ASPECTS OF THE INVASION OF SOUTHERN TALL GRASSVELD BY *ARISTIDA JUNCIFORMIS* SUBSP. *JUNCIFORMIS* TRIN. ET RUPR.

by

DOUGLAS DIRK VAN ZYL

Submitted in partial fulfilment of the requirements for the

Degree of Master of Science

in the

Department of Botany,

University of Natal

Pietermaritzburg

1998

ABSTRACT

Aristida junciformis subsp. *junciformis* Trin. et Rupr. is an indigenous, densely tufted, evergreen perennial grass associated with the degeneration of grasslands over large areas of South Africa. More than two hundred thousand square kilometres of veld, c. 17% of the total land area of South Africa, contains *A. junciformis*. The aim of this study was to improve our understanding of the mechanisms by which this species invades and dominates grassland, specifically in this study, Southern Tall Grassveld.

Aristida junciformis also has a low nutritional value resulting in a very low grazing value. The unpalatability of the plant is due to the high tensile strength of the leaves, whose hard, fibrous laminas are very difficult for a grazing animal to crop once their length attains 30 cm or more. This species lack of response to conventional grazing practices has often resulted in a grassland in which the carrying capacity has diminished to such an extent as to be virtually useless for grazing in a relatively short time.

The extent of encroachment of veld by *A. junciformis* appears dependant on the frequency of disturbance and rest afforded to the veld. Annual burning and mowing maintained the species composition of *A. junciformis* at levels <10% whilst protection from fire, burning or grazing allows this species to dominate the herbaceous layer at levels approaching 90%. *Aristida junciformis* does not become moribund and is unlikely to die if left undefoliated. As the abundance of *A. junciformis* increases, veld deterioration gradually accelerates through increased selective grazing on remaining palatable species.

Competition from adult *A. junciformis* plants increases the mortality of seedlings and constrains growth of surviving seedlings. Tiller production of *Aristida junciformis* seedlings declined from an average of 5.2 tillers per seedling in a no competition situation to 2.2 tillers per seedling when subjected to full competition. Tiller production of *T. triandra* seedlings decreased from 9.6 tillers per seedling free from competition to 3.3 tillers per seedling subject to full competition for resources.

Once these seedlings have become adult plants they are avoided by grazing animals and grazing pressure on the remaining palatable species consequently increases. This allows the *A. junciformis* plants to increase their size and density in the sward. Once this density is sufficiently high, grass seedlings of either *A. junciformis* or more desirable grass species such as *T. triandra* are unable to establish, eventually resulting in a monospecific stand of *A. junciformis* if left undisturbed.

Large amounts of caryopses are produced by *A. junciformis* - up to a 19 000 caryopses from a large mature plant (c. 38 000 caryopses/m^2). Of these c. 40% is likely to be infertile but the remaining c. 60% viable caryopses are dispersed in a typically leptokurtic distribution, the number of caryopses dispersed rapidly declining within a 10 metre radius. A large proportion of the caryopses was trapped in surrounding foliage but in open swards caryopses had greater opportunity to be blown further distances than in a closed sward. The density of *A. junciformis* caryopses on the soil surface was positively correlated with the density of flowering adult plants in the area and varied from 400 caryopses/m^2 (density of parent plants c. 0.6 plants/m^2) in less effected areas to 11 000 caryopses/m^2 (density of adult plants c. 6 plants/m^2) in severely encroached areas.

The primary function of the three awns appears to be orientating the caryopsis correctly for in its descent from the parent plant to expedite germination. Caryopses orientated vertically with the awns uppermost exhibited the highest and most rapid germination (67%) compared to caryopses lying horizontally (35%) whilst only 1% of inverted caryopses germinated. Caryopses trapped in litter and effectively held off the soil surface failed to germinate. Removal of the glumes from *A. junciformis* seed greatly enhanced the rate and overall germination of the seed except for inverted seed of which <1% germinated.

