ability of vetiver's grass under different soil nutrient levels with the aim of answering the following three questions:

1. Does vetiver exert a competitive effect on neighbouring native grasses with a strong (*Eragrostis curvula* and *Digitaria eriantha*) and weak (*Panicum maximum* and *Hyparrhenia hirta*) competitive ability?
2. Does vetiver density influence the competitive effect experienced by native grasses?
3. Does soil nutrient addition influence this interaction?

Three hypotheses for this study were; firstly, that vetiver will exert a competitive effect on native grasses, and that nutrient addition will increase vetiver's competitive effect. Secondly, increasing the number of vetiver tufts will increase the competitive effect on native grasses irrespective of soil nutrient addition. Lastly, native grasses will differ in their competitive response under low and high nutrient status, with highly competitive grasses experiencing a lower competitive effect than weakly competitive grasses.

4.3 MATERIALS AND METHODS

4.3.1 Study site and species

The study was run from November 2016 to April 2017 (6 months) at the University of KwaZulu-Natal NM Tainton Arboretum, Pietermaritzburg, KwaZulu-Natal, South Africa. The region has a mean annual rainfall of about 844mm, with most of the rain falling in summer between October and March. Summers are hot, with a mean daily maximum temperature of approximately 26.4°C, while winters are mild with occasional frost and mean daily temperature of about 8.8ºC. The winter is coolest in June, and summer is warmest in February and March (Fynn et al., 2009). The growing season of this region is controlled mainly by temperature and rainfall, with most of the grass biomass production taking place between October and April (Fynn et al., 2009).

Four native grass species, *Eragrostis curvula* (Schrad.) Nees*, Digitaria eriantha* Steud., *Panicum maximum* Jacq., and *Hyparrhenia hirta* Stapf., commonly occurring in South African rangelands and useful in soil erosion control and rangeland rehabilitation were used in this study (Tainton et al., 1976; Morris, 2016). These species differ largely in their competitive ability (Laan et al., 2008; Morris, 2016), morphological traits (Meredith, 1955; Fish et al. 2015), and response to soil nutrient addition (Fynn and O'Connor, 2005; Fynn and Naiken, 2009). *Eragrostis curvula* and *Digitaria eriantha*, even though differing in their morphological traits, compete well under both low and high soil nutrient status, and were hence classified as strong competitors (McDonald et al., 1998; Fynn and Naiken, 2009). *Digitaria eriantha* is a tall broad-leaved grass, with robust roots, and is usually stoloniferous (Van Oudtshoorn, 2012). By contrast, *E. curvula* is a tall narrow-leaved grass, with fine roots, but has no stolons or rhizomes (Meredith, 1955). The other two species, *Panicum maximum* and *Hyparrhenia hirta* were classified as weak competitors because their competitive ability is quite variable and soil nutrient dependent, with *P. maximum* shown to compete strongly in nutrient rich soils (Fynn and O'Connor, 2005) and *H. hirta* in nutrient poor-soils (Fynn and O'Connor, 2005; Zwerts et al., 2015). These two species also differ in terms of morphological traits. *Panicum maximum* is a broad-leaved grass, which prefers growing under shade, and has robust roots usually with a short creeping rhizome (Meredith, 1955). By contrast, *H. hirta* is a narrow-leaved grass, which is relatively shade intolerant, and has a dense fibrous root system (Van Oudtshoorn, 2012).

4.3.2 Experimental design

These native grass species (*Eragrostis curvula, Digitaria eriantha*, *Panicum maximum* and *Hyparrhenia hirta*) were propagated from wild-collected tillers and planted into 6L pots filled with coarse, nutrient-poor sand. The tufts (equal numbers of tillers and similar height) of each of these species were grown as a phytometer. These tufts were grown alone (control), with one vetiver tuft (low density competition), and between two vetiver tufts which were planted 15 centimeters apart (high density competition). Both the vetiver and native grasses were of similar size at the beginning of the experiment. All the competition treatments were subject to both high and low soil nutrient conditions. The high fertility treatment was watered with 300 mL of 80% Hoagland's nutrient solution (N = 172, P = 25, K = 188 mg L/1) (Hoagland and Arnon, 1950) every 4 days while the low fertility treatment was given no nutrient addition (Tedder et al., 2012). The experiment was a full factorial design, laid out in a completely randomized arrangement with six replicates of each treatment combination, and 24 treatment combinations in total. To ensure that water was not a limiting factor, pots were irrigated with municipal water daily, provided there was no natural rainfall.

4.3.3 Data collection

After 6 months, the native grass aboveground biomass was harvested. The aboveground biomass of each species from each pot was put separately into paper bags, which were then oven dried for 48 hours at 60°C before weighing to determine the final dry biomass. Growth traits of each native species, including leaf table height, basal circumference, and number of tillers, were also measured before harvesting. The results for the growth traits are shown in Appendix 4.1 for two reasons, 1) growth traits measured (e.g. leaf table height) are a weak measure of competitive effect compared to aboveground biomass, 2) most of these traits supported the findings of the RII derived from aboveground biomass.

4.3.4 Data analysis

Relative interaction indices (RII) were calculated using the aboveground biomass of the native grasses within each treatment combination to determine the level of competition exerted by vetiver (Armas et al., 2004). RII is a ratio with values that range between -1 to 1, with negative values indicating competition, zero indicating symmetry, and positive values indicating facilitation (Armas et al., 2004). Therefore, RII represents the net gain or loss of a measurable trait, generally biomass, because of the presence of inter-specific interaction relative to when that inter-specific interaction is absent. RII is calculated using the following equation:

$$\mathrm{RII} = (B_w - B_o)/(B_w + B_o)$$

With B_W representing the aboveground biomass of a native grass growing with interspecific interaction (either one or two vetiver tufts) and B_O representing the aboveground biomass of a native grass growing alone (Armas et al., 2004).

As the residuals were not normally distributed, these data were analysed using generalized linear models (GLZM) with a linear distribution and an identity link function in SPSS version 24 (IBM Inc.2016) to assess the effect of one and two vetiver tufts, nutrient level, and their interaction on native grass growth in terms of RII based on aboveground biomass. GLZMs were used as they have more statistical power than other commonly used non-parametric tests because they use the actual data and not ranked data (Quinn and Keough, 2002).

Where the model revealed significant differences, the sequential sidak procedure was used for multiple comparisons ($\alpha = 0.05$).

To assess the effect of nutrient addition on biomass production in native grasses, the percentage change in yield (Ry) was calculated using the following equation:

$Ry=\{ [(Y_H-Y_L)/Y_L]*100\}$

Where Y_H is the mean growth in terms of aboveground biomass of all replicates in the control treatment, one vetiver tuft, or two vetiver tuft treatments growing at a high nutrient level, and Y_L is the mean growth in terms of aboveground biomass under the same three treatments growing at a low nutrient level. As the residuals did not conform to the assumptions of analysis of variance (ANOVA), these data were analyzed using generalized linear models with a linear distribution and an identity link function. Where the model revealed significant differences, the sequential sidak procedure was used to adjust for multiple comparisons ($\alpha = 0.05$).

4.4 RESULTS

4.4.1 Relative interaction index (RII)

Main effects

Overall, all four native grasses experienced competition from vetiver. However, all four-native species responded differently to competition exerted by vetiver grass tufts ($P<0.0001$; Table 4.1), with *E. curvula* and *H. hirta* experiencing the most competition and *P. maximum* and *D. eriantha* experiencing less (Figure 4.1A). Competition (one and two vetiver tufts) ($p=0.015$; Table 4.1) and nutrient level (low and high) ($p<0.0001$; Table 4.1) significantly affected the relative interaction index overall. In addition, grass species responded differently to different levels of competition and to different nutrient levels ($p<0.0001$; Table 4.1). There was also a significant influence of the interaction between species, nutrients, and competition ($p<0.021$). However, there was no significant difference in the interaction between competition and nutrient level ($p=0.157$; Table 4.1).

Table 4.1: Results of a generalized linear model, with a linear distribution and an identity link function, showing the main effects and interactions of grass species, competition exerted by vetiver, and nutrient level on the relative interaction index (RII) showing chi-square likelihood ratio, degrees of freedom, and p-values. Significant p-values ($p < 0.05$) are in bold

Source of variation	RII		
	χ^2	Df	*P*
Species (S)	22.244	3	**<0.0001**
Competition (C)	5.883	1	**0.015**
Nutrient Level (N)	51.986	1	**<0.0001**
Species * Competition	26.411	3	**<0.0001**
Species * Nutrient Level	23.139	3	**<0.0001**
Competition * Nutrient Level	2.002	1	0.157
Species * Competition * Nutrient Level	9.689	3	**0.021**

Competition; main effect and their relevant two-way interactions

Two vetiver tufts exerted a stronger competitive effect overall than one vetiver tuft (Figure 4.1B). The four native grasses did not differ in their response to competition exerted by one vetiver tuft but differed significantly when growing with two vetiver tufts (Figure 4.2A). *Digitaria eriantha* and *P. maximum* experienced less competition (less than 10% reduction in their above ground biomass) compared to *E. curvula* and *H. hirta* (approximately 30% reduction in their biomass) (Figure 4.2A). Surprisingly, *D. eriantha* and *P. maximum* did not differ significantly between one another and within themselves in their response to competition exerted by both one and two vetiver tufts. By contrast, *E. curvula* and *H. hirta* experienced a substantially greater competitive effect when growing with two vetiver tufts compared to one vetiver tuft, but these species did not differ from each other (Figure 4.2A). Generally, vetiver has a negative effect on the growth of these native species, but some species are more resistant to competition than others.

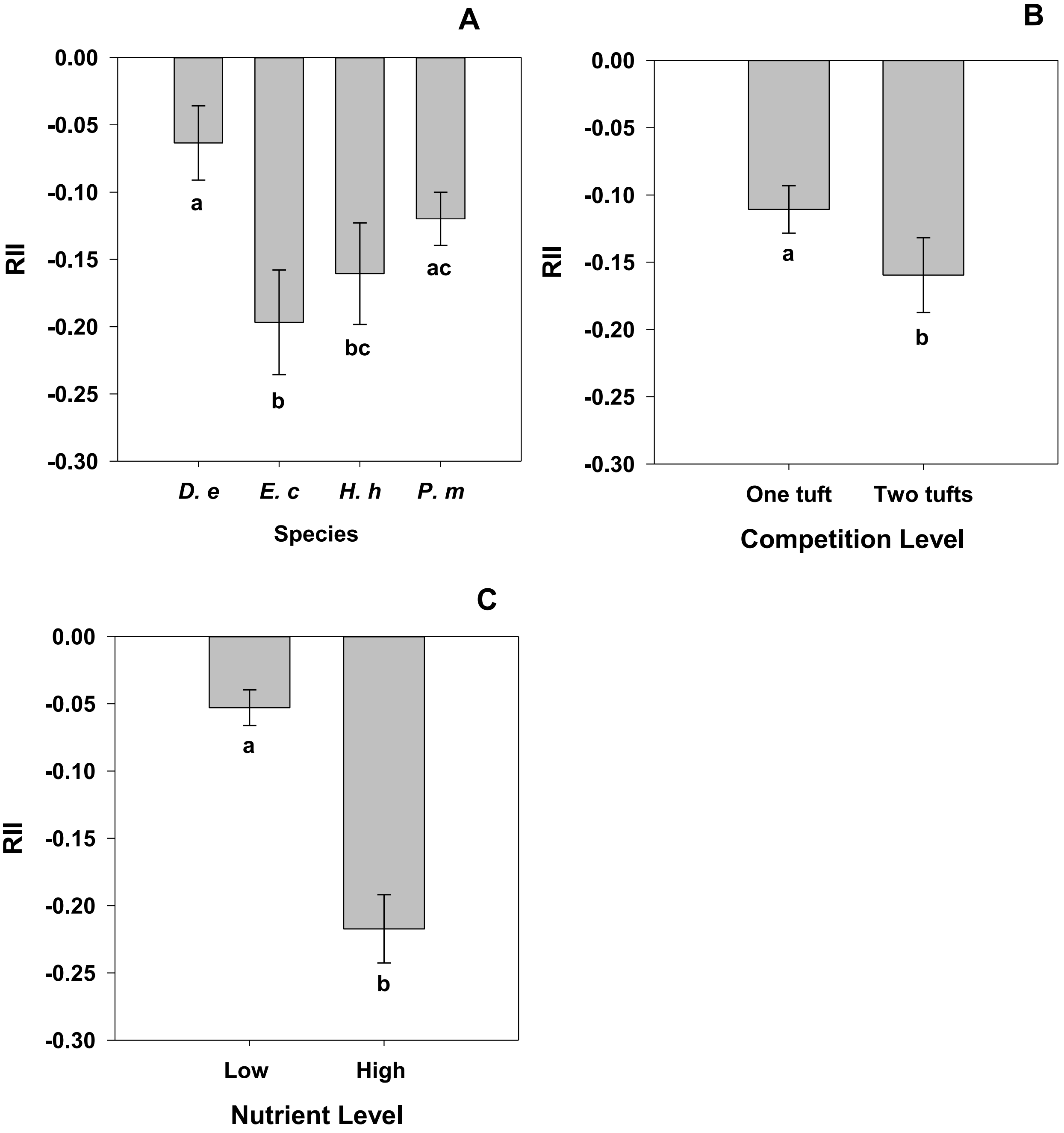

Figure 4.1: Mean (± SE) relative interaction index (RII) based on the final aboveground biomass for the main effects of species (A), vetiver competition level (B), and nutrient level (C). Different letters represent a significant difference between treatments ($p<0.05$)**.** Species (A) are as follows, ***D.e- Digitaria eriantha, E.c- Eragrostis curvula, H.h- Hyparrhenia hirta, and P.m- Panicum maximum.***

