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

By

LINDOKUHLE XOLANI DLAMINI

Submitted in fulfilment of the academic requirements for the degree of

MASTER OF SCIENCE

In the Discipline of Grassland Science

School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg

South Africa

MAY 2018
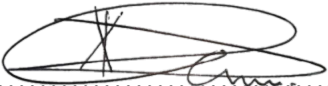
PREFACE

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.

Signed ……………………….. Date ……10../..08../.2018

Lindokuhle Xolani Dlamini

Signed ………………………. Date ……/……/……

Dr. Michelle J Tedder (Supervisor)

Signed ………………………. Date ……/……/……

 Prof. Kevin P Kirkman (Co-supervisor)

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;

(iv) This dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

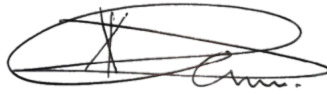a) Their words have been re-written but the general information attributed to them has been referenced;

b) Where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(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;

(vii) This dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

_____

Signed: Lindokuhle Xolani Dlamini

Date: 25 May 2018

76   **ABSTRACT**

77   Vetiver grass *(Chrysopogon zizanioides)* is a perennial C_4 grass that originates from central

78   India. This grass is used worldwide for soil (e.g. erosion control) and water conservation (e.g.

79   wetland and river rehabilitation) because it is a fast-growing tufted grass with a dense root

80   system that reaches 3 meters deep forming a wall-like structure that binds soil particles. Vetiver

81   is a very hardy grass, allowing it to withstand environmental hazards such as drought, frost, and

82   floods. The most commonly used cultivars produce infertile seeds or even no seeds, hence it

83   reproduces vegetatively. To date, no study has investigated the competitive ability of vetiver,

84   factors influencing its competitive ability, whether it inhibits germination and establishment of

85   native grasses, and its role in secondary succession of native grasses. The predicted global

86   increase in atmospheric nitrogen deposition and excessive use of agricultural fertilizers will

87   result in changes in soil nutrient status, hence altering the plant competitive trade-offs that drive

88   species coexistence. Introduced plants, for example, are often more adapted to environmental

89   changes and this may lead to invasion through competition with native plants. This study had

90   three aims; 1) to examine the behaviour of vetiver and its association with native grasses in the

91   field; 2) to investigate the effect of established vetiver tufts on native grasses (*E. curvula* and *P.*

92   *maximum*) seed germination and seedling establishment. Within this aim, the effect of different

93   sowing method on seed germination and establishment, and the effect of vetiver tufts when root

94   competition is excluded was also investigated. Lastly, to investigate the competitive effect of

95   established vetiver tufts and soil nutrient status on mature native grasses (*Eragrostis curvula,*

96   *Digitaria eriantha*, *Panicum maximum,* and *Hyparrhenia hirta*). The last two aims were

97   investigated using a pot trial. The most important results from the surveyed sites were the

98   marked increase in grass species richness with an increase in distance away from planted vetiver,

99   the abundance of bare ground around planted vetiver, and the presence of the recruited vetiver

100 away from planted vetiver. However, in the pot trial, presence of vetiver tufts facilitated seed

101 germination in both *E. curvula* and *P. maximum*, and seeds sown on the surface had a greater

102 germination percentage compared to other sowing methods. However, vetiver presence inhibited

103 seedling establishment of these grasses, even when the root competition was excluded. Vetiver

104 shade could be retaining soil moisture and hence, creating a favourable environment for the

105 seeds of native grasses to germinate. A combination of vetiver shade, direct root competition,

106 and allelopathy (possibly from oil produced by the roots) could be causing an inhibitory effect on

107   the establishment of these native grasses. Vetiver tufts exerted a weak competitive effect on all

108   native grass tufts, except for *D. eriantha*, under low nutrient status. Vetiver exerted a facilitative

109   effect on *D. eriantha* under low nutrient status. However, vetiver exerted a strong competitive

110   effect on all native grass species under high nutrient status, except for *P. maximum,* which

111   responded similarly under low and high nutrient conditions. Overall, narrow-leaved grasses (*E.*

112   *curvula* and *H. hirta*) had a weak competitive ability compared to broad-leaved grasses (*P.*

113   *maximum* and *Digitaria eriantha*). Therefore, morphological traits are important in competition

114   studies and can predict species that might coexist with vetiver. As soil nitrogen continues to

115   increase globally, this will affect coexistence between native grasses and vetiver, with vetiver

116   gaining competitive advantage over native grass. There is no doubt that vetiver is beneficial for

117   soil and water conservation; however, this study shows that vetiver persists for decades, native

118   grasses fail to successfully recruit in close proximity to vetiver, and vetiver is a strong competitor

119   under both low and high nutrient soils. Irrespective of the predicted increase in soil nutrient

120   status, vetiver is unlikely to be succeeded by the native grasses and therefore, should be used

121   only in heavily degraded sites (e.g. gully erosion) for cover (soil protection) and not for the

122   purpose of retaining or promoting species diversity.

123

LIST OF CHAPTERS

1 Table of Contents

217

218

290

291

1   CHAPTER ONE: THE ROLE AND DYNAMICS OF VETIVER GRASS IN

356   **REHABILITATION OF GRASSLANDS IN SOUTH AFRICA**

357   **1.1   INTRODUCTION**

358   **1.1.1   Grasslands in South Africa**

359   *Importance and classification*

360   Grasslands are economically and ecologically important ecosystems, and they cover a large

361   proportion of the earth's surface. In South Africa, they constitute approximately 28.4% of the

362   land surface (Tainton, 1999; Fish et al. 2015). They contribute significantly to agriculture,

363   provide numerous ecosystem services (e.g. water), and are rich in biodiversity (Palmer and

364   Ainslie, 2005). Variability in grassland systems is driven mostly by environmental factors and

365   disturbance (i.e. grazing and fire) (Tainton, 1999). Grasslands are managed and maintained

366   through a top-down approach by means of grazing, fire or an interaction between the two

367   (Tainton, 1981a). Milchunas et al. (1988), defined grasslands by categorizing them as either

368   being climatically determined (climatic climax), successional, or agricultural. Climatic climax

369   grasslands have insufficient soil water to support a forest ecosystem but sufficient to maintain the

370   grass layer (Milchunas et al., 1988). Milchunas et al. (1988), suggested that savanna or shrub

371   steppe ecosystems (i.e. ecotone between grassland and forest) with an annual rainfall that is

372   between 250 - 1000mm, are also classified as climatic climax grasslands. Successional or

373   agricultural grasslands are those that result from clearing of forests, hence are maintained by

374   agronomic or other management practices (Acocks, 1988; Milchunas et al., 1988). However, not

375   all fire dependant grasslands are as a result of forests clearing. Some are naturally grasslands but

376   become encroached by woody plants when fire frequency decreases. These grasslands are not at

377   equilibrium with climate and Acocks (1988) termed them "false grasslands" as they require fire

378   to maintain the grassy layer. These grasslands are known as fire climax grasslands, similar to

379   what Milchunas et al. (1988) called successional or agricultural grasslands. The major focus of

380   grassland management is to maintain species diversity and good veld condition. In order to do

381   this, proper management of both fire and grazing is important in grasslands to avoid veld

382   degradation, mostly through soil erosion or species loss (Tainton, 1999).

383

384

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

443   successfully for decades, for rehabilitation of eroded soils, phytoremediation (as it roots can
444   absorb toxic heavy metals/chemicals), wetland rehabilitation, slope stabilization, and soil
445   conservation, in India and worldwide. The oil from its roots is used in the cosmetic and
446   pharmaceutical industries as it has antifungal and anti-microbial properties. These applications
447   have popularized the use of this grass, but in South Africa, it is mainly used for soil erosion
448   control, rehabilitating mine waste, roadside slope stabilization, and waste water treatment
449   (George et al., 2001; Truong and Loch, 2004; Mulder and Brent, 2006).

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

453   **1.2 VETIVER GRASS (CHRYSOPOGON ZIZANIOIDES (L.) ROBERTY)**

454   **1.2.1   Growth and behaviour of vetiver grass**

455   Different grasses with different growth forms require different environmental and
456   climatic conditions for germination, establishment, and maturity. Growth form is of ecological
457   significance as it can provide important information about the life history of the grass. Vetiver
458   grass growth is highly dependent on its root system and vegetative reproduction because it
459   produces infertile seeds (Dalton et al., 1996). The reason for this infertility is unknown (Council,
460   1993). Most researchers have speculated that perhaps the plants are "sterile" or conditions for
461   germination are seldom present. However, there are two varieties of vetiver grass which have the
462   same botanical name (Council, 1993). The "colonizer" wild variety from North India, and the
463   "sunshine" commercially propagated variety from south or central India. The "colonizer" is an
464   aggressive grass capable of spreading, and Council (1993) stated that, if this variety is
465   mistakenly used for soil stabilization, it could become a weed. The sunshine variety was
466   believed to be seedless, with only vegetative reproduction but it has been observed to produce
467   infertile seeds. The question of why would it invest its resources producing infertile seeds,
468   remains unanswered. For this reason the 'sunshine' variety is said to not spread.

469   It is not easy to differentiate between these two varieties, particularly when there are no
470   flowers. Researchers have relied on morphological and physiological characteristics to
471   differentiate between these two varieties. The commercially propagated variety is said to have a
472   thicker stem, roots with less branching, and wider leaves (1.1cm on average) than the wild

473   variety but these characteristics may be too simple to be truly diagnostic (Council, 1993).

474   Furthermore, the commercially propagated variety produces more root biomass and hence more

475   oil (Council, 1993). Initially, vetiver was utilized for its oil and therefore, domestication could

476   have been aimed at producing greater oil yields, not at inhibiting sexual reproduction. This is

477   further evidenced by the fact that utilization of oil was initiated in India, the country of origin, so

478   negating the need for a sterile cultivar. Therefore, vetiver grass having infertile or sterile seeds

479   could have been a by-product of breeding for maximum oil production. Both the commercially

480   propagated, which have many cultivars, and the wild variety are dominant in the tropical and

481   subtropical plains throughout northern India. Both these grasses, particularly the wild variety,

482   prefer low-lying, damp (i.e. swamps and bogs) sites or even river margins (Council, 1993;

483   Dalton et al., 1996).

484   Adams et al. (2003) suggest that the origin of a non-seeding variety is unknown.

485   However, because there is still a wild vetiver (found in the northern part of India), researchers

486   have begun to use DNA fingerprinting to understand differences between wild vetiver and all

487   other known cultivars. Adams and Dafforn (1997) found that 86 % of 121 plants sampled

488   originated from a single clone (no variation in genetic material). Furthermore, Adams et al.

489   (1998) examined the vetiver wild variety, cultivars, and related genera (*Sorghum* and

490   *Chrysopogon*) using DNA fingerprinting, which led to Veldkamp (1999) combining DNA

491   fingerprinting and morphological data to show that species under *Vetiveria* actually fall under

492   *Chrysopogon*. Therefore, *Vetiveria zizanioides* (L.) Nash. was changed to *Chrysopogon*

493   *zizanioides* (L.) Roberty (Veldkamp, 1999; Adams and Center, 2000). An important finding of

494   this work was that the genetic material revealed no substantial differences between the wild and

495   commercially propagated vetiver. The only differences relate to reproduction, root biomass and

496   oil production (Adams and Dafforn, 1997; Adams et al., 1998; Adams et al., 2003).

497   Vetiver grass development is affected by daily temperature, soil moisture, and soil texture

498   (Wang, 2000; Nix et al., 2006). As it is a tropical grass it is adapted to high rainfall and

499   extremely warm conditions with deep soils, resulting in the extensive root systems that make it

500   useful for soil stabilization. Subfreezing conditions have been documented to significantly

501   reduce vetiver grass growth (Nix et al., 2006). For example, in China from Hainan Island (10°N

502   latitude) to Tianjing (39°N latitude)), when vetiver grass was grown in areas with a mean

503 temperature of -4^0C with the minimum temperature reaching -22^0C, the grass showed a slow

504 growth of about 0.5cm daily (Xu, 2002). Cheng et al. (1994) showed that vetiver started to grow

505 well when mean temperatures reached $10\text{-}15^o$C, the fast growth seen between 20 and 30^oC or

506 higher with a daily growth of 2-3 cm in height. Many studies supported these findings,

507 suggesting that at higher temperatures, vetiver grass started tillering and flowering (Xia et al.,

508 1998; Huang, 1999; Xu, 2002). However, when temperatures reach 40^oC or above, the growth

509 slowed (0.5cm height increase daily) (Xia et al., 1998), suggesting that both very low and high

510 temperatures negatively affect the growth of this grass. Temperature fluctuations have not been

511 reported to cause mortality in vetiver.

512   Huang, (1999) noted that vetiver grass height and biomass is more dependent on soil

513 fertility rather than temperature. For example, vetiver grass grew up to 3 m in a fertile loam soil

514 in China compared to a white sandy soil where the grass only grew up to 1m over the growing

515 season with similar temperatures (Huang, 1999). Fertile soils do promote growth and survival of

516 vetiver grass. Studies have shown that vetiver grass growth and leaf quality is mostly influenced

517 by soil phosphorus availability (Huang, 1999; Xu, 2002; Wagner et al., 2003). Soils with limited

518 phosphorus availability result in a slow growth or sometimes mortality in vetiver grass. In

519 contrast, vetiver grass has shown enhanced growth under high levels of soil nitrogen and

520 phosphorus

521   Vetiver can grow in a variety of environmental conditions (e.g. arid to semi-arid to high

522 humid regions), however, even though it can tolerate drought and salinity, it prefers nutrient-rich

523 and high rainfall areas (Truong et al., 1999; Maffei, 2003). A study in China showed that vetiver

524 grows better than the well-known drought-tolerant grass, *Paspalum notatum* during drought (Xu,

525 2002). Edelstein et al. (2009) suggested that salinity levels between 3 and 6 deciSiemens per

526 metre (**dS/m**) do not cause significant reduction in growth and mortality in vetiver grass.

527 However, salinity levels above 6dS/m caused extensive reduction in yield, leaf and root quality

528 and even increased tuft mortality (Xu, 2002; Edelstein et al., 2009). This, therefore, is one of the

529 main reasons why vetiver performs poorly in arid regions. In contrast, vetiver grass grows well

530 in wetlands and swamp areas. The grass can even grow in soilless water, when only the leaves

531 are not covered by water (Xu, 1998, 2002). However, vetiver cannot stand long-term

532 waterlogging; for example, Xu (2002) showed that it does not survive when water levels are

533 higher than the base of the tillers during the growing season.

534 **1.2.2   Effect of disturbances on vetiver grass**

535   Grass behaviour cannot be extensively understood without considering the effect of

536 disturbance. Disturbance can be either natural or anthropogenic through grassland management.

537 The two main grassland disturbances utilized in management are fire and grazing. These two

538 disturbances are important in the understanding of grassland ecosystems as they are key factors

539 that influence grassland composition and maintain the dominant grass layer (Tainton, 1981a;

540 Tainton, 1981b, 1999). These two factors either promote or reduce plant diversity by means of

541 promoting the dominance of disturbance-tolerant, grazing resistant, and unpalatable grasses

542 (Tainton, 1981b). For these reasons, it is important to consider how vetiver responds to

543 management through fire and grazing.

544   Vetiver grass invests extensively in its root system and is said to be highly dependent on

545 roots for regrowth, survival and spreading (Council, 1993; Truong, 2000b; Xu, 2002). Fire does

546 not affect the root systems, therefore, vetiver grass is assumed to be tolerant to both hot and cool

547 fires (Council, 1993). Furthermore, vetiver stays green even in the dormant season which could

548 affect its flammability, and thus fire behaviour. However, no specific study has addressed how

549 vetiver responds to fire. The evidence that exists is anecdotal from small-scale farmers and

550 projects (Xu, 1998, 2002). As such, no scientific experiments, to the best of my knowledge, have

551 been done to evaluate the response and regrowth of vetiver after fire. Furthermore, not much is

552 known about how vetiver responds to fire intensity and frequency. However, considering vetiver

553 grass morphology and growth, it would be feasible to speculate that vetiver could withstand fires

554 because of its low flammability resulting from staying green even in the dormant season. Fire

555 also could result in the regrowth of those few tillers and leaves that were dormant in the time of

556 fire (Council, 1993).

557   Growth and survival of palatable plants are the two factors most frequently affected by

558 grazing, although trampling also influences germination and establishment through compacting

559 or breaking up compacted soil. However, the outcome of trampling is mostly dependent on the

560 soil physical properties. Vetiver grass has been observed being eaten by most livestock, which

561 suggests that it is relatively palatable when still young and not very fibrous (Council, 1993).

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

570   Vetiver is more fibrous and has sharp edges in resource-poor regions or cold areas (Xu,
571   2002). Therefore, vetiver grass could only be eaten when it is young and when preferred grasses
572   are limited (Xu, 2002). This could result in its dominance in areas with unmanaged grazing
573   (selective grazed patches) or overgrazing. Integration of fire might increase the likelihood of
574   grazing as the regrowth might be palatable. However, to my knowledge, no studies have looked
575   closely at the palatability and digestibility of vetiver grass at different growth levels.

576   **1.2.3   Vetiver grass uses**
577   Environmental degradation has become a major problem worldwide, more specifically in
578   developing countries such as South Africa. Land degradation includes, but is not limited to,
579   species loss (decreasing diversity and richness), soil loss (erosion and pollution of arable soil),
580   water pollution and water reduction/loss (through changes in catchment vegetation - domination
581   of alien trees which uses more water e.g. eucalyptus species) (Bojö, 1996; Faria et al., 2015).
582   Drought, flooding and other environmental hazards which are as a result of climate change are
583   contributing extensively to land degradation (Bojö, 1996; Faria et al., 2015). These hazards or
584   climate change at large, are believed to be accelerated by changes in land use which are caused
585   by the human population growing exponentially (Faria et al., 2015). The growing demands for
586   food (hence, increase in industrial agriculture- extensive use of fertilizer) and energy (growing
587   demand for oil, coal and gas extraction, hence increase in carbon dioxide (CO_2) in the
588   atmosphere) are a by-product of human population growth (Change, 2001; Guillebaud and
589   Hayes, 2008). The collective effect of changes in land use on soils are; 1) ecosystem
590   eutrophication through nitrogen deposition, and 2) soil contamination through heavy metals

591 deposition [e.g. Zinc (Zn), lead (Pb), and Cadmium (Cd)] from mines (O'Rourke et al., 2016).

592 This then affects the aboveground vegetation, soil microbes, and water health.

593 Soil contamination degrades ecosystem health, affecting human lives indirectly through

594 the loss of agricultural lands and water pollution, and directly through public health, as many

595 pollutants are linked or associated with cancer and neurological disorders (O'Rourke et al.,

596 2016), and reduced agricultural productivity, through the loss of nutrient-rich topsoil and thus the

597 reduction in arable land (Fey, 2010). Therefore, the unique structure and tolerance of vetiver

598 grass to different disturbances, environmental catastrophes, and soil conditions, popularized its

599 use for environmental protection and rehabilitation (i.e. soil and water conservation). In 1956

600 John Greenfield used vetiver grass to plant contours on eroded hillsides in Fiji (Council, 1993).

601 This intervention slowed run-off, retained nutrient-rich topsoil, and enabled him to plant

602 sugarcane successfully between the vetiver contours. This initiated research into vetiver grass

603 application in erosion control, agriculture, wastewater treatment, and phytoremediation. The

604 widespread application of vetiver grass known as vetiver grass technology (VGT) was initiated

605 in India by the World Bank for soil and water conservation around the 1980s (Truong et al.,

606 1999; Truong, 2000a; Greenfield, 2002).

607 This research funded by the World Bank and conducted for several decades has

608 demonstrated that vetiver grass technology is an effective, safe and low-cost natural method of

609 environmental protection (Council, 1993; Adigun and Are, 2015). For this reason, vetiver grass

610 has been used successfully for soil protection and rehabilitation of rill and gully erosion (Cao et

611 al., 2015). It has been shown to successfully reduce soil loss up to 100% through binding the soil

612 with roots and creating a new root level on a culm depending on the new soil level (see Figure.

613 1.1). In addition, it can increase water conservation up to 60% (Dalton et al., 1996; Xu, 2002;

614 Cao et al., 2015). The ability of vetiver to absorb toxic chemicals and heavy metals effectively

615 has also led to its use as a phytoremediation plant (Truong et al., 1999). Vetiver has been used

616 successfully all over the world for rehabilitating abandoned mine sites and it has proven effective

617 in restoring and maintaining soil health on those sites (Truong et al., 1999). Furthermore, vetiver

618 has recently been used as a floating island in contaminated or nutrient-rich dams to absorb excess

619 nutrients and contaminants, cleaning the water and restoring ecosystem function (Truong, 2000a;

620   Truong, 2000b; Truong et al., 2001). Vetiver also has been used successfully in wastewater

621   treatment (phytoremediation) and in rehabilitating landfill sites (Truong et al., 2001).

622   Recent studies have also shown that vetiver grass can be used as an anti-pest or insect

623   trap species to improve agricultural productivity, through drawing insect pests away from crops

624   (Shengluan and Jiayou, 1998). Vetiver grass has been reported to be eaten by most herbivorous

625   insects, mostly termites (Shengluan and Jiayou, 1998). However, most studies, both

626   observational and experimental, indicate that vetiver does not die as a result of herbivory

627   (Shengluan and Jiayou, 1998; Van den Berg et al., 2003). The highest recorded damage caused

628   by termites on the stem is 39% (Shangwen, 1999; Zhu et al., 2001). Van den Berg et al. (2003)

629   conducted a two-choice greenhouse and laboratory study to understand whether vetiver grass is

630   preferred by female *Chilo partellus,* a problematic moth in maize farming, and whether vetiver

631   can be used as a pest control plant. They used maize, vetiver, and napier grass (*Pennisetum*

632   *purpureum*), a grass that is widely used in Africa as a trap crop for stem borers. They showed

633   that vetiver grass was highly preferred for oviposition; however, larval survival on vetiver grass

634   was extremely low, significantly lower than on the napier grass (Van den Berg et al., 2003).

635   Therefore, their study supported the notion that vetiver grass could be used as a trap plant for

636   insect pest control, as it attracts the insects away from the crops and reduces their survival. For

637   this reason, vetiver has great application in agriculture and mostly in subsistence farming.

638   In windy areas, vetiver has been used as a windbreak for crops (e.g. maize) mostly by

639   small-scale farmers (Shengluan and Jiayou, 1998). This is done by planting vetiver in contours

640   and the crop plant between those contours. Under these circumstances not only does vetiver

641   reduce soil erosion but increases agricultural productivity by reducing wind damage (Shengluan

642   and Jiayou, 1998; Everson et al., 2007). The space between vetiver contours and the space

643   between vetiver tufts planted in rows is dependent on the topography and the purpose of planting

644   vetiver (Greenfield, 2002; Everson et al., 2007). Spaces between contours in the agricultural

645   fields are generally wider than those of slope stabilization (e.g. roadside) or soil erosion control

646   (i.e. sheet, rill or galleys) (Greenfield, 2002; Maffei, 2003). Generally, for soil erosion control,

647   tufts are planted 15cm to 30cm apart; however, between vetiver contours, the landscape, and the

648   purpose are usually the key determinants of spacing, with most scholars advocating two meters

649   (Council, 1993; Greenfield, 2002; Maffei, 2003; Everson et al., 2007).

650   Aside from rehabilitation, remediation, and agriculture, the commercial uses of vetiver
651   grass mainly pertain to the extraction of vetiver oil through distillation of the roots. Vetiver oil
652   has extensive applications in the cosmetic industry (e.g. soaps, deodorants and refreshing sprays)
653   and is also used as an anti-microbial and anti-fungal agent in the pharmaceutical industry
654   (Chomchalow, 2001). Furthermore, vetiver is also used in the manufacturing of handy-crafts,
655   thatching of houses, and organic compost production.
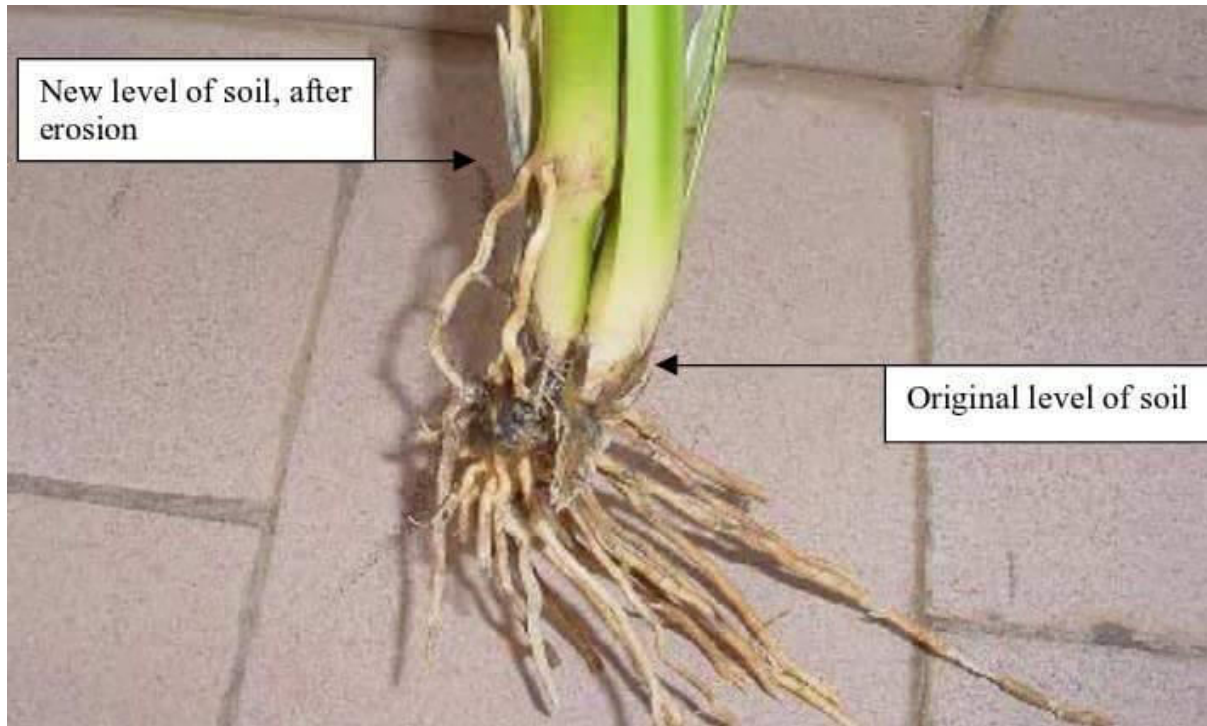
656

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

659

1.2.4   Competition and nutrient addition

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

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

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

677 **1.3   COMPETITION**

678 **1.3.1   Role of competition in grasslands**

679 *Importance of competition*

680 Grasslands are maintained mostly through a top-down effect where perturbations (outside
681 influence, i.e. disturbance such a fire and grazing) are of significance and control the ecosystem
682 stability. There is agreement among ecologists with regard to the importance of perturbations,
683 mostly because of their effect on plant interactions (Kirkman, 1988; Robinson and Rorison,
684 1988; Tainton, 1999). While ecologists agree that competition is important in structuring
685 grasslands there is uncertainty regarding whether competition promotes or reduces species
686 richness and diversity.

687 The definition of competition has been a subject of discussion among ecologists for
688 decades. However, because the experimental design used to study competition is fairly standard,
689 a general definition could be created. The basic experimental design involves a target species
690 growing in the presence or absence of neighbouring species, with the manipulation of limiting
691 resources (Goldberg, 1996; Cahill, 1999, 2002). Wall and Begon (1985) offered a simplified
692 definition of interspecific competition, suggesting that competition is "an interaction between
693 individuals, brought about by a shared requirement for a resource in limited supply, and leading
694 to a reduction in the survivorship, growth and/or reproduction of the competing individuals
695 concerned". As this definition is fairly broad, one can extract a definition that suits the objectives

696 of the study. Hence, here we define competition as a negative interference, being either direct or
697 indirect suppression of one plant by another through resource utilization differences (Fowler,
698 1986). This is seen when one plants' ability or utilization of resources decreases or influences the
699 growth, fecundity, and survival of a neighbouring plant (Casper and Jackson, 1997). Competition
700 is measured using functional traits such as plant height, shoot/leaf production, biomass, and
701 tillering. However, the most effective measure is biomass (both above and below ground)
702 because it has been shown to give conclusive results (Peltzer et al., 1998) that are useful in
703 explaining the effect of competition in structuring plant communities (Tedder et al., 2012).

704 Interspecific competition among ecologically similar species is suggested to be a major
705 driver of plant community structure (Wall and Begon, 1985). Studies have shown that
706 interspecific competition could drive certain species to local extinction or could promote
707 diversity (Hardin, 1960; Wall and Begon, 1985). For example, in a 12 year field trial, Fynn et al.
708 (2009) showed that grasses differ in their ability to resist invasion by other grasses, and that plant
709 functional traits can be used to predict species invasion and invasibility in restored grasslands.
710 Therefore, they suggested that restoration of diverse grasslands should use grasses with short
711 stature, low leaf mass, slow growth, few tillers, and high specific leaf area which may facilitate
712 succession by other native species, thereby increasing species richness (Fynn et al., 2009). This
713 is because such grasses had weak competitive effects as predicted by their traits. Interspecific
714 competition, therefore, can work to maintain species diversity in grasslands. However, the
715 grasses must be able to coexist spatially and temporally within the confines of limiting resources.

716 ***Competition theories***

717 Plant species coexistence has been the subject of controversial debate among ecologists
718 for decades. Therefore, there have been many theories proposed to explain how different species
719 with similar ecological requirements could coexist (Grime, 1977; Tilman, 1980; Thompson,
720 1987; Craine, 2005). These theories differ in their objectives but all of them aim to further our
721 understanding of plant community structure. They each try to understand different topics,
722 ranging from the importance of competition and the role of competition in plant community
723 structure (i.e. Grime, 1977 and Tilman, 1980) to invasive plants (i.e. enemy escape theories and
724 novel weapons hypothesis) (Keane and Crawley, 2002; Wolfe, 2002; Colautti et al., 2004).

13

725 ***Grime and Tilman***

726   Grime (1977) elucidating on his theory, suggested that there are two external factors
727 limiting plant biomass. The first one is stress, defined as 'conditions that restrict production e.g.
728 shortages of light, water, or mineral nutrients and suboptimal temperatures" (Grime, 1977),
729 which relates directly to competition because competition is dependent on the availability of
730 resources. The second one is disturbance, defined as "the partial or total destruction of plant
731 biomass" (Grime, 1977), e.g. fire, herbivory, pathogens, wind damage, frost, desiccation, soil
732 erosion, and anthropogenic actives (i.e. mowing, ploughing, and trampling). Grime used the
733 interaction between these two external factors to suggest that there are three possible
734 combinations of stress and disturbance, which result in three plant strategies (Campbell et al.,
735 1991b; Campbell and Grime, 1992). These strategies are 1) competitive plants, which dominate
736 in low stress, resource rich environments with low disturbance, 2) stress-tolerant plants,
737 dominant under high stress resource poor conditions with low disturbance, and 3) ruderal plants,
738 which thrive in low stress resource rich environments with high disturbance (Grime, 1977;
739 Grace, 1991). This theory will be referred in short as the CSR theory.

740   In short, Grime's CSR theory suggests that species with the maximum capacity for
741 resource capture, thus having the highest growth rate will be superior competitors (Grime, 1977).
742 Therefore, competition is more apparent in resource-rich environments than in resource-poor
743 environments. For example, Mahmoud and Grime (1976) conducted a study focusing on the
744 competitive ability of three grasses under low nitrogen (resource-poor environment) and high
745 nitrogen (resource-rich environment) conditions. The grass species were *Festuca ovina*
746 (dominant in unproductive regions), *Agrostis tenius* (dominant in intermediate-fertility regions)
747 and *Arrhenatherum elatius* (dominant in productive regions). Overall, they showed that
748 competition decreases in importance as resources availability decreases (Mahmoud and Grime,
749 1976). This was shown through the complete elimination of one species in each pair and the
750 order of competitive ability (*Arrhenatherum elatius> Agrostis tenuis> Festuca ovina)* showing
751 that grasses adapted to productive regions are more competitive than the ones adapted to
752 resource-poor environments (Mahmoud and Grime, 1976). Many studies have shown that
753 fertilization causes decline in species diversity, which is in support of this theory (Campbell et
754 al., 1991b; Campbell and Grime, 1992; Rajaniemi, 2002).

755   In contrast to Grime's CSR theory, David Tilman's R* model of differential resource

756 utilisation suggests that species with a lower minimum resource requirement (R*), the point at

757 which population decline or loss equals population growth, will be superior competitors (Tilman,

758 1980, 1985; Tilman, 1987; Begon et al., 1990). This suggests that plant species with a low R*

759 are more competitive in resource poor-environments. To explain how coexistence in plants takes

760 place in his theory, the use of illustrations is required (see Fig. 1.2 below). The basis of this

761 model is the zero net growth isocline (ZNGI), which is defined in simple terms by Begon et al.

762 (1990) as "the boundary between the resource combinations which allow the species to survive

763 and reproduce, and the resource combinations which do not". However, for this theory to predict

764 the outcome of two competing species, consumption vectors (C_A and C_B, in Fig.1.2) should be

765 included. Therefore, where resource 1 (R1) is limiting, species A dominates, but where resource

766 2 (R2) is limiting, species B dominates. Furthermore, above where the consumption vectors

767 cross, the two species coexist. The consumption vectors indicate resource consumption of each

768 species. If both species consume more of the resource that limits their own growth, the two will

769 exhibit a stable coexistence, but when these species consume more of the resource that limits the

770 other species, coexistence is not possible (i.e. if the consumption vectors are switched in Fig. 1.2)

771 (Tilman, 1985; Grace, 1991).
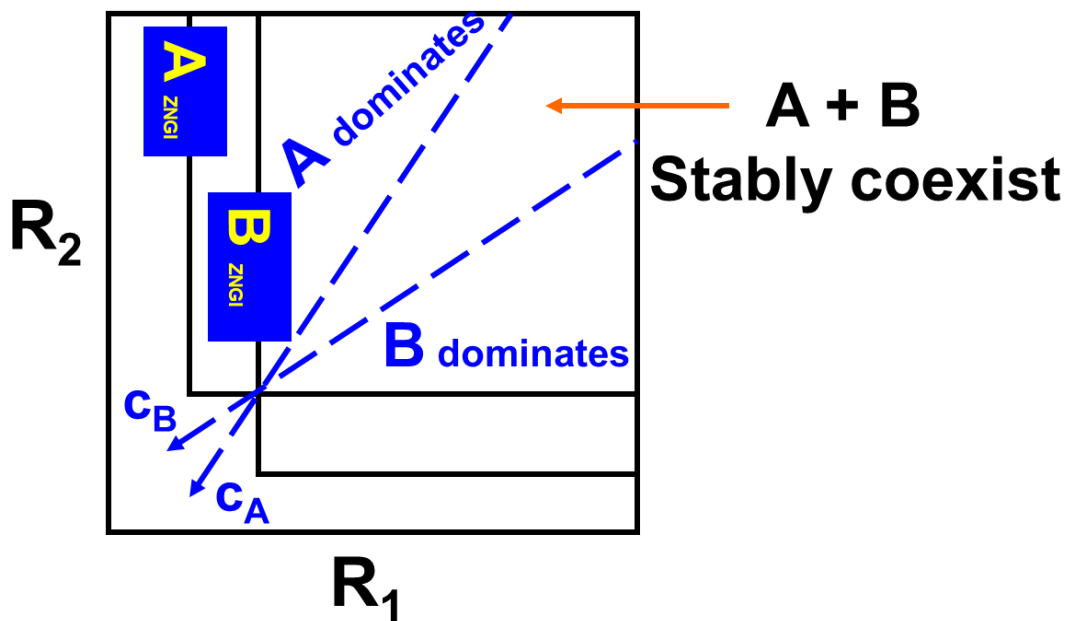
772

773 Figure 1.2: Tilman's differentiation resource utilization model (R*) modified from Begon et al.
774 (1990), with A ZNGI and B ZNGI representing isoclines (ZNGI) of species A and B, R1 and R2
775 representing resources, and CA and CB representing consumption vectors of species A and B.