The highest numbers of *A. junciformis* seedlings (32 seedlings/m^2) were found in those areas with the highest density of caryopses on the soil surface. Despite the large amounts of caryopses produced, dispersed and landing in apparently suitable micro-sites for germination, comparatively few *A. junciformis* seedlings (n=992) were found and overall germination ranged between 1% and 4% of the initial caryopses density on the soil surface. Seedling survival through winter was low with only 13% surviving to the following spring. The basal areas of *A. junciformis* increased overall by 66% whilst that of other grass species increased overall by only 3% in the time monitored. These results suggest that the primary method of encroachment of *A. junciformis* in the grass sward appears to be through vegetative expansion and not seedling recruitment.

Frequent defoliation of the sward and avoidance of overgrazing to enhance the competitive abilities of palatable species and provide as high a fuel load as possible appear to be the most economically and logistically feasible ways to remove or at least inhibit *A. junciformis* veld encroachment at present.

PREFACE

The work described in this dissertation was carried out in the Department of Botany, University of Natal, Pietermaritzburg, from February 1993 to December 1995, under the supervision of Dr. J.E. Granger and Dr. P.J.K. Zacharias. The long delay in production of the thesis was due to taking up employment and the consequent relegation of the thesis to part-time status.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

LIST OF CONTENTS

Chapter 1 - Distribution, Morphology and Physiology of *Aristida junciformis*

Chapter 2 - Response to Defoliation

2.4. Line ellipse-intercept Method

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I would particularly like to thank my supervisors Dr. J.E. Granger of the Botany Department and Dr. P.J.K. Zacharias of the Department of Range and Forage Science for their many hours of time and help, patience, encouragement, and critical input which considerably improved the final product.

In addition I would like to thank Professor J. van Staden, Head of the Department of Botany, and Professor Dick Yeaton, formerly of the Department of Botany, UN(P) for their input and guidance, and particularly Professor van Staden for the use of the facilities and equipment. I would also like to thank Craig Morris, Chippie du Toit, and Jerry Naiken of the Department of Range and Forage Science; Craig for some helpful and informative discussions, and Chippie and Jerry for assistance with equipment and support in the field. Thanks are also due to Barry Dudley who taught me how to use the Kontron equipment and wrote a major part of the programme, and to the members of the E.M. unit for their unfailing helpfulness and support. I would also like to express my gratitude to the Foundation for Research and Development (FRD) for their financial support. And finally for my family for all their love and encouragement.

CHAPTER ONE

DISTRIBUTION, MORPHOLOGY AND PHYSIOLOGY OF *ARISTIDA JUNCIFORMIS*

1.1. Introduction

Encroachment of productive land by unpalatable indigenous plants is often a far more serious problem than encroachment by exotic species. *Aristida junciformis* subsp. *junciformis* Trin. et Rupr. is such a species. Commonly known as 'wiregrass' or by its Zulu name, 'ngongoni,' a word which appears to have no direct translation but rather alludes to the strength of the leaves, this indigenous, densely tufted perennial grass is now associated with the degeneration of grasslands over large areas of South Africa as a result of poor veld management (Edwards, Jones and Tainton, 1979).

*Aristida junciformis*t led these authors to remark that: *"large areas of Natal's moister warm regions are dominated by this unusable plant, which covers many of the province's rolling hills with a verdant cloak of promise, but where grazing animals might be seen standing belly deep in grass, starving."*
(Edwards, et al. 1979).

A variable and very widely distributed sub-species, *A. junciformis* subsp. *junciformis* Trin. et Rupr. is an aggressive invader where the rainfall is high and selective overgrazing takes place, such as in the sour mountain grasslands in parts of KwaZulu-Natal (de Winter, 1965). This species readily invades overgrazed or similarly disturbed grass swards, yet is able to persist through most grassland successional stages whether the current grazing regime is retained or the grassland is rested. This species may normally occur as a small plant amongst other grasses in a rich, dense, healthy sward. However, when the other grasses are weakened the small tufts then enlarge, with an indistinct border which shifts and changes shape during the growing season (Edwards, *et al.* 1979). Large bare spaces are usually observed around the bigger *A. junciformis* tufts (Edwards, *et al.* 1979; pers. obs.) which can lead to substantial soil erosion. The loss of topsoil from these bare patches makes the successful re-colonization of the area by more desirable species highly unlikely (Edwards, *et al.* 1979).