Nutrient level; main effect and their relevant two-way interactions

Nutrient addition had a significant influence on the competitive effect exerted by vetiver on native grasses, with native grass biomass reduced by around 20% under high nutrient conditions, compared to about 5% under low nutrient conditions (Figure 4.1C). All grass species except for *P. maximum* experience greater competition under high nutrients than under low (Figure 4.2B). By contrast, *D. eriantha* and *P. maximum* did not differ significantly in their response under high nutrient conditions but both experienced a weak competitive effect (Figure 4.2B). However, *E. curvula* and *H. hirta* experienced a substantially greater competitive effect under high nutrient conditions compared to all grasses under low nutrient conditions, and compared to *P. maximum* under high nutrient conditions (Figure 4.2B). *Digitaria eriantha* shifted from experiencing a slight facilitation under low nutrients to a moderate competitive effect under high nutrient conditions, while *P. maximum* experienced similar competitive effects both under low and high nutrient conditions (Figure 4.2B).

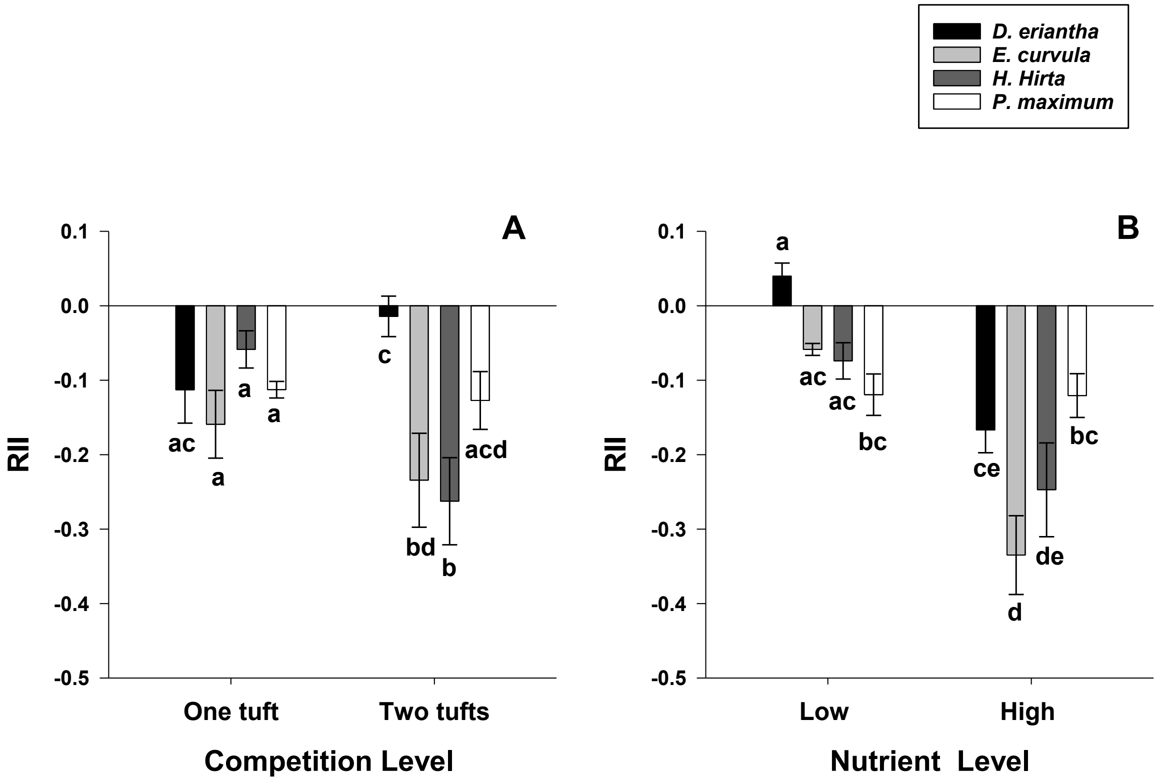

Figure 4.2: Mean (± SE) relative interaction index (RII) based on the final aboveground biomass for interaction between species and the effect of competition level (A) and nutrient level (B). Different letters represent a significant difference between treatments ($p<0.05$).

Species, competition and nutrient level interaction

Panicum maximum and *H. hirta* responded in a similar manner regardless of the level of competition and the nutrient status (Figure 4.3). By contrast, *D. eriantha* and *E. curvula* were affected by both competition and nutrient level, with *D. eriantha* experiencing little effect when growing with both one and two vetiver tufts under low nutrient conditions and two vetiver tufts under high nutrient conditions, but experiencing greater competition when growing with one vetiver tuft under high nutrient conditions. Additionally, *E. curvula* experienced a weak competitive effect under low nutrient conditions regardless of the number of vetiver tufts; however, experienced a greater competitive effect under high nutrient conditions (Figure 4.3).

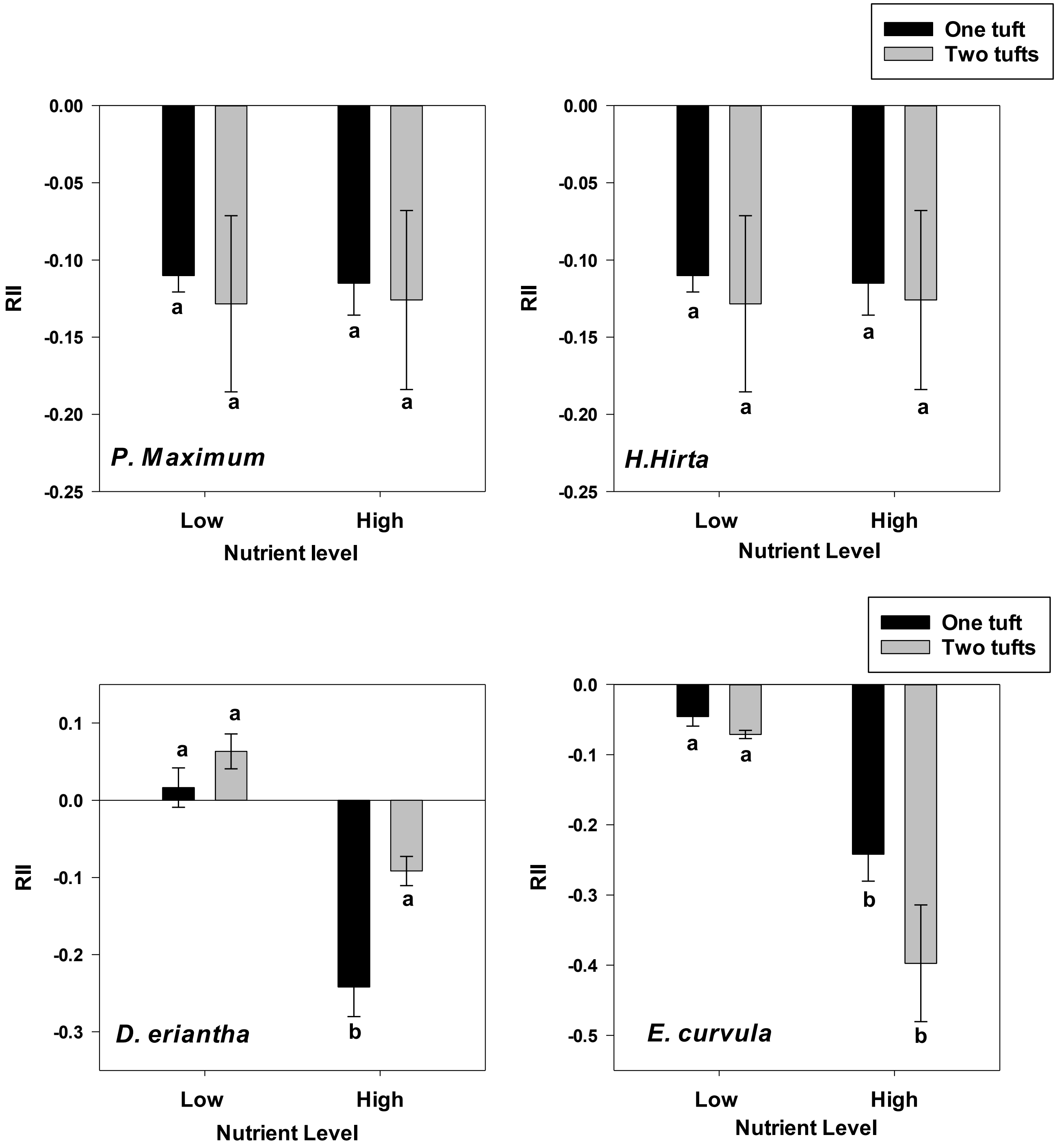

Figure 4.3: Mean (± SE) relative interaction index (RII) based on the final aboveground biomass for the interaction between competition level and nutrient level for each native species response individually. Different letters represent a significant difference between treatments ($p<0.05$).

4.4.2 Percentage change in yield (RY)

Main effect

The percentage change in yield (Ry) indicates how much native grass aboveground biomass was gained as a result of nutrient addition. Competition exerted by vetiver had a significant effect on the percentage change in yield of all species combined ($P<0.0001$; Table 4.2). It reduced the percentage change in yield overall, but there was no significant difference between one and two vetiver grass tufts (Figure 4.4A). Overall, native species were affected by nutrient addition ($P<0.0001$; Table 4.2), with *D. eriantha* gaining substantially greater aboveground biomass (271.9% ± 23.9) as a result of nutrient addition compared to *E. curvula* (181.9% ± 28.27), *H. hirta* (192.27% ± 24.25), and *P. maximum* (169.48% ± 10.92), which did not differ significantly from one another (Figure 4.4B). In addition, the percentage change in yield of native species was individually affected by competition exerted by vetiver grass tufts ($p=0.002$; Table 4.2).

Interaction between species and competition

There was no change in yield of *P. maximum* as a result of vetiver competition, but all other species showed differences (Figure 4.5). *Digitaria eriantha* and *E. curvula* biomass production was suppressed by vetiver competition but unaffected by the number of tufts, while *H. hirta* showed increasing biomass suppression with increasing vetiver competition (Figure 4.5).

Table 4.2: Results of a generalized linear model, with a linear distribution and identity link function, showing the main effect and interaction of species and competition exerted by vetiver tufts on the percentage change in yield (Ry) in four native grass species, showing likelihood chi-square value, degrees of freedom, and p-values. Significant p-values ($p< 0.05$) are in bold.