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

788 Ward (2010), using water and nitrogen as limiting resources controlling the competition
789 between acacia trees and grasses, showed that Tilman's model can be used to understand the
790 effect of climate change on bush encroachment. He suggested that acacia trees (woody C_3 plants)
791 fix nitrogen, hence, they have a low R^* for nitrogen (Ward, 2010). Contrastingly, grasses can
792 easily access water from the upper soil layer; hence, they have a lower R^* for water (Ward,
793 2010). Therefore, he showed, using Tilman's model and a field experiment, that increases in
794 water availability will favour acacia trees and that increases in nitrogen availability will favour
795 grasses (i.e. Fig 1.2) (Kraaij and Ward, 2006). He suggested that the resource ratio model is
796 likely to be used as a predictor model once atmospheric CO_2 is about 450 ppm, which will result
797 in a shift from the higher net photosynthetic rate of C4 plants to C3 plants (Ward, 2010).

798 Both Grime and Tilman's theories are fundamental to our understanding of plant community
799 structure and how competition plays a role in ecosystem function. Given that these two scholars
800 differ in the way they define competition the comparison of these two theories has proven
801 difficult (Grace, 1990; Grace, 1991). However, Austin (1986) conducted a broad comparison and
802 suggested that both Grime and Tilman agree that soil nutrient levels, light, and disturbance are

803 important factors and hold the answers to understanding plant community structure. Grace
804 (1990) pointed out that a limitation of both theories is that they fail to distinguish between
805 adaptation to resource levels and adaptation to non-resource conditions (i.e. soil salinity).
806 Additionally, Craine (2005) commented that these two theories attempt to unify the disparate
807 theories regarding plant community structure, and the role the environment plays in the assembly
808 of these communities. Natural plant communities are inherently complex and dynamic, which is
809 why it has proven difficult to have one unified theory (Austin, 1986; Craine, 2005). Therefore,
810 these two theories both have important ideas about how some species might dominate in a
811 habitat and their response when resource availability changes.

Plant invasions and theories?

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

826 The ERH is underpinned by the assumption that a plant species in its native range
827 experiences suppression from combined enemies (i.e. competitors, pathogens and herbivores).
828 Competition with other plant species for resources, while experiencing suppression from both
829 specialist and generalist herbivores, results in the plant investing resources into survival, defense
830 or/and regrowth rather than on maximising reproductive output (Bakker and Wilson, 2001;
831 Wolfe, 2002; Bakker et al., 2003). However, the new habitat might lack all or some of the
832 aforementioned factors which allow the plant to reallocate available resources to rapid growth

833   resulting in invasion. The assumptions of the ERH are mostly related to insect herbivores and
834   specialist enemies, which are not the focus of this study. However, another hypothesis which
835   focuses more on competition is the "evolution of increased competitive ability hypothesis"
836   (Blossey and Notzold, 1995). This hypothesis states that, a historically introduced plant could
837   relocate resources previously used for defence to increase its competitive ability, because of
838   release from natural enemies (Blossey and Notzold, 1995; Blossey and Kamil, 1996). This
839   incorporates both competitive ability and time, suggesting that shifts in resource allocation take
840   time and which explains why some invasive species take time to show signs of invasion. This
841   hypothesis is supported by the minimum residence time (time since first record or introduction of
842   an alien species) which has been shown to explain patterns and plant invasion dynamics (Castro
843   et al., 2005; Visser et al., 2016). For example, in South Africa Visser et al. (2016) showed that
844   non-invasive alien grasses had a shorter resident time compared to naturalized or   invasive
845   grasses.

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

856   ***Plant succession and erosion control***

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

18

863   Clements, 1928; Tainton, 1999). Primary succession is initiated in an environment which

864   previously did not support vegetation (e.g. recently exposed bare ground or rock) (Tainton,

865   1999). Plants which can decompose rocks and which survive under extreme environmental and

866   climatic conditions, such as lichens, are usually the first colonizers (pioneer species) (Clements,

867   1928; Tainton, 1999). Secondary succession links well with the subject of this study. It is

868   initiated after disturbance, which resulted in the destruction of plant communities which were at

869   equilibrium (Clements, 1928; Tainton, 1999).

870   Soil erosion involves soil and vegetation removal; thus, restoration or rehabilitation of

871   eroded areas is expected to take place via plant succession. Because soil erosion in grasslands

872   results from poor management (e.g. overgrazing) coupled with intense rainfall, the top nutrient-

873   rich soil has generally been lost (Tainton, 1999). Therefore, rehabilitation or restoration requires

874   the introduction of plants (i.e. grasses) that can grow in low nutrient soils. Similar to plant

875   succession, those grasses should hold and modify the soil to allow native grasses to colonize. In a

876   humid environment, early succession usually starts with broad-leaved weeds and annual grasses

877   (Clements, 1928; Tainton, 1999), for example, *Setaria pallide-fusca*, *Digitaria sanguinalis* and

878   *Panicum laevifolium* (Tainton, 1999). Later communities are often dominated by perennial

879   grasses. For example, *Eragrostis* and *Sporobolus* species, which are followed by *Hyparrhenia*

880   species. Such succession is usually rapid because the initial conditions are usually suited to plant

881   growth (Clements, 1928; Tainton, 1999). Restoration is highly dependent on inter and intra-

882   specific competition (Clements, 1928; Tilman, 1985; Tainton, 1999). The rehabilitation process

883   of eroded sites does not usually follow traditional successional pathways because species like

884   vetiver grass (also long rooted broad-leaved grass) are usually introduced to quickly stabilize the

885   soil. The effect of these introduced species on plant succession and colonization by native

886   species is not fully understood.

887   ***Grass on grass competition***

888   Understanding plant succession in grassland ecosystems requires the understanding of

889   grass on grass interaction and the interplay of inter and intra-specific competition. Sometimes,

890   for different species growing together to coexist, they must escape direct competition by utilizing

891   different resources or drawing resources from different soil depths (Tainton, 1999). For example,

892   deep-rooted plants could extract nutrients and water from lower soil horizons allowing shallow-

893   rooted plants to extract soil resources from the top horizon (Clements, 1928; Tilman, 1994;

894   Tainton, 1999). Furthermore, winter growing plants can associate with summer growing plants

895   because they demand resources at different times (Tainton, 1999). However, direct competition

896   is usually observed in grassland ecosystems and usually leads to the domination of some species

897   over others.

898   Interspecific competition in grasslands could regulate the abundance and diversity of

899   coexisting grass species (Silletti et al., 2004). For example, Silletti et al. (2004) investigated the

900   interplay of competition in the tall grass prairie by examining interspecific competition between

901   *Andropogon gerardii* Vitman (dominant species) and *Sorghastrum nutans* L. Nash (codominant

902   species), and the effect of fertilization. They showed that there was asymmetric competition

903   favouring *A. gerardii*; however, *S. nutans* growth was boosted by fertilization with no significant

904   impact on *A. gerardii* (Silletti et al., 2004). Their results are consistent with the dominance of *A.*

905   *gerardii* in grass prairies, while the ability of *S. nutans* to perform well under nutrient rich soils

906   could be a mechanism to avoid competitive exclusion (Silletti et al., 2004). However,

907   intraspecific competition has been seen to favour species diversity (Tainton, 1999). Intraspecific

908   competition weakens one species' competitive ability and in so doing allows other grasses to

909   coexist with it. Both inter- and intra-specific competition are important in maintaining grassland

910   ecosystems.

911   Grass on grass competition differs also between grass growth stages. For example,

912   mature grass plant and seedling interactions have been said to be both facilitative and

913   competitive (Aguiar et al., 1992; Tedder et al., 2011). Aguiar et al. (1992) showed that when

914   water is not limited in the soil layer, a seedling growing near adult grass tufts suffers some

915   reduction in biomass. However, during the dry season where water is limited in the soil layer,

916   seedlings growing near adult tufts did not only suffer a reduction in biomass but an increase in

917   mortality (Aguiar et al., 1992). This proves that through competitive interaction, adult grass

918   plants can prevent the establishment of other grass seedlings, thus creating a space of bare

919   ground around them (Aguiar et al., 1992; Tedder et al., 2011). However, some grasses do

920   facilitate seed germination and seedling establishment around them. Many studies have shown

921   that some grasses create a favourable microclimate through shade, making the soil surface damp,

922   for grass seedlings to establish (Foster, 1999; Navarro and Guitian, 2003; Tedder et al., 2011).

923   This is known as the nurse plant theory (Bruno et al., 2003).

924   Pairwise greenhouse experiments and some field experiments looking at grass on grass

925   competition have shown that different grass species have different competitive abilities in

926   different environments (Mynhardt et al., 1994; Silletti et al., 2004; Suding et al., 2004).

927   Therefore, different grasses are adapted to different environmental conditions, ranging from high

928   rainfall areas and deep soils to dry areas and shallow soils. For example, Tedder et al. (2011)

929   showed that grass biomass of *Themeda triandra* and *Panicum maximum*, increases with

930   increasing soil depth, and thus increasing soil fertility, suggesting an increase in aboveground

931   competition, as per Grime's theory. However, not all grasses showed this trend; for example,

932   *Eragrostis racemosa* showed no significant difference in biomass between shallow, medium, and

933   deep soils (Tedder et al., 2012). This is because of the physical traits of this grass (being a short

934   grass) and because it is highly adapted to shallow, rocky soils (Van Oudtshoorn, 2012).

935   Furthermore, different environmental conditions allow for differences in allocation of

936   resources in grass species. Some grasses show massive investment in the aboveground material

937   (high productivity), while others show greater investment in below ground material (Peltzer et

938   al., 1998). Therefore, two grass species growing next to each other may either compete

939   asymmetrically, symmetrically or not compete at all, depending on each species resource

940   acquisition strategies (Weiner, 1990). While grass species differ in their resource acquisition,

941   they also differ in their response to different available resources, either through biomass

942   accumulation or/and tillering patterns (Tedder et al., 2011). However, the presence of a

943   neighbour in any soil type could alter the growth (biomass accumulation and tillering) and

944   resource acquisition of a grass species (Fynn et al., 2005; Fynn et al., 2009).

945   *Competition between alien and native grasses*

946   Alien grasses, like all alien plants, have proven problematic in natural veld. Even though

947   alien grasses are often overlooked, their dominance has been linked to their competitive ability

948   and local disturbance regimes. In grasslands, disturbance and competition have been shown to be

949   correlated. For example, disturbance by means of fire or grazing can open space and reduce

950   competitive interference from native grasses, hence, allowing introduced grasses to germinate,

951 establish and sometimes become invasive (Brooks, 2000; Milton, 2004). Therefore,
952 understanding the interaction between introduced grasses and native grasses is important for
953 grassland restoration and biodiversity maintenance at large.

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

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

972 ***Above- and Belowground competition***

973   Plants (especially grasses) show differences in their competitive ability above ground (for
974 light) and belowground (for soil nutrients). Goldberg's definition of belowground competition is
975 the most extensively used because it integrates both plant behaviour (response and effect) and
976 resource utility (Goldberg, 1990; Casper and Jackson, 1997). In grasses, belowground
977 competition takes place when the neighbouring grasses or swards suppresses the growth,
978 survival, or reproduction of the other grasses through depletion of available soil resources
979 (Casper and Jackson, 1997). Therefore, belowground competition is correlated with factors such

980   as root surface area, root density, and plasticity in roots or enzymic function involved in the
981   nutrient uptake (Wilson, 1993). Root plasticity is defined as the ability of the root system to
982   facilitate growth through changing its morphology under varying soil conditions to moderate the
983   effect of stress and maintain greater plant productivity (Campbell et al., 1991a; Derner and
984   Briske, 1999; Suralta et al., 2016).

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

994   Physiological studies have found three mechanisms by which soil nutrients reach the root
995   surface of plants. Firstly, root interception, where roots grow and capture nutrients as they grow.
996   This accounts for less than 10% of the total nutrient gain in plants (Casper and Jackson, 1997;
997   Casper et al., 2003). Secondly, mass flow which is dependent on the amount of water and
998   dissolved nutrients in the soil solution and is driven by plant transpiration. This is essential for
999   nitrate (nitrogen) and water uptake in plants (Casper and Jackson, 1997). Lastly, diffusion of
1000   nutrients, which happens simultaneously with mass flow; however, is responsible for potassium
1001   and phosphorus uptake (Casper and Jackson, 1997). Nutrient diffusion takes place when soil
1002   nutrient uptake has exceeded the supply by mass flow, creating a local concentration gradient.
1003   There are experimental difficulties when trying to separate mass flow and diffusion of nutrients,
1004   because they both supply important nutrients and take place simultaneously (Casper and Jackson,
1005   1997). These three resource acquisition mechanisms are important for understanding plant
1006   resource (mostly soil nutrients) competition. However, they are more physiologically based
1007   while this study is focusing more on plant performance (response and effect of competition).

1008   With a basic understanding of nutrient acquisition, one can seek to understand the
1009   mechanisms of plant response or performance, which are likely to improve or reduce plant

23

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

1040   the depletion of a shared soil resource which leads to the suppression of one species or
1041   population (Schoener, 1983). Secondly, pre-emptive, where plant species compete for space in
1042   areas where it is limiting (Connell, 1983; Goldberg and Barton, 1992). Thirdly, symmetric,
1043   where each species or population suppresses the growth of the other species or population
1044   equally (Weiner, 1990). Fourthly, asymmetric, which is a one-sided competition where one
1045   species or population suppresses other species or populations (Weiner, 1990). And lastly,
1046   interference, which is the most difficult to quantify, where the species or population behaves in a
1047   manner that reduces the preference and exploration efficiency of other species or populations
1048   (Schoener, 1983; Callaway and Ridenour, 2004). Allelopathic behaviour falls under interference
1049   competition and plays a major role in belowground competition as it leads to asymmetric
1050   competition.

1051   Above- and belowground competition have been shown to be interdependent, because of
1052   the shift in resource allocation in plants. Aboveground, competition is strongly related to light
1053   and to a limited extent, space. Grime's CSR model states that competition for both light and soil
1054   resources increases with an increase in productivity, while Tilman's R* model states that
1055   competition shifts from belowground to aboveground with an increase in productivity and
1056   changes in species composition (Grime, 1977; Tilman, 1985; Peltzer et al., 1998). Peltzer et al.
1057   (1998) investigated these conceptual models in an old, low diversity field with no species
1058   turnover. In this field, forty plots were fertilized with different levels of nitrogen annually for
1059   five years creating a nutrient gradient. They planted *Agropyron cristatum* along the nutrient
1060   gradient with no neighbours, roots of neighbours, and whole neighbouring plants to quantify root
1061   and shoot competition. They showed that *A. cristatum* biomass was 22-165% greater where there
1062   was no competition compared to when it was competing with roots of neighbours along the soil
1063   nutrient gradient, (Peltzer et al., 1998). This suggests that root competition was suppressing
1064   growth of *A. cristatum* along a nutrient gradient (Peltzer et al., 1998). Their study, therefore,
1065   suggests that the shift from root to shoot competition is not attributed to resource availability
1066   (fertilization) or to neighbour biomass along a productivity gradient in an area with low
1067   diversity. They concluded that such a conceptual model of plant competition oversimplifies the
1068   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,

1099   shoot biomass (i.e. aboveground biomass) has been used as the proxy for the long-term effect of
1100   neighbours.

Effect of competition on germination and seedling establishment

1102   The interplay of both above- and belowground competition on seedling establishment has
1103   not been discussed fully. Therefore, because the study considers allelopathic behaviour,
1104   understanding the mechanism involved and how competition affects not only grass seedlings but
1105   also seed germination, is important.

1106   Conditions that allow seed germination are well established; however, different species
1107   require different conditions. In general, seed germination requires specific temperature, moisture,
1108   and light regimes. However, moisture and warm temperatures are the major requirements for
1109   seed germination of most plant species (Ghebrehiwot et al., 2009; Kolb et al., 2016). Different
1110   species are adapted to different environmental conditions, where different management occurs
1111   (e.g. fire); therefore, seed germination in some species is triggered by such management (e.g.
1112   smoke) (Ghebrehiwot et al., 2009). For example, fire-adapted species germinated better in smoke
1113   water than in distilled water (control) when incubated under different temperatures (15°C, 20°C,
1114   25°C, 30°C, and 35°C) with temperature also increasing the germination percentage
1115   (Ghebrehiwot et al., 2009). As previously stated, plants compete for both light and soil resources
1116   (e.g. water); therefore, competition can be expected to influence seed germination. Even though
1117   this seems correlated, considering that larger plants can limit light availability reducing
1118   temperatures and hence affecting seed germination, field studies show that the evidence relating
1119   to the effect of light competition on seed germination is limited (Cideciyan and Malloch, 1982;
1120   Kolb et al., 2016). However, there are studies which show that root competition and allelopathy
1121   do affect recruitment of grass species (Gallagher and Wagenius, 2016; Kolb et al., 2016).
1122   Allelopathy is usually seen in exotic plants and affects native plants because they lack adaptation
1123   to that allelopathic chemical, hence reducing germination success (Gentle and Duggin, 1997;
1124   Dias et al., 2016).

1125   Aguiar et al. (1992) investigated the effect of plant competition (negative interaction) and
1126   facilitation (positive interaction) in the recruitment of the perennial grass species, *Bromus pictus*.
1127   The focus was on root competition because it has been documented to affect germination and

1128 establishment of native grasses. They showed that seedling survival and establishment was
1129 indeed affected by root competition because in areas where root competition was excluded,
1130 mortality decreased and growth increased (i.e. number of leaves increased) (Aguiar et al., 1992).
1131 Haugland and Fround-Williams (1999) supported their study, by showing that even with the
1132 addition of soil nutrients and water, root competition still affected seedling growth and
1133 establishment. This may suggest that other factors, such as allelopathy, are causing the observed
1134 effect or roots were competing directly for space and not for soil resources (Haugland and Froud-
1135 Williams, 1999).

1136 Allelopathy first dominated the field of agriculture as a form of weed control (Dias et al.,
1137 2016). The chemicals which inhibit the growth of other species were extracted and used as an
1138 herbicide to inhibit germination and growth of weed species (Gentle and Duggin, 1997; Dias et
1139 al., 2016). Vetiver grass roots produce oil which is a mixture of various sesquiterpenes (part of
1140 phytotoxic agent) and their precursors (Kim et al., 2005; Mao et al., 2006). This oil has many
1141 biological uses in the plant as it also contains secondary metabolites which are involved in
1142 defence (mostly from insect herbivory), in addition to allowing the plant to be territorial through
1143 interference competition (Weyerstahl et al., 1996). Mao et al. (2004) investigated whether vetiver
1144 oil has allelopathic properties which may inhibit germination and growth of six weed species.
1145 The study showed that vetiver oil inhibited seed germination and seedling growth of five out of
1146 six weed species, which led to the conclusion that vetiver oil may indeed be used as a herbicide
1147 (Mao et al., 2004). Therefore, vetiver grass could be using such oil as interference competition
1148 (allelopathic competition).

1149 However, not only competition affects plant (especially seedling) performance, since the
1150 ability of the plant to convert soil resources to biomass, known as water-use-efficiency and/or
1151 nutrient-use-efficiency, can be as effective as the competition itself (Casper and Jackson, 1997;
1152 Casper et al., 2003). Water-use-efficiency and nutrient-use-efficiency both can affect the relative
1153 growth of the plant at different points along a resource gradient (Casper and Jackson, 1997).

1154 **1.3.2   Competitive response and effect**
1155 Understanding the effects of plant competition on seed germination, seedling and adult
1156 grass growth at a species level (e.g. vetiver grass, in this case) or individual level, requires an
1157 understanding of their competitive ability (Goldberg and Landa, 1991). Competitive ability is a

1158   way to compare and measure individual plant competition in a community or population, which

1159   offers an understanding of the short-term and long-term community structure and species

1160   composition of that region (Campbell and Grime, 1992). Competitive ability of an individual or

1161   species can be examined using two components, competitive response and competitive effect

1162   (Goldberg, 1990; Goldberg and Landa, 1991). The ability of a plant to survive, grow and

1163   reproduce well in the presence of neighbours is known as competitive response (Goldberg and

1164   Fleetwood, 1987; Goldberg and Landa, 1991). While the ability of a plant or neighbours to

1165   suppress the survival, growth, and reproduction of the species is known as competitive effect

1166   (Goldberg and Fleetwood, 1987; Goldberg and Landa, 1991).

1167   Competitive response can be measured as the change in the biomass (above- or

1168   belowground, or both) of the target plant when growing with the neighbours (Goldberg, 1990).

1169   Most studies use a small target plant because seedlings are more sensitive to competition and

1170   environmental effect than adult plants (Tedder et al., 2011). Competitive response determines

1171   which species can persist in a habitat and so can infer the effects on the diversity and

1172   productivity at a community level. Thus, species with a strong competitive response can

1173   withstand resource shortages imposed on them by neighbouring species and are therefore likely

1174   to persist under nutrient-rich conditions (Goldberg and Fleetwood, 1987; Goldberg, 1990).

1175   Competitive response is important in grassland research because differences in competitive

1176   response among grass species can determine species position within a competitive hierarchy,

1177   hence, determining their distribution along a resource gradient, and allowing the prediction of

1178   their relative abundance in a community (Grime, 1977; Keddy and Shipley, 1989).

1179   By contrast, competitive effect is measured as per-unit-mass or per-plant reduction in the

1180   target plant or species (Goldberg and Fleetwood, 1987; Goldberg, 1990). This focuses more on

1181   whether the presence of neighbours results in some negative effect on the target plant or not.

1182   Competitive effect measures the effect of neighbours on the target plant, not of one individual

1183   plant on the other, therefore, it assumed that neighbours exact an equivalent effect on the target

1184   plant without taking into account that the number of neighbouring plants has an effect also

1185   (Goldberg and Fleetwood, 1987; Goldberg and Scheiner, 2001). The assumption is grounded in

1186   the notion that all plants use similar resources (light, water, and soil nutrients), and these

1187   resources occur along a gradient of availability (Goldberg and Landa, 1991). However, such

1188 assumptions are still being tested by ecologists. For example, Wedin and Tilman (1993) showed

1189 that competitive effect differs in grasses that grow in different successional stages. Late-

1190 successional grasses lowered nitrogen availability greater than early-successional grasses, which

1191 explains their dominance in matured old field grasslands (Wedin and Tilman, 1993).

1192 Furthermore, introduced grasses have been shown to exact a strong competitive effect on native

1193 grasses (Bakker and Wilson, 2001; Bakker et al., 2003). Bakker and Wilson (2001) showed that

1194 competitive effects have the ability to prevent establishment of native grass seedlings in the

1195 *Agropyron*-dominated regions (an exotic grass species in a mixed grassland of southern

1196 Saskatchewan, Canada).

1197 It should be noted that grassland ecosystems are maintained through a variety of

1198 disturbance factors (e.g. grazing and fire). These disturbances and environmental stresses play a

1199 significant role in the competitive ability of species, which could be the reason why they are used

1200 to maintain such ecosystems. However, competitive response and effect of neighbouring species

1201 under these stresses could either follow Tilman's R* theory or Grime's CSR theory or be an

1202 interplay of both. Furthermore, competitive response and effect under such stress, mostly in

1203 grasses, has been shown to be species specific (Goldberg and Fleetwood, 1987; Bakker and

1204 Wilson, 2001). Therefore, it is important to understand each species' competitive ability

1205 (competitive response) against other species (interspecific competition) and with individuals of

1206 the same species (intra-specific competitive ability).

1207 **1.3.3 Rehabilitation, restoration, and management of grasslands**

1208 In South Africa, the largest, most transformed and degraded biome is grassland (Palmer

1209 and Ainslie, 2005). Most river catchment areas in South Africa are in grasslands, which indicates

1210 how important grasslands are, not only for carbon cycling and fodder production, but for water

1211 resources (Van Oudtshoorn, 1999; Palmer and Ainslie, 2005; Everson et al., 2007). Considering

1212 that South Africa is a water scarce country, one would assume that grasslands are well-protected

1213 and managed ecosystems, however, that is not the case. Out of all African flora, grasses are often

1214 overlooked and even the impact of alien grasses on grassland ecosystems is generally overlooked

1215 (Milton, 2004). The first peer-reviewed paper focusing on alien grasses in South Africa by

1216 Milton (2004), outlined mostly the level of uncertainty regarding alien grasses distribution and

1217 the gaps on our understanding of the dynamics of alien grasses in South Africa. After her

1218 review, few other studies have expanded on her work. For example, Visser et al. (2017) showed

1219 that there are 256 alien grasses in South Africa, of which 122 species have been naturalized, and

1220 37 species have become invasive. The paper offers further evidence of the level of uncertainty

1221 specifically in relation to alien grass species distribution, abundance, and impact on the

1222 ecosystem. For example, out of the total alien grass species found, 33% of species only had one

1223 record of occurrence.

1224 Even though South Africa seems to have fewer alien grasses compared to other regions of the

1225 world, South African native grasses are among the most dominant, problematic, and widespread

1226 invasive grasses in other parts of the world, proving the existence of a donor-recipient

1227 asymmetry. Visser et al. (2016) showed that, even though possible, it is unlikely that such donor-

1228 recipient asymmetry is a reflection of bias in sampling method and in introduction dynamics, but

1229 could because of two reasons. Firstly, a large proportion of palatable tropical forage grasses are

1230 native to Africa, with most occurring in South Africa, hence South Africa is likely to have

1231 imported few species from other continents for forage related purposes (Visser et al. 2016).

1232 Secondly, South African grasses are adapted to high fire frequencies and as a results, such

1233 adaptations give them a competitive advantage (regenerate faster after fire) in other regions,

1234 while fire frequency in South Africa is predicted to be limiting the invasion of alien grasses as

1235 there are not adapted to such fire regimes (Visser et al. 2017). For example, Visser et al. (2016)

1236 showed that the distribution of alien non-invasive grasses was limited to areas with infrequent

1237 fire, supporting that notion that fire is limiting the invasion of alien grasses in South Africa.

1238 However, species which stay green even during the dormant season (e.g. vetiver, and *Festuca*

1239 *costata*) have the ability to alter fire regimes through reducing fuel bed, and fuel load

1240 (McGranahan et al., 2018).   International studies have shown that conversion of natural

1241 grasslands to those dominated by introduced grasses or even alien invasive grasses poses a threat

1242 to grassland ecosystems, through alteration of fire regimes, water and nutrient cycling, and

1243 erosion (Humphrey and Schupp, 2004). For example, in North America, *Bromus tectorum* (an

1244 alien grass) has dominated hectares of native grassland, altering regeneration structure and the

1245 effect of fire (Humphrey and Schupp, 2004). Its seeds germinate faster than those of native

1246 grasses and gain a head start after fire, hence gaining a competitive advantage and therefore,

1247 impending germination and establishment of native grass seeds (Humphrey and Schupp, 2004).

1248   Even though fire is a widely-used management tool, uncontrolled fires can destroy native
1249   perennial grasses' seeds, hence reducing the perennial grass seed bank, which then affects native
1250   perennial grass regeneration and establishment (Tainton, 1999; Humphrey and Schupp, 2004).
1251   Uncontrolled fires combined with overgrazing could result in grassland degradation or
1252   environmental degradation in the form of species loss (domination of unpalatable grasses) and
1253   soil erosion. Eroded grasslands, either through rill, sheet or gully erosion, become unable to
1254   support productive grasses and have reduced basal cover (Van Oudtshoorn, 2012). Reasons for
1255   this loss of productivity are, the removal of topsoil resulting in the exposure of less fertile soil
1256   which cannot support grass growth (Everson et al., 2007; Van Oudtshoorn, 2012), and patches of
1257   bare soil and sparse grass cover which become unable to effectively capture water resulting in
1258   reduced soil moisture, increased evaporation and greater soil temperatures (Everson et al., 2007;
1259   Van Oudtshoorn, 2012). Therefore, rehabilitation of such grasslands is sometimes difficult and
1260   involves the use of geo-textiles, stone packs and gabions (Everson et al., 2007). Alien grasses
1261   which are adapted to harsh environments (e.g. vetiver grass) are usually used to reduce water
1262   runoff and to restore the soil so that native grasses can establish (Everson et al., 2007; Van
1263   Oudtshoorn, 2012). These alien grasses, used for rehabilitation or slope stabilization (e.g.
1264   pampas grass), often outcompete native grasses and sometimes become invasive. Understanding
1265   their ecology, mostly in terms of competitive ability (response and effect), could provide
1266   information about their invasion potential and ability to allow native grasses to establish, which
1267   will then restore the productivity and function of that ecosystem.

1268   Vetiver grass, has been used successfully for decades to rehabilitate eroded sites,
1269   abandoned mine sites, to stabilize roadside slopes, and for wastewater treatment. Many claims
1270   have been made which relate to the ecology of the grass; however, some of them have been
1271   found to be false. For example, the idea that the domesticated vetiver does not flower nor does it
1272   produce seeds does not seem to hold, as the presence of flowers and seeds has been reported (Xu,
1273   2002). Therefore, the broad assumption that it will not be invasive raises questions. These
1274   questions emphasize the importance of understanding vetiver grass' competitive ability and the
1275   interplay of soil nutrients on competitive ability. Therefore, this study will contribute to the
1276   understanding of vetiver grass, rehabilitation of eroded sites, and the management of grassland
1277   ecosystems through increasing the knowledge of alien grass species' effect on native grass seed

1278 germination, seedling establishment, and grass diversity to contribute to regeneration and
1279 restoration ecology.

1280   This study aims to addresses the following questions:

1281 **1.4   LIST OF QUESTIONS PER CHAPTER**

1282 **1.4.1   Chapter Two: which native grasses grow in close proximity with vetiver grass?**

1283 1.   Are native grasses recruiting and coexisting with vetiver in these sites?

1284 2.   Which native grasses are present in these rehabilitated sites?

1285 3.   How far from the lines of vetiver planted for rehabilitation do these grasses grow?

1286 4.   Is vetiver recruiting in areas where it was not originally planted?

1287 **1.4.2   Chapter Three: does vetiver allow germination and establishment of native grasses?**

1288   1. Do vetiver grass tufts inhibit or facilitate seed germination in native grasses?

1289   2. Is the germination rate of native grasses affected by the seed sowing method?

1290   3. Do vetiver grass tufts inhibit establishment of native grasses?

1291   4. Does the exclusion of direct root interaction decrease the competitive effect exerted on
1292   native grass seedlings?

1293   5. Does vetiver root density differ from indigenous grass root density?

1294   For this chapter *Eragrostis curvula* and *Panicum maximum* will be used to represent native
1295 grasses, and the details regarding the ecology of these species and those of the following chapter
1296 can be found in appendix A.

1297 **1.4.3   Chapter Four: effect of vetiver competition and soil nutrients on native grasses.**

1298   1. Does vetiver exert a competitive effect on neighbouring native grasses with a strong
1299   (*Eragrostis curvula* and *Digitaria eriantha*) and weak (*Panicum maximum* and
1300   *Hyparrhenia hirta*) competitive ability?

1301   2. Does vetiver density influence the competitive effect experienced by native grasses?

1302   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.

1329 Adams, R.P., Pandey, R.N., Dafforn, M.R., James, S.A., 2003. Vetiver DNA-fingerprinted
1330   cultivars: effects of environment on growth, oil yields and composition. Journal of
1331   Essential Oil Research 15, 363-371.

1332 Adigun, M., Are, K., 2015. Comparatives effectiveness of two vetiveria grasses species
1333   *Chrysopogon zizanioides* and *Chrysopogon nigritana* for the remediation of soils
1334   contaminated with heavy metals. American Journal of Experimental Agriculture 8, 361-
1335   366.

1336 Aguiar, M., Soriano, A., Sala, O., 1992. Competition and facilitation in the recruitment of
1337   seedlings in Patagonian steppe. Functional Ecology 6, 66-70.

1338 Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental
1339   stress in the spread of non-native plants. Perspectives in plant ecology, evolution and
1340   systematics 3, 52-66.

1341 Austin, M., 1986. The theoretical basis of vegetation science. Trends in Ecology & Evolution 1,
1342   161-164.

1343 Bakker, J., Wilson, S., 2001. Competitive abilities of introduced and native grasses. Plant
1344   Ecology 157, 119-127.

1345 Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G., Waddington, J., 2003.
1346   Contingency of grassland restoration on year, site, and competition from introduced
1347   grasses. Ecological Applications 13, 137-153.

1348 Begon, M., Townsend, C., Harper, J., 1990. Ecology: Individuals, Populations and Communities,
1349   Second Edition ed. Blackwell Science Inc, Massachusetts, USA.

1350 Blossey, B., Kamil, J., 1996. What determines the increased competitive ability of invasive non-
1351   indigenous plants, Proceedings of the IX international symposium on the biological
1352   control of weeds. University of Cape Town, Stellenbosch, 3-9.

1353 Blossey, B., Notzold, R., 1995. Evolution of increased competitive ability in invasive
1354   nonindigenous plants: a hypothesis. Journal of Ecology 83, 887-889.

1355 Bojö, J., 1996. The costs of land degradation in Sub-Saharan Africa. Ecological economics 16,
1356   161-173.

1357 Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the
1358   Mojave Desert. The American Midland Naturalist 144, 92-108.

1359 Brown, J.R., Archer, S., 1999. Shrub invasion of grassland: recruitment is continuous and not
1360   regulated by herbaceous biomass or density. Ecology 80, 2385-2396.

1361 Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological
1362   theory. Trends in Ecology & Evolution 18, 119-125.

1363 Cahill Jr, J.F., Casper, B.B., 2000. Investigating the relationship between neighbor root biomass
1364   and belowground competition: field evidence for symmetric competition belowground.
1365   Oikos 90, 311-320.

1366 Cahill, J.F., 1999. Fertilization effects on interactions between above-and belowground
1367   competition in an old field. Ecology 80, 466-480.

1368 Cahill, J.F., 2002. What evidence is necessary in studies which separate root and shoot
1369   competition along productivity gradients? Journal of Ecology 90, 201-205.

1370 Cahill, J.F., 2003. Lack of relationship between below-ground competition and allocation to
1371   roots in 10 grassland species. Journal of Ecology 91, 532-540.

1372 Caldwell, M.M., Manwaring, J., Durham, S., 1991. The microscale distribution of neighbouring
1373   plant roots in fertile soil microsites. Functional Ecology, 765-772.

1374 Callaway, R.M., Ridenour, W.M., 2004. Novel weapons: invasive success and the evolution of
1375   increased competitive ability. Frontiers in Ecology and the Environment 2, 436-443.

1376 Campbell, B., Grime, J., Mackey, J., 1991a. A trade-off between scale and precision in resource
1377   foraging. Oecologia 87, 532-538.

1378 Campbell, B., Grime, J., Mackey, J., Jalili, A., 1991b. The quest for a mechanistic understanding
1379   of resource competition in plant communities: the role of experiments. Functional
1380   Ecology 5, 241-253.

1381 Campbell, B.D., Grime, J.P., 1992. An experimental test of plant strategy theory. Ecology 73,
1382   15-29.

1383 Cao, L., Zhang, Y., Lu, H., Yuan, J., Zhu, Y., Liang, Y., 2015. Grass hedge effects on controlling
1384   soil loss from concentrated flow: A case study in the red soil region of China. Soil and
1385   Tillage Research 148, 97-105.

1386 Casper, B.B., Jackson, R.B., 1997. Plant competition underground. Annual Review of Ecology
1387   and Systematics 28, 545-570.

1388 Casper, B.B., Schenk, H.J., Jackson, R.B., 2003. Defining a plant's belowground zone of
1389   influence. Ecology 84, 2313-2321.

1390 Castro, S. A., Figueroa, J. A., Muñoz-Schick, M., Jaksic, F. M., 2005. Minimum residence time,
1391   biogeographical origin, and life cycle as determinants of the geographical extent of
1392   naturalized plants in continental Chile. Diversity and Distributions 11, 183-191.

1393 Change, I.P.O.C., 2001. Climate change 2007: impacts, adaptation and vulnerability. Genebra,
1394   Suíça.

1395 Cheng,K.,Hu,G.Q., Rao,H.M., Xu, L.H.,and Wu, H.Q., 1994 Ecological effects of planting
1396   vetiver grass in citrus groves on slopping red soil fields. Acta Ecologica sinice 14, 21-25.

1397 Chōmchalao, N., 2001. Utilization of vetiver as medicinal and aromatic plants. Office of the
1398   Royal Development Projects Board.

1399 Cideciyan, M.A., Malloch, A.J., 1982. Effects of seed size on the germination, growth and
1400   competitive ability of *Rumex crispus* and *Rumex obtusifolius*. The Journal of Ecology 70,
1401   227-232.

1402 Clements, F.E., 1916. Plant succession: an analysis of the development of vegetation. Carnegie
1403   Institution of Washington.

1404 Clements, F.E., 1928. Plant succession and indicators. Hafner Press; New York,; Collier
1405   Macmillan Publishers; London.