1.3. Distribution

The Aristideae are primarily subtropical in distribution occurring in drier areas with relatively high winter temperatures (de Winter, 1965). The genus *Aristida* occurs in the tropics and subtropics of both hemispheres. The distribution of the species lies mainly along the Tropic of Cancer in the northern and the Tropic of Capricorn in the southern hemisphere. The genus is well developed in terms of number of species in both hemispheres with a slight bias in the number of species in the southern hemisphere (de Winter, 1965).

The areas with the highest concentration of species all fall within regions which have a 10°C mean for the midwinter month, and no species are found in regions which have very cold winters (de Winter, 1965). Rainfall seems to have less an effect on distribution, but few species occur in areas with more than 1500 mm per year while the number of species tolerating less than 250-500 mm per year is also relatively small (de Winter, 1965). The majority of species of *Aristida* occur in areas with an annual rainfall of 250 to 750 mm. Even those occurring in areas where the rainfall is high usually grow in localities where the available moisture is limited. In areas of Gauteng, Namibia, and Angola, with an annual rainfall of less than 750 mm *A. junciformis* is found exclusively in depressions and gullies where water collects and remains for long periods during the rainy season (de Winter, 1965).

1.3.1. Distribution in South Africa

Before 1920 the precise distribution of *A. junciformis* in South Africa is unclear. Subsequent to this date the gradual spread and extant distribution of this species is better known and has been described by several authors over three decades (Edwards, 1974; Edwards *et al.*, 1979; Acocks, 1988; Gibbs Russell *et al.*, 1990). More than 200 000 km² of veld, approximately 17% of the total land area of South Africa, comprise communities in which *A. junciformis* is present in varying amounts.

Such suitable areas include the southern and eastern coastal regions of the Cape Province (Edwards *et al.*, 1979). This belt expands in KwaZulu-Natal to include most of the area between the Drakensberg foothills and the Indian Ocean (excluding the deep valleys) as far as Swaziland. A second belt extends from Wepener in the Free State, to Lydenburg in Gauteng, mostly in the lee of the Drakensberg but is more than 150 km wide in places (Edwards *et al.*, 1965). The distribution of *Aristida junciformis* subsp. *junciformis* in southern Africa is shown in Figure 1.1.