	Ry		
Source of variation	χ^2	Df	*P*
Species	21.938	3	**<0.0001**
Competition	34.619	2	**<0.0001**
Species * Competition	21.348	6	**0.002**

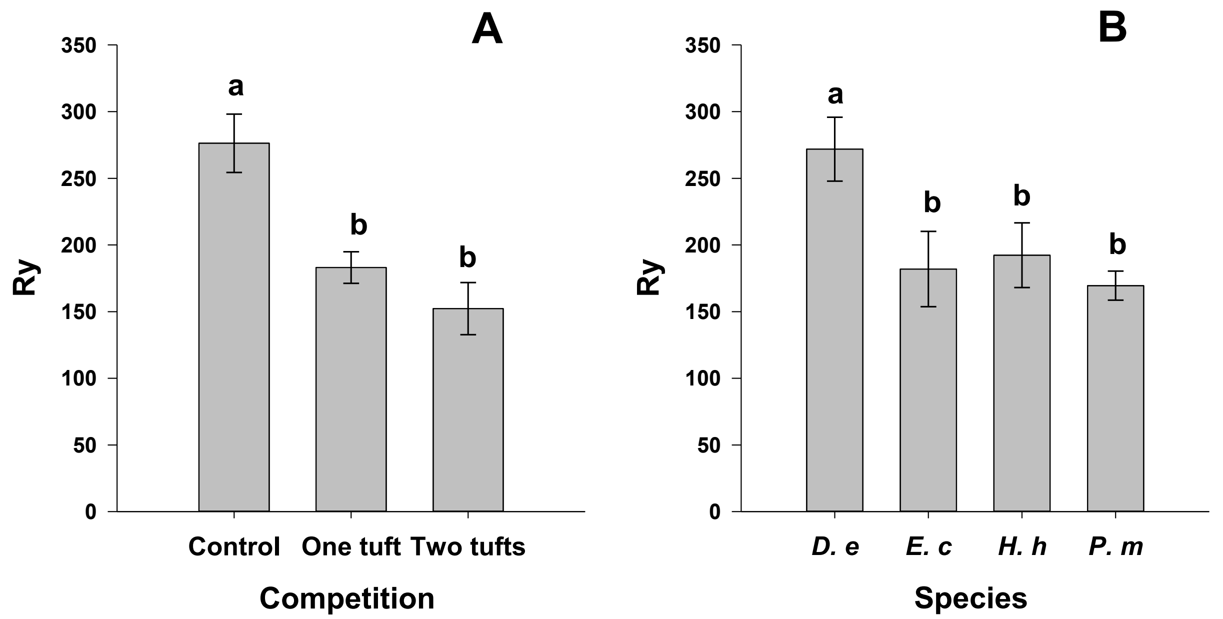

Figure 4.4: Mean (± SE) percentage change in yield (Ry) as a result of nutrient addition, based on the final aboveground biomass for the main effects of competition level (A) and species (B). Different letters represent a significant difference between treatments ($p<0.05$).

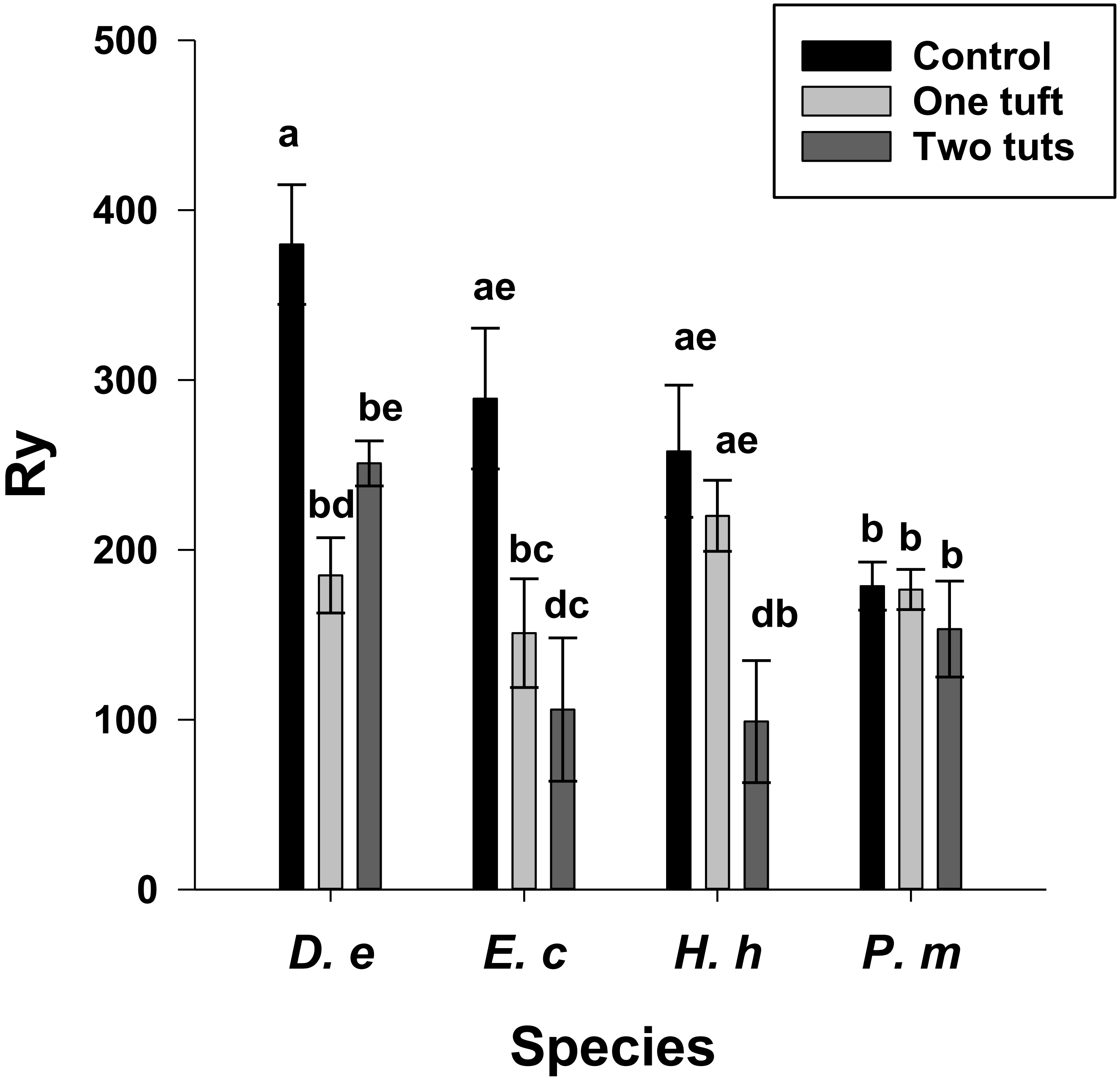

Figure 4.5: Mean (± SE) percentage change in yield (Ry) as a result of nutrient addition, based on the final aboveground biomass for interaction between the effect of competition level and native species (B). Different letters represent a significant difference between treatments (p<0.05).

4.5 DISCUSSION

This study investigated the competitive effect of one and two vetiver tufts on four native grasses, and the interplay of soil nutrients on the above interactions. The competitive effect exerted by one and two vetiver tufts under low and high soil nutrients was assessed using the relative interaction index (RII), while native grass biomass gained as a result of soil nutrient addition was assessed using the percentage change in yield (Ry). Irrespective of soil nutrient status, two vetiver tufts exerted a stronger competitive effect on all four native grasses combined, compared to one vetiver tuft, as expected. Considering that vetiver is always planted in a number of rows consisting of two, or more tufts to block eroding soil (Dalton et al., 1996; Donjadee and Chinnarasri, 2012), it is clear that vetiver will compete directly with native grasses present or recruiting into the area. Vetiver is a densely tufted, tall, broad-leaved grass, with an extensive root system. Therefore, having two adjacent tufts results in more shade and denser root biomass taking up most of the available soil space (Donjadee and Chinnarasri, 2012), which might explain why native grasses experienced increased competition when growing with two vetiver tufts. Even though increasing the space between vetiver tufts planted in the rows might offer a solution by reducing the competitive effect, increased space between vetiver tufts has been shown to reduce the effectiveness in soil erosion control, particularly on steep slopes because water can form rills between the vetiver tufts (Greenfield, 2002; Donjadee and Chinnarasri, 2012).

It was expected that *D. eriantha* and *E. curvula* would be strong competitors, and vice versa for *P. maximum* and *H. hirta*. However, this study did not support this hypothesis but suggests that species with similar morphological traits respond similarly to competition exerted by vetiver. For example, *D. eriantha* and *P. maximum*, both broad-leaved grasses, experienced similar levels of competition even when growing with two vetiver tufts. However, *E. curvula* and *H. hirta*, both fine-leaved grasses, experienced a stronger competitive effect from two vetiver tufts than in one vetiver tuft. This suggests that categorising these species in terms of their morphological traits, rather than their possible competitive ability, may be more useful to determine which species may colonise areas stabilised with vetiver. This further confirms that a species can be a strong competitor with one species but become a weak competitor with another, depending on their resource requirements and functional similarities (Tilman, 1984; Tilman, 1990). Functionally similar species compete more strongly than functionally dissimilar species

(Tilman, 1984; Wedin and Tilman, 1993). For example, vetiver is a broad-leaved grass with a robust dense root system, and is more similar morphologically to *D. eriantha* and *P. maximum*, than it is to *E. curvula* and *H. hirta*. Grime (1977) argued that a strong competitor plant, is a species that is leafy (i.e. broad-leaved and produces more leaves), fast growing, and has an extensive investment in root systems, which further qualifies these two native species (*D. eriantha* and *P. maximum*) as well as vetiver as strong competitor species.

Morphological traits are important in understanding species competitive ability (Grime, 1977; Tilman, 1985). For example, Fynn et al. (2009) investigated vegetative traits of 18 native grasses and compared them to their competitive effect exerted on a phytometer. The study consisted of a field trial where four seedlings of each grass species were grown around a phytometer (*Themeda triandra*), and a pot trial containing only a phytometer to measure growth when competition is absent (Fynn et al., 2009). They showed that vegetative traits such as high total leaf mass, many tillers and low specific leaf area (SLA) were linked to invasiveness and ability to resist invasion by other grasses (Fynn et al., 2009). This further suggests that grouping species in terms of their traits could be a good predictor of their ability to resist invasion, ability to invade, and competitive ability. However, their study showed the importance of considering soil nutrient addition, as it affects species investment in these traits, explained further by resource allocation trade-offs (Fynn et al., 2005; Fynn et al., 2009). Species either allocate more resources to aboveground material for light capture, and less to belowground material for soil resource acquisition, or vice versa or even to both below and aboveground material, although this is dependent on resource availability and competitive pressure (Tilman, 1990).

Changes in the soil nutrient status have been linked with changes in species composition in grasslands, with soil nutrient limitation (i.e. mostly nitrogen) seen as a major factor contributing to species diversity, as it is linked directly to plant growth and plant competition (Harpole and Tilman, 2007; Harpole et al., 2016). Nitrogen is the most limiting soil nutrient for plant growth (Campbell et al., 1991). Atmospheric nitrogen deposition resulting from anthropogenic practices (i.e. commercial agriculture practices and industrial emissions) has been shown to increase nitrogen enrichment in the soil (Clark and Tilman, 2008; Bobbink et al., 2010). This study showed that the addition of nutrients increased the competitive effect exerted by vetiver on native grasses in general, and changed the competitive response of native grasses from categorizing them in terms of their traits to focusing on their individual species responses. However, broad leaved species, even though they experienced competition, still remained strong competitors compared to narrow-leaved grasses. For example, *D. eriantha* experienced a slight facilitative effect under low soil nutrients but shifted to experiencing a moderate competitive effect under high soil nutrient conditions. Whereas, *P. maximum*'s competitive response was not affected by soil nutrient addition, suggesting that it was a strong competitor under both low and high nutrient conditions, which is contrary to our expectations. It was expected that *P. maximum* would be a weak competitor and would increase its competitive ability in high nutrient soils as most studies have previously reported (Fynn et al., 2005; Fynn and O'Connor, 2005; Tedder et al., 2012), but that was not the case. *Panicum maximum* is a very variable grass, varying mostly in terms of height and length of creeping rhizome (Meredith, 1955; Van Oudtshoorn, 2012). These features could be rendering this grass a strong competitor against vetiver. Height (accompanied by broad-leaves) could be allowing easy light capture, and creeping rhizomes could be creating a new resource niche through foraging for resources where vetiver roots are not reaching (Silvertown, 2004; Laan et al., 2008; Van Oudtshoorn, 2012).