1406 Colautti, R.I., Ricciardi, A., Grigorovich, I.A., MacIsaac, H.J., 2004. Is invasion success
1407   explained by the enemy release hypothesis? Ecology Letters 7, 721-733.

1408   Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist 122, 661-696.

1410   Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

1411   Craine, J.M., 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of Ecology 93, 1041-1052.

1413   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.

1415   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.

1417   Dias, L., Pereira, I.P., Dias, A.S., 2016. Allelopathy, seed germination, weed control and bioassay methods. Allelopathy Journal 37, 31-40.

1419   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.

1421   Eagles, C., 1972. Competition for light and nutrients between natural populations of *Dactylis glomerata*. Journal of Applied Ecology, 141-151.

1423   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.

1426   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.

1429   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.

1432   Fey, M., 2010. Soils of South Africa. Cambridge University Press.

1433   Fish, L., Mashau, A. C., Moeaha, M. J., Nembudani, M.T., 2015. Identification guide to southern
1434   African grasses. An identification manual with keys, descriptions and distributions.
1435   Strelitzia 36. South African National Biodiversity Institute, South Africa.

1436   Foster, B.L., 1999. Establishment, competition and the distribution of native grasses among
1437   Michigan old-fields. Journal of Ecology 87, 476-489.

1438   Fowler, N., 1986. The role of competition in plant communities in arid and semiarid regions.
1439   Annual Review of Ecology and Systematics 17, 89-110.

1440   Fynn, R., Morris, C., Kirkman, K., 2005. Plant strategies and trait trade-offs influence trends in
1441   competitive ability along gradients of soil fertility and disturbance. Journal of Ecology
1442   93, 384-394.

1443   Fynn, R.W., O'Connor, T.G., 2005. Determinants of community organization of a South African
1444   mesic grassland. Journal of Vegetation Science 16, 93-102.

1445   Fynn, R.W., Wragg, P., Morris, C., Kirkman, K., Naiken, J., 2009. Vegetative traits predict grass
1446   species' invasiveness and the invasibility of restored grassland. African Journal of Range
1447   & Forage Science 26, 59-68.

1448   Gallagher, M.K., Wagenius, S., 2016. Seed source impacts germination and early establishment
1449   of dominant grasses in prairie restorations. Journal of Applied Ecology 53, 251-263.

1450   Gentle, C., Duggin, J., 1997. Allelopathy as a competitive strategy in persistent thickets of
1451   *Lantana camara* L. in three Australian forest communities. Plant Ecology 132, 85-95.

1452   George, J., Laing, M., Drewes, S., 2001. Phytochemical research in South Africa. South African
1453   Journal of Science 97, 93-105.

1454   Ghebrehiwot, H.M., Kulkarni, M.G., Kirkman, K.P., Van Staden, J., 2009. Smoke solutions and
1455   temperature influence the germination and seedling growth of South African mesic
1456   grassland species. Rangeland Ecology & Management 62, 572-578.

1457   Goldberg, D.E., 1990. Components of resource competition in plant communities. Perspectives
1458   on Plant Competition, 27-49.

1459   Goldberg, D.E., 1996. Competitive ability: definitions, contingency and correlated traits.
1460   Philosophical Transactions of the Royal Society of London B: Biological Sciences 351,
1461   1377-1385.

1462   Goldberg, D.E., Barton, A.M., 1992. Patterns and consequences of interspecific competition in
1463   natural communities: a review of field experiments with plants. The American Naturalist
1464   139, 771-801.

1465   Goldberg, D.E., Fleetwood, L., 1987. Competitive effect and response in four annual plants. The
1466   Journal of Ecology 75, 1131-1143.

1467   Goldberg, D.E., Landa, K., 1991. Competitive effect and response: hierarchies and correlated
1468   traits in the early stages of competition. The Journal of Ecology 79, 1013-1030.

1469   Goldberg, D.E., Scheiner, S.M., 2001. ANOVA and ANCOVA: field competition experiments.
1470   Design and analysis of ecological experiments 2, 69-93.

1471   Gough, L., Osenberg, C.W., Gross, K.L., Collins, S.L., 2000. Fertilization effects on species
1472   density and primary productivity in herbaceous plant communities. Oikos 89, 428-439.

1473   Grace, J., 1991. A clarification of the debate between Grime and Tilman. Functional Ecology 5,
1474   583-587.

1475   Grace, J.B., 1990. On the relationship between plant traits and competitive ability. Perspectives
1476   on Plant Competition, 51-65.

1477   Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth.
1478   Infinity Publishing.

1479   Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its
1480   relevance to ecological and evolutionary theory. The American Naturalist 111, 1169-
1481   1194.

1482   Guillebaud, J., Hayes, P., 2008. Population growth and climate change. British Medical Journal
1483   Publishing Group.

1484   Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292-1297.

1485 Haugland, E., Froud-Williams, R.J., 1999. Improving grasslands: the influence of soil moisture
1486   and nitrogen fertilization on the establishment of seedlings. Journal of Applied Ecology
1487   36, 263-270.

1488 Huang, X., 1999. Introduction of vetiver grass in Huangshan area, Annual Report. China Vetiver
1489   Development Foundation, Nanjing.

1490 Humphrey, L.D., Schupp, E.W., 2004. Competition as a barrier to establishment of a native
1491   perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*)
1492   communities. Journal of Arid Environments 58, 405-422.

1493 Jurena, P., Archer, S., 2003. Woody plant establishment and spatial heterogeneity in grasslands.
1494   Ecology 84, 907-919.

1495 Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis.
1496   Trends in Ecology & Evolution 17, 164-170.

1497 Keddy, P.A., Shipley, B., 1989. Competitive hierarchies in herbaceous plant communities.
1498   Oikos, 234-241.

1499 Kim, H.-J., Chen, F., Wang, X., Chung, H.Y., Jin, Z., 2005. Evaluation of antioxidant activity of
1500   vetiver (*Vetiveria zizanioides* L.) oil and identification of its antioxidant constituents.
1501   Journal of Agricultural and Food Chemistry 53, 7691-7695.

1502 Kirkman, K.P., 1988. Factors affecting the seasonal variation of veld quality in South Africa.
1503   Unpublished Master's Thesis, University of KwaZulu-Natal, South Africa.

1504 Kolb, R.M., Pilon, N.A.L., Durigan, G., 2016. Factors influencing seed germination in Cerrado
1505   grasses. Acta Botanica Brasílica 30, 87-92.

1506 Kraaij, T., Ward, D., 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and
1507   early survival in bush-encroached savanna, South Africa. Plant Ecology 186, 235-246.

1508 Maffei, M., 2003. *Vetiveria*: the genus *Vetiveria*. CRC Press.

1509 Mahmoud, A., Grime, J., 1976. An analysis of competitive ability in three perennial grasses.
1510   New Phytologist 77, 431-435.

1511   Mao, L., Henderson, G., Bourgeois, W.J., Vaughn, J.A., Laine, R.A., 2006. Vetiver oil and
1512   nootkatone effects on the growth of pea and citrus. Industrial Crops and Products 23,
1513   327-332.

1514   Mao, L., Henderson, G., Laine, R.A., 2004. Germination of various weed species in response to
1515   vetiver oil and nootkatone 1. Weed Technology 18, 263-267.

1516   McGranahan, D. A., Archibald, S., Kirkman, K. P., and O'Connor, T. G., 2018. A native C 3
1517   grass alters fuels and fire spread in montane grassland of South Africa. Plant Ecology, 1-
1518   12.

1519   Milchunas, D., Sala, O., Lauenroth, W.K., 1988. A generalized model of the effects of grazing
1520   by large herbivores on grassland community structure. The American Naturalist 132, 87-
1521   106.

1522   Milton, S.J., 2004. Grasses as invasive alien plants in South Africa: working for water. South
1523   African Journal of Science 100, 69-75.

1524   Mulder, J., Brent, A.C., 2006. Selection of sustainable rural agriculture projects in South Africa:
1525   Case studies in the LandCare programme. Journal of Sustainable Agriculture 28, 55-84.

1526   Mynhardt, J.E., Van Rooyen, M., Theron, G., 1994. Competitive ability of two grass species:
1527   *Anthephora pubescens* and *Eragrostis curvula*. 1. Yield and biomass allocation. South
1528   African Journal of Botany 60, 261-268.

1529   Navarro, L., Guitian, J., 2003. Seed germination and seedling survival of two threatened endemic
1530   species of the northwest Iberian Peninsula. Biological Conservation 109, 313-320.

1531   Nix, K.E., Henderson, G., Zhu, B.C., Laine, R.A., 2006. Evaluation of vetiver grass root growth,
1532   oil distribution, and repellency against formosan subterranean termites. HortScience 41,
1533   167-171.

1534   O'Rourke, S., Minasny, B., Holden, N., McBratney, A., 2016. Synergistic use of Vis-NIR, MIR,
1535   and XRF spectroscopy for the determination of soil geochemistry. Soil Science Society
1536   of America Journal 80, 888-899.

1537   Palmer, A.R., Ainslie, A.M., 2005. Grasslands of South Africa. Grasslands of the World 34, 77.

1538   Peltzer, D.A., Wilson, S.D., Gerry, A.K., 1998. Competition intensity along a productivity
1539   gradient in a low-diversity grassland. The American Naturalist 151, 465-476.

1540   Rajaniemi, T.K., 2002. Why does fertilization reduce plant species diversity? Testing three
1541   competition-based hypotheses. Journal of Ecology 90, 316-324.

1542   Remison, S.U., Snaydon, R.W., 1978. Yield, seasonal-changes in root competitive ability and
1543   competition for nutrients among grass species. Journal of Agricultural Science, The 90,
1544   115-124.

1545   Robinson, D., Rorison, I., 1988. Plasticity in grass species in relation to nitrogen supply.
1546   Functional Ecology 2, 249-257.

1547   Sala, O., Lauenroth, W., McNaughton, S., Rusch, G., Zhang, X., 1996. 6 Biodiversity and
1548   Ecosystem Functioning in Grasslands.

1549   Schoener, T.W., 1983. Field experiments on interspecific competition. The American Naturalist
1550   122, 240-285.

1551   Shangwen, C., 1999. Insects on vetiver hedges. The Vetiver Newsletter 23, 17-18.

1552   Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions.
1553   Trends in Ecology & Evolution 17, 170-176.

1554   Shengluan, L., Jiayou, Z., 1998. Contribution of vetiver grass to sustainable agricultural
1555   development in the hilly red soil region In: Xu Liyu (ed) Vetiver Research and
1556   Development. 132-137. China Agriculture Scientech Press, Beijing.

1557   Silletti, A.M., Knapp, A.K., Blair, J.M., 2004. Competition and coexistence in grassland
1558   codominants: responses to neighbour removal and resource availability. Canadian Journal
1559   of Botany 82, 450-460.

1560   Suding, K.N., LeJeune, K.D., Seastedt, T.R., 2004. Competitive impacts and responses of an
1561   invasive weed: dependencies on nitrogen and phosphorus availability. Oecologia 141,
1562   526-535.

1563   Suralta, R.R., Kano-Nakata, M., Niones, J.M., Inukai, Y., Kameoka, E., Tran, T.T., Menge, D.,
1564   Mitsuya, S., Yamauchi, A., 2016. Root plasticity for maintenance of productivity under

1565   abiotic stressed soil environments in rice: Progress and prospects. Field Crops Research
1566   220, 57-66.

1567 Tainton, N., 1981a. ecology of the main grazing lands of South Africa. Veld and pasture
1568   management in South Africa.

1569 Tainton, N.M., 1981b. Veld and pasture management in South Africa. Shuter & Shooter;
1570   University of Natal Press.

1571 Tainton, N.M., 1999. Veld Management in South Africa. University of Natal press.

1572 Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2011. Grass-on-grass competition along a catenal
1573   gradient in mesic grassland, South Africa. African Journal of Range & Forage Science
1574   28, 79-85.

1575 Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2012. Do soil nutrients mediate competition
1576   between grasses and Acacia saplings? Grassland Science 58, 238-245.

1577 The Vetiver Network International, 2017. 20 JUNE The Vetiver Network International, 2017,
1578   http://vetiver.org/.

1579 Thompson, K., 1987. The resource ratio hypothesis and the meaning of competition. Functional
1580   Ecology 1, 297-303.

1581 Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation.
1582   The American Naturalist 116, 362-393.

1583 Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist
1584   125, 827-852.

1585 Tilman, D., 1987. On the meaning of competition and the mechanisms of competitive
1586   superiority. Functional Ecology 1, 304-315.

1587 Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2-
1588   16.

1589 Truong, P., 2000a. Application of the vetiver system for phytoremediation of mercury pollution
1590   in the Lake and Yolo Counties, Northern California. Proceedings of pollution solutions,
1591   1-13.

1592   Truong, P., 2000b. The global impact of vetiver grass technology on the environment.
1593   Proceedings of the Second International Conference on Vetiver, 48-61.

1594   Truong, P., Chomchalow, N., Vessabutr, S., 1999. Vetiver grass technology for mine
1595   rehabilitation. Pacific Rim Vetiver Network Technology 2, 1-19.

1596   Truong, P., Hart, B., Chomchalow, N., Sombatpanit, S., 2001. Vetiver system for wastewater
1597   treatment. Office of the Royal Development Projects Board.

1598   Truong, P., Loch, R., 2004. Vetiver system for erosion and sediment control. Proceeding of 13th
1599   international soil conservation organization conference, 1-6.

1600   Van den Berg, J., Midega, C., Wadhams, L., Khan, Z., 2003. Can Vetiver grass be used to
1601   manage insect pests on crops? Proceedings of the Third International Conference on
1602   Vetiver and Exhibition, 254-264.

1603   Van Oudtshoorn, F.v., 1999. Guide to grasses of Southern Africa. Briza Publications.

1604   Van Oudtshoorn, F.v., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza
1605   Publications.

1606   Veldkamp, J., 1999. A revision of *Chrysopogon* Trin. including *Vetiveria* Bory (Poaceae) in
1607   Thailand and Malesia with notes on some other species from Africa and Australia.
1608   Austrobaileya 5, 503-533.

1609   Visser, V., Wilson, J. R., Canavan, K., Canavan, S., Fish, L., Maitre, D. L., Kumschick, S., 2017.
1610   Grasses as invasive plants in South Africa revisited: Patterns, pathways and
1611   management. Bothalia-African Biodiversity & Conservation 47, 1-29.

1612   Visser, V., Wilson, J. R., Fish, L., Brown, C., Cook, G. D., Richardson, D. M., 2016. Much more
1613   give than take: South Africa as a major donor but infrequent recipient of invasive non-
1614   native grasses. Global Ecology and Biogeography, 25, 679-692.

1615   Vourlitis, G.L., Kroon, J.L., 2013. Growth and resource use of the invasive grass, pampasgrass
1616   (*Cortaderia selloana*), in response to nitrogen and water availability. Weed Science 61,
1617   117-125.

1618   Wagner, S., Truong, P., Vieritz, A., Smeal, C., 2003. Response of vetiver grass to extreme
1619   nitrogen and phosphorus supply. Proceedings of the Third International Conference on
1620   Vetiver and Exhibition, Guangzhou, China.

1621   Wall, R., Begon, M., 1985. Competition and fitness. Oikos, 356-360.

1622   Wang, Y.-W., 2000. The root extension rate of vetiver under different temperature treatments.
1623   Proceedings   of   the   Second   International   Conference   on   Vetiver.
1624   http://www.vetiver.org/TAI_temp.pdf.

1625   Ward, D., 2010. A resource ratio model of the effects of changes in CO2 on woody plant
1626   invasion. Plant Ecology 209, 147-152.

1627   Wedin, D., Tilman, D., 1993. Competition among grasses along a nitrogen gradient: initial
1628   conditions and mechanisms of competition. Ecological Monographs 63, 199-229.

1629   Weiner, J., 1990. Asymmetric competition in plant populations. Trends in Ecology & Evolution
1630   5, 360-364.

1631   Weyerstahl, P., Marschall, H., Splittgerber, U., Wolf, D., 1996. New sesquiterpene ethers from
1632   Vetiver oil. Liebigs Annalen 1996, 1195-1199.

1633   Wilson, S.D., 1993. Belowground competition in forest and prairie. Oikos 68, 146-150.

1634   Wolfe, L.M., 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis.
1635   The American Naturalist 160, 705-711.

1636   Xia, H., 1995. Effect of shading and cutting on the growth of vetiver. Vetiver Grass for Soil and
1637   Water Conservation, 178-179.

1638   Xia, H., Ao, H., He, D., 1998. The effect of environmental factors on the growth of vetiver
1639   growth. Vetiver Research and Development, 39-44.

1640   Xu, L., 1998. Vetiver research and development, Proceedings of International Vetiver
1641   Workshop, Fuzhou, China. Agricultural Science and Technology Press of China, Beijing.

1642   Xu, L., 2002. Vetiver research and development: A decade experience from China, Proceedings:
1643   The Second International Vetiver Conference, ORDPB, Bangkok, 311-322.

1644   Zaloumis, N. P., and Bond, W. J. 2011. Grassland restoration after afforestation: No direction
1645   home?. Austral Ecology 36, 357-366.

1646   Zhu, B.C., Henderson, G., Chen, F., Maistrello, L., Laine, R.A., 2001. Nootkatone is a repellent
1647   for Formosan subterranean termite (*Coptotermes formosanus*). Journal of Chemical
1648   Ecology 27, 523-531.

1649

1650   **2   CHAPTER TWO: WHICH NATIVE GRASSES GROW IN CLOSE PROXIMITY**

1651   **WITH VETIVER GRASS?**

1652   **2.1   ABSTRACT**

1653   Soil erosion has become a major problem affecting agricultural and rangeland productivity,

1654   especially in developing countries. To combat this problem, a fast-growing, densely rooted, and

1655   drought resistant grass called vetiver (*Chrysopogon zizanioides*) has been widely used, mostly in

1656   developing countries. Its use is grounded in two claims, firstly that it does not compete with

1657   neighbouring plants, and secondly, that it does not spread as it produces non-viable seeds.

1658   However, no study has evaluated areas rehabilitated using vetiver to verify these claims. The

1659   contiguous quadrat method was used to survey six sites rehabilitated using vetiver with the aim

1660   to determine how far native grasses grow from planted vetiver and the extent of plant succession

1661   in these rehabilitated sites. The most important results of this study were the marked increase in

1662   grass species richness with an increase in distance away from planted vetiver, the abundance of

1663   bare ground around planted vetiver, and the presence of the recruiting vetiver grass away from

1664   planted vetiver. The presence of bare ground could either indicate a strong competitive ability of

1665   vetiver, and/or an allelophatic effect (possibly from the oil produced by the roots), hence

1666   challenging the first claim. The second claim is challenged by the presence of recruiting vetiver,

1667   indicating signs of spreading. These sites were dominated by unpalatable subclimax species e.g.

1668   *Aristida bipartite*, climax species e.g. *Hyparrhenia hirta*, and only one unpalatable pioneer grass

1669   i.e. *Aristida congesta* subsp *barbicollis* occurring only in one site. The marked dominance of

1670   increaser grasses was as a result of overgrazing because the area surveyed is a communal

1671   rangeland with poorly controlled grazing. There is no doubt that vetiver is beneficial for soil

1672   conservation; however, this study shows that vetiver persists for decades with no sign of being

1673   succeeded by native grasses, and native grasses do not grow in close proximity to vetiver.

1674   **2.2   INTRODUCTION**

1675   Rangeland degradation in the form of soil erosion has become a worldwide problem,

1676   especially in developing countries (Tainton, 1999; O'Rourke et al., 2016). For decades, research

1677   has focused on understanding the causes of soil erosion, mapping erosion over time, and

1678   implementing environmentally sound ways to combat soil erosion (Boardman and Poesen, 2006;

1679   Morgan, 2009). Even though soil erosion is a natural process, it is accelerated by factors such as

1680   clearing of vegetation, overgrazing, and soil tillage, which are directly linked to human activities

1681 (Morgan, 2009). Grasses have been shown to effectively stabilize the soil, increase water
1682 infiltration and reduce surface runoff, hence preventing or reducing the occurrence of soil
1683 erosion (Council, 1993; Everson et al., 2007). However, poor management of rangelands, such as
1684 overgrazing, exposes the topsoil making it susceptible to sheet or rill erosion during rainfall
1685 events (Boardman and Poesen, 2006; Everson et al., 2007). Soil erosion removes the nutrient-
1686 rich topsoil, exposing the nutrient-poor subsoil which prevents re-establishment of native
1687 grasses. Through top soil removal, the soil seed bank is also lost, further reducing the likelihood
1688 of reestablishment (Zhang et al., 2001; DeFalco et al., 2009). Therefore, attempts to rehabilitate
1689 these degraded areas require the re-introduction of native species by means of seeds or tufts to
1690 regain the lost vegetation (Everson et al., 2007). However, not all plant species can grow in these
1691 nutrient poor conditions. Fast growing grass species that can tolerate low nutrient soils and harsh
1692 environmental conditions have been seen as a practical solution to combat soil erosion (Council,
1693 1993). These grasses stabilise the soil and help to capture topsoil runoff with the view to
1694 allowing recolonization of the more sensitive native species. Many indigenous species do not
1695 grow in these nutrient-poor eroded soils and so some exotic species have been propagated for
1696 this purpose.

1697 Vetiver (*Chrysopogon zizanioides* (L.) Roberty) is an exotic grass originating in India
1698 which has been extensively used for controlling soil erosion (Chen et al., 1993; Grimshaw,
1699 1993). It is a fast-growing grass with an extensive root system that extends down to 4m, binding
1700 soil particles together. Vetiver grass tolerates many harsh environmental conditions, such as
1701 drought, floods, nutrient poor soil, and salinity and it is resistant to fires (Chen et al., 1993;
1702 Grimshaw, 1993; Edelstein et al., 2009). A number of claims have been made by promoters of
1703 vetiver grass (The Vetiver Network International, 2017) relating to its competitive ability and
1704 coexistence with other species, which have been used to support and popularize the use of this
1705 grass. The first claim is, vetiver grass does not compete with adjacent crops (Council, 1993;
1706 Vieritz et al., 2003). This means that, after vetiver has established, it should trap the top soil and
1707 restore the nutrient status to allow for establishment of native grasses. However, the evidence
1708 that exists for such claims is from crop plants only, not naturally occurring grasses (Council,
1709 1993; Vieritz et al., 2003). For example, compared with other vegetative barriers (*Leucaena*
1710 *leucocephala*, *Cymbopogon flexuosus*, and *Chrysopogon martini*), vetiver grass resulted in a
1711 25.5% greater yield in seed cotton (*Gossypium hirsutum*) compared to the control, 24% more

1712 compared to *L. leucocephala*, 15% more compared to *Cymbopogon flexuosus*, and 11% more
1713 compared to *Chrysopogon martini* (Vieritz et al., 2003). It is therefore, assumed that even in
1714 rangelands, indigenous grasses will coexist with vetiver and that vetiver will enhance their
1715 recruitment process. The second claim is, vetiver grass does not spread because it produces non-
1716 viable seeds, and has no stolons or rhizomes (Council, 1993). However, no study has properly
1717 evaluated the validity of these claims in rangelands. In rangelands, rehabilitation does not only
1718 involve reestablishing aboveground cover and preventing soil erosion, it also involves promoting
1719 species diversity and retaining naturally occurring species to promote rangeland productivity.

1720   This study aimed to evaluate areas rehabilitated using vetiver grass to determine which
1721 species grow in close proximity to vetiver grass. The three following questions were addressed in
1722 this study:

1723 1.   Are native grasses recruiting and coexisting with vetiver in these sites?

1724 2.   Which native grasses are present in these rehabilitated sites?

1725 3.   How far from the lines of vetiver planted for rehabilitation do these grasses grow?

1726 4.   Is vetiver recruiting in areas where it was not originally planted?

1727 There is so much uncertainty and anecdotal evidence relating to other species' association with
1728 vetiver; therefore, this study is exploratory in that regard.

1729 **2.3 MATERIALS AND METHODS**

1730 **2.3.1 Study site**

1731   The study was conducted in the Okhombe valley, located at the foot of the Northern
1732 Drakensberg Mountains, Bergville, KwaZulu-Natal, South Africa. The Okhombe valley is a
1733 communal rangeland which receives a mean annual rainfall of 800 – 1000 mm, with about 82%
1734 of the rainfall received during summer (Mansour et al., 2012). The mean altitude of this area
1735 ranges from 1200 to 3350 m, with a mean monthly minimum temperature of $11.5^{o}C$ to $16^{o}C$ in
1736 summer (October to March) and below $5^{o}C$ in winter (June to July), with frost and snow
1737 occurring almost every year (Temme, 2008; Mansour et al., 2012). The area has a mixed
1738 geology, ranging from mudstone and sandstone to ampholite, basalt, and tillite with increasing
1739 altitude (Mansour et al., 2012). The mixed geology, rainfall, and topography give rise to mostly

1740 oxidic, well-drained soils with Griffin, Hutton (Oxisol) and Clovelly (Alfisol) on the slopes, and
1741 shallower soils, such as Mispah on top of the catena (Mansour et al., 2012).

1742   The grazing camps are situated on top of the ridges surrounding the settlements in the
1743 bottom of the valley (Fig. 2.1). This presents a management problem because livestock have to
1744 move up to the grazing camps every morning and down to the settlements at night. This
1745 movement creates paths on the slopes which then get easily eroded during intense rainfall
1746 periods. As a result, these soils have become heavily eroded and so rehabilitation programmes
1747 have been initiated. Vetiver grass was planted as one of the techniques employed for a
1748 programme that aimed at rehabilitation and management of degraded catchments, funded by the
1749 Department of Environmental Affairs, and run by staff from the University of KwaZulu-Natal.
1750 This programme trained local people in the basic causes and effects of soil erosion, the
1751 importance of rehabilitation, ways to rehabilitate eroded sites (e.g. how to plant vetiver), and
1752 formed the Okhombe Monitoring Group. This programme aimed to empower the community
1753 and utilize simple techniques, such as vetiver planting, and stone packs, to rehabilitate degraded
1754 catchments (see Everson et al. 2007 for more detail).

1755   The area is primary grassland, classified as upland moist grassland (Mucina and
1756 Rutherford, 2006). The most dominant grasses in the region are *Hyparrhenia* species, *Eragrostis*
1757 species, *Aristida* species, *Themeda triandra, Digitaria* species, *Panicum* species, *Cymbopogon*
1758 species, *Monocymbium ceresiiforme*, *Sporobolus* species, and *Miscanthus capense* (O'Connor
1759 and Bredenkamp, 1997; Mansour et al., 2012). The area has a long history of research and
1760 collaboration with the University of KwaZulu-Natal as it is a catchment for the Tugela River,
1761 and therefore, a number of different rehabilitation and management programmes have been run
1762 over the last two decades commencing in about 1992. For this work, six sites where vetiver grass
1763 has been used to rehabilitate eroded areas were identified. These sites were rehabilitated between
1764 1992 and 2015.
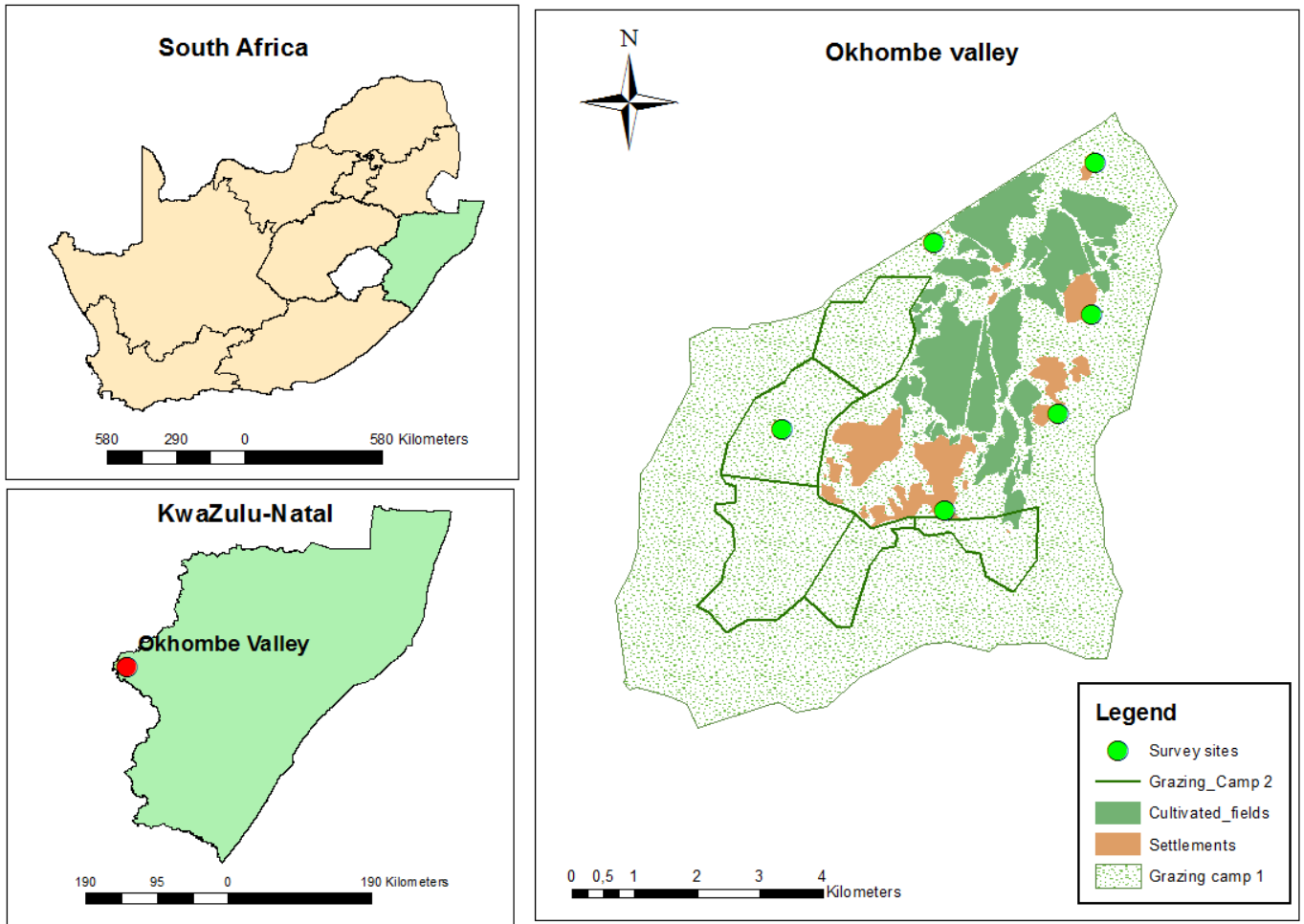
1765

1766   Figure 2.1: The Okhombe Valley in KwaZulu-Natal showing the location and the six survey sites

1767   and the different forms of land use in the region (Mansour et al., 2012).

1768

1769   2.3.2   **Data collection**

1770   The contiguous quadrat method was used when recording species composition and cover

1771   data. All species in each quadrat were identified and their aerial cover was estimated. Starting at

1772   the edge of the planted vetiver grass row, a 0.5m x 0.5m quadrat was placed and then turned over

1773   six times to cover a distance of 3m. This was replicated four times per sites. GPS coordinates

1774   were also recorded at all sites.

1775   **2.3.3   Statistical analysis**

1776   The quadrat data were used to calculate species richness and species abundance. The

1777   residuals for species richness were normally distributed; therefore, the relationship between

1778   species richness and distance from vetiver grass was analysed using linear regression in SPSS

1779   software version 24 (IBM Inc).

1780   Given the rapid species turnover within the dataset, a unimodal method, correspondence

1781   analysis (CA), was used for the ordination of species composition and abundance (species

1782   cover), assessing which species are associated with vetiver grass in relation to years since

1783   rehabilitation and distance from planted vetiver grass rows. Distance from planted vetiver rows

1784   and years since rehabilitation were overlaid as environmental variables. The CA was performed

1785   using Canoco, and the ordination graph drawn using CanoDraw (Ter Braak and Smilauer, 1997).

1786   **2.4 RESULTS**

1787   Overall, a total of ten grass species, one *Helichrysum* species, and one sedge were found

1788   within 3m of vetiver planted in rows (Table 1). *Aristida bipartita, Sporobolus africanus,*

1789   *Eragrostis plana, Eragrostis curvula, and Paspalum notatum* were present in all sites, while

1790   *Hyparrhenia hirta* and *Cymbopogon caesius* were present in most sites except the site that was

1791   rehabilitated in 1992 (Table 2.1). *Aristida congesta,* and *Helichrysum* species were present in

1792   sites rehabilitated in 1992*,* while *Chloris gayana,* and sedges were found in sites rehabilitated in

1793   2011 and 2002, respectively (Table 2.1). Surprisingly, there were two sites (2002 and 2011) that

1794   had vetiver grass recruiting where it was not originally planted (Table 2.1). Species richness

1795   significantly increased with increasing distance from planted vetiver grass rows (R^2=0.4606;

1796   p<0.0001; Figure. 2.2; Table 2.2). However, an increase in variability in species richness moving

1797   away from the planted vetiver grass rows was evidenced (Fig. 2.2).

1798

1799

1800

1801

1802

1803

1804   Table 2.1: Species found in areas rehabilitated using vetiver grass in different years, and their

1805   successional and ecological status. Two sites were rehabilitated in 2002 while other sites were

1806   rehabilitated in different years. In the table below, (**x**) indicates that the species was present, and

1807   (**-**) 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

1808

1809   Table 2.2: Analysis of variance for a linear regression of species richness against distance from

1810   planted vetiver grass rows (m) in all sites rehabilitated using vetiver grass in Okhombe Valley,

1811   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		

1816

y = 1.419x + 2.2667
R² = 0.4606
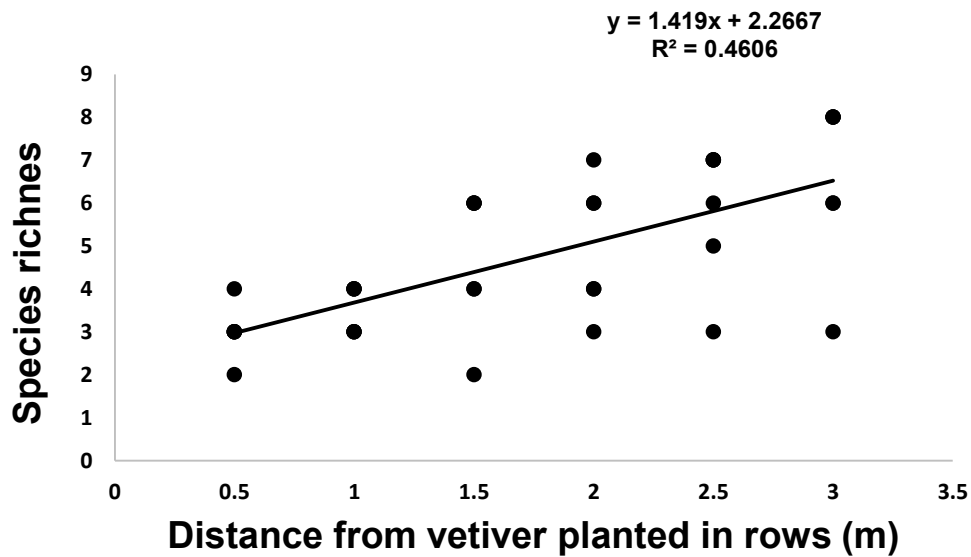
Figure 2.2: Relationship between species richness and distance from vetiver grass in areas rehabilitated using vetiver grass between 1992 and 2015 in the Okhombe Valley, Bergville, KwaZulu-Natal.