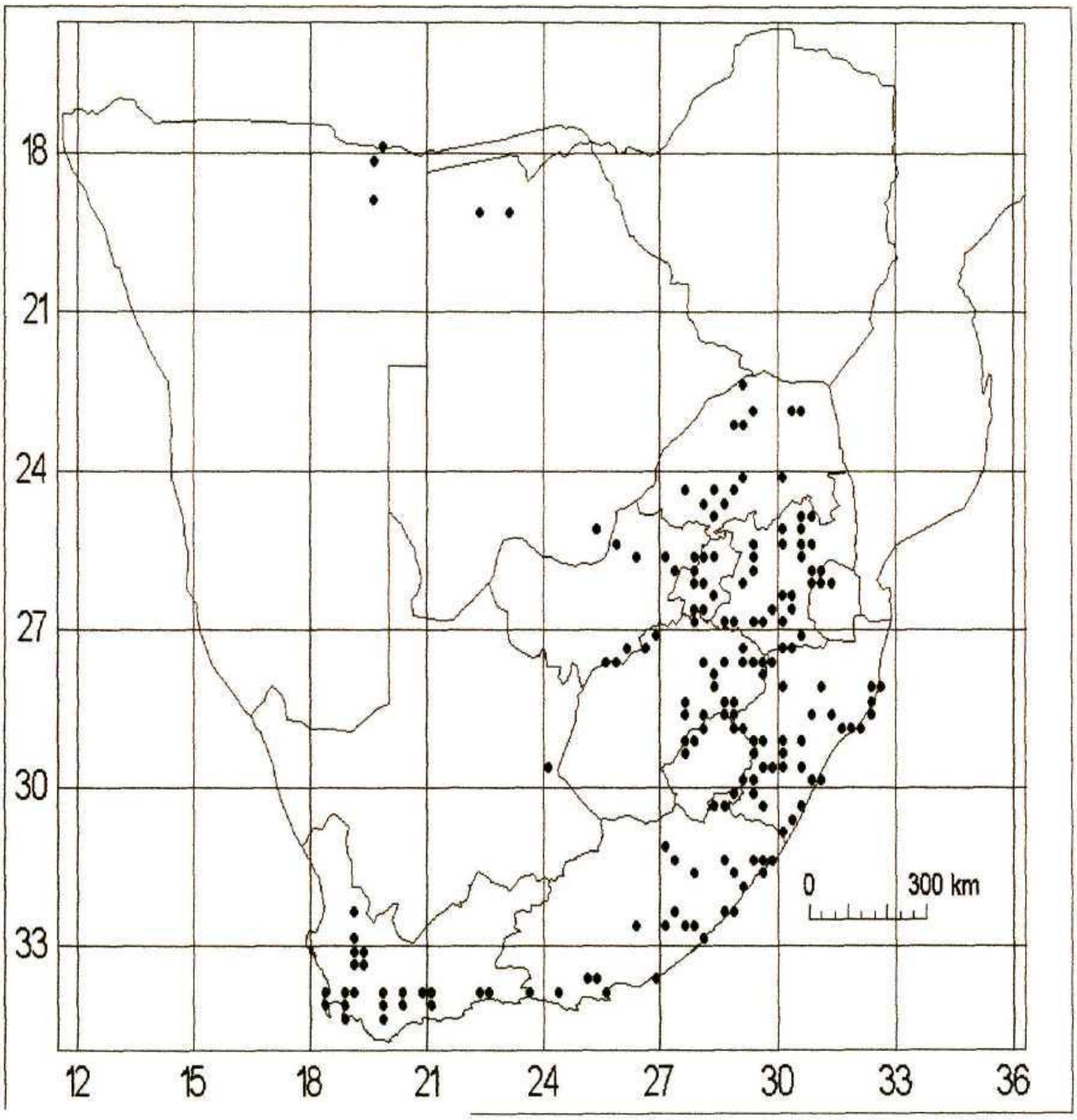


Figure 1.1. The distribution of *Aristida junciformis* in southern Africa (Source: National Botanical Institute of South Africa).

1.3.2. Distribution in KwaZulu-Natal

Aristida junciformis is best adapted to warm moist conditions, consequently in KwaZulu-Natal the grass is restricted to areas below approximately 1250 metres that do not have cool, dry summers. Drier summers limit its spread down into warm river valleys, but it can often be found on seaward, southeast facing slopes. The grass can be found at higher altitudes but is normally restricted to the warmer, north facing slopes in these areas (Edwards *et al.*, 1965).

Nineteen of South Africa's 70 veld types as described by Acocks (1988) include the species in varying degrees of abundance. The veld types in which Acocks cites it as most abundant include: Coastal Forest and Thornveld (1), Pondoland Coastal Plateau Sourveld (3), Ngongoni Veld (5), Zululand Thornveld (6), and the Natal Mist Belt Ngongoni (45) (Edwards *et al.*, 1979). Within Highland Sourveld (44) and Southern Tall Grassveld (65) infestation by *A. junciformis* appears to be on the increase (Venter, 1968; Edwards *et al.*, 1979). The cooler summers prevent *A. junciformis* being as troublesome in the Highland Sourveld as in the Ngongoni Mistbelt immediately adjacent, though there are many instances where this species is prolific on warmer north-facing slopes (Edwards *et al.*, 1979). In some areas (specific locations not stated) *A. junciformis* is also invading Valley Bushveld (23) (Venter, 1968).

In Ngongoni veld (Acocks, 1988) *A. junciformis* forms large stands in areas which are apparently not very wet. The Natal Mountain sourveld has an annual rainfall of between 750 and 1500 mm which is probably high enough to support growth even in apparently dry habitats. This preference for high rainfall, or habitats where moisture collects during the rainy seasons in areas of lower rainfall, may explain why there is no tendency for *A. junciformis* to extend its distribution and form pure stands in over-grazed areas in drier regions (de Winter, 1965).