Two of the native narrow-leaved grasses showed a relatively strong competitive ability in low nutrient soils, but experienced a strong competitive effect in high nutrient soils. These findings are consistent with those of Fynn and O’Connor (2005), even though they used field trial not pot trials, and they did not fertilize with a nutrient mixture but added granular of nitrogen and phosphorus. However, they showed that sites with both nitrogen and phosphorus added had a greater aboveground net primary production (ANPP) and were dominated by tall broad-leaved grasses (i.e. *P. maximum*) (Fynn and O'Connor, 2005). Whereas, sites with no nutrient addition were dominated by mixture of short grasses and tall narrow-leaved grasses (e.g. *T. triandra*, *E. curvula* and *H. hirta*) (Fynn and O'Connor, 2005). They showed a trade-off between greater ANPP and light availability, therefore, as soil nutrient status increases, these species allocate resources to producing aboveground biomass, shifting competition importance from soil nutrients to light, with competition for light favouring tall broad-leaved grasses because they can capture light more efficiently than narrow-leaved grasses (Fynn and O'Connor, 2005). Therefore, this could explain why narrow-leaved grasses (mostly *E. curvula*) experienced a greater competitive effect under high nutrient levels than broad-leaved grasses.

Numerous studies have reported that *H. hirta* is a strong competitor in nutrient-poor environments and its competitive ability shifts when soil nutrients are no longer limiting (Fynn et al., 2009; Chejara et al., 2010; Zwerts et al., 2015). This means that *H. hirta* has a low R* for essential soil nutrients like nitrogen (Tilman, 1985), but it is known to have a weak competitive response (ability to resist invasion) (Zwerts et al., 2015), which might explain why it still experienced some competitive effect even in nutrient-poor soils. Nitrogen enrichment will therefore, have a massive effect on the competitive ability of *H. hirta,* and *E. curvula,* as they are more sensitive to shade than broad-leaved species. Even though *E. curvula* was expected to be a strong competitor because of its ability to increase biomass production irrespective of soil nutrient availability, and its fine root structure that allows easy resource acquisition (Fynn and Naiken, 2009), this grass was only shown to be a strong competitor against vetiver in nutrient-poor soils. Therefore, the competitive ability of *E. curvula* is not only dependant on nutrient availability but also on the species it is competing with. In this case, vetiver, which is a robust grass, allocates more resources to leaf, stem and root production than *E. curvula*, hence allowing it to substantially supress *E. curvula* growth and performance. However, *E. curvula* has been shown to dominate areas limited by phosphorus (Fynn and O'Connor, 2005), while vetiver growth is highly limited by phosphorus, limiting mostly leaf production (Wagner et al., 2003) . These species might coexist in areas with high nitrogen but low phosphorus, with nitrogen boosting vetiver competitive ability, and phosphorus limitation making *E. curvula* more competitive against vetiver. Such a trade-off in resource utilization and resource ratio (R*) would separate niches for these species and could potentially promote coexistence (Tilman, 1987; Silvertown, 2004; Harpole and Suding, 2011).

The three-way interaction between species, competition and nutrient level, showed that species which were strong competitors under low nutrient conditions hardly retained their competitive ability under high nutrient conditions, suggesting an alteration of the trade-off through nutrient addition (Harpole and Tilman, 2007; Harpole and Suding, 2011). Native species responded differently to nutrient addition when growing either with one or two vetiver tufts, with *P. maximum* and *H. hirta* responding in a similar manner, but *D. eriantha* and *E. curvula* differing in their response. For example, *D. eriantha*'s competitive ability was strong under low nutrient conditions and did not differ between one and two tufts, but under high nutrient conditions it experienced a high competitive effect only when growing with one vetiver tuft. The ability of *D. eriantha* to grow under shade through effective utilization of light could explain the observed results, and the ability of this species to dominate in nutrient-rich soils. Furthermore, *D. eriantha* gained the most aboveground biomass as a result of nutrient addition compared to other species, so could be investing more in aboveground biomass in areas where competition for light becomes increasingly important (e.g. under high nutrient conditions with two vetiver tufts). Interspecific competition exerted by *D. eriantha* could be stronger than the intraspecific competition between vetiver tufts, hence explaining why *D. eriantha* experienced less competition when growing with two tufts than when growing with one. However, this would need to be tested because no study has investigated intraspecific competition between vetiver tufts. Numerous studies have however, shown that strong intraspecific competition and weak interspecific competition drives species coexistence and could allow invasion (Tilman, 1985; Wilson and Tilman, 1993; Fynn et al., 2009).

It was observed that *H. hirta* changed its usually upright growth form to grow more horizontally when growing with two vetiver tufts. This could have been a mechanism for exposing the leaves to sunlight, which might explain why it responded similarly to *P. maximum* in the three-way interaction, showing no effect of either one or two vetiver tufts under both nutrient conditions. However, this mechanism is only possible in pot trials and not in field trials where a species will be a phytometer surrounded by numerous vetiver tufts, blocking it from growing horizontally to gain light exposure. Therefore, should this be examined in a field trial, *H. hirta* should experience a stronger competitive effect under nutrient rich conditions. Competition studies that focus on native grasses either incorporate response to defoliation, or are field trials, because these are a realistic representation of what takes place in natural grasslands (Morris, 2016). Pot trials could be forcing competition between grasses because of limited space, while in field trials space is not usually as limiting. This might explain why species like *E. curvula* had a weak competitive ability, because their fine roots are able to absorb soil resources easily and avoid direct competition when space is not limiting (Schenk et al., 1999; Fynn and Naiken, 2009). Therefore, in the field *E. curvula* may have a strong competitive ability compared to pot trials.

Even though the hypothesis that competition shifts from belowground to aboveground when the resource gradient increases has been subject of debate among grassland ecologists

(Wilson and Tilman, 1993; Peltzer et al., 1998; Rajaniemi, 2002), the findings of this study could be explained by this notion. Other studies showed similar findings, for example, Wilson and Tilman (1993) using a field trial showed that belowground competition was more intense in areas with low nitrogen, while aboveground competition became intense in nitrogen rich soils, but whole plant competition was similar in both low and high nitrogen soils. However, even though this hypothesis might support some of our findings, Peltzer et al. (1998) showed that in low diversity grasslands, root competition suppressed *Agropyron cristatum* even in nutrient-rich soils. Rajaniemi (2002) also showed that even though shadecloth and increased aboveground biomass through fertilizer addition reduced the same amount of light availability, shadecloth did not decrease species diversity but fertilizer addition did. This indicates that it is not competition for light alone producing this effect, even though it becomes important in nutrient rich soils, but the interplay between roots and aboveground competition is responsible for competitive exclusion of less competitive species (Rajaniemi, 2002; Rajaniemi et al., 2003). Therefore, it could be that vetiver roots are also responsible for the suppression of native grasses even when soil nutrients are high. A study separating vetiver root and shoot competition could give clarity on this, but this was outside the scope and focus of this study.

A theoretical explanation that accounts for differences in soil resources which has gained popularity, mostly in studies of species coexistence and diversity, is the niche dimensionality hypothesis (Hutchinson, 1957). First proposed 50 years ago by George Evelyn Hutchinson, this hypothesis predicts that there are multi-dimensional nonoverlapping soil resources, and few aboveground resources (light and space) which allow species coexistence (Hutchinson, 1957; Harpole and Suding, 2011). Therefore, addition of a nutrient mixture and water every day, made these resources non-limiting, thereby altering soil resource niches and competitive trade-offs, increasing biomass production, which in turn shifted competition from multi-dimensional soil resources to a few aboveground resources (Tedder et al., 2012; Harpole et al., 2016). Considering that this was a pot trial, it is possible that both competition for space and light became important as in nutrient rich soils, because all species invested in their aboveground material. Therefore, resource competition theory, even though used mostly to explain large scale studies of species coexistence and species diversity (Tilman, 1994) forms a basis for understanding plant interactions and their interaction with the environment. However, it is important to understand individual plant trade-offs or niches to understand how plants will coexist with other species (Tilman, 1985).

This study disproved the claim that vetiver grass does not compete with neighbouring plants, and to a limited extent the second claim that vetiver is not invasive (Vieritz et al., 2003). The hypothesis that vetiver will exert a competitive effect on native grasses, and that nutrient addition will increase vetiver's competitive effect, is supported. Therefore, the increase in nitrogen, as a result of nitrogen deposition should be expected to increase vetiver's competitive ability and possibly shift the species composition in areas rehabilitated using vetiver. However, this study shows that vetiver is a strong competitor species irrespective of nutrient addition. Extensive investment of vetiver to both above- and belowground material allows it to be competitive in both low and high nutrient soils and could be the mechanism for survival and recruitment as this grass does not produce viable seeds.

4.6 REFERENCES

Adigun, M., Are, K., 2015. Comparatives effectiveness of two vetiveria grasses species *Chrysopogon zizanioides* and *Chrysopogon nigritana* for the remediation of soils contaminated with heavy metals. American Journal of Experimental Agriculture 8, 361-366.

Armas, C., Ordiales, R., Pugnaire, F.I., 2004. Measuring plant interactions: a new comparative index. Ecology 85, 2682-2686.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological applications 20, 30-59.

Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. The American Midland Naturalist 144, 92-108.

Campbell, B., Grime, J., Mackey, J., 1991. A trade-off between scale and precision in resource foraging. Oecologia 87, 532-538.

Campbell, B.D., Grime, J.P., 1992. An experimental test of plant strategy theory. Ecology 73, 15-29.

Chejara, V., Kriticos, D., Kristiansen, P., Sindel, B., Whalley, R., Nadolny, C., 2010. The current and future potential geographical distribution of *Hyparrhenia hirta*. Weed Research 50, 174-184.

Clark, C.M., Tilman, D., 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. Nature 451, 712-715.

Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

Dalton, P., Smith, R., Truong, P., 1996. Vetiver grass hedges for erosion control on a cropped flood plain: hedge hydraulics. Agricultural Water Management 31, 91-104.

Donjadee, S., Chinnarasri, C., 2012. Effects of rainfall intensity and slope gradient on the application of vetiver grass mulch in soil and water conservation. International Journal of Sediment Research 27, 168-177.

Fey, M., 2010. Soils of South Africa. Cambridge University Press.

Fish, L., Mashau, A. C., Moeaha, M. J., Nembudani, M.T., 2015. Identification guide to southern African grasses. An identification manual with keys, descriptions and distributions. Strelitzia 36. South African National Biodiversity Institute, South Africa.

Fynn, R., Morris, C., Kirkman, K., 2005. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. Journal of Ecology 93, 384-394.

Fynn, R., Naiken, J., 2009. Different responses of *Eragrostis curvula* and *Themeda triandra* to rapid-and slow-release fertilisers: insights into their ecology and implications for fertiliser selection in pot experiments. African Journal of Range and Forage Science 26, 43-46.

Fynn, R.W., O'Connor, T.G., 2005. Determinants of community organization of a South African mesic grassland. Journal of Vegetation Science 16, 93-102.

Fynn, R.W., Wragg, P., Morris, C., Kirkman, K., Naiken, J., 2009. Vegetative traits predict grass species' invasiveness and the invasibility of restored grassland. African Journal of Range & Forage Science 26, 59-68.

Goldberg, D.E., 1996. Competitive ability: definitions, contingency and correlated traits. Philosophical Transactions of the Royal Society of London B: Biological Sciences 351, 1377-1385.

Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth. Infinity Publishing.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111, 1169-1194.

Harpole, W.S., Suding, K.N., 2011. A test of the niche dimension hypothesis in an arid annual grassland. Oecologia 166, 197-205.

Harpole, W.S., Sullivan, L.L., Lind, E.M., Firn, J., Adler, P.B., Borer, E.T., Chase, J., Fay, P.A., Hautier, Y., Hillebrand, H., 2016. Addition of multiple limiting resources reduces grassland diversity. Nature 537, 93-96.

Harpole, W.S., Tilman, D., 2007. Grassland species loss resulting from reduced niche dimension. Nature 446, 791-793.

Hoagland, D.R., Arnon, D.I., 1950. The water-culture method for growing plants without soil. California Agricultural Experiment Station 347.

Hutchinson, G.E., 1957. Concluding remarks. quantitative biology 22, 415-427.