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).
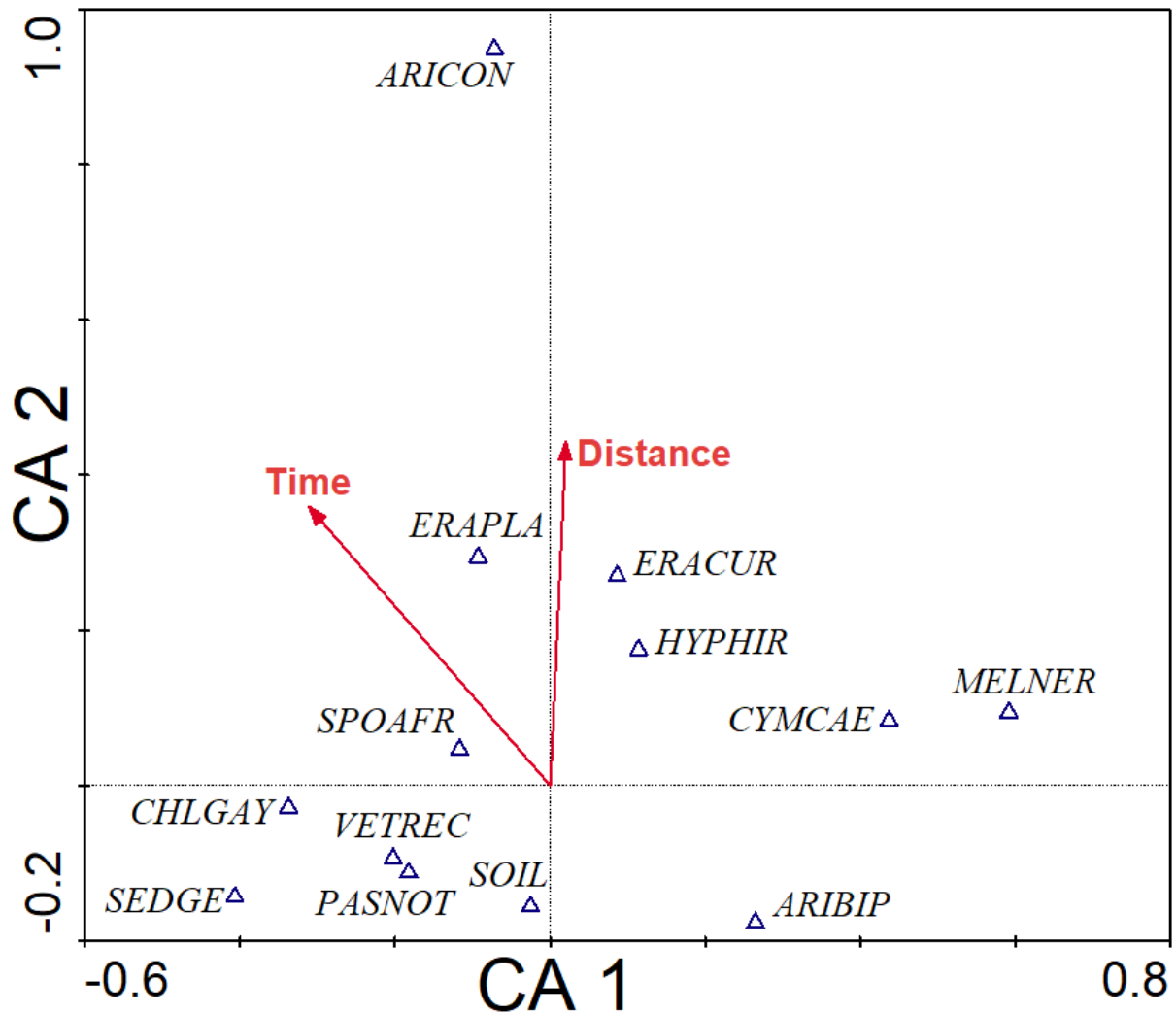
Figure 2.3: Correspondence analysis (CA) ordination of species composition and their basal cover from sites rehabilitated using vetiver grass in different years (i.e. time) correlated with distance from planted vetiver grass (i.e. distance), at Okhombe valley, Bergville, KwaZulu-Natal, South Africa. 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

1845

1846 The most consequential results of this study were the marked increase in grass species
1847 richness with an increase in distance away from the planted vetiver, the abundance of bare
1848 ground around the planted vetiver, and the presence of the recruiting vetiver grass away from the
1849 planted vetiver. Native grasses, therefore, appear to fail to recruit in close proximity with
1850 vetiver, with only a few species managing to successfully recruit half a meter to a meter away
1851 from planted vetiver. The surveyed sites were in a communal rangeland with continuous grazing
1852 (Everson et al., 2007; Mansour et al., 2012). The grass community in these sites, therefore,
1853 reflects both the effect of selective grazing and/or overgrazing, and the extent of secondary
1854 succession as influenced by planting of vetiver (Mansour et al., 2012). The general secondary
1855 successional pattern in grasslands usually follows this order, pioneer grasses — subclimax
1856 grasses — climax grasses (Tainton, 1981, 1999; Van Oudtshoorn, 2012). The pioneers, being
1857 annual grasses which allocate more resources to seed production and have effective seed
1858 dispersal strategies, a trade-off between leaf production and seed production, giving them a
1859 relatively low grazing potential (Van Oudtshoorn, 2012). Subclimax grasses are more densely
1860 tufted and produce more leaf material than annual pioneer grasses (Meredith, 1955; Van
1861 Oudtshoorn, 2012). These grasses offer more soil protection, there are much denser and better at
1862 resource capture e.g. light and nutrients (Meredith, 1955; Tainton, 1999). They outcompete
1863 pioneer grasses and dominate either in areas with moderate rainfall and low soil nutrient status or
1864 moderate soil nutrient status and low rainfall (Tainton, 1999). The grazing potential of most
1865 subclimax grasses range from poor to relatively good (Van Oudtshoorn, 2012). Lastly, climax
1866 grasses are strongly perennial and tufted which vary greatly in their environmental requirements
1867 but grow in normal, optimal conditions that support long-term survival (Van Oudtshoorn, 2012).
1868 These grasses also vary greatly in their grazing potential, with very unpalatable grasses e.g.
1869 *Aristida junciformis*, and very palatable grasses e.g. *Themeda triandra* (Tainton, 1999; Van
1870 Oudtshoorn, 2012).

1871 Selective grazing resulting from a continuous grazing regime could result in the
1872 dominance of unpalatable grasses, which may include unpalatable pioneer, subclimax, and
1873 climax grasses (Tainton, 1999). As grazers select for palatable grasses, less palatable grasses
1874 gain competitive ability and reproduce successfully, hence dominating the sward (Tainton et al.,
1875 1980; Tainton, 1999). Grazing in these rehabilitating sites acts as a second disturbance (Cramer

1876   et al., 2008) which could, therefore, potentially alter the general successional pattern, resulting in

1877   vegetation that is a mixture of unpalatable subclimax and climax species, and even some strong

1878   competitive pioneer species (Tainton, 1999; Cramer et al., 2008). This is evidenced in this study

1879   as the surveyed plots were dominated by unpalatable subclimax species e.g. *Aristida bipartita,*

1880   *Sporobolus africanus,* and climax species e.g. *Hyparrhenia hirta* and *Cymbopogon caesius*, with

1881   only one unpalatable pioneer grass i.e. *Aristida congesta* subsp *barbicollis* occurring only in one

1882   site. The only palatable grass i.e. *Chloris gayana* occurred only in one site and was not a

1883   dominant species. This grass reproduces by both seeds and vegetatively- through a creeping

1884   stolon. It adopts several seed dispersal strategies, namely wind, water, and animal agents

1885   (Meredith, 1955). Therefore, this grass could have established from seeds which were either

1886   attached to livestock skin, collected from palatable climax patches dominated by *Chloris gayana*

1887   in the surrounding areas, or/and wind-dispersed seeds. There are previous studies in this village

1888   which used hyperspectral remotely sensed data to discriminate patches dominated by palatable

1889   climax grasses (e.g. *Themeda triandra*) to those dominated by less palatable climax grass (e.g.

1890   *Hyparrhenia hirta*) as a management approach (Mansour et al., 2012; Mansour et al., 2016).

1891   They showed that it is possible to discriminate between these patches using remotely sensed data

1892   and that there are still patches dominated by palatable climax species in these continuously

1893   grazed grasslands (Mansour et al., 2012; Mansour et al., 2016). This, therefore, means that these

1894   patches could have been the source for *Chloris gayana* seeds. However, it is fair to assume that

1895   some surveyed sites did not have patches dominated by palatable species near them, hence why

1896   only one out of the six surveyed sites had *Chloris gayana* out of the six surveyed sites. *Chloris*

1897   *gayana* seeds have a relatively good germination potential, thus explaining the recruitment

1898   success, and it is usually a preferred grass for reseeding, mostly with the aim to stabilize the soil

1899   (Meredith, 1955; Van Oudtshoorn, 2012).

1900   These rehabilitated rangelands can be classified as unpalatable climax grassland, as they

1901   were dominated by more climax species than subclimax species. The subclimax species occurred

1902   relatively close to the planted vetiver compared to the climax species. However, there was no

1903   clear relationship between successional stages and years since rehabilitation. These findings are

1904   relatively similar to those reported by studies of plant succession in old-fields or abandoned

1905   agricultural fields (Bonet, 2004; Bonet and Pausas, 2004). For example, Bonet (2004) in a

1906   vegetation change study examining a 60 year old abandoned agricultural field, showed that there

1907   was a nonlinear relationship between years since abandonment and plant successional status, and
1908   rather there was a clear coexistence of different plant functional groups. The progress of plant
1909   succession and species turnover is dependent on many factors e.g. seed dispersal, soil and
1910   climatic conditions, and availability of a seed bank in that rehabilitating area(Tainton, 1999;
1911   Bonet, 2004). The soil and climatic factors determine which species can recruit; however, if
1912   there are no dispersed seeds or no buried seeds (seed bank) of native plants, such species will not
1913   recruit in that area (Tainton, 1999). For example, climax grass species usually have a poor seed
1914   dispersal ability; therefore, their recruitment is usually dependent on an existing seed bank,
1915   although they can only recruit when the soil and climatic conditions are favourable (Tainton,
1916   1999). Soil erosion usually removes the topsoil and hence the seed bank, therefore, grass species
1917   which have poor dispersal abilities are unlikely to be found in these sites, unless the sites are
1918   reseeded (Tainton, 1999). Therefore, a combined effect of planted vetiver (possibly competition),
1919   grazing, and lack of dispersed and buried seeds could determine the community structure of
1920   these previously eroded sites.

1921   This study showed a relatively clear progressive succession moving away from planted
1922   vetiver, i.e. a clear turnover of subclimax to climax species accompanied by an increased species
1923   richness. The ecological and successional status of these plant communities can be related to
1924   specific species responses to defoliation (i.e. grazing) or the decreaser-increaser concept
1925   described by Foran et al (1978) and modified by Tainton et al (1980). Decreaser species are
1926   grasses which dominate in good veld, but decreases in abundance with poor management i.e.
1927   overgrazing or undergrazing (Foran et al., 1978). These grasses are palatable subclimax and
1928   climax grasses, which are usually preferred by grazing animals (Van Oudtshoorn, 2012).
1929   Increaser I species are grasses which dominate in undergrazed or underutilized veld (Foran et al.,
1930   1978). These are usually robust climax, unpalatable species which usually grow well without any
1931   form of defoliation (Van Oudtshoorn, 2012). Increaser II species are subclimax and pioneer grass
1932   species which dominate in overgrazed veld (Foran et al., 1978). These species are a mixture of
1933   palatable and less palatable grasses, and are usually associated with low rainfall areas, but can be
1934   found in high rainfall areas which are overgrazed and have nutrient-poor soils (Van Oudtshoorn,
1935   2012). Increaser III species are climax grass species which dominate in selectively grazed veld
1936   (Tainton et al., 1980). These are usually very unpalatable robust tufted perennials, which are

1937 strong competitors and increase when climax palatable grasses are weakened by being
1938 overgrazed (Tainton et al., 1980; Van Oudtshoorn, 2012).

1939   The species dominating in all sites were mostly increaser II (i.e. *Aristida bipartita,*
1940 *Eragrostis plana, Eragrostis curvula*) and increaser III (i.e. *Sporobolus africanus*), and one
1941 invasive (i.e. *Paspalum notatum*) species (Van Oudtshoorn, 2012). This is a clear indication of
1942 the effect of grazing on the succession status and community structure of these rehabilitating
1943 sites. *Paspalum notatum* was sown concurrently with vetiver, as part of the rehabilitation
1944 programme (Everson et al., 2007). This grass is an alien grass from Mexico, the Caribbean, and
1945 South America, tolerant to drought, increases in abundance when grazed because of its deep
1946 roots and strong creeping rhizomes, and this is thus useful for soil erosion control (Van
1947 Oudtshoorn, 2012). However, even this creeping strong competitive grass could not cover the
1948 bare ground around vetiver (Van Oudtshoorn, 2012), suggesting that either the competitive
1949 ability of vetiver and/or allelopathy from oil produced in the roots is inhibiting the recruitment of
1950 other grasses near vetiver (Van den Berg et al., 2003). This therefore, challenges the two claims
1951 made about vetiver competitive ability and coexistence with other grasses. These claims are 1)
1952 vetiver does not compete with adjacent crops, and 2) vetiver does not spread because it produces
1953 non-viable seeds, and has no stolon or rhizomes (Vieritz et al., 2003). For these claims to hold,
1954 other grasses should coexist well with vetiver, and there should be no signs of vetiver recruiting
1955 outside of the planted areas. Unfortunately, the presence of bare ground around the vetiver plants
1956 and the evidence of vetiver recruiting, where it was not planted, strongly challenges the validity
1957 of these claims.

1958   Council (1993) reported that there are few incidences where vetiver was reported to have
1959 recruited, showing signs of spreading, although this was anecdotal evidence from interviews with
1960 the farmers. Whether vetiver recruited using suckers developed from roots or if the environment
1961 became favourable to allow a few seeds to be produced and to germinate, is not known. These
1962 surveyed sites need to be monitored regularly to understand whether or not the recruitment is
1963 accidental through the washing away of few vetiver reproductive roots to a nearby location, or
1964 whether these are initial signs of vetiver spreading. However, it is clear that it did recruit, even
1965 though only a few tufts were seen, suggesting that even through recruiting, probably, there are
1966 still unknown inhibitory factors that inhibit recruitment and spreading of this grass. Vetiver grass

1967 is very dependent on its belowground material for reproduction, thus clipped upper surface roots
1968 alone can give rise to new plants (Greenfield, 2002).

1969   From this study and the published literature, there are many unanswered questions
1970 relating to: 1) vetiver reproductive potential, seed germination and the extent of vegetative
1971 reproduction; 2) the effect of established vetiver on seed germination and seedling establishment
1972 of indigenous species and; 3) the competitive interaction between established vetiver and mature
1973 native grass tufts. These questions will help develop a better understanding of vetiver ecology
1974 and, particularly questions 2 and 3 will help to understand what causes the bare areas around
1975 planted vetiver. In addition, all these questions are important to understand the potential of
1976 vetiver becoming invasive. From this study, it is clear that the previously mentioned two claims
1977 about vetiver do not hold and have to be revisited. While there is no doubt that the use of vetiver
1978 is beneficial for soil and water conservation and allows (to a limited extent) progressive
1979 vegetation succession, the availability of bare ground around planted vetiver could indicate that
1980 vetiver is a territorial grass. Vegetative regeneration by means of tillering adopted by vetiver is
1981 an extremely slow process (Tainton, 1999; Greenfield, 2002). For this reason, vetiver is unlikely
1982 to become a problem but can become a permanent feature in rehabilitated areas, reducing forage
1983 availability. Even though these rehabilitated sites showed progress in terms of plant succession
1984 and increases in species richness within 3m of planted vetiver, suggesting that vetiver does help
1985 retain topsoil allowing other grasses to grow, this study shows that native grasses do not grow in
1986 particularly close proximity to vetiver, supporting the notion that it may develop permanent
1987 monotypic patches.

1988 **2.6 REFERENCES**

1989 Boardman, J., Poesen, J., 2006. Soil erosion in Europe: major processes, causes and
1990   consequences, in: Boardman, J., Poesen, J. (Eds.), Soil Erosion in Europe. Wiley.,
1991   Chichester, pp. 477-487.

1992 Bonet, A., 2004. Secondary succession of semi-arid Mediterranean old-fields in south-eastern
1993   Spain: insights for conservation and restoration of degraded lands. Journal of Arid
1994   Environments 56, 213-233.

1995 Bonet, A., Pausas, J.G., 2004. Species richness and cover along a 60-year chronosequence in old-
1996   fields of southeastern Spain. Plant Ecology 174, 257-270.

1997   Chen, K., Hu, G., Rao, H., Xu, L., Hu, H., 1993. Ecological effects of planting vetiver grass in
1998   citrus groves in sloping red soil fields. Acta Ecologica Sinica 14, 249-254.

1999   Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

2000   Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land
2001   abandonment and ecosystem assembly. Trends in Ecology & Evolution 23, 104-112.

2002   DeFalco, L., Esque, T., Kane, J., Nicklas, M., 2009. Seed banks in a degraded desert shrubland:
2003   influence of soil surface condition and harvester ant activity on seed abundance. Journal
2004   of Arid Environments 73, 885-893.

2005   Edelstein, M., Plaut, Z., Dudai, N., Ben-Hur, M., 2009. Vetiver (*Vetiveria zizanioides*) responses
2006   to fertilization and salinity under irrigation conditions. Journal of Environmental
2007   Management 91, 215-221.

2008   Everson, T.M., Everson, C.S., Zuma, K., 2007. Community based research on the influence of
2009   rehabilitation techniques on the management of degraded catchments. Water Research
2010   Commission.

2011   Foran, B., Tainton, N., Booysen, P.d.V., 1978. The development of a method for assessing veld
2012   condition in three grassveld types in Natal. Proceedings of the Annual Congresses of the
2013   Grassland Society of Southern Africa 13, 27-33.

2014   Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth.
2015   Infinity Publishing.

2016   Grimshaw, R.G., 1993. The role of vetiver grass in sustaining agricultural productivity. Asia
2017   Technical Department. The World Bank, Washington DC USA.

2018   Mansour, K., Mutanga, O., Adam, E., Abdel-Rahman, E.M., 2016. Multispectral remote sensing
2019   for mapping grassland degradation using the key indicators of grass species and edaphic
2020   factors. Geocarto International 31, 477-491.

2021   Mansour, K., Mutanga, O., Everson, T., Adam, E., 2012. Discriminating indicator grass species
2022   for rangeland degradation assessment using hyperspectral data resampled to AISA Eagle
2023   resolution. ISPRS Journal of Photogrammetry and Remote Sensing 70, 56-65.

2024   Meredith, D., 1955. The grasses and pastures of South Africa. The grasses and pastures of South
2025   Africa.

2026   Morgan, R.P.C., 2009. Soil erosion and conservation. John Wiley & Sons.

2027   Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland.
2028   South African National Biodiversity Institute.

2029   O'Connor, T.G., Bredenkamp, G.J., 1997. Grassland. In: Cowling, R.M., Richardson, D.M.,
2030   Pierce, S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press,
2031   Cambridge, 215–257.

2032   O'Rourke, S., Minasny, B., Holden, N., McBratney, A., 2016. Synergistic use of Vis-NIR, MIR,
2033   and XRF spectroscopy for the determination of soil geochemistry. Soil Science Society
2034   of America Journal 80, 888-899.

2035   Tainton, N., Edwards, P., Mentis, M., 1980. A revised method for assessing veld condition.
2036   Proceedings of the Annual Congresses of the Grassland Society of Southern Africa 15,
2037   37-42.

2038   Tainton, N.M., 1981. Veld and pasture management in South Africa. Shuter & Shooter;
2039   University of Natal Press.

2040   Tainton, N.M., 1999. Veld Management in South Africa. University of Natal press.

2041   Temme, A., 2008. Understanding Landscape Dynamics over Thousand Years: Combining Field
2042   and Model Work: With Case Study in the Drakensberg Foothill. KwaZulu-Natal, South
2043   Africa.

2044   Ter Braak, C., Smilauer, P., 1997. Canoco for Windows, Biometrics. Plant Research
2045   International, Wageningen, The Netherlands.

2046   The Vetiver Network International, 2017. 20 June, The Vetiver Network International, 2017,
2047   http://vetiver.org/.

2048   Van den Berg, J., Midega, C., Wadhams, L., Khan, Z., 2003. Can Vetiver grass be used to
2049   manage insect pests on crops? Proceedings of the Third International Conference on
2050   Vetiver and Exhibition (ed. by RG Grimshaw), 254–264.

2051   Van Oudtshoorn, F.v., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza
2052   Publications.

2053   Vieritz, A., Truong, P., Gardner, T., Smeal, C., 2003. Modelling Monto vetiver growth and
2054   nutrient uptake for effluent irrigation schemes. Proceedings of the Third International
2055   Conference on Vetiver and Exhibition, 254-264.

2056   Zhang, Z., Shu, W., Lan, C., Wong, M., 2001. Soil seed bank as an input of seed source in
2057   revegetation of lead/zinc mine tailings. Restoration Ecology 9, 378-385.

2058 **3 CHAPTER 3: DOES VETIVER ALLOW GERMINATION AND ESTABLISHMENT**
2059 **OF NATIVE GRASSES?**

2060 **3.1 ABSTRACT**

2061 Vetiver grass (*Chrysopogon zizanioides* (L.) Roberty) is a tufted perennial grass from India, used
2062 worldwide for rehabilitating eroded rangelands and for other soil and water conservation
2063 practices. Morphological features e.g. dense extensive root system (4m deep), and the claim that
2064 it allows recruitment of other grasses around it has popularized the use of this grass. However,
2065 this claim has not been extensively examined. The effect of vetiver tufts and sowing method on
2066 seed germination and seedling establishment of *Eragrostis curvula* and *Panicum maximum* was
2067 examined using pot trials. One hundred seeds of each species were planted alone, around one
2068 vetiver tuft and between two vetiver tufts planted fifteen centimeters apart. These native grass
2069 seeds were sown on the soil surface, buried, and mixed with a water retention gel. Native grass
2070 seedling response when root interaction was excluded using a 42-micron nitex mesh was also
2071 investigated as a follow-up pot trial. The root profile picture taken from cutting the soil-root
2072 material of vetiver and *E. curvula* was analyzed using NIS-Element BR software to quantify the
2073 amount of space available around each species for other species to colonize. Vetiver tufts
2074 facilitated seed germination in both *E. curvula* and *P. maximum*, and seeds sown on the soil
2075 surface had a greater germination percentage compared to other sowing methods. However,
2076 vetiver tufts inhibited seedling establishment of these grasses, even when the root competition
2077 was excluded. Vetiver had less root space available for other species to colonize compared to *E.*
2078 *curvula*, which suggests that dense roots of vetiver could be causing direct root competition for
2079 space and thus, inhibiting establishment of native grasses. Shading by vetiver could be retaining
2080 soil moisture and hence creating a favorable environment for the seeds of native grasses to
2081 germinate. A combination of vetiver shade, direct root competition, and allelopathy (possibly
2082 from oil produced by the roots) could be causing an inhibitory effect on native grass seedling
2083 establishment. These findings, therefore, suggest that it is unlikely that vetiver will allow
2084 recruitment of native grasses, which means rehabilitation using vetiver is unlikely to allow
2085 succession by native grasses.

2086

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

66

2118 and inhibit seed germination and seeding establishment through direct root competition and/or
2119 allelopathy (Schenk et al., 1999).

2120   Territoriality in plants relates to both root spatial segregation and allelopathy (Schenk et
2121 al., 1999; Dias et al., 2016). Plants with spatially segregated roots occupy vacant soil volumes
2122 and by so doing, they avoid direct root competition from the neighboring plants (Schenk et al.,
2123 1999). However, some plants with dense roots and those with creeping stolons or rhizomes can
2124 utilize most soil space around them, creating an unfavorable microclimate for recruitment of
2125 other grasses (Schenk et al., 1999; Schenk and Jackson, 2002). Allelopathy does not require
2126 segregated or clumped roots because it involves the release of allelochemicals which inhibit seed
2127 germination and establishment of other grasses (Ghebrehiwot et al., 2014; Dias et al., 2016).
2128 These two behaviors are seen as territoriality because they usually result in bare soil around that
2129 grass plant (Ghebrehiwot et al., 2014). If these bare soil areas are large, a soil crust could
2130 develop, lacking soil moisture and thus further inhibiting seed germination and seedling
2131 establishment of native grasses (Morgan, 2009). Vetiver oil has been shown to have allelopathic
2132 propitiates that inhibit weed species germination and establishment (Mao et al., 2004). This
2133 allelopathic behaviour could also inhibit native grasses germination and establishment; however,
2134 no study has addressed this question. Therefore, vetiver research should shift from the
2135 application of vetiver in soil and water conservation to questions surrounding its ecology such as,
2136 its effect on native grasses germination and seedling recruitment because seedlings are more
2137 sensitive to competition than adult plants. Moreover, the focus of rangeland rehabilitation
2138 projects has shifted from soil protection alone to promoting species diversity with the aim of
2139 improving grassland productively (Bakker et al., 2003).

2140 It is for these reasons that this study was conducted, and aimed to answer the following
2141 questions:

2142   1. Do vetiver grass tufts inhibit or facilitate seed germination in native grasses?

2143   2. Is the germination rate of native grasses affected by the seed sowing method?

2144   3. Do vetiver grass tufts inhibit establishment of native grasses?

2145   4. Does the exclusion of direct root interaction decrease the competitive effect exerted on
2146   native grass seedlings?

2147   5. Does vetiver root density differ from indigenous grass root density?

2148   An improved understanding of whether vetiver allows recruitment of native grasses, and
2149   how to sow native grass seeds to promote successful coexistence with vetiver grass will help to
2150   explain the patterns observed in areas already rehabilitated using vetiver. Furthermore, it will
2151   help to formulate a practical guide to using vetiver not only for soil erosion control but for
2152   promoting grassland productivity.

2153   **3.3   MATERIALS AND METHODS**

2154   **3.3.1   Study area and species**

2155   The study was conducted under greenhouse conditions at the NM Tainton Arboretum at the
2156   University of KwaZulu-Natal, Pietermaritzburg campus, South Africa, (S 29°37′47″, E
2157   30°24′07″).

2158   Two native grass species, *Eragrostis curvula* and *Panicum maximum* (also known as
2159   *Megathyrsus maximus*) were used in this study. These two native grasses were chosen because
2160   they have contrasting physical and ecological traits but are both used for rehabilitation. For
2161   example, *E. curvula* is a pioneer grass, producing large numbers of small seed with a high
2162   germination percentage, while *P. maximum* is a late seral grass, producing fewer, larger seeds
2163   with lower viability (Meredith, 1955; Adkins et al., 2000: Fish et al. 2015). *Eragrostis curvula* is
2164   a densely tufted perennial grass with an open panicle (6-30cm) and leaves that are crowded at the
2165   base, but it is an increaser grass species which is extremely variable with many different forms
2166   (Meredith, 1955; Tainton et al., 1976; Van Oudtshoorn, 2012). *P. maximum* is a tufted perennial,
2167   shade tolerant grass usually with a creeping rhizome and an open panicle (20-30 cm), and has
2168   broad leaves (Meredith, 1955; Tainton et al., 1976; Van Oudtshoorn, 2012). It is a decreaser
2169   species grass which is exceedingly variable in height (up 200 cm) and is invasive in other parts
2170   of the world (Meredith, 1955; Bogdan, 1977; Van Oudtshoorn, 2012).

2171   In order to maximize germination potential, the seeds of these grasses were bought from a
2172   commercial supplier (McDonald's Seeds, 2 Trek road, Mkondeni, Pietermaritzburg, South
2173   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

2203 did not have full root interaction (full root interaction vs. none) because it would have given us
2204 results which are similar to the previous trial, and therefore, the only control was the native
2205 species growing alone. *Panicum maximum* had a slow germination rate and low germination
2206 percentage and so was omitted from this follow-up study, with *E. curvula* being the only native
2207 grass used. The interaction between the roots of vetiver and those of *E. curvula* was prevented
2208 using a 42-micron Nitex mesh (purchased at Meshcape Industries (Pty) Ltd, 30 Nipper Rd, New
2209 Germany, South Africa).

2210 Three-week-old *E. curvula* seedlings were planted alone, with one vetiver tuft, and with
2211 two vetiver tufts, with the roots of these species carefully separated by pasting the Nitex mesh
2212 into the pots to create two, or three chambers using a strong waterproof epoxy (Epidermix 372
2213 purchased at Hayfields Mica Hardware, Pietermaritzburg) (See Fig. 3.1). Five seedlings of *E.*
2214 *curvula* were planted in each pot, and there were six replicates of each treatment. The Nitex
2215 mesh prevents direct root interaction but allows chemicals and nutrients to pass through it (Fig
2216 3.1). Therefore, it excludes root competition but allows any allelopathic behavior and shading to
2217 be investigated. The experiment had six replicates, laid out in a completely randomized
2218 arrangement. Pots were watered every second day and the water that appeared in the tray under
2219 the pot was used also to re-water the pots to ensure that any compounds released by the vetiver
2220 were not lost.

2221 The trial ran for 4 months (March to June 2017) and seedling height, number of leaves
2222 per seedling, and number of tillers per seedling were recorded every second week. The
2223 aboveground biomass was harvested at the end of the trial, oven dried for 48 hours at 60°C and
2224 then weighed.

2225 ***Root density analysis***

2226 Previous studies have found that measuring root density has proven difficult because fine
2227 roots are easily washed out and lost during the root extraction process (Cahill, 2002). For this
2228 reason, a different approach was used to quantify how much space is available for other roots to
2229 colonize using the plants in the control pots (grasses that were grown alone). Four replicates of
2230 representative pots containing one vetiver tuft, two vetiver tufts and mature *E. curvula* growing
2231 alone, were selected. The soil and root material was carefully removed from the pot and cut in
2232 half, without disturbing the soil, to form a root profile. A photograph of the root profile was

2233 taken and analyzed using NIS-Element BR software (Nikon Inc.). The NIS-Element BR software
2234 analyzed pixel colour of roots and the soil and by setting the intensity of the colours as a constant
2235 (roots coloured blue and soil coloured red with the intensity of both colours standardized to 80%)
2236 the total area comprised of by roots (blue) and soil (red) was calculated (Fig.3.2). This data was
2237 then used to determine the percentage (%) space taken up by the roots and percentage space
2238 available for other roots to colonize.

3.3.3 Statistical analysis

2240   Generalized linear models (GZLM) in SPSS version 24 (IBM Inc. 2016) were used to
2241 analyze the data because the data violated the assumptions of the analysis of variance (ANOVA)
2242 even when transformed (Quinn and Keough, 2002). A gamma distribution with a log link
2243 function was used for scale data such as the mean number of leaves per seedling, mean seedling
2244 height (cm), and mean number of tillers per seedling to assess the effect of vetiver presence (full
2245 competition) and sowing method in the germination and establishment trial.

2246   However, for count data, in this case the number of germinated seeds, a Poisson
2247 distribution was used, with over-dispersion of the data controlled. To assess the effect of
2248 competition and sowing method on seedling survival a binomial distribution with a logit link
2249 function was used, where survival (number of seedlings that survived) was an event and the
2250 number of germinated seeds was a trial. For the survival data, where the generalized linear
2251 models were not appropriate, because of a lack of variance (e.g. in *P. maximum* where there was
2252 one seed germinated and one seedling survived), a single value was substituted, which made the
2253 test more conservative (Kiepiel and Johnson, 2014). Values from a linear scale were back-
2254 transformed to obtain marginal means which resulted in asymmetrical standard errors (Kiepiel
2255 and Johnson, 2014).

2256   For the root exclusion trial, a linear distribution with an identity link function was used to
2257 assess the effect of vetiver presence (competition) on the mean seedling height (cm), mean
2258 number of leaves per seedling, mean number of tillers per seedling, and aboveground biomass
2259 (g). Furthermore, a linear distribution with an identity link function was used to assess whether
2260 there was a significant difference in soil space occupied by roots of *E. curvula*, and one or two
2261 vetiver grass tufts. For all these analyses, where the model showed significant differences,
2262 sequential Sidak was used to adjust for multiple comparisons ($\alpha = 0.05$).
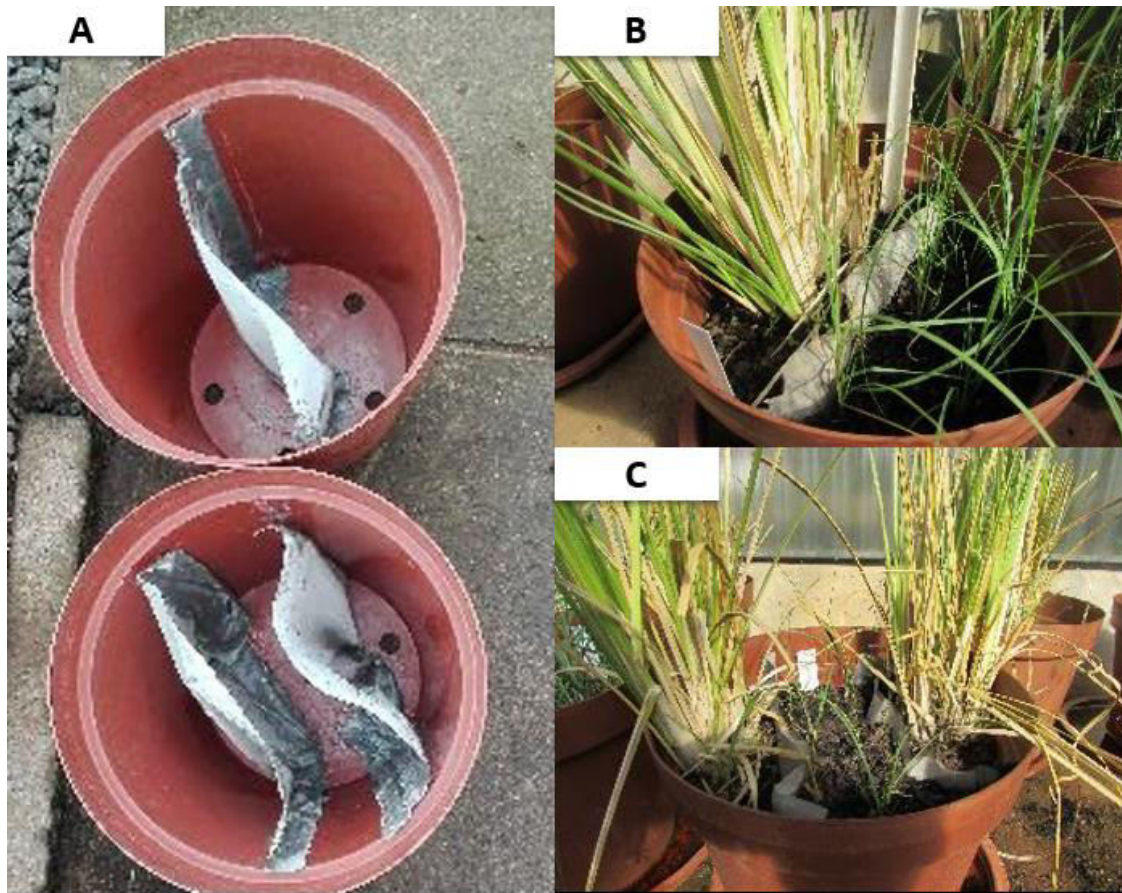
2263

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**).

2267
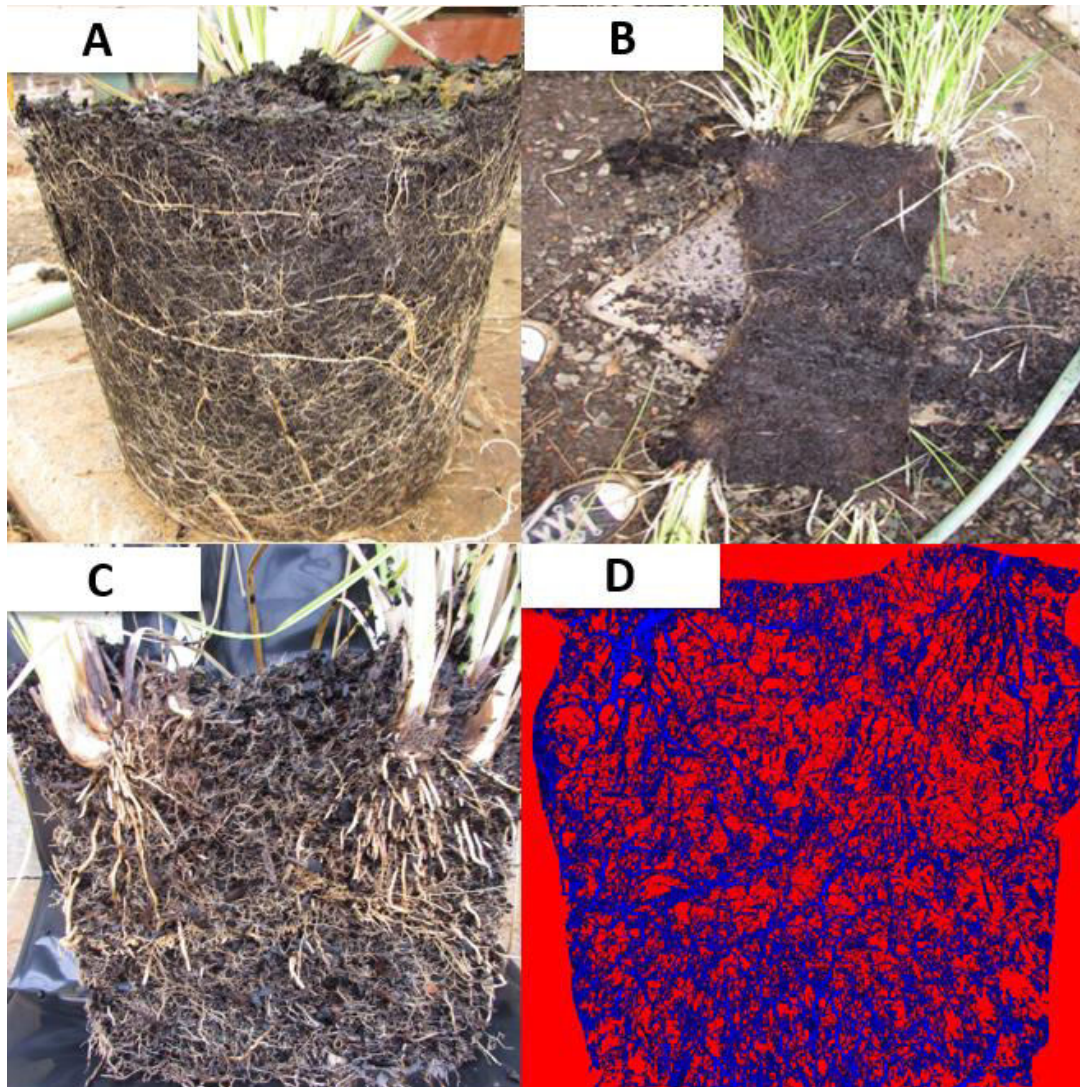
2268

2269 Figure 3.2: The root-soil profile used for analyzing root density and the illustration of the steps
2270 involved from the careful removal of roots and soil from the pot (**A**), cutting of a soil profile (**B**),
2271 Taking a picture (**C**), and root pixel analysis (**D**).