1.4. Encroachment in KwaZulu-Natal

In KwaZulu-Natal the most rapid deterioration of grasslands has taken place in the Ngongoni veld types (Acocks, 1988) within the last 60 years (Edwards, 1981). This expansion of *A. junciformis* has left much of this Ngongoni veld in an extremely poor condition, severely affected areas providing grazing for approximately 10 weeks of the year. From an agricultural perspective Farr (1992) called it "one of the most useless veld grasses in our country" and doubted whether it could produce 20 kg/ha of live mass gain yearly. From an ecological perspective, little published research appears to have been done on the direct impacts of *A. junciformis* on both plant and animal biodiversity in heavily encroached areas.

The position of Southern Tall Grassveld wedged as it is between the two Ngongoni veld types of KwaZulu-Natal makes it extremely prone to encroachment by *A. junciformis* (Tainton, 1972). Eighty years ago *A.junciformis* was absent from experimental plots in veld at Cedara Agricultural Research Station and Howick (Sawer, 1911). Twenty years later it was still absent in some plots but was found in plots subjected to heavy grazing without burning (Staples, 1930). By 1979 all of these experimental plots were reported as being dominated by *A.junciformis* (Edwards *et al.*, 1979).

In most instances the increase in *A. junciformis* and consequent change in species composition appears to have been at the expense of palatable species such as *T. triandra*, the normally dominant species in such grasslands (Staples and Taylor, 1929; Venter, 1962, 1968; Edwards, 1981; Tainton, 1981; McKenzie, 1982). Bayer (1955) categorized *A. junciformis* dominated grasslands as secondary grasslands and suggested that prior to the arrival of western agricultural practices these grasslands existed only as a successional stage on shallower soils. Bayer (1955) reasoned that the unpalatability of *A. junciformis* coupled with high caryopsis production on the shallower soils gave the species a distinct advantage over more palatable species, out competed them and became the dominant plant in the landscape. This dominance of *A. junciformis* increased as the impact of grazing on this species lessened but escalated for the surrounding palatable species. This dominance had allowed it to invade *Themeda* dominated grasslands where its unpalatability then prevented it from being grazed out. *Aristida junciformis's* largely evergreen habit, dense basal area, and comparatively deep root system would also have reduced the detrimental effects of burning (McKenzie, 1982).

1.5. Description of *Aristida junciformis*

Mature plants consist of a tuft of dense, stiff, erect culms up to 900 mm in height, with a fascicled base (de Winter, 1965; Gibbs Russell *et al*, 1990). The leaf blades are up to 300 mm long to 3 mm wide (Gibbs Russell *et al*, 1990). The culms are unbranched to branched at some nodes, leaves mainly cauline, and the culms are clearly visible for most of their lengths (Gibbs Russell *et al*, 1990). The nodes are glabrous and compressed below the nodes. The leaf sheaths are glabrous or sparsely woolly (de

Winter, 1965).

The inflorescence is contracted, dense to lax, the branches erect to spreading up to 45 degrees from the main axis. Spikelets are 20-30 mm long (including awns). The lower awned glume is up to ⅔ the length of the upper, the lemma is narrowly lanceolate, up to 90 mm long, distinctly tapering into a beak or column, articulation is absent. There are three awns, the laterals being well developed. The central awn is 12-35 mm long, the lateral awns 9-28 mm long (de Winter, 1965). The callus is bearded with backwardly directed (antrorse) barbs; the tip of the callus is naked, swollen and is rounded to truncate. The ligule is inconspicuous (de Winter, 1965; Gibbs Russell *et al*, 1990). The caryopsis of *A. junciformis* is linear and terete (de Winter, 1965) (Figure 1.2).

The bases of the tufts are branched and often produce short, branched rhizomes (de Winter, 1965). The roots are very tough and are covered by a white spongy layer. They have been described as very thick (dimensions not stated), almost spongy (de Winter, 1965) or as consisting of two distinct types by Venter (1968) who reported that "some of the roots were well divided and permeated throughout the depth (not stated) of the soil profile examined, while others, in which branching was restricted, were thick and had a more restricted distribution. This latter system was difficult to distinguish from the numerous rhizomes which arose from the crown and grew downwards, frequently giving rise to subterranean crowns which in turn produced roots."