Laan, M.v.d., Reinhardt, C., Belz, R., Truter, W., Foxcroft, L., Hurle, K., 2008. Interference potential of the perennial grasses *Eragrostis curvula*, *Panicum maximum* and *Digitaria eriantha* with *Parthenium hysterophorus*. Tropical Grasslands 42, 88-95.

McDonald, C.J., Jones RM; Tothill, JC, 1998. Growth and spread of *Digitaria eriantha* cv. Premier and *Urochloa mosambicensis* cv. Nixon oversown into native speargrass

(*Heteropogon contortus*) pasture in south-east Queensland. Tropical Grasslands 32, 41-49.

Meredith, D., 1955. The grasses and pastures of South Africa.

Morris, C.D., 2016. Is the grazing tolerance of mesic decreaser and increaser grasses altered by soil nutrients and competition? African Journal of Range & Forage Science 33, 235-245.

Peltzer, D.A., Wilson, S.D., Gerry, A.K., 1998. Competition intensity along a productivity gradient in a low-diversity grassland. The American Naturalist 151, 465-476.

Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press.

Rajaniemi, T.K., 2002. Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. Journal of Ecology 90, 316-324.

Rajaniemi, T.K., Allison, V.J., Goldberg, D.E., 2003. Root competition can cause a decline in diversity with increased productivity. Journal of Ecology 91, 407-416.

Roongtanakiat, N., Chairoj, P., 2001. Uptake potential of some heavy metals by vetiver grass. Kasetsart Journal: Natural Science 35, 46-50.

Schenk, H.J., Callaway, R.M., Mahall, B., 1999. Spatial root segregation: are plants territorial? Advances in Ecological Research 28, 145-180.

Silvertown, J., 2004. Plant coexistence and the niche. Trends in Ecology & Evolution 19, 605-611.

Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J., 2004. Impact of nitrogen deposition on the species richness of grasslands. Science 303, 1876-1879.

Tainton, N.M., Bransby, D., Booysen, P.d.V., 1976. Common veld and pasture grasses of Natal. Shuter & Shooter.

Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2012. Do soil nutrients mediate competition between grasses and Acacia saplings? Grassland Science 58, 238-245.

Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation. The American Naturalist 116, 362-393.

Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist 125, 827-852.

Tilman, D., 1987. On the meaning of competition and the mechanisms of competitive superiority. Functional Ecology 1, 304-315.

Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58, 3-15.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2-16.

Tilman, D., Wedin, D., 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72, 1038-1049.

Tilman, G.D., 1984. Plant dominance along an experimental nutrient gradient. Ecology 65, 1445-1453.

Truong, P., Chomchalow, N., Vessabutr, S., 1999. Vetiver grass technology for mine rehabilitation. Pacific Rim Vetiver Network, Tech. Bull. No. 1999/2, PRVN / RDPB, Bangkok, Thailand.

Truong, P., Hart, B., Chomchalow, N., Sombatpanit, S., 2001. Vetiver system for wastewater treatment. Office of the Royal Development Projects Board.

Van Oudtshoorn, F.v., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza Publications.

Vieritz, A., Truong, P., Gardner, T., Smeal, C., 2003. Modelling Monto vetiver growth and nutrient uptake for effluent irrigation schemes. Proceedings of the Third International Conference on Vetiver and Exhibition, 254-264.

Vilà, M., Gómez, A., Maron, J.L., 2003. Are alien plants more competitive than their native conspecifics? A test using *Hypericum perforatum* L. Oecologia 137, 211-215.

Wagner, S., Truong, P., Vieritz, A., Smeal, C., 2003. Response of vetiver grass to extreme nitrogen and phosphorus supply. Proceedings of the Third International Conference on Vetiver and Exhibition, Guangzhou, China.

Wedin, D., Tilman, D., 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecological Monographs 63, 199-229.

Wilson, S.D., Tilman, D., 1993. Plant competition and resource availability in response to disturbance and fertilization. Ecology 74, 599-611.

Wilson, S.D., Tilman, D., 1995. Competitive responses of eight old-field plant species in four environments. Ecology 76, 1169-1180.

Xia, H., Ao, H., He, D., 1998. The effect of environmental factors on the growth of vetiver growth. Vetiver Research and Development 2, 39-44.

Xu, L., 1998. Vetiver research and development, proceedings of International Vetiver Workshop, Fuzhou, China. Agricultural Science and Technology Press of China, Beijing.

Xu, L., 2002. Vetiver research and development: A decade experience from China, Proceedings: The Second International Vetiver Conference, ORDPB, Bangkok, 311-322.

Zwerts, J., Prins, H., Bomhoff, D., Verhagen, I., Swart, J., de Boer, W., 2015. Competition between a Lawn-Forming *Cynodon dactylon* and a Tufted Grass Species *Hyparrhenia hirta* on a South-African Dystrophic Savanna. PloS one 10, 1-17.

5 CHAPTER 5: SYNTHESIS, IMPLICATIONS, AND RECOMMENDATIONS

Anthropogenic activities exact enormous pressure on the environment, mostly through agriculture, mining, and development (Tilman and Wedin, 1991; Xia, 2004). However, even though these practices are designed to be beneficial, they also have negative effects through pollution and reduction of natural resources (Wessels et al., 2007). For example, high stocking rates with unmanaged grazing could cause soil erosion (Boardman and Poesen, 2006; Morgan, 2009). The negative impacts of soil erosion on agricultural productivity (i.e. removal of arable, nutrient-rich topsoil), rivers and dams (i.e. sediment deposition), and hence, on the economy of the country, are well studied and known (Truong and Loch, 2004; Morgan, 2009). Similarly, intense use of fertilizers, increases in industrial emissions (atmospheric nitrogen depositions) (Clark and Tilman, 2008; Bobbink et al., 2010), and mining (acid mine drainage wastewater) results in soil and groundwater contamination through increasing soil nutrient status and acid mine drainage (low pH, high electric conductivity, and metal elements) (O'Rourke et al., 2016; Kiiskila et al., 2017). This, then affects/reduces floral, faunal and aquatic ecosystem health and function (O'Rourke et al., 2016). These are forms of environmental degradation and require human intervention to rehabilitate eroded and contaminated sites through the use of plants that are adapted to such extreme environmental conditions.

Vetiver grass is an exotic grass from India, which has proven to be a useful low cost, sustainable tool in rehabilitation (Adams et al., 2004; Chahal et al., 2015). Its extensive root systems and hard tufts allow it to withstand environmental hazards such as floods, droughts, and fires (Council, 1993; Chiu et al., 2006). Moreover, these features allow it to bind soil particles together and protect the soil by providing ground cover; hence, its use in soil and water conservation (Dalton et al., 1996). In addition, this grass is extremely adapted to low pH, nutrient rich soils, and can absorb acid mine drainage, hence its use in phytoremediation (Chiu et al., 2006; Kiiskila et al., 2017). For example, Kiiskila et al. (2017) showed that vetiver grass grew well in acid mine drainage wastewater and changed the pH from 2.50 to 4.35 within 30 days. Furthermore, vetiver reduced the electrical conductivity of the water from 3250 to 1750 microsecond (µS), Sulfate ion concentration (SO_4^{2-}) from 2750 to 1500 milligram/liter (mg SO_4^{2-} L^{-1}), and all metal elements by about 50% with 30 days (Kiiskila et al., 2017). This is a clear indication of the potential of vetiver grass in restoring soil and water health.

There is no doubt that vetiver is useful for environmental protection and rehabilitation. However, this study had a different approach, as it investigated the competitive ability of vetiver and how it behaves in areas where it has been used; whether it allows seed germination and seedling establishment of native grasses, as well as its competitive effect on mature native grass tufts on both high and low nutrient soils. This was with a broad aim to understand whether vetiver can coexist with native grasses or even be succeeded by native grasses, and therefore, predict the potential of vetiver to become invasive. This study showed that vetiver does show some signs of recruitment in areas where it was not originally planted, and that species richness increases with increasing distance away from planted vetiver in areas rehabilitated using vetiver. Moreover, while vetiver does facilitate seed germination it negatively affects seedling establishment. Vetiver is a very competitive grass, mostly in nutrient rich soils, but native species with similar traits (broad-leaved, robust root system, and sometimes stoloniferous or with rhizomes) experience less competitive suppression than species with dissimilar traits (narrow-leaved, fine roots, and no stolons or rhizomes). Species coexistence, therefore, is related to species traits and so can be understood through understanding species quantitative trade-offs that link to their resource utilization.

The most basic trade-off that is well researched is that a strong competitor species (investing more resources into competitive traits) usually has limited seed production, poor seed germination, and poor seed dispersal (Tilman, 1980, 1990, 1994). This is true with vetiver, as this study shows that vetiver is a strong competitor but shows limited signs of spreading, possibly because seeds are suggested to be non-viable (Council, 1993). It also reproduces vegetatively by means of tillers, which is a slower process (Greenfield, 2002). Such trade-offs, according to Tilman, can allow other species with contrasting seed related traits to coexist with it (Tilman, 1980, 1985, 1990). This means that vetiver should be able to coexist with native species which produce an abundant number of seeds with a high germination rate and effective dispersal. One can thus argue that *E. curvula* can coexist with vetiver but not in close proximity, as vetiver seems to be territorial as evidenced by having bare ground around it. However, in this study, *E. curvula* and *H. hirta* which are narrow-leaved species were mostly supressed by the vetiver competitive effect.

This study showed that species with similar morphological traits to vetiver grass but with greater seed production, germination success, and seed dispersal can potentially coexist with vetiver even in close proximity e.g. *Digiteria eriantha* and *P. maximum*. However, it is highly unlikely that these species will succeed or outcompete vetiver, even though they are able to withstand vetiver competitive effect. *Digiteria eriantha* has a strong competitive ability with high seed production and germination rates (Meredith, 1955). The combination of these traits could allow greater coexistence between vetiver and *D. eriantha*, mostly because vetiver increases the germination rate of native grasses around it, but affects seedling survival and so limits native species recruitment. There is a better chance that seedlings of *D. eriantha* can survive the competitive effect and/or the allelopathic effect exacted by vetiver oil because mature tufts benefited from growing with vetiver grass. Such coexistence can reduce the vegetative spreading of vetiver grass through competing directly with vetiver and making sure that it serves only its intended purpose of stabilizing and conserving the soil, thus reducing soil erosion.

It should be noted that because few species seem to have potential to coexist with vetiver grass, diversity in areas rehabilitated using vetiver should be expected to be low, thus also low grassland productivity. Vetiver, as our knowledge stands, lives longer than other grass species, and seems to stay as a permanent feature, which is beneficial for prevention of soil erosion through providing aboveground cover and binding the soils, but not for promoting species diversity and rangeland productivity (Grimshaw, 1993; Dalton et al., 1996; Huston, 2004). Broad-leaved native species with strong competitive ability, shade tolerance, and the potential for reducing soil erosion should be the target species for reseeding or vegetative planting in areas rehabilitated using vetiver. Management approaches that aim to remove or suppress vetiver after it has served its purpose should be developed so that these rehabilitating rangelands can regain a relatively good species diversity and increase grassland productivity. Development of a management protocol for vetiver grass is important for two reasons: 1) vetiver's grass is not a preferred grass by grazers and its leaves hardens as it matures thus reducing its palatability and digestibility (Grimshaw, 1993). In areas with unmanaged grazing and/or selective grazing, selection for native grasses could allow the dominance and even the invasion of vetiver as native grasses will allocate more resources to regrowth than to competing with vetiver (Tainton, 1999). This is evidenced in the second chapter, where an area having unmanaged continuous grazing had signs of vetiver recruiting where it was not originally planted. 2) Vetiver growth behavior allows it to stay green all year round, which in turn reduces the available fuel load, and hence fire intensity and frequency (Gnansounou et al., 2017). In fire climax grasslands, this can alter fire regimes, which might allow woody plant encroachment in areas where encroachment is managed through fire and might drive fire-adapted species to local extinction (Bond et al., 2003; Hoffmann and Solbrig, 2003). Furthermore, an expected increase in atmospheric nitrogen deposition is likely to favour vetiver grass through increasing its competitive ability; hence, the need for development of a management protocol that will take such effects into account is needed.