2272 **3.4 RESULTS**

2273 **3.4.1   Seed germination**

2274 *Main effects*

2275   *Eragrostis curvula* and *Panicum maximum* differed significantly in their germination
2276 percentage (P <0.0001) (Table 3.1), with *E. curvula* (39% ± 1.683) having a greater germination
2277 percentage than *P. maximum* (2.20% ± 0.279). The presence of vetiver tufts and sowing method
2278 significantly affected seed germination overall (P<0.0001) (Table 3.1). *Eragrostis curvula* and

73

2279 *P. maximum* responded differently to competition ($P<0.0001$) but not to sowing method ($P=$
2280 0.448). The interaction between competition and sowing method had no significant effect on
2281 germination overall ($P= 0.260$) or on each species individually ($P=0.245$) (Table 3.1).

2282 Table 3.1: The effect of the presence of vetiver (competition), sowing method, and their
2283 interaction using a generalized linear model on seed germination (Poisson distribution) and
2284 seedling survival (%) (Binary distribution, events by trials) of two native grass species
2285 (*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

2286

Effect of competition

2288   Overall the native grasses germinated better in the presence of vetiver tufts compared to
2289 the control, but there was no significant difference in percentage germination between one
2290 vetiver tuft and two vetiver tufts (Fig.3.3A). Individually, these species showed a similar trend,
2291 although, *E. curvula* germination was substantially greater than *P. maximum* with *E. curvula*
2292 having a maximum percentage germination of about 45% and a minimum of 30%, compared to 6
2293 % and 1% maximum and minimum germination by *P. maximum,* respectively (Fig.3.3B).

Sowing method

2295   Seeds sown on the soil surface germinated better than those that were buried and those
2296 mixed with water retention gel, but there was no significant difference between seeds buried and
2297 those mixed with a water retention gel (Fig. 3.4).

2298
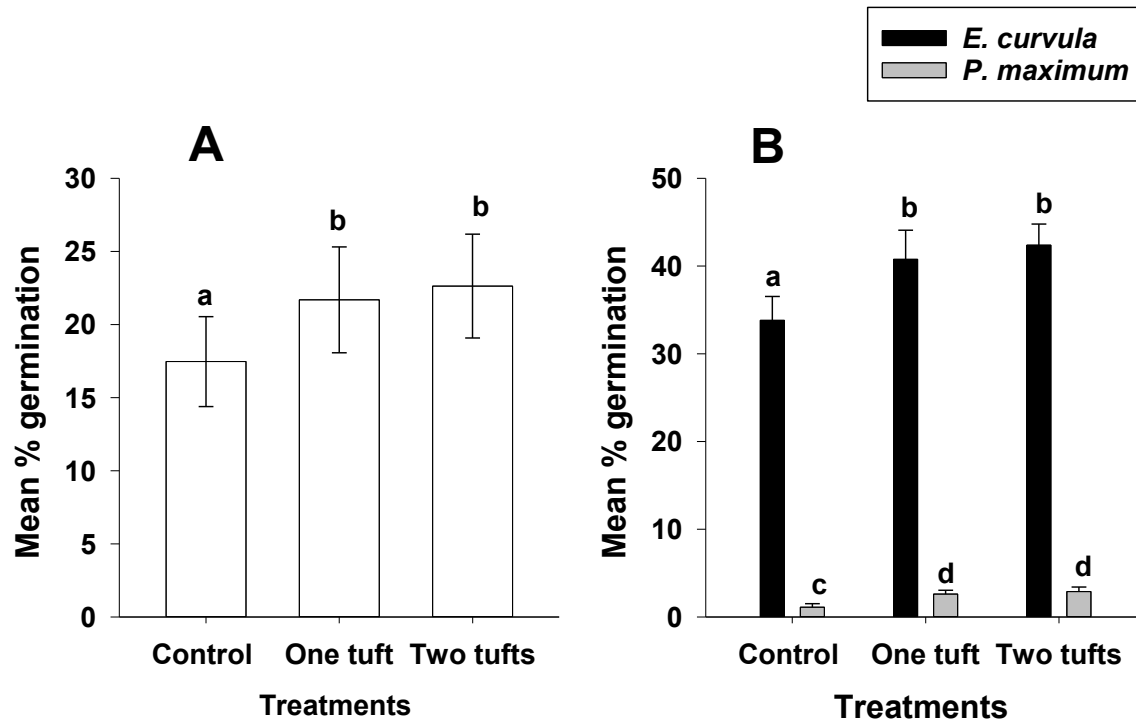
2299

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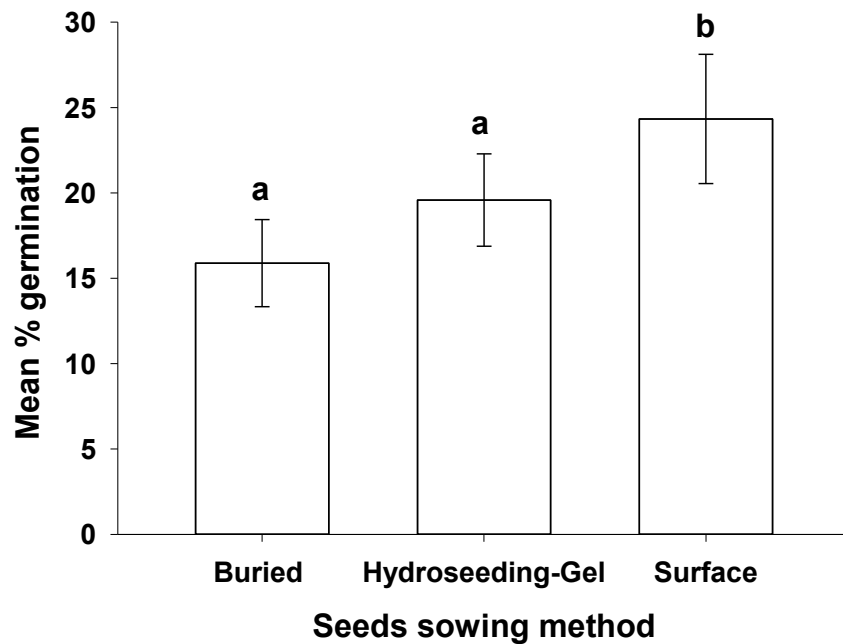
Figure 3.4: Main effect of sowing method on mean germination percentage (± SE) of *Eragrostis curvula* and *Panicum maximum* overall. Different letters represent a significant difference between treatments (p<0.05).

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).
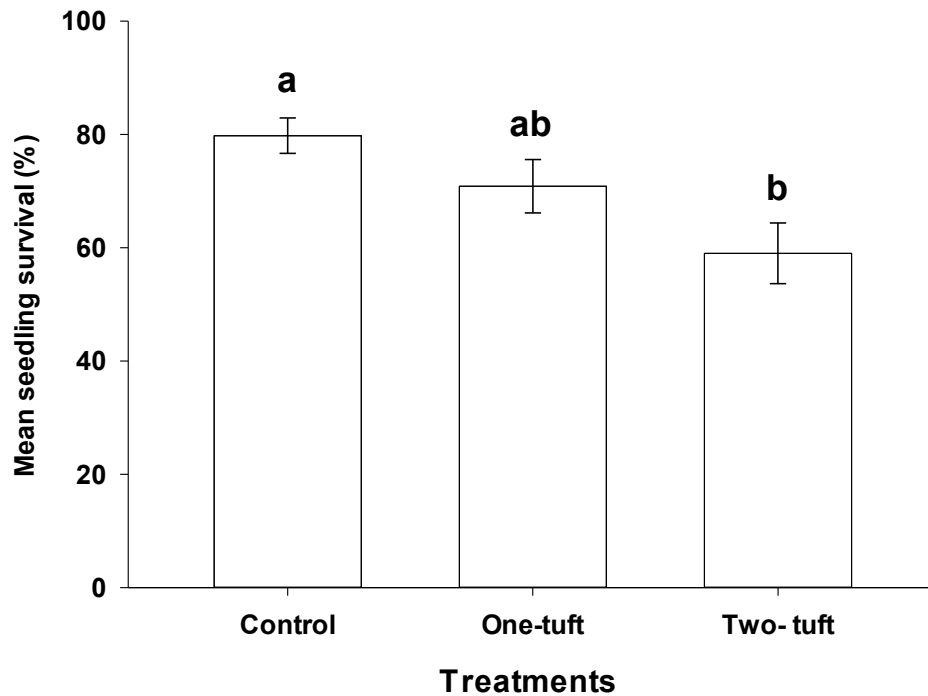
2320

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.

2337   Sowing method; however, did not affect seedling height (P=0.238), number of tillers per

2338   seedling (P=0.372), and number of leaves per seedling of both native species (P=0.843).

2339   *Eragrostis curvula* and *P. maximum* responded differently to competition in terms of seedling

2340   height (P= 0.007), but not number of tillers per seedling (P=0.071), and number of leaves per

2341   seedling (P=0.539). Seedling height of *P. maximum* was significantly greater than that of *E.*

2342   *curvula* in the control but these species did not differ significantly in their seedling height when

2343   growing with one, or two vetiver tufts (Fig. 3.7). Both these species experienced a reduced

2344   seedling height when growing with one and two vetiver tufts, but there was no significant

2345   difference between one and two tufts (Fig. 3.7). Sowing method, and the interaction between

2346   competition and sowing method had no effect on any of the variables measured (Table 3.2).

2347   Table 3.2: The effect of the presence of vetiver (competition), sowing method, and their

2348   interaction on seedling height (cm), number of leaves per seedling, and number of tillers per

2349   seedling of two native grass species (*Eragrostis curvula* and *Panicum maximum*) using a

2350   generalized linear model with a gamma distribution and a log link function. Significant p-values

2351   (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

2352
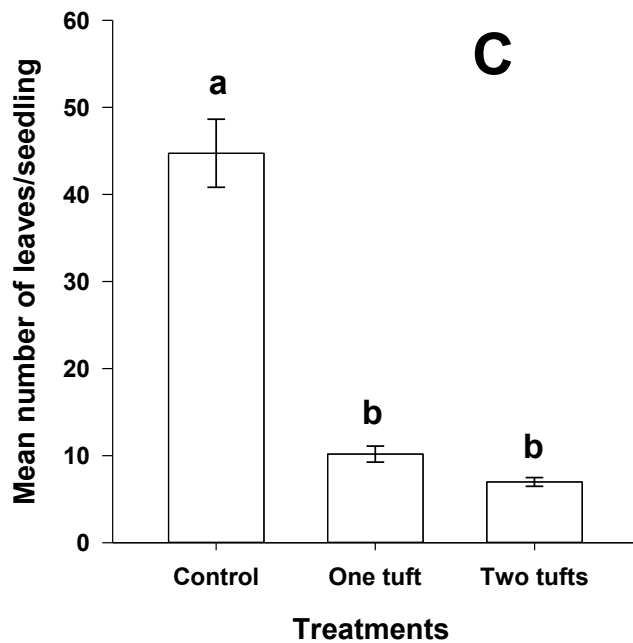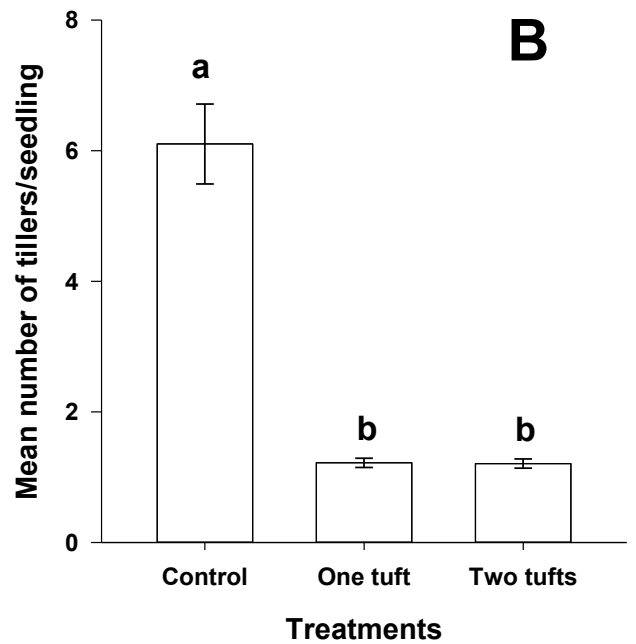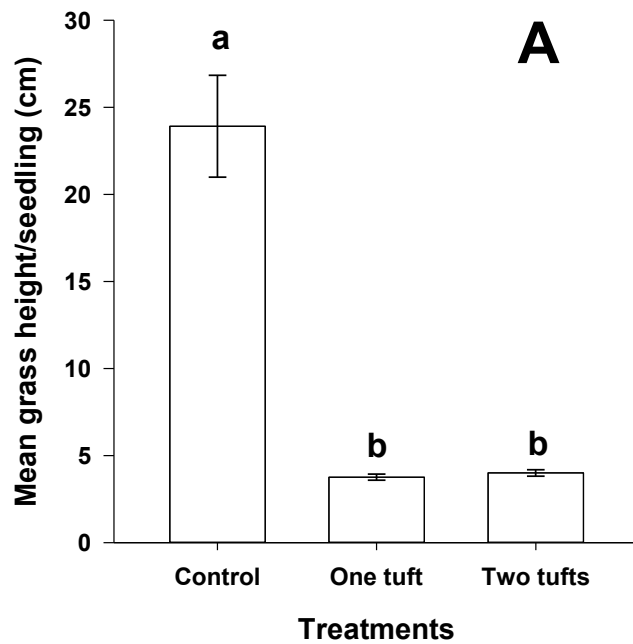
2353

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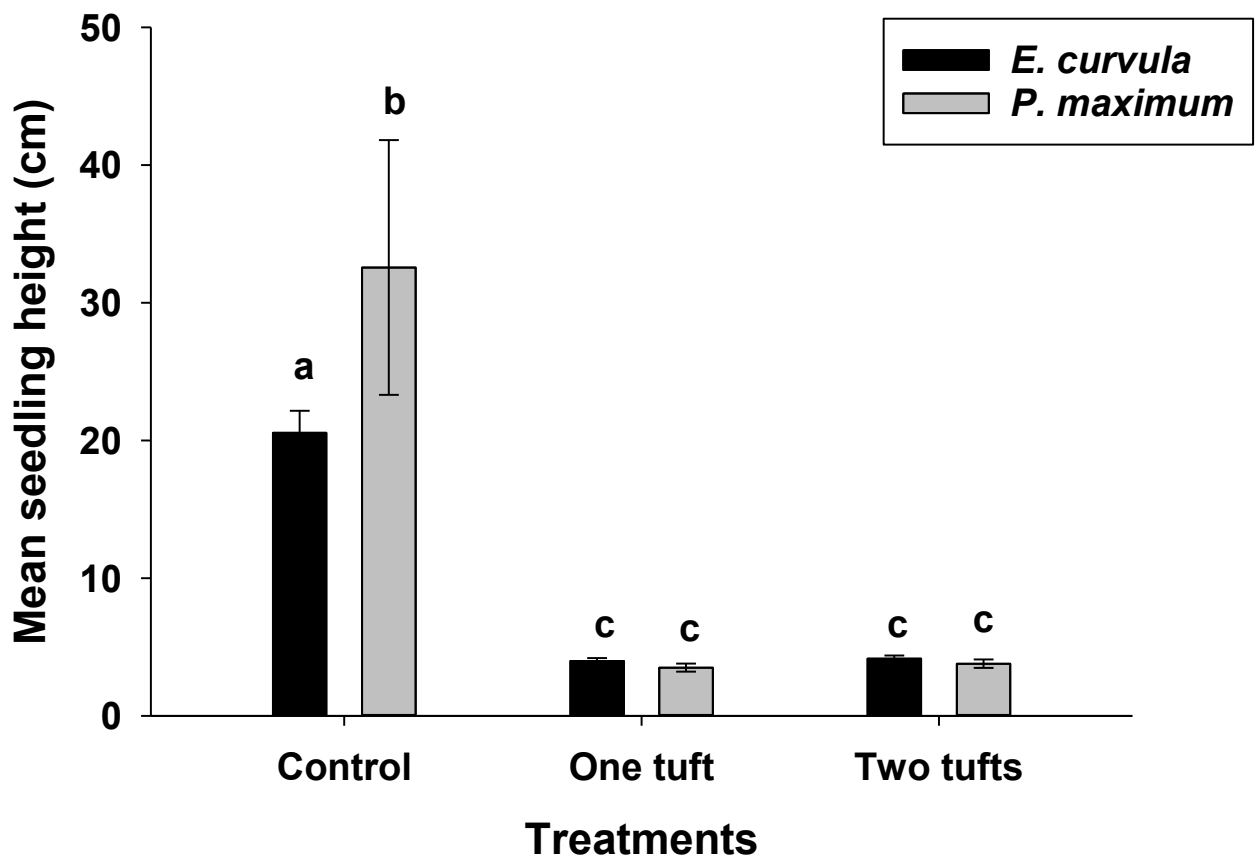
Figure 3.7: Effect of vetiver (full competition) on the mean seedling height (± SE) of the interaction between *Eragrostis curvula* and *Panicum maximum*. Different letters represent a significant difference between treatments (p<0.05).

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

2372 number of tillers per seedling (χ^2=39.128, df=2, P< 0.0001). *Eragrostis curvula* tufts still

2373 experienced a reduction in growth even with the exclusion of vetiver roots. *Eragrostis curvula*

2374 still produced more aboveground biomass (Fig.3.8A), grew taller (Fig.3.8B), produced more

2375 tillers per seedling (Fig.3.8C), and more leaves per seedling (Fig.3.8D) when growing alone

2376 (control) compared to when growing with one and two vetiver grass tufts. Surprisingly, *E.*

2377 *curvula* also grew better when growing with one vetiver grass tuft (Fig.3.8 A, B, and C)

2378 compared to when growing with two vetiver tufts (Fig.3.8A, B, and C), which is contrary to

2379 when growing with full competition (vetiver roots present, Figure 3.6 and 3.7).
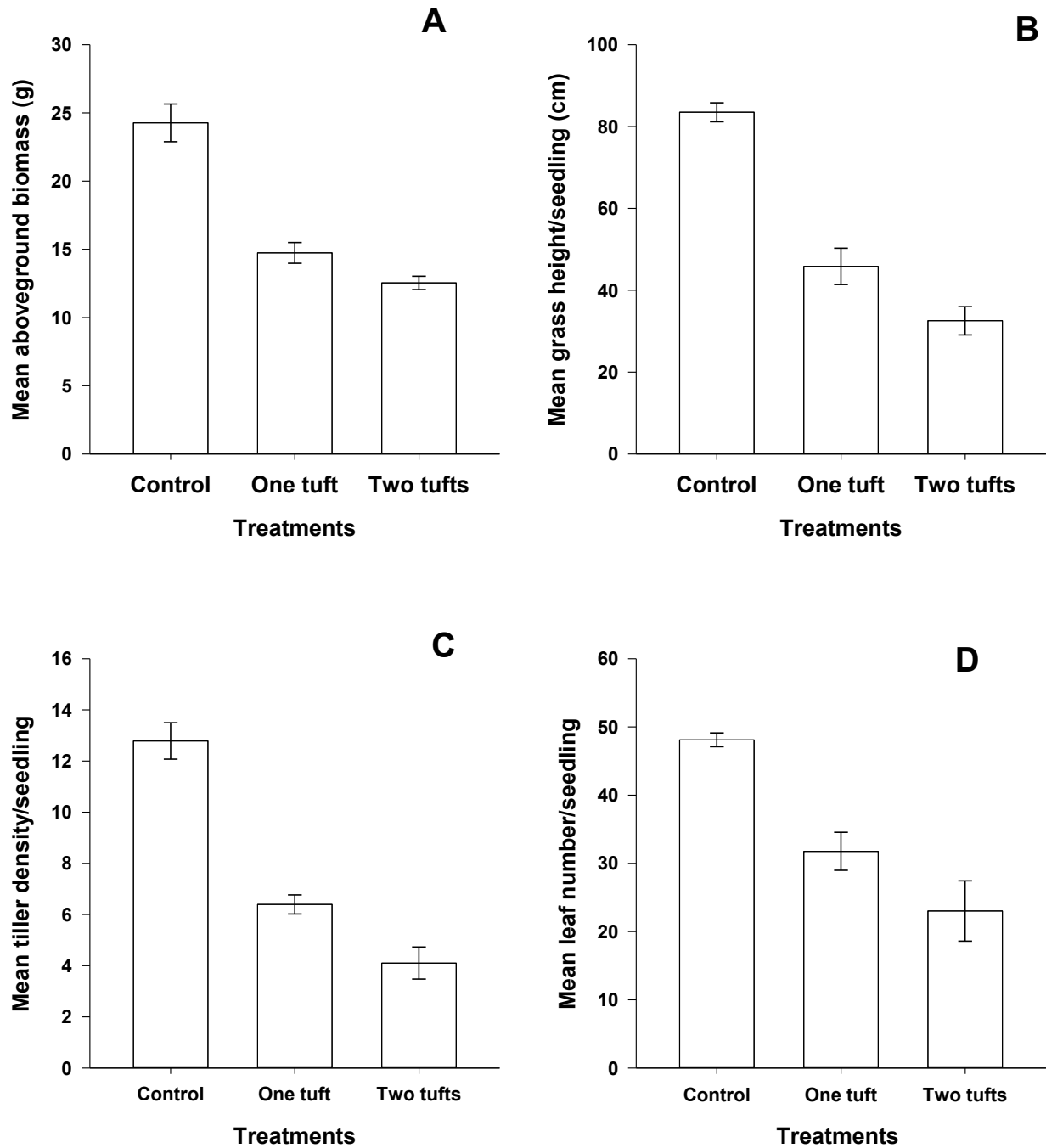
2380

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.*

2384 **3.4.5 Roots density analysis**

2385   The space available around one and two vetiver tufts was examined and compared it to

2386 the space available around *E. curvula* roots to understand whether vetiver root density could also

2387 be limiting the growth and survival of native grasses. There was a significant difference in the

2388 space available (unoccupied soil space) around vetiver roots compared to *E. curvula* roots

2389 (χ^2=28.865, df =2, *P<0.001*). *Eragrostis curvula* (60.27% ± 4.517) had significantly more soil

2390 space unoccupied by roots compared to one (30.913% ± 1.820) and two vetiver tufts (23.87% ±

2391 0.957; Figure 3.9). Furthermore, one vetiver tuft has significantly more soil space unoccupied by

2392 roots when compared to two vetiver tufts (Fig.3.9). Therefore, there is limited soil space around

2393 vetiver tufts that can allow the establishment of native grasses.
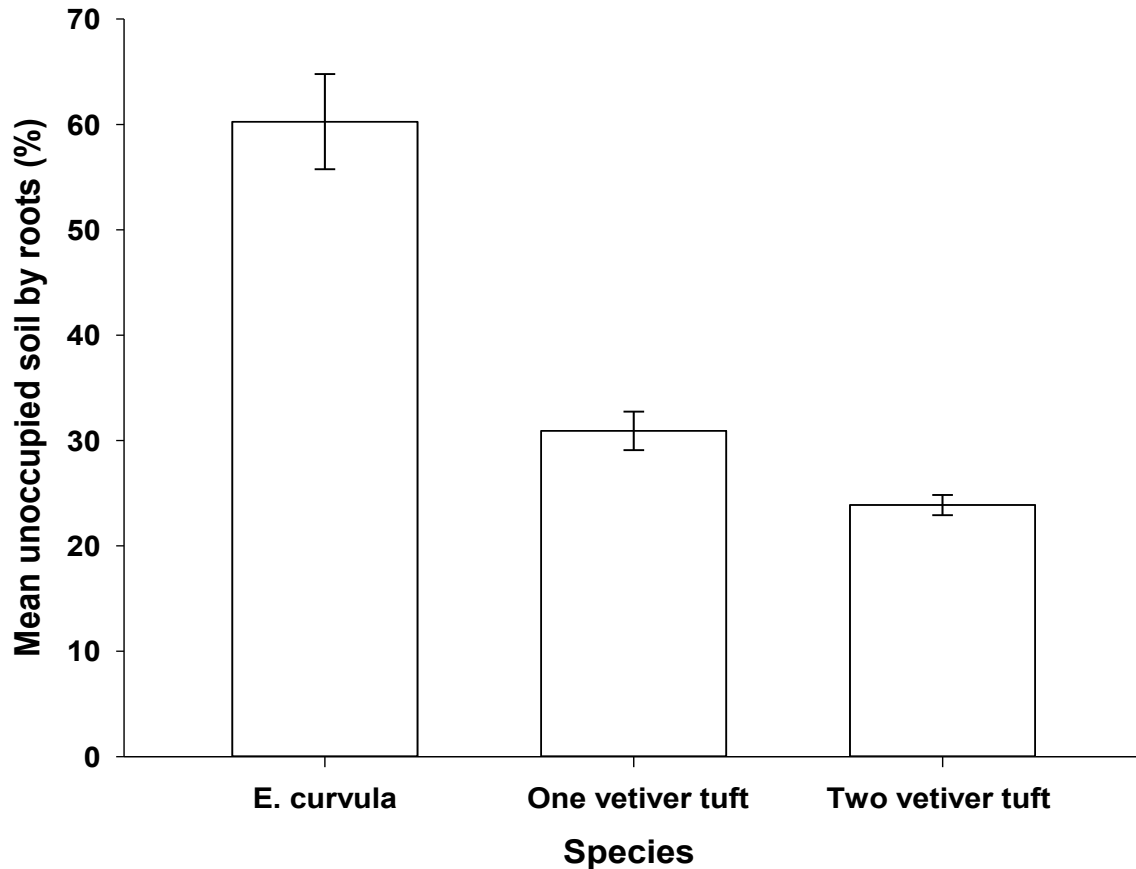
2394   :

2395 Figure 3.9: Mean (± SE) soil space unoccupied by the roots of one and two vetiver grass tufts

2396 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

2428 et al. 2015). This might explain why the presence of a neighboring plant boosted seed

2429 germination. However, because *E. curvula* is more of a pioneer type species which produces

2430 small abundant seeds with greater viability compared to *P. maximum*, which is a late seral

2431 species producing large fewer seeds with reduced viability (Meredith, 1955), it germinated better

2432 than *P. maximum* in all treatments. This also suggests that *E. curvula* has a wider microclimate

2433 tolerance for seed germination compared to *P. maximum.* Furthermore, seed size has been shown

2434 to also affect germination, with most studies reporting an increase in germination percentage rate

2435 with a decrease in seed size (Silvertown, 1981; Gross, 1984; Aldrete and Mexal, 2005), which

2436 supports these findings.

2437 Seed sowing method is also one of the factors that affects seed germination, but it is

2438 mostly studied using commercially important crops (e.g. maize and sorghum) and trees (e.g. pine

2439 trees) (Aldrete and Mexal, 2005). Few studies looked at naturally occurring rangeland grasses

2440 (Maun and Lapierre, 1986). This study is among the first to investigate the influence of sowing

2441 method in rangeland grasses, and it showed that surface sowed seeds germinate better than

2442 buried seeds or seeds mixed with a water retention gel. Several studies have shown that burying

2443 seeds reduces germination percentage by increasing seed mortality (Maun and Lapierre, 1986;

2444 Harris, 1996; Aldrete and Mexal, 2005). However, this is dependent on sowing depth, with an

2445 increase in sowing depth resulting in a decrease in seed germination rate. For example, Maun

2446 and Lapierre (1986) showed that seed germination, the rate of emergence of those germinated

2447 seeds, and the total emergence of dune species (*Elymus canadensis*, *Cakile edentula*, and

2448 *Corispermum hyssopifolium*) decreased with an increase in seed burial depth in sandy soils.

2449 Aldrete and Mexal (2005), using potting soil, also showed a clear decrease in seed

2450 germination and seedling emergence of three pine species with an increase in sowing depth.

2451 Even though our study did not compare different sowing depths, the differences between surface

2452 sowing and buried seeds (2cm) support these examples. However, should water be a liming

2453 factor (i.e. arid regions), one should expect better germination of buried seeds and those seeds

2454 mixed with a water retention gel compared to surface sown seeds. These sowing methods

2455 maintain moisture for longer periods compared to surface sowing (Ren et al., 2008). For this

2456 study, watering was done frequently (watered every second day), thus water availability is

2457 excluded as a limiting factor, which explains the findings obtained. Harris (1996), studied the

2458 effect of sowing depth on seed germination and seedling emergence of *Sorghum bicolor* in semi-
2459 arid Botswana. He showed that the soil dried quickly, indicating that even though deeper sowing
2460 depth reduced seed germination and emergence, shallow sowing (not surface sowing) retained
2461 moisture longer resulting in quicker seedling emergence and did not result in seed mortality
2462 (Harris, 1996). Microsites that favours seed germination are those that do not allow seed
2463 desiccation (Fenner, 1978). Some studies use mulching or water retention gel to combat quick
2464 drying of the top soil which in turn reduces seed germination (Pill, 1991).

2465 Even though vetiver facilitated seed germination, it also reduced the establishment of
2466 those germinated seeds resulting in a slow seedling growth and increased seedling mortality.
2467 This is contrary to the claim that vetiver promotes reestablishment in native grasses. Numerous
2468 studies have demonstrated that established surrounding swards have a negative effect on seedling
2469 establishment of either invading species or of the same species (Fenner, 1978; Snaydon and
2470 Howe, 1986; Fowler, 1986a). This is because the seedling stage is a critical stage in plant
2471 development and requires enough above and belowground resources, hence why seedlings tend
2472 to be more sensitive to competition than mature plants. For example, in a field trial, Snaydon and
2473 Howe (1986) studied the effect of shoot, root, and full competition exerted by established
2474 ryegrass (*Lolium perenne*) on the establishment of *Poa annua*, *P. trivialis*, and *Festuca rubra*.
2475 They showed that full competition and root competition affected the seedling establishment of
2476 these grasses by reducing the dry weight of seedlings by about sevenfold (Snaydon and Howe,
2477 1986). Their findings suggested that seedlings are more severely affected by belowground
2478 competition than aboveground competition as shoot competition had little effect on seedling
2479 growth (Snaydon and Howe, 1986). Vetiver has an extensive investment in belowground
2480 material, which may explain why seedling growth was substantially reduced by the presence of
2481 vetiver.

2482 This study showed similar results to those of Fowler (1986a), Fenner (1978), and Wesson
2483 and Wareing (1969). Fowler (1986a) used a field trial to investigate the effect of established
2484 grasses on seed germination, seedling establishment, and survival of other grasses. He showed
2485 that established grasses had no negative effect on seed germination but rather had a slight
2486 positive effect, despite substantially reducing the number of tillers in *Bouteloua rigidiseta*
2487 (Fowler, 1986a). Using artificial swards, Fenner (1978) showed that seed germination in ruderals

2488   was not negatively affected by established grass swards mostly in short turf treatment. However,

2489   seedlings of ruderal species could not establish successfully in these swards (Fenner, 1978).

2490   Wesson and Wareing (1969), focused on the effect of grass swards on buried seeds of weed

2491   species e.g. *Veronica persica* and *Sinapis arvensis*. They showed that seeds of these plants

2492   germinated well within established grass swards but failed to establish (Wesson and Wareing,

2493   1969). This provides further evidence that the microclimate requirements for seeds and seedlings

2494   can be different. Seeds require specific abiotic conditions to trigger germination, while seedlings

2495   are influenced by both abiotic and biotic factors with competition for resources being the key

2496   determinant of seedling survival (Aguiar et al., 1992). In these grass sward conditions, seedling

2497   fail to recruit because they have no fully developed shoots and roots which can help them

2498   compete effectively for both aboveground and belowground resources with surrounding swards

2499   community (Fenner, 1978).

2500   Factors responsible for hindering growth and establishment of native grasses were then

2501   investigated in more detail. Vetiver root density was compared to that of *E. curvula* with the aim

2502   of understanding how much space is available for other species to utilize around these two

2503   species. *Eragrostis curvula* had more space around its roots compared to vetiver, suggesting that

2504   there is limited space for the establishment of native grasses around vetiver. Reduced space

2505   could result in direct root competition between recruiting seedlings and vetiver roots (Schenk et

2506   al., 1999). Numerous studies have shown that when there is enough available soil space, roots

2507   tends to avoid direct root competition by foraging in unoccupied soil resource patches (Schenk

2508   and Jackson, 2002; Bliss et al., 2002; Hutchings and John, 2003). However, changes in available

2509   soil space force direct root competition between mature grasses and seedlings (Schenk et al.,

2510   1999), with seedlings experiencing substantial negative effect because of their sensitivity to

2511   competition.

2512   Above- and belowground competition interacts simultaneously in a natural ecosystem,

2513   but can exert different pressures on recruiting species, with one being more important than the

2514   other (Cahill, 1999). For this reason, an additional trial which excluded root competition was

2515   conducted. This tried to understand if the exclusion of root competition reduced the negative

2516   effect exerted by vetiver on native grass seedlings or if other factors i.e. shade and/or allelopathy

2517   were important in explaining the observed results. Seedlings still suffered a substantial decrease

2518 in growth even though root competition was excluded, which means either shade or allelopathy
2519 or both were responsible for reducing seedling growth. Surprisingly, there was also a difference
2520 between one and two vetiver tufts, with two tufts exerting more negative effect than one tuft.
2521 This is contrary to what was observed in the trial with no root exclusion (i.e. no difference
2522 between one and two tufts). The existence of strong root intraspecific competition between
2523 vetiver tufts could explain these findings. Root competition between vetiver tufts could be
2524 reducing the interspecific competition exerted by two vetiver tufts to the same level as that of
2525 one tuft. Strong intraspecific competition has been suggested to reduce the magnitude of
2526 interspecific competition when the density (the number of species per unit areas) of the
2527 competing species increases, allowing other species coexistence between those two species
2528 (Wedin and Tilman, 1993; Tilman, 1994).