Aristida junciformis subsp. *junciformis*

(Magnification x 6)

Themeda triandra
(Magnification x 1.8)

Figure 1.2. Diagrammatic representation of an *Aristida junciformis* caryopsis with a caryopsis of *Themeda triandra* (Illustration by P. Brown).

The unpalatability of the plant is due to the high tensile strength of the leaves the cell walls of which are unusually thick as a result of the distribution of the lignin. The hard fibrous leaves are very difficult for a grazing animal to crop once lengths greater than 30 cm or more are attained. The only time grazing animals will utilize the herbage is where leaf growth, or regrowth after prior grazing is less than 20 cm. The young inflorescences are also selected for a week or two after emergence in late January to early February. In addition *A. junciformis* also has a low nutritional value despite having a high dry matter content (Theron, 1966) resulting in a very low grazing value. By midsummer the leaf blades have a nitrogen content of <1% and a digestibility of <25% (Zacharias pers. com., 1998).

Compared with the generally highly palatable species *T. triandra* the growth of *A. junciformis* is reportedly slow (Venter, 1968). The terminal bud of *T. triandra* elevates at a rate of c. 20 mm per day during December while the terminal bud of an *A. junciformis* tiller remains less than five cm above the surface until January, and then it starts elevating at a rate of 6mm/day. Flowering is day-length dependant, the first inflorescences emerging in late January, two months later the caryopses are shed (Edwards *et al.*, 1979) of which Venter (1968) calculated that a typical tuft produces 18 000 viable caryopses each season which have a high germination success (Zacharias, Tainton, and Oberholster, 1988).

Apart from the high tensile leaf strength and caryopsis production another outstanding feature of *Aristida junciformis* is that it does not become moribund and is unlikely to die if left undefoliated unless it becomes permanently shaded by trees and shrubs. Well established plants growing in grassland planted to *Eucalyptus* spp. trees in the Hilton area were still alive though very moribund after eight years (pers. obs., 1995).

In open grassland undisturbed plants form large tufts with a high proportion of the canopy consisting of dead tillers. These dead tillers eventually form a thick mulch on the soil surface which appears to inhibit seed germination of other herbaceous species. This is vividly illustrated by the high abundance of *A. junciformis* in experimental sites in the Southern Tall Grassveld that have remained relatively undisturbed by either fire or grazing for over 35 years, the plots having been defoliated by two arson fires in 35 years (unpublished data, Department of Range and Forage Science, University of Natal, Pietermaritzburg cited in Morris and Tainton, 1993). *Aristida junciformis* also appears to be a potentially long lived species as some individual plants have appeared to survive for over 20 years in these protected plots (Edwards *et al.* 1979).

Figure 1.3. Veld heavily encroached by *A. junciformis* "has the aspect of a field of ripe barley, being knee high, straw coloured, and apparently (if not actually) monospecific" (Edwards, Jones and Tainton 1979). Photograph taken in March 1994 on Ukulinga Plateau in Burning/ Grazing Trial.

In these undisturbed plots, *A. junciformis* totally dominates the herbaceous layer(average percentage composition = 92%, n=3; average basal diameter = 16.2 cm, n=173) and which in turn is gradually displaced by dicotyledonous species such as *Rhus dentata*, Seringa (*Melia azedarach*), wattle (*Acacia decurrens*), and *Acacia karroo* if left unburnt. This invasion of woody species in the absence of fire is to be expected, as in common with most of KwaZulu-Natal's grasslands, these Southern Tall grasslands are recognized as fire climax grasslands (Tainton, 1981).

1.6. Objectives of this study

The overall objective of this study was to improve the understanding of the mechanisms by which *A. junciformis* is capable of encroaching and dominating grasslands so successfully and recommend management practices that will reduce the composition of *A. junciformis* in the sward. Within this broad objective (illustrated in Figure 1.4) several key questions were posed, namely:

- What effect does burning, grazing and mowing have on *A. junciformis*?
- Is the frequency of such disturbance important?
- How does *A. junciformis* out-compete other species in the sward and how does it spread - by vegetative expansion, seedling recruitment or both?
- Does the high caryopsis production of *A. junciformis* and dispersal play a role?
- Is the three-awned structure of the diaspore important in it's dispersal and a important factor in the encroachment success of this species?
- Does alteration of light quality and temperature play an important role in the germination success of the *A. junciformis* seed?