Although the method used to answer questioned asked in this study were mostly of a short spatial and temporal scale, but the study acts as a first step toward understanding vetiver ecology and use in grasslands rehabilitation. This study recommends that vetiver should continue to be used for the following environmental and agricultural purposes.

- For soil and water conservation but not for maintaining and promoting species diversity.
- In heavy degraded/eroded sites (e.g. gully erosion) where soil cover is more important than species diversity.
- In agriculture (planted in contours) for avoiding soil erosion, maintaining soil health, and for use as an insect pest trap. Vetiver attracts herbivorous insect pests away from the main agricultural crops.
- For phytoremediation in dams, rivers, and contaminated lands, where native grasses cannot grow. In dams and rivers, it should be used as a floating wetland treatment system (removable floating islands). However, in abandoned mine sites and landfill sites, proper management that will allow reseeding and establishment of native species after vetiver has restored the soil health should be formulated.

There is no argument against the usefulness and potential of vetiver in soil and water conservation, although research should redirect its focus to management questions and improving the spatial and temporal scale of this current study. These are the questions/areas that still need addressing:

- Separating the effect of shade, root interaction, and allelopathy. This work would follow on from the work outlined in chapter 3, to give a clear indication of whether it is allelopathy, root competition, shade or all these factors combined that inhibit native grass seedling survival and growth. It would be good also to increase the number of native species, from two to at least four (possibly two broad-leaved and two fine-leaved species) to strengthen the recommendations and conclusions of this study.
- Study the competitive effect exerted by the broad-leaved and fine-leaved native grasses on vetiver grass under low and high soil nutrient conditions, to understand whether some native grasses can suppress vetiver grass. This is because it could be that competition is symmetrical, rather than asymmetrical. This would involve a reverse of the study in chapter 4.
- There are limited studies and only anecdotal evidence on vetiver grass's response to disturbance such as fire, frost, and grazing. Future studies, therefore, should also try to address these gaps, through studying vetiver's response to the effect of these disturbance factors. An example of a question that still needs addressing is, can vetiver alter fire behaviour when planted in fire climax grasslands as it stays green even during the dormant season?
- Grazing also is dependent upon species palatability and digestibility among other factors; however, it is not fully known whether vetiver is digestible and palatable enough to be eaten by livestock and wild grazers. If it is, at what growth stage is it most palatable and digestible? Future studies should also try to answer these questions.
- The results presented in this thesis are mostly from pot trials. While pot trials are useful mostly for the manipulation of species responses, these pots have limited space and that could over-emphasize competition between these species. Therefore, studies should consider conducting a field experiment which aims to validate the results obtained in this study.
- Furthermore, studies should also combine all information known about vetiver and try to develop a practical guide that points out ways that will guarantee that vetiver is succeeded/suppressed by native grasses. For example, combining possible disturbances

that might be useful to suppress vetiver and allow secondary succession of native grasses. Also, outline if any specific planting or sowing method can encourage species coexistence. The list of possible species that may be useful for competing directly with vetiver or coexist well with vetiver, possibly broad-leaved species, could also be developed.

5.1 REFERENCES

Adams, R.P., Habte, M., Park, S., Dafforn, M.R., 2004. Preliminary comparison of vetiver root essential oils from cleansed (bacteria-and fungus-free) versus non-cleansed (normal) vetiver plants. Biochemical Systematics and Ecology 32, 1137-1144.

Boardman, J., Poesen, J., 2006. Soil erosion in Europe: major processes, causes and consequences. Soil erosion in Europe, 477-487.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological applications 20, 30-59.

Bond, W., Midgley, G., Woodward, F., Hoffman, M., Cowling, R., 2003. What controls South African vegetation—climate or fire? South African Journal of Botany 69, 79-91.

Chahal, K.K., Kaushal, S., Sandhu, A.K., 2015. Chemical composition and biological properties of *Chrysopogon zizanioides* (L.) Roberty syn. *Vetiveria zizanioides* (L.) Nash-A Review. Indian Journal of Natural Products and Resources [Formerly as Natural Product Radiance] 6, 251-260.

Chiu, K., Ye, Z., Wong, M., 2006. Growth of *Vetiveria zizanioides* and *Phragmities australis* on Pb/Zn and Cu mine tailings amended with manure compost and sewage sludge: a greenhouse study. Bioresource Technology 97, 158-170.

Clark, C.M., Tilman, D., 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. Nature 451, 712-715.

Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

Dalton, P., Smith, R., Truong, P., 1996. Vetiver grass hedges for erosion control on a cropped flood plain: hedge hydraulics. Agricultural Water Management 31, 91-104.

Gnansounou, E., Alves, C.M., Raman, J.K., 2017. Multiple applications of vetiver grass–A review. International Journal of Environmental. Sciences 2, 125-141.

Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth. Infinity Publishing.

Grimshaw, R.G., 1993. The role of vetiver grass in sustaining agricultural productivity. Asia Technical Department. The World Bank, Washington DC USA.

Hoffmann, W.A., Solbrig, O.T., 2003. The role of topkill in the differential response of savanna woody species to fire. Forest Ecology and Management 180, 273-286.

Huston, M.A., 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Diversity and Distributions 10, 167-178.

Kiiskila, J.D., Sarkar, D., Feuerstein, K.A., Datta, R., 2017. A preliminary study to design a floating treatment wetland for remediating acid mine drainage-impacted water using vetiver grass (*Chrysopogon zizanioides*). Environmental Science and Pollution Research 24, 27985-27993.

Meredith, D., 1955. The grasses and pastures of South Africa.

Morgan, R.P.C., 2009. Soil erosion and conservation. John Wiley & Sons.

O’Rourke, S., Minasny, B., Holden, N., McBratney, A., 2016. Synergistic use of Vis-NIR, MIR, and XRF spectroscopy for the determination of soil geochemistry. Soil Science Society of America Journal 80, 888-899.

Tainton, N.M., 1999. Veld Management in South Africa. University of Natal press.

Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation. The American Naturalist 116, 362-393.

Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist 125, 827-852.

Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58, 3-15.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2-16.

Tilman, D., Wedin, D., 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72, 1038-1049.

Truong, P., Loch, R., 2004. Vetiver system for erosion and sediment control. Proceeding of 13th international soil conservation organization conference, 1-6.

Wessels, K., Prince, S., Malherbe, J., Small, J., Frost, P., VanZyl, D., 2007. Can human-induced land degradation be distinguished from the effects of rainfall variability? A case study in South Africa. Journal of Arid Environments 68, 271-297.

Xia, H., 2004. Ecological rehabilitation and phytoremediation with four grasses in oil shale mined land. Chemosphere 54, 345-353.

6 APPENDICES

6.1 APPENDIX A: Study species

The native grasses listed here are used for soil stabilization, grassland restoration, and could be a better option for integration with vetiver; however they differ in their competitive ability, and whether they can coexist with vetiver is still an answered question. Descriptions, distribution, ecology and uses of these grasses are further discussed to give an elucidated background and reason for their use in this study.

1. Strong competitors

1.1 *Eragrostis curvula*

1.1.1 Description

Eragrostis curvula (Schrad.) Nees., commonly known as a Weeping love grass, is a robust densely tufted perennial native grass. It has many lax and drooping leaves (Fish et al., 2015). The inflorescence differs with ecotypes but most have an open branched panicle. However, some ecotypes found in the Eastern, Western and Northern Cape, sometimes have a contracted panicle (Tainton et al., 1976; Van Oudtshoorn, 1999). Therefore, *E. curvula* is a variable grass with many localized ecotypes which differ in height, inflorescence structure, leaf structure and productivity (Van Oudtshoorn, 2012). The leaves (up to 60cm long, and 10mm wide) are usually concentrated from the base of the plant but are not curled (Van Oudtshoorn, 2012). The stem height ranges from 60cm to 120cm or sometimes more depending on the environment and the soil fertility (Tainton et al., 1976). Roots are fine, dense, and fibrous allowing the grass to be effective in soil resource capture (Meredith, 1955).

1.1.2 Distribution

It originates in southern and eastern Africa but is now widely spread in other countries as a weed or fodder crop (Van Oudtshoorn, 2012; Fish et al., 2015). *Eragrostis curvula* covers a vast area of South Africa occurring in parts of the Nama-karroo, grassland, savanna, and forest biomes (Tainton et al., 1976; Van Oudtshoorn, 2012). It is widely spread in disturbed sites and badly managed veld. It prefers areas with high rainfall (above 600mm, mostly in overgrazed areas) and well-drained soils but will grow in low rainfall areas and on sandy and acidic soils (Tainton et al., 1976).

1.1.3 Ecology and uses

Eragrostis curvula produces abundant high-quality seeds which germinate easily, hence allowing it to spread (Fynn and Naiken, 2009). It flowers in the growing season between August and June, and usually stays green until mid-winter (Van Oudtshoorn, 2012). Weeping lovegrass has an extensive root system which grows both downward (down to 5m) and horizontally (stretching 1m), hence making it drought tolerant through efficient use of light rain and allowing it to prevent other plants from establishing.

This grass is a strong competitor which is moderately shade tolerant and adapted to heavy grazing (Mynhardt et al., 1994; Fynn and Naiken, 2009). For example, Mynhardt et al. (1994) investigated the competitive ability (both intra- and inter-specific) of *E. curvula* and *Anthephora pubescens* using biomass allocation and yield. Relative yield and biomass allocation showed that *E. curvula* could outcompete *A. pubescens* because it is a strong interspecific competitor but showed no significant differences in intraspecific competition, while *A. pubescens* was a weak competitor for both intra- and inter-specific competition (Mynhardt et al., 1994). Leaf and root extracts of *E. curvula* have been shown to have allelopathic properties that inhibit germination and growth of other species (Ghebrehiwot et al., 2014). For this reason, it had become invasive in some countries such as Australia (Firn et al., 2010).

Nitrogen addition has been shown to increase both biomass and tussock diameter of many grasses, but not all grasses are limited by nitrogen. For example, Fynn and Naiken (2009) evaluated the response of *Eragrostis curvula* and *Themeda triandra* to different levels of nitrogen addition. They showed that these species increased their biomass with an increase in nitrogen availability (Fynn and Naiken, 2009). However, *T triandra* grew to its full potential at intermediate nitrogen availability, while *E. curvula* continued growing, increasing its biomass even at high nitrogen availability (Fynn and Naiken, 2009). Furthermore, *E. curvula* competed well under both high and low soil nutrient levels because of its root structure and ability to increase biomass production in both high and low nutrient soils.

Eragrostis curvula is a relatively variable grass with a moderate grazing value but is planted as a pasture grass in South Africa and Africa at large. This is because it establishes easily even in poor environmental conditions, has high leaf production and produce high-quality seeds (Mynhardt et al., 1994; Fynn and Naiken, 2009). Furthermore, because of these abilities and the extensive root system, *E. curvula* has been used for soil erosion control, rehabilitation and stabilizing highway embankments (Van Oudtshoorn, 1999, 2012).

1.2 *Digitaria eriantha*

1.2.1 Description

Digitaria eriantha Steud., was previously classified as a number of different species e.g *D. umfolozi*, *D. decumbens*, *D. pentzii*, *D. setivalva*, *D. smutsii*, *D. valida* (Van Oudtshoorn, 1999, 2012; Fish et al., 2015). The combining of these species has made *D. eriantha* a very variable species, with some having a stolon and a branched culm, a stolon and unbranched culm, and others without both the stolon and branched culm (Tainton et al., 1976). In general, *D. eriantha* is known as "common finger grass", and is a broad-leaved robust tufted perennial grass with digitate or semi-digitate inflorescences, with a very long, thin raceme (4-20cm long, fingers) (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012). The spikelets are found on opposite sides of the main branch of the raceme (Van Oudtshoorn, 2012). The lowermost part of the leaf sheath is densely hairy but the leaves are usually not hairy (Tainton et al., 1976). The culms of this grass range in height from 40cm to over 1.8 m (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012). It has a robust, sometimes stoloniferous root systems making the grass more competitive belowground (Meredith, 1955; Tainton, 1981b).

1.2.2 Distribution

Known to be native only in southern Africa (including Angola and Zambia) (Fish et al., 2015), this grass; however, has been introduced in many countries for different agricultural reasons (McDonald et al., 1998; Van Oudtshoorn, 1999, 2012). *D. eriantha* is occurs in most of South Africa in sandy and gravelly soils in arid regions, but also in well-drained, damp soils near wetlands in wetter regions of the country. It is often seen along roadsides, stream banks in tall grasslands, and in grasslands near forest margins (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012).