2529   Shade is not expected to be a major limiting factor affecting seedling establishment, as
2530 results from the full competition and roots exclusion trials were not similar, even though shade
2531 between these trials (i.e. one and two tufts) should have been relatively similar, because vetiver
2532 tufts in both trials were of a relatively equal height. However, the amount of oil produced by the
2533 roots can be affected by root intraspecific competition because it is closely related to metabolism
2534 in roots which is affected by both abiotic and biotic factors (Massardo et al., 2006). Oil
2535 production is influenced by soil resource availability also (Adams et al., 2003), hence
2536 intraspecific competition could result in a trade-off in resource allocation to either growth and oil
2537 production. Therefore, two vetiver tufts can produce a relatively similar amount of oil to that of
2538 one vetiver tuft as a result of intraspecific competition between the two vetiver tufts. Vetiver oil
2539 has been reported to have allelopathic compounds that negatively affect the seedling
2540 establishment of other plants (Mao et al., 2004; Mao et al., 2006). For example, Mao et al. (2004)
2541 investigated the effect of vetiver oil on seed germination and seedling growth of six weed
2542 species. They showed that vetiver oil inhibited seed germination and seedling establishment in
2543 five out of six weed species providing evidence for the existence of an allelopathic behaviour by
2544 vetiver grass (Mao et al., 2006). However, this argument does not completely exclude
2545 competition for light as a contributing factor, it only suggests that allelopathic effects appears to
2546 be major contributing factor to the result found in the root exclusion trial. Furthermore, *P.*
2547 *maximum* is a shade tolerant species, and *E. curvula* is also a moderately shade-tolerant species,
2548 meaning they can both grow in a shaded environment. A simple trial separating allelopathy

2549 interference, root competition, and shading effect is needed to understand which factor is
2550 responsible for the suppression of growth in native grasses.

2551 Surface sowing and the presence of vetiver are beneficial only for seed germination but
2552 not for seedling establishment as vetiver reduced the seedling growth and survival of native
2553 grasses. The reduction could be caused by one or the combination of these factors: 1) Direct root
2554 competition between vetiver roots and seedlings roots; 2) vetiver shade, reducing the
2555 photosynthetic activity in native grass seedlings; and 3) possibly an allelopathic effect caused by
2556 vetiver oil produced by the roots. Results of this study, therefore, suggest that it is unlikely that
2557 vetiver grass will allow recruitment of native grasses, which means rehabilitation using vetiver is
2558 unlikely to allow succession by native grasses.

3.6 REFERENCES

2560 Adams, R.P., Pandey, R.N., Dafforn, M.R., James, S.A., 2003. Vetiver DNA-fingerprinted
2561 cultivars: effects of environment on growth, oil yields and composition. Journal of
2562 Essential Oil Research 15, 363-371.

2563 Adkins, S., Davidson, P., Matthew, L., Navie, S., Wills, D., Taylor, I., Bellairs, S., 2000. Smoke
2564 and germination of arable and rangeland weeds. Seed biology: advances and applications.
2565 CABI Publishing, New York, 347-359.

2566 Aguiar, M., Soriano, A., Sala, O., 1992. Competition and facilitation in the recruitment of
2567 seedlings in Patagonian steppe. Functional Ecology 6, 66-70.

2568 Aldrete, A., Mexal, J., 2005. Sowing depth, media, and seed size interact to influence emergence
2569 of three pine species. Tree planters' notes.

2570 Ammondt, S.A., Litton, C.M., 2012. Competition between native Hawaiian plants and the
2571 invasive grass *Megathyrsus maximus*: implications of functional diversity for ecological
2572 restoration. Restoration Ecology 20, 638-646.

2573 Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G., Waddington, J., 2003.
2574 Contingency of grassland restoration on year, site, and competition from introduced
2575 grasses. Ecological Applications 13, 137-153.

2576 Bliss, K.M., Jones, R.H., Mitchell, R.J., Mou, P.P., 2002. Are competitive interactions
2577   influenced by spatial nutrient heterogeneity and root foraging behavior? New Phytologist
2578   154, 409-417.

2579 Bogdan, A., 1977. Tropical pasture and fodder plants. Longman.

2580 Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G.,
2581   Liancourt, P., Tielbörger, K., Travis, J.M., Anthelme, F., 2008. Facilitation in plant
2582   communities: the past, the present, and the future. Journal of Ecology 96, 18-34.

2583 Cahill, J.F., 1999. Fertilization effects on interactions between above-and belowground
2584   competition in an old field. Ecology 80, 466-480.

2585 Cahill, J.F., 2002. What evidence is necessary in studies which separate root and shoot
2586   competition along productivity gradients? Journal of Ecology 90, 201-205.

2587 Chahal, K.K., Kaushal, S., Sandhu, A.K., 2015. Chemical composition and biological properties
2588   of *Chrysopogon zizanioides* (L.) Roberty syn. *Vetiveria zizanioides* (L.) Nash-A Review.
2589   Indian Journal of Natural Products and Resources [Formerly as Natural Product
2590   Radiance] 6, 251-260.

2591 Chōmchalao, N., 2001. utilization of vetiver as medicinal and aromatic plants. Office of the
2592   Royal Development Projects Board.

2593 Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

2594 Dalton, P., Smith, R., Truong, P., 1996. Vetiver grass hedges for erosion control on a cropped
2595   flood plain: hedge hydraulics. Agricultural Water Management 31, 91-104.

2596 Danh, L.T., Truong, P., Mammucari, R., Foster, N., 2010. Extraction of vetiver essential oil by
2597   ethanol-modified supercritical carbon dioxide. Chemical Engineering Journal 165, 26-34.

2598 Dias, L., Pereira, I.P., Dias, A.S., 2016. Allelopathy, seed germination, weed control and
2599   bioassay methods. Allelopathy Journal 37, 31-40.

2600 Fenner, M., 1978. A comparison of the abilities of colonizers and closed-turf species to establish
2601   from seed in artificial swards. The Journal of Ecology 66, 953-963.

2602 Fish, L., Mashau, A. C., Moeaha, M. J., Nembudani, M.T., 2015. Identification guide to southern
2603   African grasses. An identification manual with keys, descriptions and distributions.
2604   Strelitzia 36. South African National Biodiversity Institute, South Africa.

2605 Fowler, N., 1986a. Microsite requirements for germination and establishment of three grass
2606   species. American Midland Naturalist 115, 131-145.

2607 Fowler, N., 1986b. The role of competition in plant communities in arid and semiarid regions.
2608   Annual Review of Ecology and Systematics 17, 89-110.

2609 Gallagher, M.K., Wagenius, S., 2016. Seed source impacts germination and early establishment
2610   of dominant grasses in prairie restorations. Journal of Applied Ecology 53, 251-263.

2611 Ghebrehiwot, H.M., Aremu, A.O., Van Staden, J., 2014. Evaluation of the allelopathic potential
2612   of five South African mesic grassland species. Plant Growth Regulation 72, 155-162.

2613 Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth.
2614   Infinity Publishing.

2615 Grimshaw, R.G., 1993. The role of vetiver grass in sustaining agricultural productivity. Asia
2616   Technical Department. The World Bank, Washington DC USA.

2617 Gross, K.L., 1984. Effects of seed size and growth form on seedling establishment of six
2618   monocarpic perennial plants. The Journal of Ecology 72, 369-387.

2619 Harris, D., 1996. The effects of manure, genotype, seed priming, depth and date of sowing on the
2620   emergence and early growth of *Sorghum bicolor* (L.) Moench in semi-arid Botswana.
2621   Soil and Tillage Research 40, 73-88.

2622 Hutchings, M., John, E., 2003. Distribution of roots in soil, and root foraging activity, Root
2623   ecology. Springer, pp. 33-60.

2624 Kiepiel, I., Johnson, S.D., 2014. Breeding systems in Clivia (*Amaryllidaceae*): late-acting self-
2625   incompatibility and its functional consequences. Botanical journal of the Linnean Society
2626   175, 155-168.

2627   Knipe, O., 1968. Effects of moisture stress on germination of alkali *Sacaton, Galleta*, and glue
2628   grama. Rangeland Ecology & Management/Journal of Range Management Archives 21,
2629   3-4.

2630   Kolb, R.M., Pilon, N.A.L., Durigan, G., 2016. Factors influencing seed germination in Cerrado
2631   grasses. Acta Botanica Brasílica 30, 87-92.

2632   Lenz, T.I., Facelli, J.M., 2005. The role of seed limitation and resource availability in the
2633   recruitment of native perennial grasses and exotics in a South Australian grassland.
2634   Austral Ecology 30, 684-694.

2635   Lindig-Cisneros, R., Zedler, J., 2001. Effect of light on seed germination in *Phalaris*
2636   *arundinacea* L.(reed canary grass). Plant Ecology 155, 75-78.

2637   Mao, L., Henderson, G., Bourgeois, W.J., Vaughn, J.A., Laine, R.A., 2006. Vetiver oil and
2638   nootkatone effects on the growth of pea and citrus. Industrial Crops and Products 23,
2639   327-332.

2640   Mao, L., Henderson, G., Laine, R.A., 2004. Germination of various weed species in response to
2641   vetiver oil and nootkatone 1. Weed technology 18, 263-267.

2642   Massardo, D.R., Senatore, F., Alifano, P., Del Giudice, L., Pontieri, P., 2006. Vetiver oil
2643   production correlates with early root growth. Biochemical systematics and Ecology 34,
2644   376-382.

2645   Maun, M., Lapierre, J., 1986. Effects of burial by sand on seed germination and seedling
2646   emergence of four dune species. American Journal of Botany 73, 450-455.

2647   Meredith, D., 1955. The grasses and pastures of South Africa.

2648   Morgan, R.P.C., 2009. Soil erosion and conservation. John Wiley & Sons.

2649   Pill, W.G., 1991. Advances in fluid drilling. HortTechnology 1, 59-65.

2650   Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists.
2651   Cambridge University Press.

2652   Rees, M., Brown, V.K., 1991. The effect of established plants on recruitment in the annual forb
2653   *Sinapis arvensis*. Oecologia 87, 58-62.

92

2654 Ren, H., Yang, L., Liu, N., 2008. Nurse plant theory and its application in ecological restoration
2655   in lower subtropics of China. Progress in Natural Science 18, 137-142.

2656 Schenk, H.J., Callaway, R.M., Mahall, B., 1999. Spatial root segregation: are plants territorial?
2657   Advances in Ecological Research 28, 145-180.

2658 Schenk, H.J., Jackson, R.B., 2002. Rooting depths, lateral root spreads and below-ground/above-
2659   ground allometries of plants in water-limited ecosystems. Journal of Ecology 90, 480-
2660   494.

2661 Shangwen, C., 1999. Insects on vetiver hedges. The Vetiver Newsletter 23, 17-18.

2662 Silvertown, J.W., 1981. Seed size, life span, and germination date as coadapted features of plant
2663   life history. The American Naturalist 118, 860-864.

2664 Snaydon, R., Howe, C., 1986. Root and shoot competition between established ryegrass and
2665   invading grass seedlings. Journal of Applied Ecology 23, 667-674.

2666 Tainton, N.M., Bransby, D., Booysen, P.d.V., 1976. Common veld and pasture grasses of Natal.
2667   Shuter & Shooter.

2668 Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2011. Grass-on-grass competition along a catenal
2669   gradient in mesic grassland, South Africa. African Journal of Range & Forage
2670   Science 28, 79-85.

2671 Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2-
2672   16.

2673 Truong, P., Chomchalow, N., Vessabutr, S., 1999. Vetiver grass technology for mine
2674   rehabilitation. Pacific Rim Vetiver Network Technology 2, 1-19.

2675 Truong, P., Hart, B., Chomchalow, N., Sombatpanit, S., 2001. Vetiver system for wastewater
2676   treatment. Office of the Royal Development Projects Board.

2677 Van den Berg, J., Midega, C., Wadhams, L., Khan, Z., 2003. Can Vetiver grass be used to
2678   manage insect pests on crops? Proceedings of the Third International Conference on
2679   Vetiver and Exhibition (ed. by RG Grimshaw), 254–264.

2680   Van Oudtshoorn, F.V., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza
2681   Publications.

2682   Vieritz, A., Truong, P., Gardner, T., Smeal, C., 2003. Modelling Monto vetiver growth and
2683   nutrient uptake for effluent irrigation schemes. Proceedings of the Third International
2684   Conference on Vetiver and Exhibition, 254-264.

2685   Wagner, S., Truong, P., Vieritz, A., Smeal, C., 2003. Response of vetiver grass to extreme
2686   nitrogen and phosphorus supply. Proceedings of the Third International Conference on
2687   Vetiver and Exhibition, 100-108.

2688   Wedin, D., Tilman, D., 1993. Competition among grasses along a nitrogen gradient: initial
2689   conditions and mechanisms of competition. Ecological Monographs 63, 199-229.

2690   Wesson, G., Wareing, P., 1969. The role of light in the germination of naturally occurring
2691   populations of buried weed seeds. Journal of Experimental Botany 20, 402-413.

2692   Weyerstahl, P., Marschall, H., Splittgerber, U., Wolf, D., 1996. New sesquiterpene ethers from
2693   Vetiver oil. Liebigs Annalen 1996, 1195-1199.

2694   Xia, H., Ao, H., He, D., 1998. The effect of environmental factors on the growth of vetiver
2695   growth. Vetiver Research and Development, 39-44.

2696   Xu, L., 2002. Vetiver research and development: A decade experience from China. Proceedings:
2697   The   Second   International   Vetiver   Conference,   ORDPB,   Bangkok,   311-322.

4   CHAPTER 4: EFFECT OF VETIVER COMPETITION AND SOIL NUTRIENT

2699   **STATUS ON NATIVE GRASSES**

2700   **4.1   ABSTRACT**

2701   Vetiver grass (*Chrysopogon zizanioides* (L.) Roberty) is a densely tufted perennial C_4 grass from

2702   central India, used worldwide for soil and water conservation. It is a hardy, fast-growing, and

2703   densely rooted grass enabling it to withstand most environmental hazards (drought, frost, and

2704   floods). Worldwide use of vetiver is grounded in the claims that it does not compete with

2705   neighbouring grasses and it is not invasive. Recent studies have demonstrated that nitrogen

2706   deposition has dramatically risen after the industrial and agricultural revolution, and is expected

2707   to continue rising. Such increase is predicted to alter plant species coexistence, particularly in

2708   grasslands, through making limiting resources non-limiting, hence eliminating the competitive

2709   trade-off that allows species coexistence. The claims about vetiver's competitive ability were

2710   investigated using a pot trial examining the competitive interactions between vetiver and four

2711   native grasses (*Eragrostis curvula, Digitaria eriantha*, *Panicum maximum* and *Hyparrhenia*

2712   *hirta*) under different soil nutrient levels. Nutrient addition was achieved using 80% Hoagland's

2713   solution (N=172, P=25, K=188mg/L), and the relative interaction index (RII) and the percentage

2714   change in yield (Ry) were used as indices to assess the effect of competition and nutrient status

2715   on native grasses. Vetiver exerted a weak competitive effect on all native grass tufts, except for

2716   *D. eriantha*, under low nutrient status. Vetiver exerted a facilitative effect on *D. eriantha* under

2717   low nutrient status. However, vetiver exerted a strong competitive effect on all native grass

2718   species under high nutrient status, except for *P. maximum,* which responded similarly under low

2719   and high nutrients conditions. Overall, narrow-leaved grasses (*E. curvula* and *H. hirta*) had a

2720   weak competitive ability compared to broad-leaved grasses (*P. maximum* and *Digitaria*

2721   *eriantha*). Therefore, morphological traits are important to consider in competition studies and

2722   could predict species that might coexist with vetiver. As soil nitrogen continues to increase

2723   globally, this will affect coexistence between native grasses and vetiver, with vetiver gaining an

2724   increased competitive advantage over native grasses. For this reason the claims that vetiver does

2725   not compete with neighbouring grasses need to be reconsidered and care taken when using

2726   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

2758 R*) two or more resources (e.g. water and sunlight) will be better competitors and can
2759 outcompete other species, hence altering species coexistence in that ecosystem (Tilman, 1980;
2760 Wedin and Tilman, 1993). Introduced plants are generally better at resource acquisition than
2761 native plants, hence the interaction between introduced plants and native plants can sometimes
2762 favour introduced plants resulting in their invasion (Brooks, 2000; Vilà et al., 2003).

2763 Numerous studies have shown that atmospheric nitrogen deposition has increased the
2764 levels of nitrogen in the soil and this is directly linked to the agricultural and industrial revolution
2765 (Stevens et al., 2004; Clark and Tilman, 2008; Bobbink et al., 2010). Nitrogen cycling in an
2766 ecosystem is derived from three main sources; biological N-fixation, mineralization, and
2767 atmospheric deposition, with the two dominant sources being atmospheric deposition, increased
2768 by combustion of fossil fuels, and mineralization which is directly linked to emission of NH_3
2769 from the use of fertilizer and manure in agricultural fields (Bobbink et al., 2010). These sources
2770 are driven by the human demand for food and energy, which is unlikely to decrease given the
2771 current population growth predictions (Tilman and Wedin, 1991). Nitrogen, an essential nutrient
2772 for plant growth and nutrient enrichment, as a result of atmospheric nitrogen deposition has been
2773 shown to potentially reduce species diversity, with rare species being the most sensitive (Tilman
2774 and Wedin, 1991; Stevens et al., 2004; Clark and Tilman, 2008). The mechanisms driving this
2775 decline remain unclear, but are strongly linked to plant competition, as increased nitrogen levels
2776 alter individual plant physiology (e.g. water and nutrient use efficiency) and biomass allocation
2777 patterns (e.g. root to shoot ratio) (Bobbink et al., 2010).

2778 Moreover, atmospheric nitrogen and sulphur deposition have been shown to acidify soil
2779 in the long-term, leading to lower soil pH, leaching of cations, and increased levels of toxic
2780 metals (e.g. Al) in the soil, mostly in regions with high rainfall (Bobbink et al., 2010). In South
2781 Africa, regions with high rainfall are also associated with highly dispersive soils which are
2782 susceptible to soil erosion, making these areas a prime target for the use of vetiver (Fey, 2010).
2783 Considering that vetiver can tolerate low soil pH, toxic metals, and high nitrogen levels, it is
2784 important to understand its competitive ability under these conditions to understand and predict
2785 the species shifts that can be expected in areas rehabilitated using vetiver.

2786 An improved understanding of both the competitive effect of vetiver and competitive
2787 response of selected native grasses, with both strong and weak competitive ability, and how soil

2788 nutrient levels influence these interactions will help predict the potential of vetiver to become
2789 invasive and suggest indigenous species that are likely to coexist or even outcompete vetiver.
2790 The claims about vetiver competitive ability were investigated using a pot trial by examining the
2791 competitive ability of vetiver's grass under different soil nutrient levels with the aim of
2792 answering the following three questions:

2793 1. Does vetiver exert a competitive effect on neighbouring native grasses with a strong
2794 (*Eragrostis curvula* and *Digitaria eriantha*) and weak (*Panicum maximum* and
2795 *Hyparrhenia hirta*) competitive ability?

2796 2. Does vetiver density influence the competitive effect experienced by native grasses?

2797 3. Does soil nutrient addition influence this interaction?

2798 Three hypotheses for this study were; firstly, that vetiver will exert a competitive effect on
2799 native grasses, and that nutrient addition will increase vetiver's competitive effect. Secondly,
2800 increasing the number of vetiver tufts will increase the competitive effect on native grasses
2801 irrespective of soil nutrient addition. Lastly, native grasses will differ in their competitive
2802 response under low and high nutrient status, with highly competitive grasses experiencing a
2803 lower competitive effect than weakly competitive grasses.

2804 **4.3 MATERIALS AND METHODS**

2805 **4.3.1 Study site and species**

2806 The study was run from November 2016 to April 2017 (6 months) at the University of
2807 KwaZulu-Natal NM Tainton Arboretum, Pietermaritzburg, KwaZulu-Natal, South Africa. The
2808 region has a mean annual rainfall of about 844mm, with most of the rain falling in summer
2809 between October and March. Summers are hot, with a mean daily maximum temperature of
2810 approximately 26.4°C, while winters are mild with occasional frost and mean daily temperature
2811 of about 8.8ºC. The winter is coolest in June, and summer is warmest in February and March
2812 (Fynn et al., 2009). The growing season of this region is controlled mainly by temperature and
2813 rainfall, with most of the grass biomass production taking place between October and April
2814 (Fynn et al., 2009).

2815 Four native grass species, *Eragrostis curvula* (Schrad.) Nees*, Digitaria eriantha* Steud.,
2816 *Panicum maximum* Jacq., and *Hyparrhenia hirta* Stapf., commonly occurring in South African

2817   rangelands and useful in soil erosion control and rangeland rehabilitation were used in this study

2818   (Tainton et al., 1976; Morris, 2016). These species differ largely in their competitive ability

2819   (Laan et al., 2008; Morris, 2016), morphological traits (Meredith, 1955; Fish et al. 2015), and

2820   response to soil nutrient addition (Fynn and O'Connor, 2005; Fynn and Naiken, 2009).

2821   *Eragrostis curvula* and *Digitaria eriantha*, even though differing in their morphological traits,

2822   compete well under both low and high soil nutrient status, and were hence classified as strong

2823   competitors (McDonald et al., 1998; Fynn and Naiken, 2009). *Digitaria eriantha* is a tall broad-

2824   leaved grass, with robust roots, and is usually stoloniferous (Van Oudtshoorn, 2012). By

2825   contrast, *E. curvula* is a tall narrow-leaved grass, with fine roots, but has no stolons or rhizomes

2826   (Meredith, 1955). The other two species, *Panicum maximum* and *Hyparrhenia hirta* were

2827   classified as weak competitors because their competitive ability is quite variable and soil nutrient

2828   dependent, with *P. maximum* shown to compete strongly in nutrient rich soils (Fynn and

2829   O'Connor, 2005) and *H. hirta* in nutrient poor-soils (Fynn and O'Connor, 2005; Zwerts et al.,

2830   2015). These two species also differ in terms of morphological traits. *Panicum maximum* is a

2831   broad-leaved grass, which prefers growing under shade, and has robust roots usually with a short

2832   creeping rhizome (Meredith, 1955). By contrast, *H. hirta* is a narrow-leaved grass, which is

2833   relatively shade intolerant, and has a dense fibrous root system (Van Oudtshoorn, 2012).

2834   **4.3.2   Experimental design**

2835   These native grass species (*Eragrostis curvula, Digitaria eriantha*, *Panicum maximum*

2836   and *Hyparrhenia hirta*) were propagated from wild-collected tillers and planted into 6L pots

2837   filled with coarse, nutrient-poor sand. The tufts (equal numbers of tillers and similar height) of

2838   each of these species were grown as a phytometer. These tufts were grown alone (control), with

2839   one vetiver tuft (low density competition), and between two vetiver tufts which were planted 15

2840   centimeters apart (high density competition). Both the vetiver and native grasses were of similar

2841   size at the beginning of the experiment. All the competition treatments were subject to both high

2842   and low soil nutrient conditions. The high fertility treatment was watered with 300 mL of 80%

2843   Hoagland's nutrient solution (N = 172, P = 25, K = 188 mg L/1) (Hoagland and Arnon, 1950)

2844   every 4 days while the low fertility treatment was given no nutrient addition (Tedder et al.,

2845   2012). The experiment was a full factorial design, laid out in a completely randomized

2846   arrangement with six replicates of each treatment combination, and 24 treatment combinations in

2847 total. To ensure that water was not a limiting factor, pots were irrigated with municipal water
2848 daily, provided there was no natural rainfall.

4.3.3 Data collection

2850   After 6 months, the native grass aboveground biomass was harvested. The aboveground
2851 biomass of each species from each pot was put separately into paper bags, which were then oven
2852 dried for 48 hours at 60°C before weighing to determine the final dry biomass. Growth traits of
2853 each native species, including leaf table height, basal circumference, and number of tillers, were
2854 also measured before harvesting. The results for the growth traits are shown in Appendix 4.1 for
2855 two reasons, 1) growth traits measured (e.g. leaf table height) are a weak measure of competitive
2856 effect compared to aboveground biomass, 2) most of these traits supported the findings of the RII
2857 derived from aboveground biomass.

4.3.4 Data analysis

2859   Relative interaction indices (RII) were calculated using the aboveground biomass of the
2860 native grasses within each treatment combination to determine the level of competition exerted
2861 by vetiver (Armas et al., 2004). RII is a ratio with values that range between -1 to 1, with
2862 negative values indicating competition, zero indicating symmetry, and positive values indicating
2863 facilitation (Armas et al., 2004). Therefore, RII represents the net gain or loss of a measurable
2864 trait, generally biomass, because of the presence of inter-specific interaction relative to when that
2865 inter-specific interaction is absent. RII is calculated using the following equation:

2866 $RII = (B_w - B_o)/(B_w + B_o)$

2867   With B_W representing the aboveground biomass of a native grass growing with
2868 interspecific interaction (either one or two vetiver tufts) and B_O representing the aboveground
2869 biomass of a native grass growing alone (Armas et al., 2004).

2870   As the residuals were not normally distributed, these data were analysed using
2871 generalized linear models (GLZM) with a linear distribution and an identity link function in
2872 SPSS version 24 (IBM Inc.2016) to assess the effect of one and two vetiver tufts, nutrient level,
2873 and their interaction on native grass growth in terms of RII based on aboveground biomass.
2874 GLZMs were used as they have more statistical power than other commonly used non-
2875 parametric tests because they use the actual data and not ranked data (Quinn and Keough, 2002).

2876   Where the model revealed significant differences, the sequential sidak procedure was used for

2877   multiple comparisons ($\alpha = 0.05$).

2878   To assess the effect of nutrient addition on biomass production in native grasses, the

2879   percentage change in yield (Ry) was calculated using the following equation:

2880 $Ry=\{ [(Y_H-Y_L)/Y_L]*100\}$

2881   Where Y_H is the mean growth in terms of aboveground biomass of all replicates in the

2882   control treatment, one vetiver tuft, or two vetiver tuft treatments growing at a high nutrient level,

2883   and Y_L is the mean growth in terms of aboveground biomass under the same three treatments

2884   growing at a low nutrient level. As the residuals did not conform to the assumptions of analysis

2885   of variance (ANOVA), these data were analyzed using generalized linear models with a linear

2886   distribution and an identity link function. Where the model revealed significant differences, the

2887   sequential sidak procedure was used to adjust for multiple comparisons ($\alpha = 0.05$).

2888   4.4   RESULTS

2889   4.4.1   Relative interaction index (RII)

2890   *Main effects*

2891   Overall, all four native grasses experienced competition from vetiver. However, all four-

2892   native species responded differently to competition exerted by vetiver grass tufts ($P<0.0001$;

2893   Table 4.1), with *E. curvula* and *H. hirta* experiencing the most competition and *P. maximum* and

2894   *D. eriantha* experiencing less (Figure 4.1A). Competition (one and two vetiver tufts) ($p=0.015$;

2895   Table 4.1) and nutrient level (low and high) ($p<0.0001$; Table 4.1) significantly affected the

2896   relative interaction index overall. In addition, grass species responded differently to different

2897   levels of competition and to different nutrient levels ($p<0.0001$; Table 4.1). There was also a

2898   significant influence of the interaction between species, nutrients, and competition ($p<0.021$).

2899   However, there was no significant difference in the interaction between competition and nutrient

2900   level ($p=0.157$; Table 4.1).

2901

2902

2903

101

2904   Table 4.1: Results of a generalized linear model, with a linear distribution and an identity link

2905   function, showing the main effects and interactions of grass species, competition exerted by

2906   vetiver, and nutrient level on the relative interaction index (RII) showing chi-square likelihood

2907   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**

2908

2909   ***Competition; main effect and their relevant two-way interactions***

2910   Two vetiver tufts exerted a stronger competitive effect overall than one vetiver tuft

2911   (Figure 4.1B). The four native grasses did not differ in their response to competition exerted by

2912   one vetiver tuft but differed significantly when growing with two vetiver tufts (Figure 4.2A).

2913   *Digitaria eriantha* and *P. maximum* experienced less competition (less than 10% reduction in

2914   their above ground biomass) compared to *E. curvula* and *H. hirta* (approximately 30% reduction

2915   in their biomass) (Figure 4.2A). Surprisingly, *D. eriantha* and *P. maximum* did not differ

2916   significantly between one another and within themselves in their response to competition exerted

2917   by both one and two vetiver tufts. By contrast, *E. curvula* and *H. hirta* experienced a

2918   substantially greater competitive effect when growing with two vetiver tufts compared to one

2919   vetiver tuft, but these species did not differ from each other (Figure 4.2A). Generally, vetiver has

2920   a negative effect on the growth of these native species, but some species are more resistant to

2921   competition than others.

2922
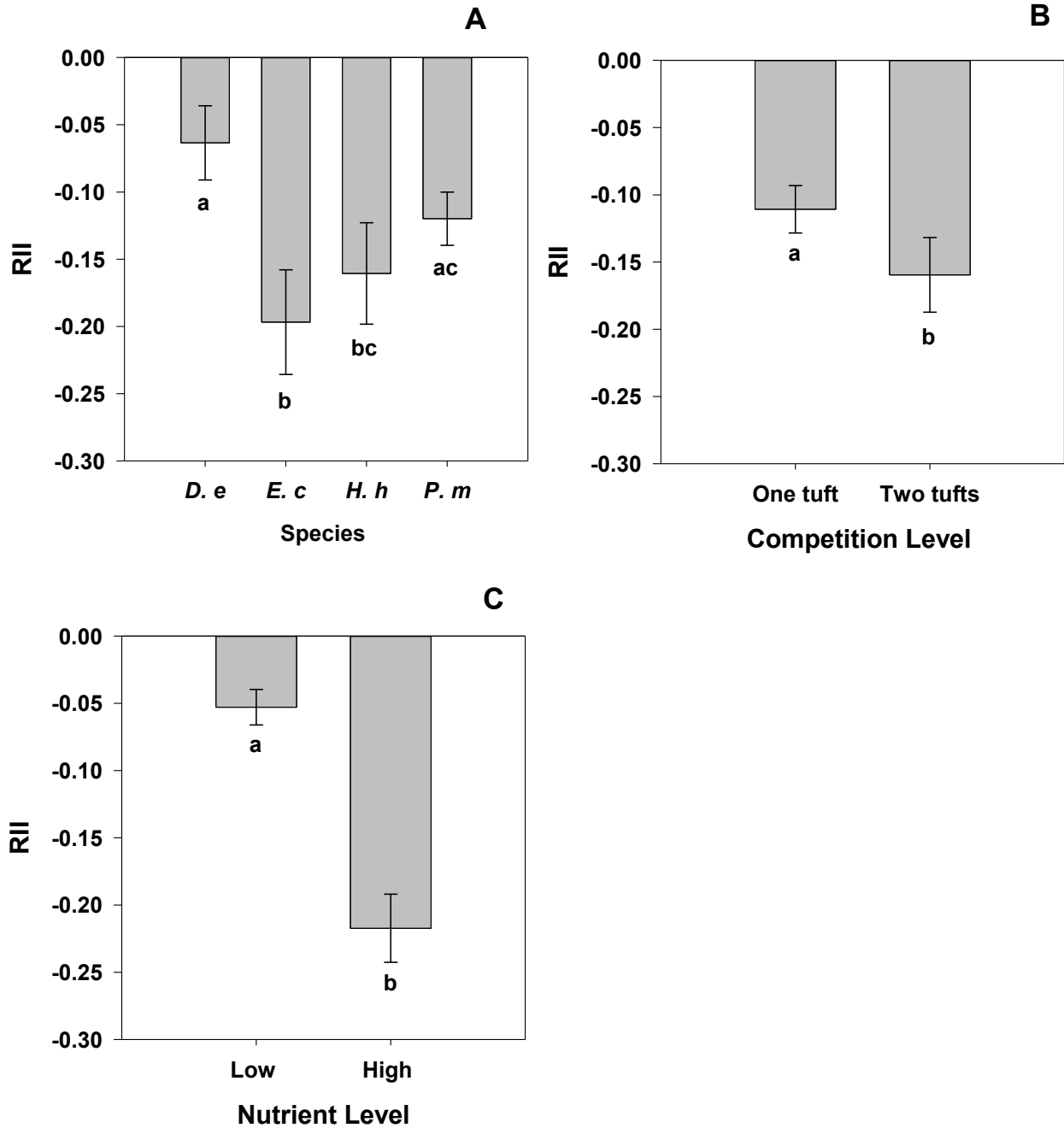
Figure 4.1: Mean (± SE) relative interaction index (RII) based on the final aboveground biomass for the main effects of species (A), vetiver competition level (B), and nutrient level (C). Different letters represent a significant difference between treatments (p<0.05)**.** Species (A) are as follows, *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

2931   Nutrient addition had a significant influence on the competitive effect exerted by vetiver

2932 on native grasses, with native grass biomass reduced by around 20% under high nutrient

2933 conditions, compared to about 5% under low nutrient conditions (Figure 4.1C). All grass species

2934 except for *P. maximum* experience greater competition under high nutrients than under low

2935 (Figure 4.2B). By contrast, *D. eriantha* and *P. maximum* did not differ significantly in their

2936 response under high nutrient conditions but both experienced a weak competitive effect (Figure

2937 4.2B). However, *E. curvula* and *H. hirta* experienced a substantially greater competitive effect

2938 under high nutrient conditions compared to all grasses under low nutrient conditions, and

2939 compared to *P. maximum* under high nutrient conditions (Figure 4.2B). *Digitaria eriantha*

2940 shifted from experiencing a slight facilitation under low nutrients to a moderate competitive

2941 effect under high nutrient conditions, while *P. maximum* experienced similar competitive effects

2942 both under low and high nutrient conditions (Figure 4.2B).

2943

2944

2945

2946

2947

2948

2949

2950

2951

2952

2953

2954

2955
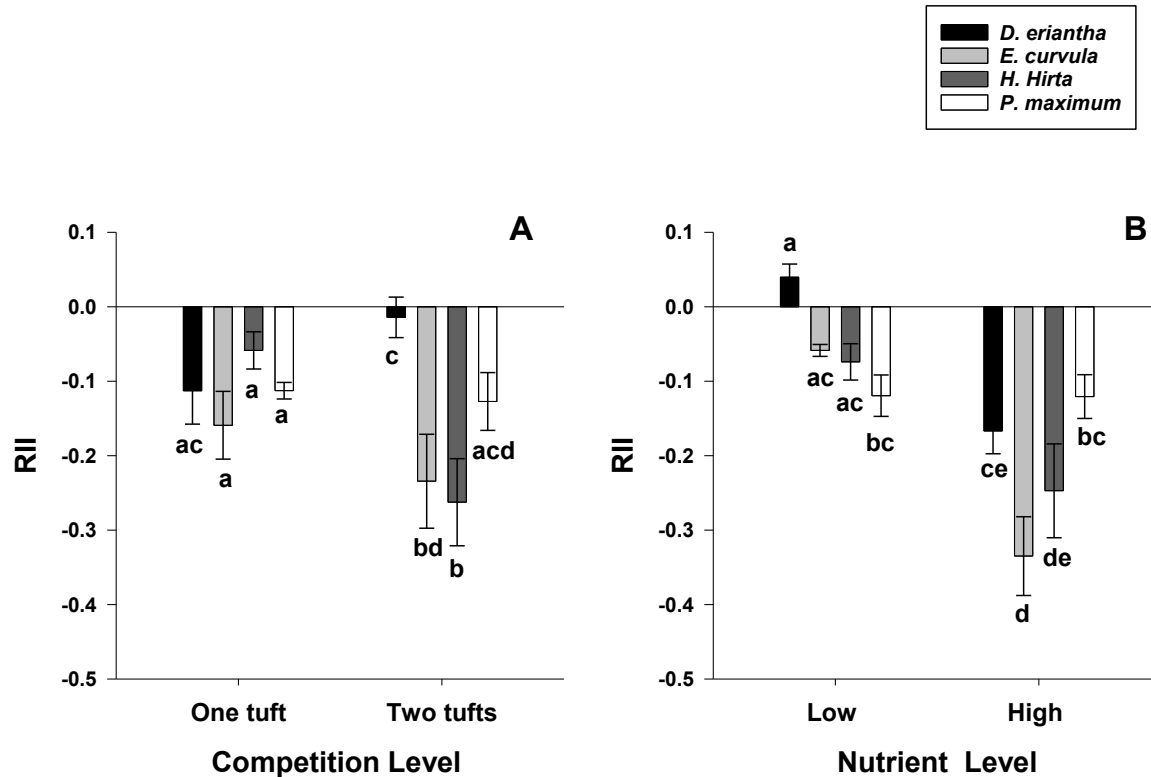
Figure 4.2: Mean (± SE) relative interaction index (RII) based on the final aboveground biomass for interaction between species and the effect of competition level (A) and nutrient level (B). Different letters represent a significant difference between treatments ($p < 0.05$).

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).
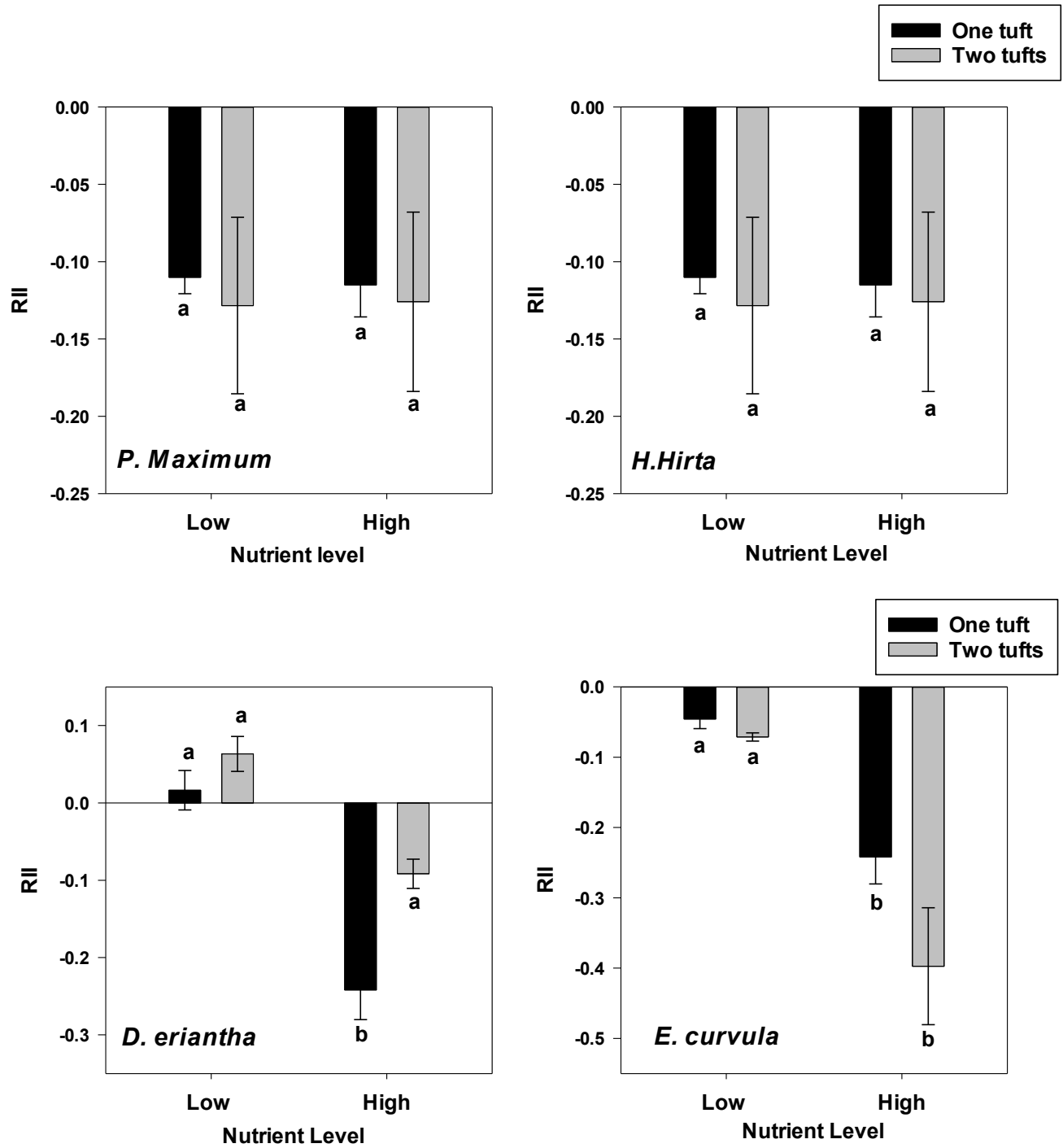
2969

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.

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**
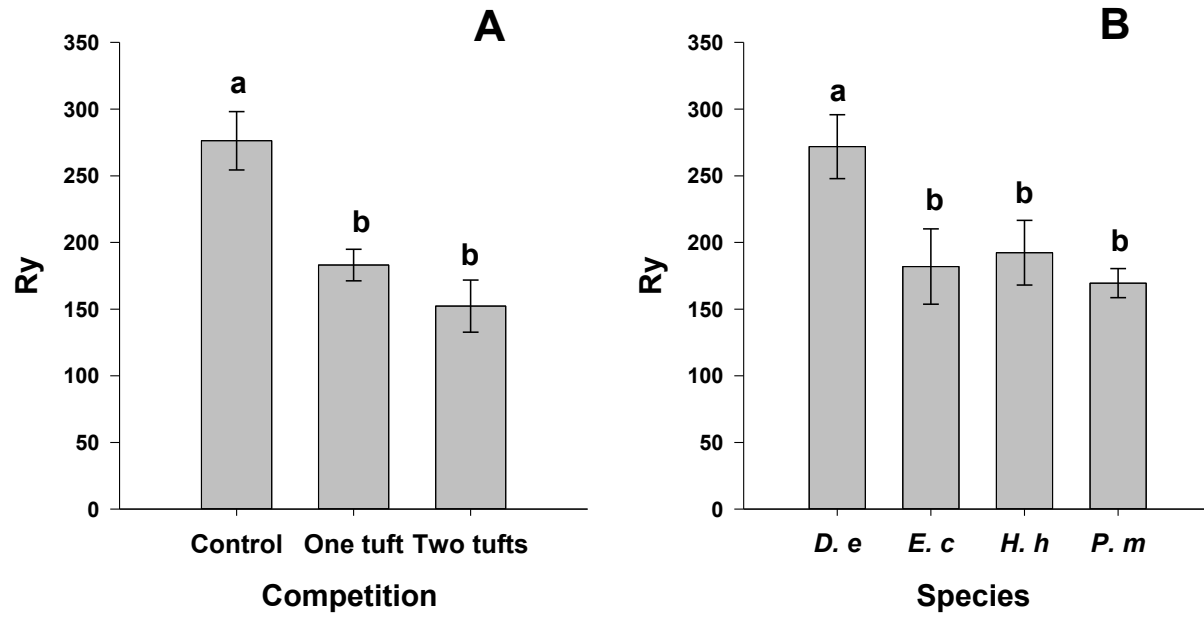
2997

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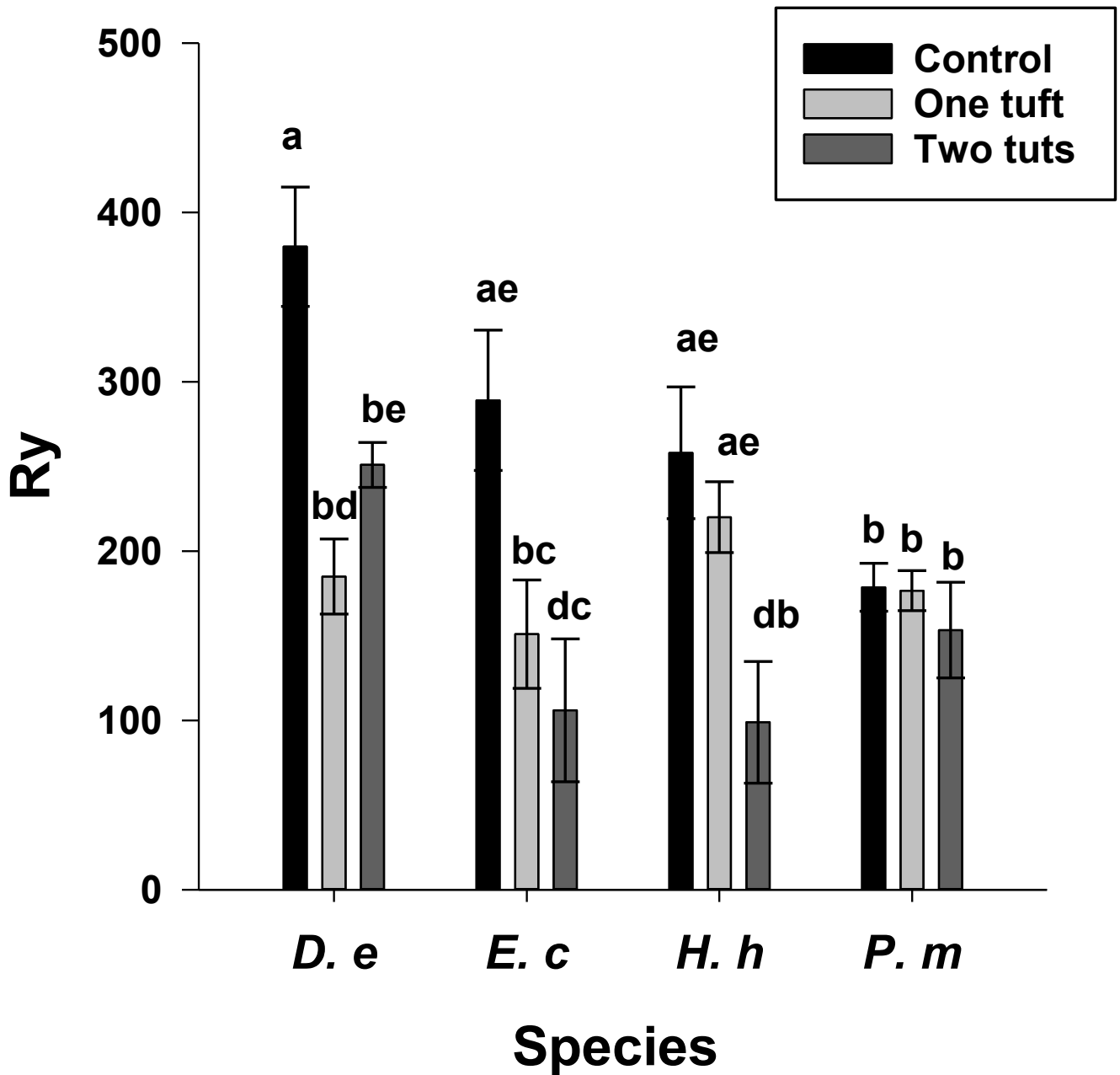
Figure 4.5: Mean (± SE) percentage change in yield (Ry) as a result of nutrient addition, based on the final aboveground biomass for interaction between the effect of competition level and native species (B). Different letters represent a significant difference between treatments ($p<0.05$).

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

3038 (Tilman, 1984; Wedin and Tilman, 1993). For example, vetiver is a broad-leaved grass with a
3039 robust dense root system, and is more similar morphologically to *D. eriantha* and *P. maximum*,
3040 than it is to *E. curvula* and *H. hirta*. Grime (1977) argued that a strong competitor plant, is a
3041 species that is leafy (i.e. broad-leaved and produces more leaves), fast growing, and has an
3042 extensive investment in root systems, which further qualifies these two native species (*D.*
3043 *eriantha* and *P. maximum*) as well as vetiver as strong competitor species.

3044   Morphological traits are important in understanding species competitive ability (Grime,
3045 1977; Tilman, 1985). For example, Fynn et al. (2009) investigated vegetative traits of 18 native
3046 grasses and compared them to their competitive effect exerted on a phytometer. The study
3047 consisted of a field trial where four seedlings of each grass species were grown around a
3048 phytometer (*Themeda triandra*), and a pot trial containing only a phytometer to measure growth
3049 when competition is absent (Fynn et al., 2009). They showed that vegetative traits such as high
3050 total leaf mass, many tillers and low specific leaf area (SLA) were linked to invasiveness and
3051 ability to resist invasion by other grasses (Fynn et al., 2009). This further suggests that grouping
3052 species in terms of their traits could be a good predictor of their ability to resist invasion, ability
3053 to invade, and competitive ability. However, their study showed the importance of considering
3054 soil nutrient addition, as it affects species investment in these traits, explained further by resource
3055 allocation trade-offs (Fynn et al., 2005; Fynn et al., 2009). Species either allocate more resources
3056 to aboveground material for light capture, and less to belowground material for soil resource
3057 acquisition, or vice versa or even to both below and aboveground material, although this is
3058 dependent on resource availability and competitive pressure (Tilman, 1990).

3059   Changes in the soil nutrient status have been linked with changes in species composition
3060 in grasslands, with soil nutrient limitation (i.e. mostly nitrogen) seen as a major factor
3061 contributing to species diversity, as it is linked directly to plant growth and plant competition
3062 (Harpole and Tilman, 2007; Harpole et al., 2016). Nitrogen is the most limiting soil nutrient for
3063 plant growth (Campbell et al., 1991). Atmospheric nitrogen deposition resulting from
3064 anthropogenic practices (i.e. commercial agriculture practices and industrial emissions) has been
3065 shown to increase nitrogen enrichment in the soil (Clark and Tilman, 2008; Bobbink et al.,
3066 2010). This study showed that the addition of nutrients increased the competitive effect exerted
3067 by vetiver on native grasses in general, and changed the competitive response of native grasses

111

3068 from categorizing them in terms of their traits to focusing on their individual species responses.
3069 However, broad leaved species, even though they experienced competition, still remained strong
3070 competitors compared to narrow-leaved grasses. For example, *D. eriantha* experienced a slight
3071 facilitative effect under low soil nutrients but shifted to experiencing a moderate competitive
3072 effect under high soil nutrient conditions. Whereas, *P. maximum*'s competitive response was not
3073 affected by soil nutrient addition, suggesting that it was a strong competitor under both low and
3074 high nutrient conditions, which is contrary to our expectations. It was expected that *P. maximum*
3075 would be a weak competitor and would increase its competitive ability in high nutrient soils as
3076 most studies have previously reported (Fynn et al., 2005; Fynn and O'Connor, 2005; Tedder et
3077 al., 2012), but that was not the case. *Panicum maximum* is a very variable grass, varying mostly
3078 in terms of height and length of creeping rhizome (Meredith, 1955; Van Oudtshoorn, 2012).
3079 These features could be rendering this grass a strong competitor against vetiver. Height
3080 (accompanied by broad-leaves) could be allowing easy light capture, and creeping rhizomes
3081 could be creating a new resource niche through foraging for resources where vetiver roots are not
3082 reaching (Silvertown, 2004; Laan et al., 2008; Van Oudtshoorn, 2012).

3083 Two of the native narrow-leaved grasses showed a relatively strong competitive ability in
3084 low nutrient soils, but experienced a strong competitive effect in high nutrient soils. These
3085 findings are consistent with those of Fynn and O'Connor (2005), even though they used field
3086 trial not pot trials, and they did not fertilize with a nutrient mixture but added granular of
3087 nitrogen and phosphorus. However, they showed that sites with both nitrogen and phosphorus
3088 added had a greater aboveground net primary production (ANPP) and were dominated by tall
3089 broad-leaved grasses (i.e. *P. maximum*) (Fynn and O'Connor, 2005). Whereas, sites with no
3090 nutrient addition were dominated by mixture of short grasses and tall narrow-leaved grasses (e.g.
3091 *T. triandra*, *E. curvula* and *H. hirta*) (Fynn and O'Connor, 2005). They showed a trade-off
3092 between greater ANPP and light availability, therefore, as soil nutrient status increases, these
3093 species allocate resources to producing aboveground biomass, shifting competition importance
3094 from soil nutrients to light, with competition for light favouring tall broad-leaved grasses because
3095 they can capture light more efficiently than narrow-leaved grasses (Fynn and O'Connor, 2005).
3096 Therefore, this could explain why narrow-leaved grasses (mostly *E. curvula*) experienced a
3097 greater competitive effect under high nutrient levels than broad-leaved grasses.

3098   Numerous studies have reported that *H. hirta* is a strong competitor in nutrient-poor
3099   environments and its competitive ability shifts when soil nutrients are no longer limiting (Fynn et
3100   al., 2009; Chejara et al., 2010; Zwerts et al., 2015). This means that *H. hirta* has a low R* for
3101   essential soil nutrients like nitrogen (Tilman, 1985), but it is known to have a weak competitive
3102   response (ability to resist invasion) (Zwerts et al., 2015), which might explain why it still
3103   experienced some competitive effect even in nutrient-poor soils. Nitrogen enrichment will
3104   therefore, have a massive effect on the competitive ability of *H. hirta,* and *E. curvula,* as they are
3105   more sensitive to shade than broad-leaved species. Even though *E. curvula* was expected to be a
3106   strong competitor because of its ability to increase biomass production irrespective of soil
3107   nutrient availability, and its fine root structure that allows easy resource acquisition (Fynn and
3108   Naiken, 2009), this grass was only shown to be a strong competitor against vetiver in nutrient-
3109   poor soils. Therefore, the competitive ability of *E. curvula* is not only dependant on nutrient
3110   availability but also on the species it is competing with. In this case, vetiver, which is a robust
3111   grass, allocates more resources to leaf, stem and root production than *E. curvula*, hence allowing
3112   it to substantially supress *E. curvula* growth and performance. However, *E. curvula* has been
3113   shown to dominate areas limited by phosphorus (Fynn and O'Connor, 2005), while vetiver
3114   growth is highly limited by phosphorus, limiting mostly leaf production (Wagner et al., 2003) .
3115   These species might coexist in areas with high nitrogen but low phosphorus, with nitrogen
3116   boosting vetiver competitive ability, and phosphorus limitation making *E. curvula* more
3117   competitive against vetiver. Such a trade-off in resource utilization and resource ratio (R*) would
3118   separate niches for these species and could potentially promote coexistence (Tilman, 1987;
3119   Silvertown, 2004; Harpole and Suding, 2011).

3120   The three-way interaction between species, competition and nutrient level, showed that
3121   species which were strong competitors under low nutrient conditions hardly retained their
3122   competitive ability under high nutrient conditions, suggesting an alteration of the trade-off
3123   through nutrient addition (Harpole and Tilman, 2007; Harpole and Suding, 2011). Native species
3124   responded differently to nutrient addition when growing either with one or two vetiver tufts, with
3125   *P. maximum* and *H. hirta* responding in a similar manner, but *D. eriantha* and *E. curvula*
3126   differing in their response. For example, *D. eriantha*'s competitive ability was strong under low
3127   nutrient conditions and did not differ between one and two tufts, but under high nutrient
3128   conditions it experienced a high competitive effect only when growing with one vetiver tuft. The

113

3129 ability of *D. eriantha* to grow under shade through effective utilization of light could explain the
3130 observed results, and the ability of this species to dominate in nutrient-rich soils. Furthermore, *D.*
3131 *eriantha* gained the most aboveground biomass as a result of nutrient addition compared to other
3132 species, so could be investing more in aboveground biomass in areas where competition for light
3133 becomes increasingly important (e.g. under high nutrient conditions with two vetiver tufts).
3134 Interspecific competition exerted by *D. eriantha* could be stronger than the intraspecific
3135 competition between vetiver tufts, hence explaining why *D. eriantha* experienced less
3136 competition when growing with two tufts than when growing with one. However, this would
3137 need to be tested because no study has investigated intraspecific competition between vetiver
3138 tufts. Numerous studies have however, shown that strong intraspecific competition and weak
3139 interspecific competition drives species coexistence and could allow invasion (Tilman, 1985;
3140 Wilson and Tilman, 1993; Fynn et al., 2009).

3141 It was observed that *H. hirta* changed its usually upright growth form to grow more
3142 horizontally when growing with two vetiver tufts. This could have been a mechanism for
3143 exposing the leaves to sunlight, which might explain why it responded similarly to *P. maximum*
3144 in the three-way interaction, showing no effect of either one or two vetiver tufts under both
3145 nutrient conditions. However, this mechanism is only possible in pot trials and not in field trials
3146 where a species will be a phytometer surrounded by numerous vetiver tufts, blocking it from
3147 growing horizontally to gain light exposure. Therefore, should this be examined in a field trial,
3148 *H. hirta* should experience a stronger competitive effect under nutrient rich conditions.
3149 Competition studies that focus on native grasses either incorporate response to defoliation, or are
3150 field trials, because these are a realistic representation of what takes place in natural grasslands
3151 (Morris, 2016). Pot trials could be forcing competition between grasses because of limited space,
3152 while in field trials space is not usually as limiting. This might explain why species like *E.*
3153 *curvula* had a weak competitive ability, because their fine roots are able to absorb soil resources
3154 easily and avoid direct competition when space is not limiting (Schenk et al., 1999; Fynn and
3155 Naiken, 2009). Therefore, in the field *E. curvula* may have a strong competitive ability compared
3156 to pot trials.

3157 Even though the hypothesis that competition shifts from belowground to aboveground
3158 when the resource gradient increases has been subject of debate among grassland ecologists

114

3159 (Wilson and Tilman, 1993; Peltzer et al., 1998; Rajaniemi, 2002), the findings of this study could
3160 be explained by this notion. Other studies showed similar findings, for example, Wilson and
3161 Tilman (1993) using a field trial showed that belowground competition was more intense in areas
3162 with low nitrogen, while aboveground competition became intense in nitrogen rich soils, but
3163 whole plant competition was similar in both low and high nitrogen soils. However, even though
3164 this hypothesis might support some of our findings, Peltzer et al. (1998) showed that in low
3165 diversity grasslands, root competition suppressed *Agropyron cristatum* even in nutrient-rich
3166 soils. Rajaniemi (2002) also showed that even though shadecloth and increased aboveground
3167 biomass through fertilizer addition reduced the same amount of light availability, shadecloth did
3168 not decrease species diversity but fertilizer addition did. This indicates that it is not competition
3169 for light alone producing this effect, even though it becomes important in nutrient rich soils, but
3170 the interplay between roots and aboveground competition is responsible for competitive
3171 exclusion of less competitive species (Rajaniemi, 2002; Rajaniemi et al., 2003). Therefore, it
3172 could be that vetiver roots are also responsible for the suppression of native grasses even when
3173 soil nutrients are high. A study separating vetiver root and shoot competition could give clarity
3174 on this, but this was outside the scope and focus of this study.

3175   A theoretical explanation that accounts for differences in soil resources which has gained
3176 popularity, mostly in studies of species coexistence and diversity, is the niche dimensionality
3177 hypothesis (Hutchinson, 1957). First proposed 50 years ago by George Evelyn Hutchinson, this
3178 hypothesis predicts that there are multi-dimensional nonoverlapping soil resources, and few
3179 aboveground resources (light and space) which allow species coexistence (Hutchinson, 1957;
3180 Harpole and Suding, 2011). Therefore, addition of a nutrient mixture and water every day, made
3181 these resources non-limiting, thereby altering soil resource niches and competitive trade-offs,
3182 increasing biomass production, which in turn shifted competition from multi-dimensional soil
3183 resources to a few aboveground resources (Tedder et al., 2012; Harpole et al., 2016).
3184 Considering that this was a pot trial, it is possible that both competition for space and light
3185 became important as in nutrient rich soils, because all species invested in their aboveground
3186 material. Therefore, resource competition theory, even though used mostly to explain large scale
3187 studies of species coexistence and species diversity (Tilman, 1994) forms a basis for
3188 understanding plant interactions and their interaction with the environment. However, it is

3189 important to understand individual plant trade-offs or niches to understand how plants will
3190 coexist with other species (Tilman, 1985).

3191 This study disproved the claim that vetiver grass does not compete with neighbouring
3192 plants, and to a limited extent the second claim that vetiver is not invasive (Vieritz et al., 2003).
3193 The hypothesis that vetiver will exert a competitive effect on native grasses, and that nutrient
3194 addition will increase vetiver's competitive effect, is supported. Therefore, the increase in
3195 nitrogen, as a result of nitrogen deposition should be expected to increase vetiver's competitive
3196 ability and possibly shift the species composition in areas rehabilitated using vetiver. However,
3197 this study shows that vetiver is a strong competitor species irrespective of nutrient addition.
3198 Extensive investment of vetiver to both above- and belowground material allows it to be
3199 competitive in both low and high nutrient soils and could be the mechanism for survival and
3200 recruitment as this grass does not produce viable seeds.

3201 **4.6   REFERENCES**
3202 Adigun, M., Are, K., 2015. Comparatives effectiveness of two vetiveria grasses species
3203   *Chrysopogon zizanioides* and *Chrysopogon nigritana* for the remediation of soils
3204   contaminated with heavy metals. American Journal of Experimental Agriculture 8, 361-
3205   366.

3206 Armas, C., Ordiales, R., Pugnaire, F.I., 2004. Measuring plant interactions: a new comparative
3207   index. Ecology 85, 2682-2686.

3208 Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante,
3209   M., Cinderby, S., Davidson, E., Dentener, F., 2010. Global assessment of nitrogen
3210   deposition effects on terrestrial plant diversity: a synthesis. Ecological applications 20,
3211   30-59.

3212 Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the
3213   Mojave Desert. The American Midland Naturalist 144, 92-108.

3214 Campbell, B., Grime, J., Mackey, J., 1991. A trade-off between scale and precision in resource
3215   foraging. Oecologia 87, 532-538.

3216   Campbell, B.D., Grime, J.P., 1992. An experimental test of plant strategy theory. Ecology 73,
3217   15-29.

3218   Chejara, V., Kriticos, D., Kristiansen, P., Sindel, B., Whalley, R., Nadolny, C., 2010. The current
3219   and future potential geographical distribution of *Hyparrhenia hirta*. Weed Research 50,
3220   174-184.

3221   Clark, C.M., Tilman, D., 2008. Loss of plant species after chronic low-level nitrogen deposition
3222   to prairie grasslands. Nature 451, 712-715.

3223   Council, N.R., 1993. Vetiver grass: a thin green line against erosion. National Academies Press.

3224   Dalton, P., Smith, R., Truong, P., 1996. Vetiver grass hedges for erosion control on a cropped
3225   flood plain: hedge hydraulics. Agricultural Water Management 31, 91-104.

3226   Donjadee, S., Chinnarasri, C., 2012. Effects of rainfall intensity and slope gradient on the
3227   application of vetiver grass mulch in soil and water conservation. International Journal of
3228   Sediment Research 27, 168-177.

3229   Fey, M., 2010. Soils of South Africa. Cambridge University Press.

3230   Fish, L., Mashau, A. C., Moeaha, M. J., Nembudani, M.T., 2015. Identification guide to southern
3231   African grasses. An identification manual with keys, descriptions and distributions.
3232   Strelitzia 36. South African National Biodiversity Institute, South Africa.

3233   Fynn, R., Morris, C., Kirkman, K., 2005. Plant strategies and trait trade-offs influence trends in
3234   competitive ability along gradients of soil fertility and disturbance. Journal of Ecology
3235   93, 384-394.

3236   Fynn, R., Naiken, J., 2009. Different responses of *Eragrostis curvula* and *Themeda triandra* to
3237   rapid-and slow-release fertilisers: insights into their ecology and implications for fertiliser
3238   selection in pot experiments. African Journal of Range and Forage Science 26, 43-46.

3239   Fynn, R.W., O'Connor, T.G., 2005. Determinants of community organization of a South African
3240   mesic grassland. Journal of Vegetation Science 16, 93-102.

3241   Fynn, R.W., Wragg, P., Morris, C., Kirkman, K., Naiken, J., 2009. Vegetative traits predict grass
3242   species' invasiveness and the invasibility of restored grassland. African Journal of Range
3243   & Forage Science 26, 59-68.

3244   Goldberg, D.E., 1996. Competitive ability: definitions, contingency and correlated traits.
3245   Philosophical Transactions of the Royal Society of London B: Biological Sciences 351,
3246   1377-1385.

3247   Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth.
3248   Infinity Publishing.

3249   Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its
3250   relevance to ecological and evolutionary theory. The American Naturalist 111, 1169-
3251   1194.

3252   Harpole, W.S., Suding, K.N., 2011. A test of the niche dimension hypothesis in an arid annual
3253   grassland. Oecologia 166, 197-205.

3254   Harpole, W.S., Sullivan, L.L., Lind, E.M., Firn, J., Adler, P.B., Borer, E.T., Chase, J., Fay, P.A.,
3255   Hautier, Y., Hillebrand, H., 2016. Addition of multiple limiting resources reduces
3256   grassland diversity. Nature 537, 93-96.

3257   Harpole, W.S., Tilman, D., 2007. Grassland species loss resulting from reduced niche dimension.
3258   Nature 446, 791-793.

3259   Hoagland, D.R., Arnon, D.I., 1950. The water-culture method for growing plants without soil.
3260   California Agricultural Experiment Station 347.

3261   Hutchinson, G.E., 1957. Concluding remarks. quantitative biology 22, 415-427.

3262   Laan, M.v.d., Reinhardt, C., Belz, R., Truter, W., Foxcroft, L., Hurle, K., 2008. Interference
3263   potential of the perennial grasses *Eragrostis curvula*, *Panicum maximum* and *Digitaria*
3264   *eriantha* with *Parthenium hysterophorus*. Tropical Grasslands 42, 88-95.

3265   McDonald, C.J., Jones RM; Tothill, JC, 1998. Growth and spread of *Digitaria eriantha* cv.
3266   Premier and *Urochloa mosambicensis* cv. Nixon oversown into native speargrass

3267   (*Heteropogon contortus*) pasture in south-east Queensland. Tropical Grasslands 32, 41-
3268   49.

3269   Meredith, D., 1955. The grasses and pastures of South Africa.

3270   Morris, C.D., 2016. Is the grazing tolerance of mesic decreaser and increaser grasses altered by
3271   soil nutrients and competition? African Journal of Range & Forage Science 33, 235-245.

3272   Peltzer, D.A., Wilson, S.D., Gerry, A.K., 1998. Competition intensity along a productivity
3273   gradient in a low-diversity grassland. The American Naturalist 151, 465-476.

3274   Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists.
3275   Cambridge University Press.

3276   Rajaniemi, T.K., 2002. Why does fertilization reduce plant species diversity? Testing three
3277   competition-based hypotheses. Journal of Ecology 90, 316-324.

3278   Rajaniemi, T.K., Allison, V.J., Goldberg, D.E., 2003. Root competition can cause a decline in
3279   diversity with increased productivity. Journal of Ecology 91, 407-416.

3280   Roongtanakiat, N., Chairoj, P., 2001. Uptake potential of some heavy metals by vetiver grass.
3281   Kasetsart Journal: Natural Science 35, 46-50.

3282   Schenk, H.J., Callaway, R.M., Mahall, B., 1999. Spatial root segregation: are plants territorial?
3283   Advances in Ecological Research 28, 145-180.

3284   Silvertown, J., 2004. Plant coexistence and the niche. Trends in Ecology & Evolution 19, 605-
3285   611.

3286   Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J., 2004. Impact of nitrogen deposition on
3287   the species richness of grasslands. Science 303, 1876-1879.

3288   Tainton, N.M., Bransby, D., Booysen, P.d.V., 1976. Common veld and pasture grasses of Natal.
3289   Shuter & Shooter.

3290   Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2012. Do soil nutrients mediate competition
3291   between grasses and Acacia saplings? Grassland Science 58, 238-245.

3292 Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation.
3293   The American Naturalist 116, 362-393.

3294 Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist
3295   125, 827-852.

3296 Tilman, D., 1987. On the meaning of competition and the mechanisms of competitive
3297   superiority. Functional Ecology 1, 304-315.

3298 Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and
3299   succession. Oikos 58, 3-15.

3300 Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2-
3301   16.

3302 Tilman, D., Wedin, D., 1991. Dynamics of nitrogen competition between successional grasses.
3303   Ecology 72, 1038-1049.

3304 Tilman, G.D., 1984. Plant dominance along an experimental nutrient gradient. Ecology 65, 1445-
3305   1453.

3306 Truong, P., Chomchalow, N., Vessabutr, S., 1999. Vetiver grass technology for mine
3307   rehabilitation. Pacific Rim Vetiver Network, Tech. Bull. No. 1999/2, PRVN / RDPB,
3308   Bangkok, Thailand.

3309 Truong, P., Hart, B., Chomchalow, N., Sombatpanit, S., 2001. Vetiver system for wastewater
3310   treatment. Office of the Royal Development Projects Board.

3311 Van Oudtshoorn, F.v., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza
3312   Publications.

3313 Vieritz, A., Truong, P., Gardner, T., Smeal, C., 2003. Modelling Monto vetiver growth and
3314   nutrient uptake for effluent irrigation schemes. Proceedings of the Third International
3315   Conference on Vetiver and Exhibition, 254-264.

3316 Vilà, M., Gómez, A., Maron, J.L., 2003. Are alien plants more competitive than their native
3317   conspecifics? A test using *Hypericum perforatum* L. Oecologia 137, 211-215.

3318   Wagner, S., Truong, P., Vieritz, A., Smeal, C., 2003. Response of vetiver grass to extreme
3319   nitrogen and phosphorus supply. Proceedings of the Third International Conference on
3320   Vetiver and Exhibition, Guangzhou, China.

3321   Wedin, D., Tilman, D., 1993. Competition among grasses along a nitrogen gradient: initial
3322   conditions and mechanisms of competition. Ecological Monographs 63, 199-229.

3323   Wilson, S.D., Tilman, D., 1993. Plant competition and resource availability in response to
3324   disturbance and fertilization. Ecology 74, 599-611.

3325   Wilson, S.D., Tilman, D., 1995. Competitive responses of eight old-field plant species in four
3326   environments. Ecology 76, 1169-1180.

3327   Xia, H., Ao, H., He, D., 1998. The effect of environmental factors on the growth of vetiver
3328   growth. Vetiver Research and Development 2, 39-44.

3329   Xu, L., 1998. Vetiver research and development, proceedings of International Vetiver Workshop,
3330   Fuzhou, China. Agricultural Science and Technology Press of China, Beijing.

3331   Xu, L., 2002. Vetiver research and development: A decade experience from China, Proceedings:
3332   The Second International Vetiver Conference, ORDPB, Bangkok, 311-322.

3333   Zwerts, J., Prins, H., Bomhoff, D., Verhagen, I., Swart, J., de Boer, W., 2015. Competition
3334   between a Lawn-Forming *Cynodon dactylon* and a Tufted Grass Species *Hyparrhenia*
3335   *hirta* on a South-African Dystrophic Savanna. PloS one 10, 1-17.

121

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.

3366   There is no doubt that vetiver is useful for environmental protection and rehabilitation.
3367 However, this study had a different approach, as it investigated the competitive ability of vetiver
3368 and how it behaves in areas where it has been used; whether it allows seed germination and
3369 seedling establishment of native grasses, as well as its competitive effect on mature native grass
3370 tufts on both high and low nutrient soils. This was with a broad aim to understand whether
3371 vetiver can coexist with native grasses or even be succeeded by native grasses, and therefore,
3372 predict the potential of vetiver to become invasive. This study showed that vetiver does show
3373 some signs of recruitment in areas where it was not originally planted, and that species richness
3374 increases with increasing distance away from planted vetiver in areas rehabilitated using vetiver.
3375 Moreover, while vetiver does facilitate seed germination it negatively affects seedling
3376 establishment. Vetiver is a very competitive grass, mostly in nutrient rich soils, but native
3377 species with similar traits (broad-leaved, robust root system, and sometimes stoloniferous or with
3378 rhizomes) experience less competitive suppression than species with dissimilar traits (narrow-
3379 leaved, fine roots, and no stolons or rhizomes). Species coexistence, therefore, is related to
3380 species traits and so can be understood through understanding species quantitative trade-offs that
3381 link to their resource utilization.

3382   The most basic trade-off that is well researched is that a strong competitor species
3383 (investing more resources into competitive traits) usually has limited seed production, poor seed
3384 germination, and poor seed dispersal (Tilman, 1980, 1990, 1994). This is true with vetiver, as
3385 this study shows that vetiver is a strong competitor but shows limited signs of spreading,
3386 possibly because seeds are suggested to be non-viable (Council, 1993). It also reproduces
3387 vegetatively by means of tillers, which is a slower process (Greenfield, 2002). Such trade-offs,
3388 according to Tilman, can allow other species with contrasting seed related traits to coexist with it
3389 (Tilman, 1980, 1985, 1990). This means that vetiver should be able to coexist with native species
3390 which produce an abundant number of seeds with a high germination rate and effective dispersal.
3391 One can thus argue that *E. curvula* can coexist with vetiver but not in close proximity, as vetiver
3392 seems to be territorial as evidenced by having bare ground around it. However, in this study, *E.*
3393 *curvula* and *H. hirta* which are narrow-leaved species were mostly supressed by the vetiver
3394 competitive effect.

3395   This study showed that species with similar morphological traits to vetiver grass but with
3396   greater seed production, germination success, and seed dispersal can potentially coexist with
3397   vetiver even in close proximity e.g. *Digiteria eriantha* and *P. maximum*. However, it is highly
3398   unlikely that these species will succeed or outcompete vetiver, even though they are able to
3399   withstand vetiver competitive effect. *Digiteria eriantha* has a strong competitive ability with
3400   high seed production and germination rates (Meredith, 1955). The combination of these traits
3401   could allow greater coexistence between vetiver and *D. eriantha*, mostly because vetiver
3402   increases the germination rate of native grasses around it, but affects seedling survival and so
3403   limits native species recruitment. There is a better chance that seedlings of *D. eriantha* can
3404   survive the competitive effect and/or the allelopathic effect exacted by vetiver oil because mature
3405   tufts benefited from growing with vetiver grass. Such coexistence can reduce the vegetative
3406   spreading of vetiver grass through competing directly with vetiver and making sure that it serves
3407   only its intended purpose of stabilizing and conserving the soil, thus reducing soil erosion.