1.2.3 Ecology and uses

In wet areas, common finger grass flowers almost throughout the growing season, but most ecotypes flower from January to late April or May (Van Oudtshoorn, 2012). The stoloniferous varieties can regenerate using both the stolon and seeds, even though they produce little or no seeds when growing in unfertile lands (McDonald, 1998; Tainton et al., 1976).

It is a strong competitor which has the ability to resist invasion by other grasses, mostly in high nutrient soils (McDonald, 1998). The stoloniferous varieties spread quickly in disturbed areas, and invade easily to nearby veld; however, *D. eriantha* is considered to grow well with other species. McDonald (1998) showed that *D. eriantha* has invaded grasslands with both low and high soil fertility, which was previously dominated by *Heteropogon contortus* and *Macroptilium atropurpureum* cv. Siratro in Australia. He furthermore suggested that common finger grass invades fertile soils and has proven to be more competitive on such soils; however, it has changed the vegetation structure of both these grasslands (low fertility and high fertility) ever since it was sown as pasture in 1979 and 1980 respectively (McDonald, 1998).

Common finger grass is favoured by large herbivores because it is highly digestible, palatable, and has high leaf production (McDonald et al., 1998; Van Oudtshoorn, 1999, 2012). In most African countries and other countries outside Africa, *D. eriantha* is used as a fodder grass and is considered as the most reliable grass as an animal feed. It is a decreaser grass, hence, dominates in good veld but decreases in abundance in overgrazed or undergrazed veld (Van Oudtshoorn, 1999, 2012). For this reason, *D. eriantha* has been used for veld improvement mostly through seeding (Ramírez and Hacker, 1996). Furthermore, because it is a variable grass with a stoloniferous variety and produces a dense root system, it has been used for soil erosion control, rehabilitation and stabilization of highway embankments (Van Oudtshoorn, 1999, 2012).

2. Weak competitors

2.1 *Panicum maximum*

2.1.1 Description

Panicum maximum Jacq., commonly known as guinea grass or white buffalo grass, is a broad-leaved tufted perennial grass with a large open panicle inflorescence (Van Oudtshoorn, 1999, 2012). The inflorescence usually has lax branches, while the lower branches are arranged in a whorl (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012). The spikelets are purple in colour when it grows in direct sunlight, but green when growing under shade (Van Oudtshoorn, 2012; Fish et al., 2015). This grass has many leaves and its leaf sheath is usually hairy but varies with different ecotypes. The height of this grass also varies with different ecotypes but ranges from 60cm to 300cm when environmental conditions are conducive and begins to form a reed like appearance (Tainton et al., 1976). The roots grow from the lower nodes and it often has short creeping rhizomes.

2.1.2 Distribution

Although originating in Africa, this grass has spread to all tropical regions of the world (Tainton et al., 1976; Fish et al., 2015). In South Africa, guinea grass is distributed along the eastern and northern parts in the grassland, savanna and Nama-karroo biomes. It prefers cool, shady, damp areas with well-drained, fertile soils, such as river margins, low-lying coastal areas and is usually found growing under shrubs and trees in open woodland regions (Tainton et al., 1976; Van Oudtshoorn, 1999; Tainton, 1999; Van Oudtshoorn, 2012).

2.1.3 Ecology and use

Even though this grass has a short creeping rhizome, it relies more on seeds for reproduction. It flowers in the growing season (September to March) and stays green until late winter. Like most grasses, it is pollinated by wind and seeds are sometimes eaten by birds (Tainton et al., 1976; Van Oudtshoorn, 1999; Tainton, 1999; Van Oudtshoorn, 2012). However, there are many different localized ecotypes of this grass in South Africa, which is why this grass is so variable.

Panicum maximum has been shown to be variable even in terms of it competitive ability. In general, this grass competes well in nutrient-rich soil, suggested to be influenced by Nitrogen (N) and Potassium (P) levels, while on nutrient-poor soils it is outcompeted by other grass species (Van Oudtshoorn, 2012; Tedder et al., 2012). For example, Fynn et al. (2005) showed that *P. maximum* outcompeted *H. hirta* in areas with high N and P; however, the reverse happened in areas with low N and P. In Hawaii, *P. maximum* was naturalized in 1871 and is now considered an invasive species. Ammondt and Litton (2012), using a pot trial, investigated competitive response of *P. maximum* when growing with the Hawaiian native species, *Myoporum sandwicense*, *Dodonaea viscosa*, and *Plumbago zeylanica* (Ammondt and Litton, 2012). The reproductive tillers and biomass (above- and belowground) of *P. maximum* was reduced when growing with one or a combination of these species (Ammondt and Litton, 2012).

This suggests that *P. maximum* can be outcompeted by these species and that it is a weak competitor against these grasses and woody plant species when nutrient availability is not taken into account. Therefore, the fluctuation in its competitiveness means that *P. maximum* is a weak competitor when competing with other grasses, and the increased performance under nutrient-rich soils could be a strategy to avoid competitive exclusion.

It is a very good grazing grass due to high leaf production and high palatability, used as a pasture grass all over Africa. Furthermore, *P. maximum* establishes quickly and has dense roots with a creeping rhizome. For this reason, *P. maximum* has is used for rehabilitation and soil protection (Van Oudtshoorn, 2012).

2.2 *Hyparrhenia hirta* Stapf

2.2.1 Descriptions

Hyparrhenia hirta Stapf. of the many species in the *Hyparrhenia* genus, is recognizable by its pairs of white villous racemes which do not bend downward, growing on a stem with narrow rough leaves and a hard basal tussock (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012). Commonly known as thatching grass, *H. hirta* is a relatively dense erect, tufted perennial grass (Van Oudtshoorn, 2012). The racemes on its spikelets have four to seven brownish awns. Culm height varies greatly and is affected by rainfall availability (Van Oudtshoorn, 1999, 2012; Fish et al., 2015). This grass is relatively tall, but its height varies from 30cm in shallow nutrient-poor soils to over 100 cm in well-drained, nutrient-rich soils. It has many tillers forming nodded stems and has a dense fibrous root system (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012).

2.2.2 Distribution

It is a dominant grass in South Africa, occurring in all provinces (Van Oudtshoorn, 1999, 2012; Fish et al., 2015). It also occurs throughout the African continent, the Mediterranean regions, and Pakistan. In some countries outside of Africa it has been considered an invasive weed (e.g. Australia) (Van Oudtshoorn, 1999, 2012; Zwerts et al., 2015). It is found in many biomes in South Africa, from mid to low altitude areas in fynbos, Nama-karroo, savanna, and grasslands. It prefers well-drained soils, particularly gravelly soil, but can also be found in shallow soils. It dominates in open grassland on rocky slopes, along river margins and roadsides, and in disturbed areas, especially old cultivated sites (Van Oudtshoorn, 1999, 2012; Zwerts et al., 2015).

2.2.3 Ecology and uses

Thatching grass spreads through tillering but also depends on seeds for reproduction, flowering between September and June. It behaves differently in different environments. For example, in terms of competitive ability, *H. hirta* competes well on nutrient-poor soils but not on nutrient-rich soils. Fynn et al. (2005) showed that there is a trade-off between *H. hirta* and *P. maximum* in terms of their competitive ability along a fertility gradient, with *H. hirta* outcompeting *P. maximum* on nutrient-poor soils, and the opposite happening on nutrient-rich soils. Furthermore, Fynn et al. (2009) showed that this grass is highly invasive. However, it has a weak competitive response (ability to resist being invaded) (Chejara et al., 2010; Zwerts et al., 2015). For example, Zwerts et al. (2015) showed that regardless of whether nutrient availability was high or low, *H. hirta* was outcompeted by *Cynodon dactylon*, mostly when there was simulated herbivory (clipping). Therefore, the previously documented invasion potential and good performance of *H. hirta* under nutrient-poor conditions does not justify it as a strong competitor, rather it shows that competitive ability of this species is species specific and nutrient specific.

H. hirta has been considered problematic in some countries through being invasive. It is not a good grazing grass because of high fibre content and low palatability (Chejara et al., 2010; Zwerts et al., 2015). It is only grazed when young, early in the growing season but decreases in palatability as it matures. It is commonly used as a thatching grass, and for making mats and baskets. Furthermore, because this grass is a fast growing plant, has dense roots and ability to invade disturbed nutrients poor soils, it has been used for rehabilitation purposes and soil protection (slope stabilization) (Van Oudtshoorn, 1999, 2012; Zwerts et al., 2015).

3. REFERENCES

Ammondt, S.A., Litton, C.M., 2012. Competition between native Hawaiian plants and the invasive grass *Megathyrsus maximus*: implications of functional diversity for ecological restoration. Restoration Ecology 20, 638-646.

Chejara, V., Kriticos, D., Kristiansen, P., Sindel, B., Whalley, R., Nadolny, C., 2010. The current and future potential geographical distribution of *Hyparrhenia hirta*. Weed Research 50, 174-184.

Firn, J., MacDougall, A.S., Schmidt, S., Buckley, Y.M., 2010. Early emergence and resource availability can competitively favour natives over a functionally similar invader. Oecologia 163, 775-784.

Fish, L., Mashau, A. C., Moeaha, M. J., Nembudani, M.T., 2015. Identification guide to southern African grasses. An identification manual with keys, descriptions and distributions. Strelitzia 36. South African National Biodiversity Institute, South Africa.

Fynn, R., Morris, C., Kirkman, K., 2005. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. Journal of Ecology 93, 384-394.

Fynn, R., Naiken, J., 2009. Different responses of *Eragrostis curvula* and *Themeda triandra* to rapid-and slow-release fertilisers: insights into their ecology and implications for fertiliser selection in pot experiments. African Journal of Range and Forage Science 26, 43-46.

Ghebrehiwot, H.M., Aremu, A.O., Van Staden, J., 2014. Evaluation of the allelopathic potential of five South African mesic grassland species. Plant Growth Regulation 72, 155-162.

McDonald, C.J., RM; Tothill, JC, 1998. Growth and spread of *Digitaria eriantha* cv. Premier and *Urochloa mosambicensis* cv. Nixon oversown into native speargrass (*Heteropogon contortus*) pasture in south-east Queensland. Tropical Grasslands 32, 41-49.

Meredith, D., 1955. The grasses and pastures of South Africa.

Mynhardt, J.E., Van Rooyen, M., Theron, G., 1994. Competitive ability of two grass species: *Anthephora pubescens* and *Eragrostis curvula*. 1. Yield and biomass allocation. South African Journal of Botany 60, 261-268.

Ramírez, L., Hacker, J., 1996. Effect of time of tiller emergence and nitrogen fertiliser on seed yield components of *Digitaria eriantha* cv. Premier. Australian Journal of Experimental Agriculture 36, 189-195.

Tainton, N.M., 1981b. Veld and pasture management in South Africa. Shuter & Shooter; University of Natal Press.

Tainton, N.M., 1999. Veld Management in South Africa. University of Natal press.

Tainton, N.M., Bransby, D., Booysen, P.d.V., 1976. Common veld and pasture grasses of Natal. Shuter & Shooter.

Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2012. Do soil nutrients mediate competition between grasses and Acacia saplings? Grassland Science 58, 238-245.

Van Oudtshoorn, F.v., 1999. Guide to grasses of Southern Africa. Briza Publications.

Van Oudtshoorn, F.v., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza Publications.

Zwerts, J., Prins, H., Bomhoff, D., Verhagen, I., Swart, J., de Boer, W., 2015. Competition between a lawn-forming *Cynodon dactylon* and a tufted grass species *Hyparrhenia hirta* on a South-African dystrophic savanna. PloS one 10,1-17.