3408   It should be noted that because few species seem to have potential to coexist with vetiver
3409   grass, diversity in areas rehabilitated using vetiver should be expected to be low, thus also low
3410   grassland productivity. Vetiver, as our knowledge stands, lives longer than other grass species,
3411   and seems to stay as a permanent feature, which is beneficial for prevention of soil erosion
3412   through providing aboveground cover and binding the soils, but not for promoting species
3413   diversity and rangeland productivity (Grimshaw, 1993; Dalton et al., 1996; Huston, 2004).
3414   Broad-leaved native species with strong competitive ability, shade tolerance, and the potential
3415   for reducing soil erosion should be the target species for reseeding or vegetative planting in areas
3416   rehabilitated using vetiver. Management approaches that aim to remove or suppress vetiver after
3417   it has served its purpose should be developed so that these rehabilitating rangelands can regain a
3418   relatively good species diversity and increase grassland productivity. Development of a
3419   management protocol for vetiver grass is important for two reasons: 1) vetiver's grass is not a
3420   preferred grass by grazers and its leaves hardens as it matures thus reducing its palatability and
3421   digestibility (Grimshaw, 1993). In areas with unmanaged grazing and/or selective grazing,
3422   selection for native grasses could allow the dominance and even the invasion of vetiver as native
3423   grasses will allocate more resources to regrowth than to competing with vetiver (Tainton, 1999).
3424   This is evidenced in the second chapter, where an area having unmanaged continuous grazing
3425   had signs of vetiver recruiting where it was not originally planted. 2) Vetiver growth behavior

3426 allows it to stay green all year round, which in turn reduces the available fuel load, and hence fire
3427 intensity and frequency (Gnansounou et al., 2017). In fire climax grasslands, this can alter fire
3428 regimes, which might allow woody plant encroachment in areas where encroachment is managed
3429 through fire and might drive fire-adapted species to local extinction (Bond et al., 2003;
3430 Hoffmann and Solbrig, 2003). Furthermore, an expected increase in atmospheric nitrogen
3431 deposition is likely to favour vetiver grass through increasing its competitive ability; hence, the
3432 need for development of a management protocol that will take such effects into account is
3433 needed.

3434 Although the method used to answer questioned asked in this study were mostly of a short spatial
3435 and temporal scale, but the study acts as a first step toward understanding vetiver ecology and
3436 use in grasslands rehabilitation. This study recommends that vetiver should continue to be used
3437 for the following environmental and agricultural purposes.

3438 • For soil and water conservation but not for maintaining and promoting species diversity.

3439 • In heavy degraded/eroded sites (e.g. gully erosion) where soil cover is more important
3440   than species diversity.

3441 • In agriculture (planted in contours) for avoiding soil erosion, maintaining soil health, and
3442   for use as an insect pest trap. Vetiver attracts herbivorous insect pests away from the
3443   main agricultural crops.

3444 • For phytoremediation in dams, rivers, and contaminated lands, where native grasses
3445   cannot grow. In dams and rivers, it should be used as a floating wetland treatment system
3446   (removable floating islands). However, in abandoned mine sites and landfill sites, proper
3447   management that will allow reseeding and establishment of native species after vetiver
3448   has restored the soil health should be formulated.

3449 There is no argument against the usefulness and potential of vetiver in soil and water
3450 conservation, although research should redirect its focus to management questions and
3451 improving the spatial and temporal scale of this current study. These are the questions/areas that
3452 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.

3509   Dalton, P., Smith, R., Truong, P., 1996. Vetiver grass hedges for erosion control on a cropped
3510   flood plain: hedge hydraulics. Agricultural Water Management 31, 91-104.

3511   Gnansounou, E., Alves, C.M., Raman, J.K., 2017. Multiple applications of vetiver grass–A
3512   review. International Journal of Environmental. Sciences 2, 125-141.

3513   Greenfield, J.C., 2002. Vetiver grass: an essential grass for the conservation of the planet earth.
3514   Infinity Publishing.

3515   Grimshaw, R.G., 1993. The role of vetiver grass in sustaining agricultural productivity. Asia
3516   Technical Department. The World Bank, Washington DC USA.

3517   Hoffmann, W.A., Solbrig, O.T., 2003. The role of topkill in the differential response of savanna
3518   woody species to fire. Forest Ecology and Management 180, 273-286.

3519   Huston, M.A., 2004. Management strategies for plant invasions: manipulating productivity,
3520   disturbance, and competition. Diversity and Distributions 10, 167-178.

3521   Kiiskila, J.D., Sarkar, D., Feuerstein, K.A., Datta, R., 2017. A preliminary study to design a
3522   floating treatment wetland for remediating acid mine drainage-impacted water using
3523   vetiver grass (*Chrysopogon zizanioides*). Environmental Science and Pollution Research
3524   24, 27985-27993.

3525   Meredith, D., 1955. The grasses and pastures of South Africa.

3526   Morgan, R.P.C., 2009. Soil erosion and conservation. John Wiley & Sons.

3527   O'Rourke, S., Minasny, B., Holden, N., McBratney, A., 2016. Synergistic use of Vis-NIR, MIR,
3528   and XRF spectroscopy for the determination of soil geochemistry. Soil Science Society
3529   of America Journal 80, 888-899.

3530   Tainton, N.M., 1999. Veld Management in South Africa. University of Natal press.

3531   Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation.
3532   The American Naturalist 116, 362-393.

3533   Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist
3534   125, 827-852.

3535 Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and
3536   succession. Oikos 58, 3-15.

3537 Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2-
3538   16.

3539 Tilman, D., Wedin, D., 1991. Dynamics of nitrogen competition between successional grasses.
3540   Ecology 72, 1038-1049.

3541 Truong, P., Loch, R., 2004. Vetiver system for erosion and sediment control. Proceeding of 13th
3542   international soil conservation organization conference, 1-6.

3543 Wessels, K., Prince, S., Malherbe, J., Small, J., Frost, P., VanZyl, D., 2007. Can human-induced
3544   land degradation be distinguished from the effects of rainfall variability? A case study in
3545   South Africa. Journal of Arid Environments 68, 271-297.

3546 Xia, H., 2004. Ecological rehabilitation and phytoremediation with four grasses in oil shale
3547   mined land. Chemosphere 54, 345-353.

6   APPENDICES

6.1 APPENDIX A: Study species

3550   The native grasses listed here are used for soil stabilization, grassland restoration, and
3551 could be a better option for integration with vetiver; however they differ in their competitive
3552 ability, and whether they can coexist with vetiver is still an answered question. Descriptions,
3553 distribution, ecology and uses of these grasses are further discussed to give an elucidated
3554 background and reason for their use in this study.

3555 1.   Strong competitors

3556 1.1   *Eragrostis curvula*

3557 1.1.1   Description

3558   *Eragrostis curvula* (Schrad.) Nees., commonly known as a Weeping love grass, is a
3559 robust densely tufted perennial native grass. It has many lax and drooping leaves (Fish et al.,
3560 2015). The inflorescence differs with ecotypes but most have an open branched panicle.
3561 However, some ecotypes found in the Eastern, Western and Northern Cape, sometimes have a
3562 contracted panicle (Tainton et al., 1976; Van Oudtshoorn, 1999). Therefore, *E. curvula* is a
3563 variable grass with many localized ecotypes which differ in height, inflorescence structure, leaf
3564 structure and productivity (Van Oudtshoorn, 2012). The leaves (up to 60cm long, and 10mm
3565 wide) are usually concentrated from the base of the plant but are not curled (Van Oudtshoorn,
3566 2012). The stem height ranges from 60cm to 120cm or sometimes more depending on the
3567 environment and the soil fertility (Tainton et al., 1976). Roots are fine, dense, and fibrous
3568 allowing the grass to be effective in soil resource capture (Meredith, 1955).

3569 1.1.2   Distribution

3570   It originates in southern and eastern Africa but is now widely spread in other countries as
3571 a weed or fodder crop (Van Oudtshoorn, 2012; Fish et al., 2015). *Eragrostis curvula* covers a
3572 vast area of South Africa occurring in parts of the Nama-karroo, grassland, savanna, and forest
3573 biomes (Tainton et al., 1976; Van Oudtshoorn, 2012). It is widely spread in disturbed sites and
3574 badly managed veld. It prefers areas with high rainfall (above 600mm, mostly in overgrazed
3575 areas) and well-drained soils but will grow in low rainfall areas and on sandy and acidic soils
3576 (Tainton et al., 1976).

3577   1.1.3   Ecology and uses

3578   *Eragrostis curvula* produces abundant high-quality seeds which germinate easily, hence
3579   allowing it to spread (Fynn and Naiken, 2009). It flowers in the growing season between August
3580   and June, and usually stays green until mid-winter (Van Oudtshoorn, 2012). Weeping lovegrass
3581   has an extensive root system which grows both downward (down to 5m) and horizontally
3582   (stretching 1m), hence making it drought tolerant through efficient use of light rain and allowing
3583   it to prevent other plants from establishing.

3584   This grass is a strong competitor which is moderately shade tolerant and adapted to heavy
3585   grazing (Mynhardt et al., 1994; Fynn and Naiken, 2009). For example, Mynhardt et al. (1994)
3586   investigated the competitive ability (both intra- and inter-specific) of *E. curvula* and *Anthephora*
3587   *pubescens* using biomass allocation and yield. Relative yield and biomass allocation showed that
3588   *E. curvula* could outcompete *A. pubescens* because it is a strong interspecific competitor but
3589   showed no significant differences in intraspecific competition, while *A. pubescens* was a weak
3590   competitor for both intra- and inter-specific competition (Mynhardt et al., 1994). Leaf and root
3591   extracts of *E. curvula* have been shown to have allelopathic properties that inhibit germination
3592   and growth of other species (Ghebrehiwot et al., 2014). For this reason, it had become invasive
3593   in some countries such as Australia (Firn et al., 2010).

3594   Nitrogen addition has been shown to increase both biomass and tussock diameter of
3595   many grasses, but not all grasses are limited by nitrogen. For example, Fynn and Naiken (2009)
3596   evaluated the response of *Eragrostis curvula* and *Themeda triandra* to different levels of
3597   nitrogen addition. They showed that these species increased their biomass with an increase in
3598   nitrogen availability (Fynn and Naiken, 2009). However, *T triandra* grew to its full potential at
3599   intermediate nitrogen availability, while *E. curvula* continued growing, increasing its biomass
3600   even at high nitrogen availability (Fynn and Naiken, 2009). Furthermore, *E. curvula* competed
3601   well under both high and low soil nutrient levels because of its root structure and ability to
3602   increase biomass production in both high and low nutrient soils.

3603   *Eragrostis curvula* is a relatively variable grass with a moderate grazing value but is
3604   planted as a pasture grass in South Africa and Africa at large. This is because it establishes easily
3605   even in poor environmental conditions, has high leaf production and produce high-quality seeds
3606   (Mynhardt et al., 1994; Fynn and Naiken, 2009). Furthermore, because of these abilities and the

131

3607 extensive root system, *E. curvula* has been used for soil erosion control, rehabilitation and
3608 stabilizing highway embankments (Van Oudtshoorn, 1999, 2012).

3609 1.2 *Digitaria eriantha*

3610 1.2.1 Description

3611 *Digitaria eriantha* Steud., was previously classified as a number of different species e.g
3612 *D. umfolozi*, *D. decumbens*, *D. pentzii*, *D. setivalva*, *D. smutsii*, *D. valida* (Van Oudtshoorn,
3613 1999, 2012; Fish et al., 2015). The combining of these species has made *D. eriantha* a very
3614 variable species, with some having a stolon and a branched culm, a stolon and unbranched culm,
3615 and others without both the stolon and branched culm (Tainton et al., 1976). In general, *D.*
3616 *eriantha* is known as "common finger grass", and is a broad-leaved robust tufted perennial grass
3617 with digitate or semi-digitate inflorescences, with a very long, thin raceme (4-20cm long,
3618 fingers) (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012). The spikelets are found on opposite
3619 sides of the main branch of the raceme (Van Oudtshoorn, 2012). The lowermost part of the leaf
3620 sheath is densely hairy but the leaves are usually not hairy (Tainton et al., 1976). The culms of
3621 this grass range in height from 40cm to over 1.8 m (Tainton et al., 1976; Van Oudtshoorn, 1999,
3622 2012). It has a robust, sometimes stoloniferous root systems making the grass more competitive
3623 belowground (Meredith, 1955; Tainton, 1981b).

3624 1.2.2 Distribution

3625 Known to be native only in southern Africa (including Angola and Zambia) (Fish et al.,
3626 2015), this grass; however, has been introduced in many countries for different agricultural
3627 reasons (McDonald et al., 1998; Van Oudtshoorn, 1999, 2012). *D. eriantha* is occurs in most of
3628 South Africa in sandy and gravelly soils in arid regions, but also in well-drained, damp soils near
3629 wetlands in wetter regions of the country. It is often seen along roadsides, stream banks in tall
3630 grasslands, and in grasslands near forest margins (Tainton et al., 1976; Van Oudtshoorn, 1999,
3631 2012).

3632 1.2.3 Ecology and uses

3633 In wet areas, common finger grass flowers almost throughout the growing season, but
3634 most ecotypes flower from January to late April or May (Van Oudtshoorn, 2012). The

3635   stoloniferous varieties can regenerate using both the stolon and seeds, even though they produce
3636   little or no seeds when growing in unfertile lands (McDonald, 1998; Tainton et al., 1976).

3637   It is a strong competitor which has the ability to resist invasion by other grasses, mostly
3638   in high nutrient soils (McDonald, 1998). The stoloniferous varieties spread quickly in disturbed
3639   areas, and invade easily to nearby veld; however, *D. eriantha* is considered to grow well with
3640   other species. McDonald (1998) showed that *D. eriantha* has invaded grasslands with both low
3641   and high soil fertility, which was previously dominated by *Heteropogon contortus* and
3642   *Macroptilium atropurpureum* cv. Siratro in Australia. He furthermore suggested that common
3643   finger grass invades fertile soils and has proven to be more competitive on such soils; however, it
3644   has changed the vegetation structure of both these grasslands (low fertility and high fertility) ever
3645   since it was sown as pasture in 1979 and 1980 respectively (McDonald, 1998).

3646   Common finger grass is favoured by large herbivores because it is highly digestible,
3647   palatable, and has high leaf production (McDonald et al., 1998; Van Oudtshoorn, 1999, 2012). In
3648   most African countries and other countries outside Africa, *D. eriantha* is used as a fodder grass
3649   and is considered as the most reliable grass as an animal feed. It is a decreaser grass, hence,
3650   dominates in good veld but decreases in abundance in overgrazed or undergrazed veld (Van
3651   Oudtshoorn, 1999, 2012). For this reason, *D. eriantha* has been used for veld improvement
3652   mostly through seeding (Ramírez and Hacker, 1996). Furthermore, because it is a variable grass
3653   with a stoloniferous variety and produces a dense root system, it has been used for soil erosion
3654   control, rehabilitation and stabilization of highway embankments (Van Oudtshoorn, 1999, 2012).

3655   2.   Weak competitors

3656   2.1   *Panicum maximum*

3657   2.1.1   Description

3658   *Panicum maximum* Jacq., commonly known as guinea grass or white buffalo grass, is a
3659   broad-leaved tufted perennial grass with a large open panicle inflorescence (Van Oudtshoorn,
3660   1999, 2012). The inflorescence usually has lax branches, while the lower branches are arranged
3661   in a whorl (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012). The spikelets are purple in colour
3662   when it grows in direct sunlight, but green when growing under shade (Van Oudtshoorn, 2012;
3663   Fish et al., 2015). This grass has many leaves and its leaf sheath is usually hairy but varies with

3664   different ecotypes. The height of this grass also varies with different ecotypes but ranges from
3665   60cm to 300cm when environmental conditions are conducive and begins to form a reed like
3666   appearance (Tainton et al., 1976). The roots grow from the lower nodes and it often has short
3667   creeping rhizomes.

3668   2.1.2   Distribution

3669   Although originating in Africa, this grass has spread to all tropical regions of the world
3670   (Tainton et al., 1976; Fish et al., 2015). In South Africa, guinea grass is distributed along the
3671   eastern and northern parts in the grassland, savanna and Nama-karroo biomes. It prefers cool,
3672   shady, damp areas with well-drained, fertile soils, such as river margins, low-lying coastal areas
3673   and is usually found growing under shrubs and trees in open woodland regions (Tainton et al.,
3674   1976; Van Oudtshoorn, 1999; Tainton, 1999; Van Oudtshoorn, 2012).

3675   2.1.3   Ecology and use

3676   Even though this grass has a short creeping rhizome, it relies more on seeds for
3677   reproduction. It flowers in the growing season (September to March) and stays green until late
3678   winter. Like most grasses, it is pollinated by wind and seeds are sometimes eaten by birds
3679   (Tainton et al., 1976; Van Oudtshoorn, 1999; Tainton, 1999; Van Oudtshoorn, 2012). However,
3680   there are many different localized ecotypes of this grass in South Africa, which is why this grass
3681   is so variable.

3682   *Panicum maximum* has been shown to be variable even in terms of it competitive ability.
3683   In general, this grass competes well in nutrient-rich soil, suggested to be influenced by Nitrogen
3684   (N) and Potassium (P) levels, while on nutrient-poor soils it is outcompeted by other grass
3685   species (Van Oudtshoorn, 2012; Tedder et al., 2012). For example, Fynn et al. (2005) showed
3686   that *P. maximum* outcompeted *H. hirta* in areas with high N and P; however, the reverse
3687   happened in areas with low N and P. In Hawaii, *P. maximum* was naturalized in 1871 and is now
3688   considered an invasive species. Ammondt and Litton (2012), using a pot trial, investigated
3689   competitive response of *P. maximum* when growing with the Hawaiian native species,
3690   *Myoporum sandwicense*, *Dodonaea viscosa*, and *Plumbago zeylanica* (Ammondt and Litton,
3691   2012). The reproductive tillers and biomass (above- and belowground) of *P. maximum* was
3692   reduced when growing with one or a combination of these species (Ammondt and Litton, 2012).

3693 This suggests that *P. maximum* can be outcompeted by these species and that it is a weak
3694 competitor against these grasses and woody plant species when nutrient availability is not taken
3695 into account. Therefore, the fluctuation in its competitiveness means that *P. maximum* is a weak
3696 competitor when competing with other grasses, and the increased performance under nutrient-
3697 rich soils could be a strategy to avoid competitive exclusion.

3698   It is a very good grazing grass due to high leaf production and high palatability, used as a
3699 pasture grass all over Africa. Furthermore, *P. maximum* establishes quickly and has dense roots
3700 with a creeping rhizome. For this reason, *P. maximum* has is used for rehabilitation and soil
3701 protection (Van Oudtshoorn, 2012).

3702 2.2   *Hyparrhenia hirta* Stapf

3703 2.2.1   Descriptions

3704   *Hyparrhenia hirta* Stapf. of the many species in the *Hyparrhenia* genus, is recognizable
3705 by its pairs of white villous racemes which do not bend downward, growing on a stem with
3706 narrow rough leaves and a hard basal tussock (Tainton et al., 1976; Van Oudtshoorn, 1999,
3707 2012). Commonly known as thatching grass, *H. hirta* is a relatively dense erect, tufted perennial
3708 grass (Van Oudtshoorn, 2012). The racemes on its spikelets have four to seven brownish awns.
3709 Culm height varies greatly and is affected by rainfall availability (Van Oudtshoorn, 1999, 2012;
3710 Fish et al., 2015). This grass is relatively tall, but its height varies from 30cm in shallow nutrient-
3711 poor soils to over 100 cm in well-drained, nutrient-rich soils. It has many tillers forming nodded
3712 stems and has a dense fibrous root system (Tainton et al., 1976; Van Oudtshoorn, 1999, 2012).

3713 2.2.2   Distribution

3714   It is a dominant grass in South Africa, occurring in all provinces (Van Oudtshoorn, 1999,
3715 2012; Fish et al., 2015). It also occurs throughout the African continent, the Mediterranean
3716 regions, and Pakistan. In some countries outside of Africa it has been considered an invasive
3717 weed (e.g. Australia) (Van Oudtshoorn, 1999, 2012; Zwerts et al., 2015). It is found in many
3718 biomes in South Africa, from mid to low altitude areas in fynbos, Nama-karroo, savanna, and
3719 grasslands. It prefers well-drained soils, particularly gravelly soil, but can also be found in
3720 shallow soils. It dominates in open grassland on rocky slopes, along river margins and roadsides,

3721 and in disturbed areas, especially old cultivated sites (Van Oudtshoorn, 1999, 2012; Zwerts et al.,
3722 2015).

3723 ### 2.2.3   Ecology and uses

3724 Thatching grass spreads through tillering but also depends on seeds for reproduction,
3725 flowering between September and June. It behaves differently in different environments. For
3726 example, in terms of competitive ability, *H. hirta* competes well on nutrient-poor soils but not on
3727 nutrient-rich soils. Fynn et al. (2005) showed that there is a trade-off between *H. hirta* and *P.*
3728 *maximum* in terms of their competitive ability along a fertility gradient, with *H. hirta*
3729 outcompeting *P. maximum* on nutrient-poor soils, and the opposite happening on nutrient-rich
3730 soils. Furthermore, Fynn et al. (2009) showed that this grass is highly invasive. However, it has a
3731 weak competitive response (ability to resist being invaded) (Chejara et al., 2010; Zwerts et al.,
3732 2015). For example, Zwerts et al. (2015) showed that regardless of whether nutrient availability
3733 was high or low, *H. hirta* was outcompeted by *Cynodon dactylon*, mostly when there was
3734 simulated herbivory (clipping). Therefore, the previously documented invasion potential and
3735 good performance of *H. hirta* under nutrient-poor conditions does not justify it as a strong
3736 competitor, rather it shows that competitive ability of this species is species specific and nutrient
3737 specific.

3738 *H. hirta* has been considered problematic in some countries through being invasive. It is
3739 not a good grazing grass because of high fibre content and low palatability (Chejara et al., 2010;
3740 Zwerts et al., 2015). It is only grazed when young, early in the growing season but decreases in
3741 palatability as it matures. It is commonly used as a thatching grass, and for making mats and
3742 baskets. Furthermore, because this grass is a fast growing plant, has dense roots and ability to
3743 invade disturbed nutrients poor soils, it has been used for rehabilitation purposes and soil
3744 protection (slope stabilization) (Van Oudtshoorn, 1999, 2012; Zwerts et al., 2015).

3745 **3. REFERENCES**

3746

3747 Ammondt, S.A., Litton, C.M., 2012. Competition between native Hawaiian plants and the
3748 invasive grass *Megathyrsus maximus*: implications of functional diversity for ecological
3749 restoration. Restoration Ecology 20, 638-646.

3750 Chejara, V., Kriticos, D., Kristiansen, P., Sindel, B., Whalley, R., Nadolny, C., 2010. The current
3751   and future potential geographical distribution of *Hyparrhenia hirta*. Weed Research 50,
3752   174-184.

3753 Firn, J., MacDougall, A.S., Schmidt, S., Buckley, Y.M., 2010. Early emergence and resource
3754   availability can competitively favour natives over a functionally similar invader.
3755   Oecologia 163, 775-784.

3756 Fish, L., Mashau, A. C., Moeaha, M. J., Nembudani, M.T., 2015. Identification guide to southern
3757   African grasses. An identification manual with keys, descriptions and distributions.
3758   Strelitzia 36. South African National Biodiversity Institute, South Africa.

3759 Fynn, R., Morris, C., Kirkman, K., 2005. Plant strategies and trait trade-offs influence trends in
3760   competitive ability along gradients of soil fertility and disturbance. Journal of Ecology
3761   93, 384-394.

3762 Fynn, R., Naiken, J., 2009. Different responses of *Eragrostis curvula* and *Themeda triandra* to
3763   rapid-and slow-release fertilisers: insights into their ecology and implications for fertiliser
3764   selection in pot experiments. African Journal of Range and Forage Science 26, 43-46.

3765 Ghebrehiwot, H.M., Aremu, A.O., Van Staden, J., 2014. Evaluation of the allelopathic potential
3766   of five South African mesic grassland species. Plant Growth Regulation 72, 155-162.

3767 McDonald, C.J., RM; Tothill, JC, 1998. Growth and spread of *Digitaria eriantha* cv. Premier
3768   and *Urochloa mosambicensis* cv. Nixon oversown into native speargrass (*Heteropogon*
3769   *contortus*) pasture in south-east Queensland. Tropical Grasslands 32, 41-49.

3770 Meredith, D., 1955. The grasses and pastures of South Africa.

3771 Mynhardt, J.E., Van Rooyen, M., Theron, G., 1994. Competitive ability of two grass species:
3772   *Anthephora pubescens* and *Eragrostis curvula*. 1. Yield and biomass allocation. South
3773   African Journal of Botany 60, 261-268.

3774 Ramírez, L., Hacker, J., 1996. Effect of time of tiller emergence and nitrogen fertiliser on seed
3775   yield components of *Digitaria eriantha* cv. Premier. Australian Journal of Experimental
3776   Agriculture 36, 189-195.

3777   Tainton, N.M., 1981b. Veld and pasture management in South Africa. Shuter & Shooter;
3778   University of Natal Press.

3779   Tainton, N.M., 1999. Veld Management in South Africa. University of Natal press.

3780   Tainton, N.M., Bransby, D., Booysen, P.d.V., 1976. Common veld and pasture grasses of Natal.
3781   Shuter & Shooter.

3782   Tedder, M., Morris, C., Fynn, R., Kirkman, K., 2012. Do soil nutrients mediate competition
3783   between grasses and Acacia saplings? Grassland Science 58, 238-245.

3784   Van Oudtshoorn, F.v., 1999. Guide to grasses of Southern Africa. Briza Publications.

3785   Van Oudtshoorn, F.v., 2012. Guide to grasses of Southern Africa, Third edition ed. Briza
3786   Publications.

3787   Zwerts, J., Prins, H., Bomhoff, D., Verhagen, I., Swart, J., de Boer, W., 2015. Competition
3788   between a lawn-forming *Cynodon dactylon* and a tufted grass species *Hyparrhenia hirta*
3789   on a South-African dystrophic savanna. PloS one 10,1-17.

3790

3791

3792

3793

3794

3795 **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*

3796

3797

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

3818
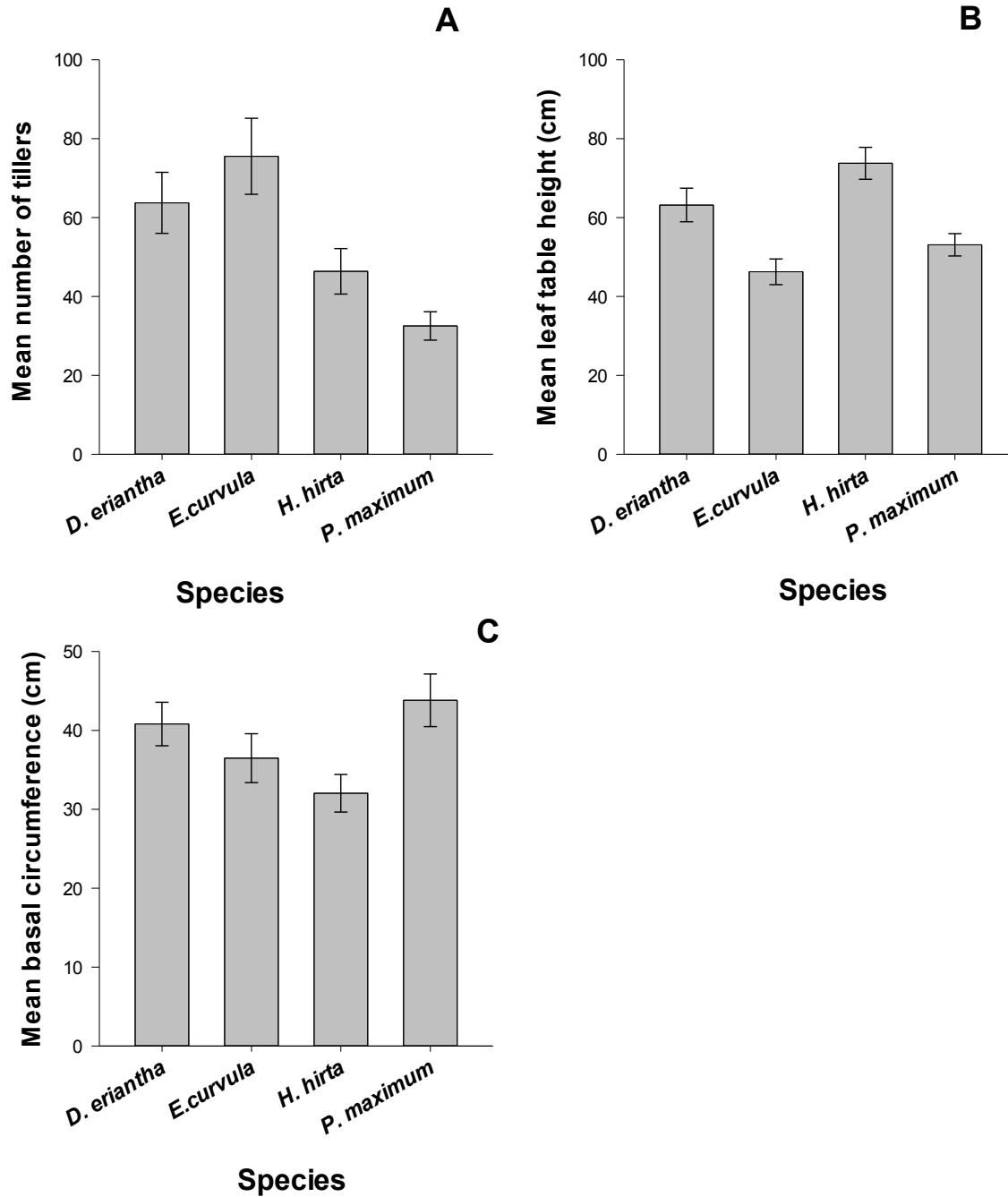
Figure 1: Main effect of vetiver competition on the mean (± SE) number of tillers (A), mean (±SE) leaf table height (B), and Mean (± SE) basal circumference (C) of four native species.
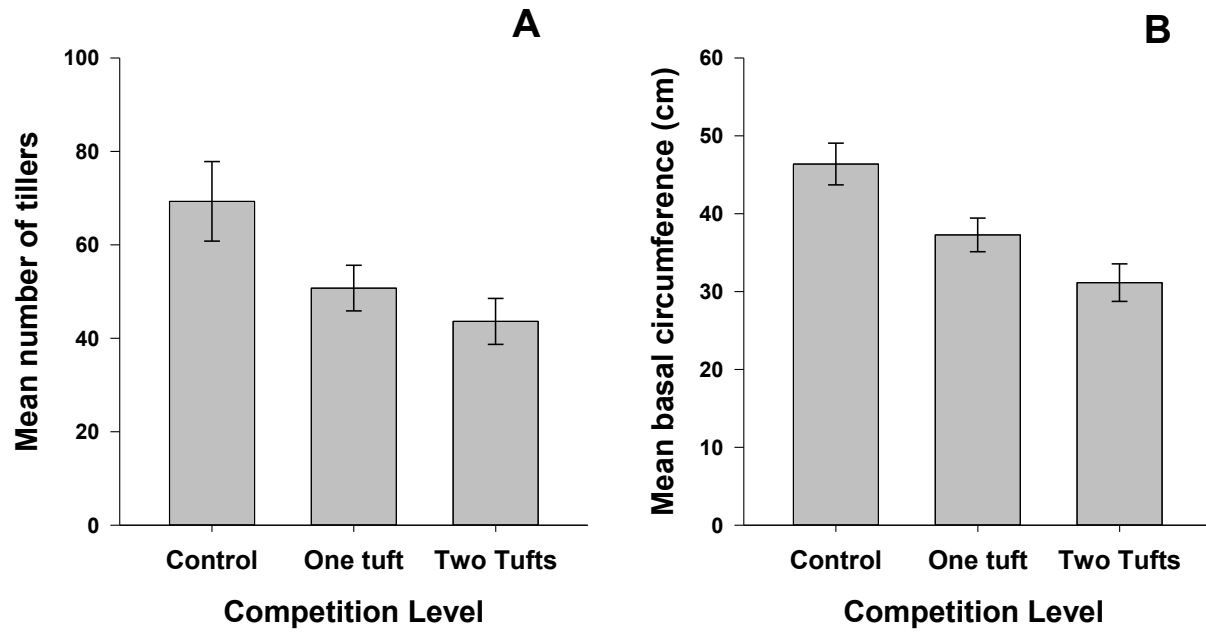
3821

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.

A

B

C
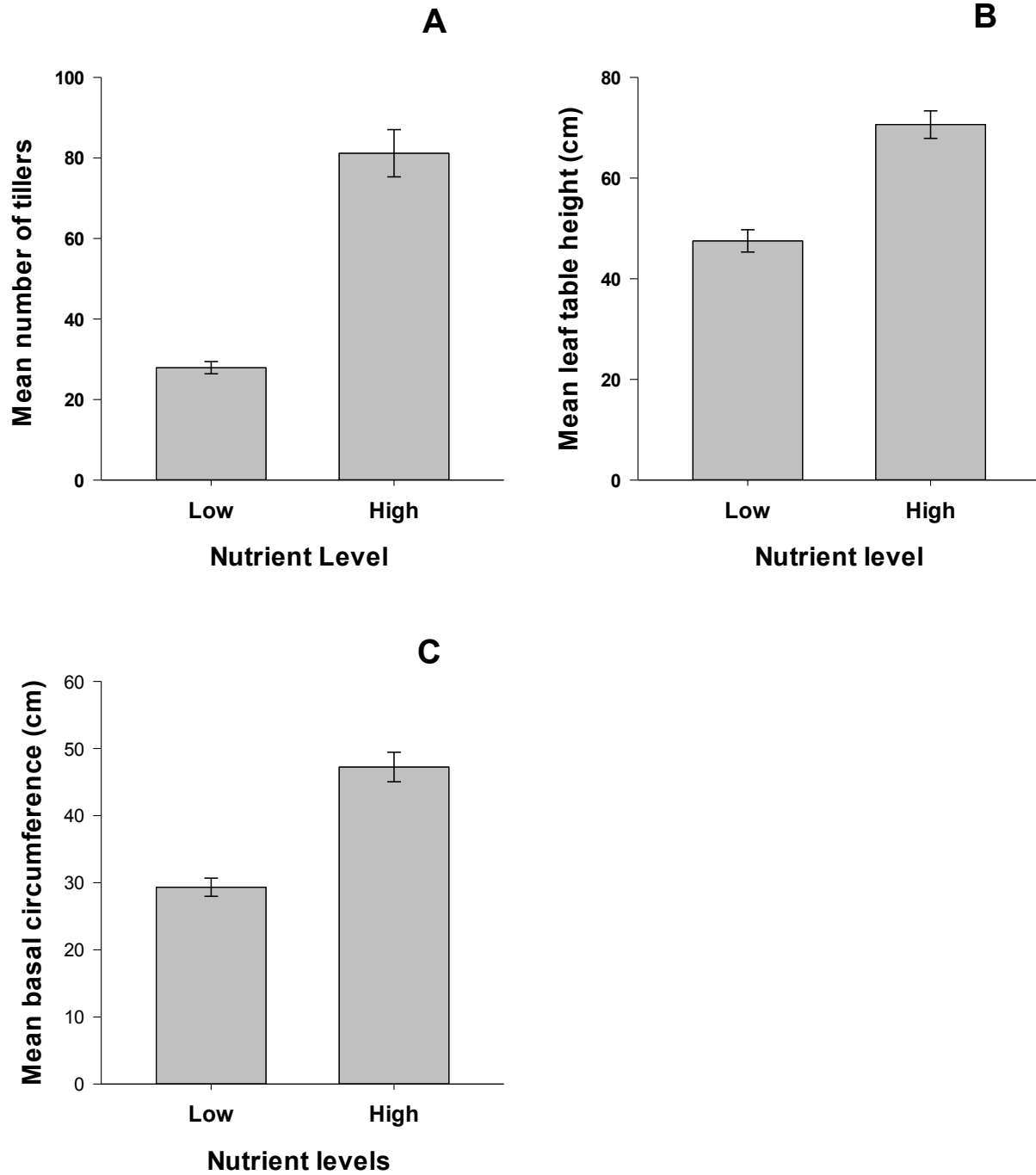
3824
3825

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.

3829