6.2 APPENDIX 2.1: Grass species and sedge abbreviations used in the CA ordination plot.

Species names	Acronym
Aristida bipartita	*ARIBIP*
Aristida congesta	*ARICON*
Chloris gayana	*CHLGAY*
Cymbopogon caesius	*CYMCAE*
Eragrostis curvula	*ERACUR*
Eragrostis plana	*ERAPLA*
Hyparrhenia hirta	*HYPHIR*
Paspalum notatum	*PASNOT*
Sporobolus africanus	*SPOAFR*
vetiver grass recruit	*VETREC*
Melinis nerviglumis	*MELNER*
Bare soil	*SOIL*
Sedge	*SEDGE*

6.3 APPENDIX 4.1. Sumplimentaly growth traits results for chapter 3; effect of vetiver competition and soil nutrients on native grasses

Table 1**:** Result of the MANOVA showing the effect of vetiver competition level (one and two tufts), nutrient level (low and high), and their interaction on leaf table height (cm), Basal circumference (cm), and number of tillers of four native grass species (*Digitaria eriantha*, *Eragrostis curvula, Hyparrhenia hirta* and *Panicum maximum*). Significant p-values ($p < 0.05$) are in bold

Source of variation	Leaf table height			Basal circumference			Number of tillers		
	df	*F*	*P*	df	*F*	*P*	DF	*F*	*P*
Species (S)	3	17.871	**<0.0001**	1	5.344	**0.02**	1	32.689	**<0.0001**
Competition Level (C)	2	1.693	0.188	2	20.095	**<0.0001**	2	16.035	**<0.0001**
Nutrient Level (N)	1	66.295	**<0.0001**	1	59.266	**<0.0001**	1	254.45	**<0.0001**
S*C	6	2.902	**0.011**	6	1.356	0.238	6	5.805	**<0.0001**
S*N	3	2.504	0.063	3	1.550	0.205	3	5.141	**0.002**
C*N	2	1.128	0.327	2	1.179	0.311	2	1.653	0.196
S*C*N	6	2.191	0.058	6	1.667	0.135	6	0.548	0.771

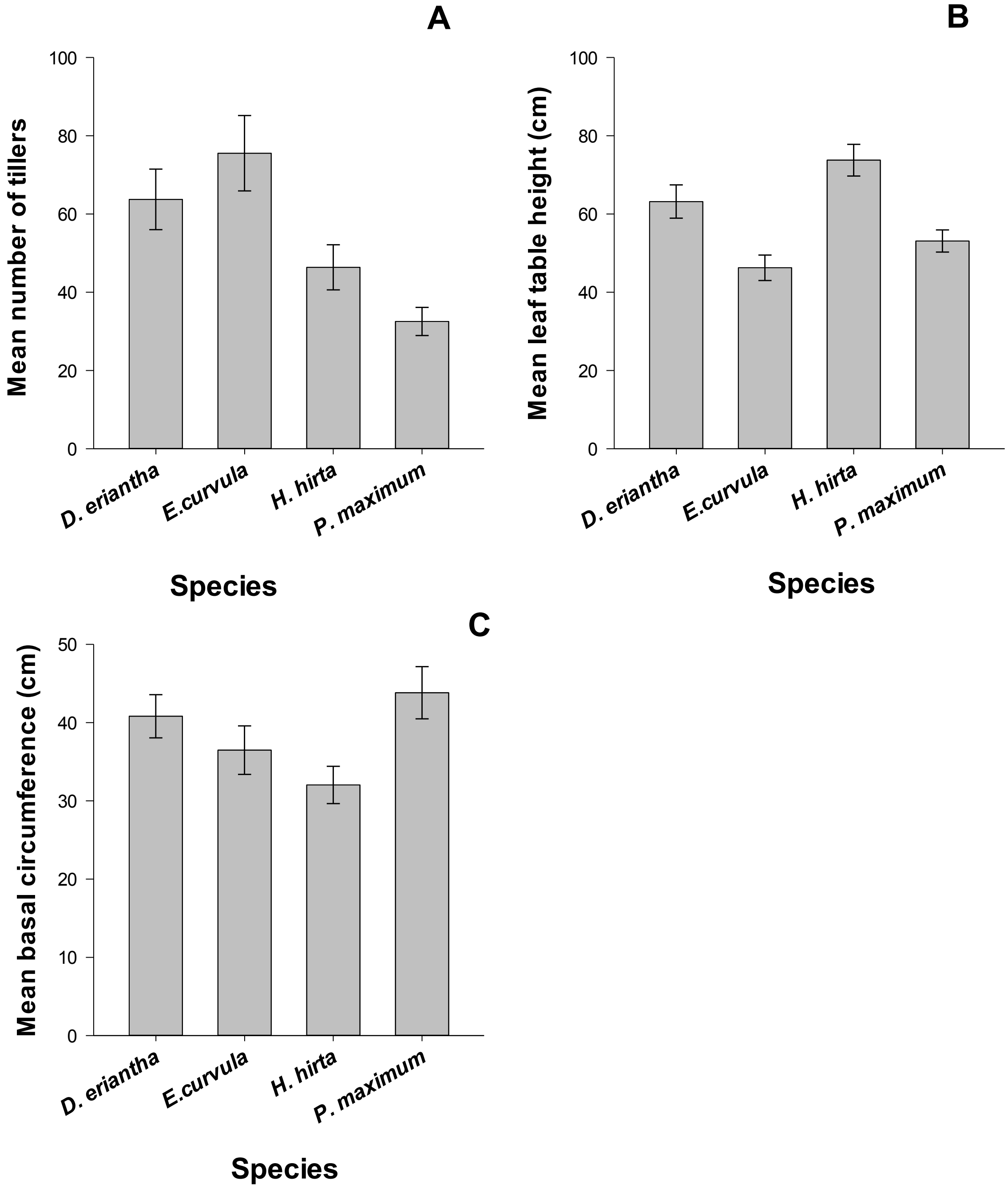

Figure 1: Main effect of vetiver competition on the mean (± SE) number of tillers (A), mean (±SE) leaf table height (B), and Mean (± SE) basal circumference (C) of four native species.

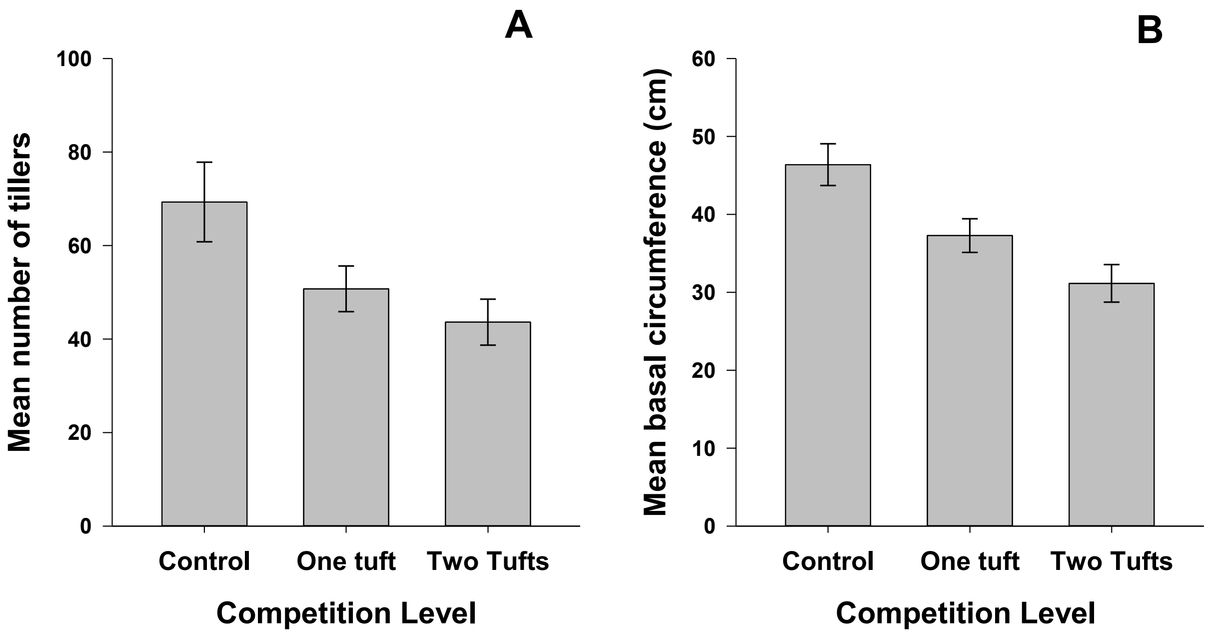

Figure 2**:** Main effect of vetiver competition level on the mean (± SE) number of tillers (A), and Mean (± SE) basal circumference (C) of four native species.

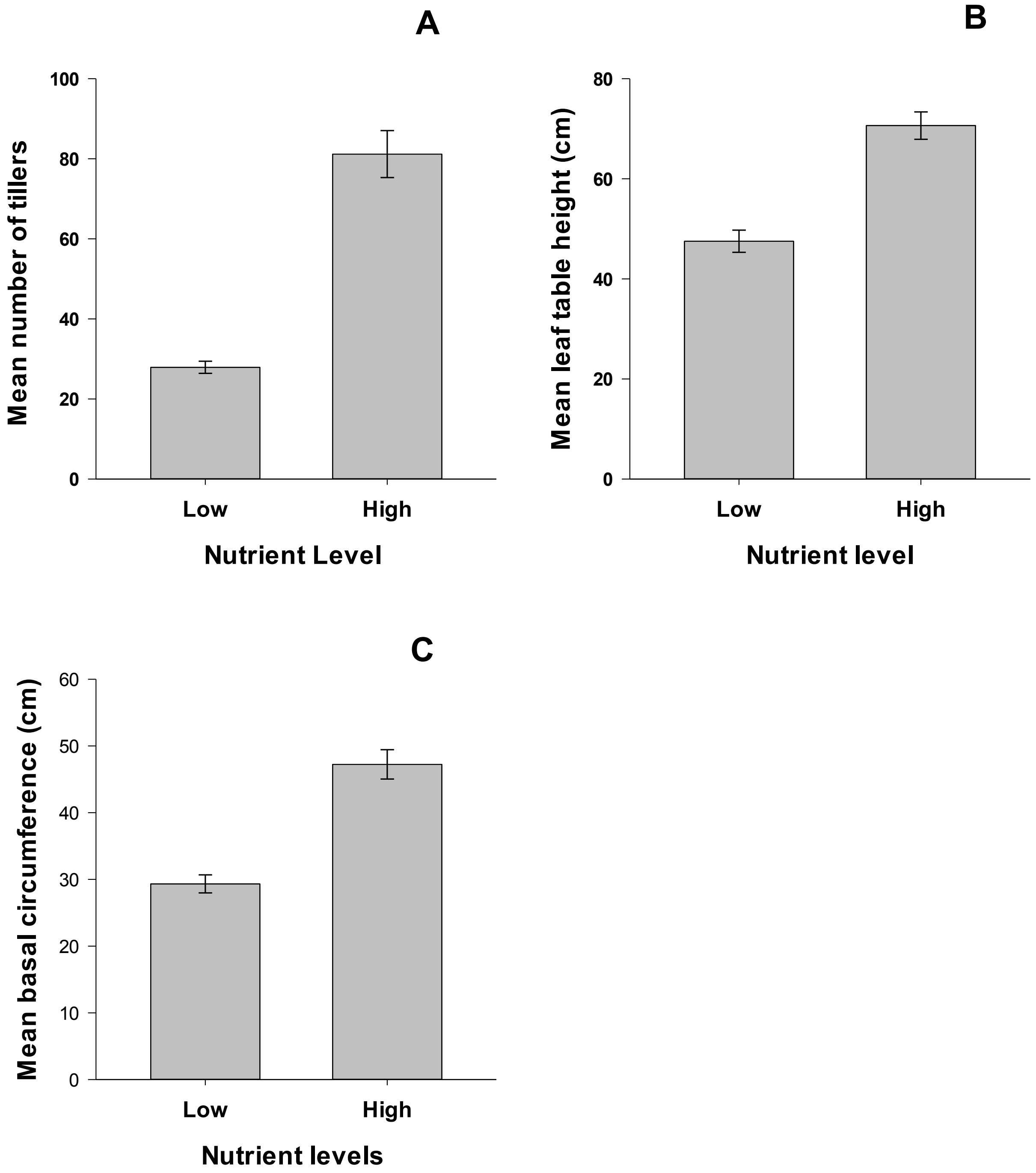

Figure 3: Main effect of nutrient level on the mean mean (± SE) number of tillers **(A),** mean (±SE) leaf table height **(B),** and Mean (± SE) basal circumference **(C)** of combined native gasses species.