To answer these questions, a combination of laboratory and greenhouse experiments were conducted in conjunction with the collection of data from extant burning, mowing and grazing trials in which the type of treatments applied, the time of application and frequency were known. The two broad themes of adult plants' competitive behaviour and the role of vegetative expansion (or contraction) and that of their seed; including it's physiology, survival, and contribution to encroachment of grassland are illustrated below in Figure 1.4.

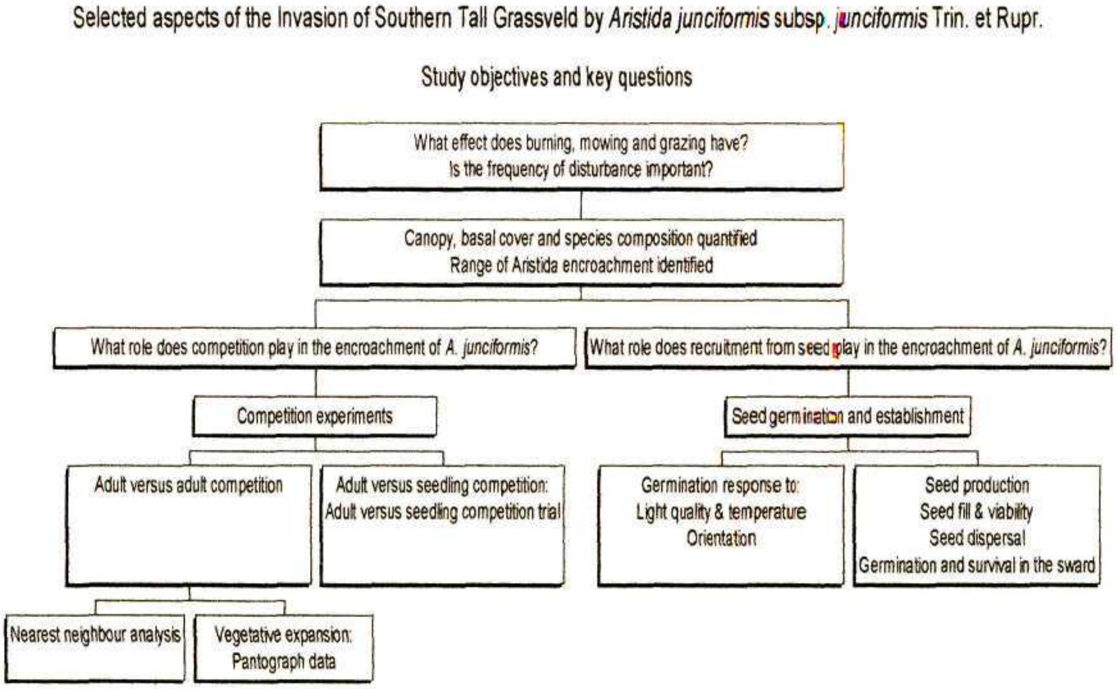


Figure 1.4. Structure of study investigating selected aspects of *Aristida junciformis* encroachment of grassland outlining key objectives and questions.

CHAPTER TWO

RESPONSE TO DEFOLIATION

2.1 Introduction

An initial objective of this study was to quantify the effects of grazing, burning, and mowing at varying intensities on the physiological and ecological behaviour of *Aristida junciformis* in the grass sward. Grass species display differing abilities to tolerate defoliation whether through burning, grazing, mowing or combinations of these factors. Many grass species require periodic defoliation to remain vigourous and competitive in the sward but vary in their response to the intensity and frequency of any particular disturbance regime. These differences in response between species are largely associated with variation in morphology (Tainton, 1988) which in mixed swards subject to defoliation may favour some species over others. It has become quite apparent that *A. junciformis* does not respond to conventional grazing and burning practices in the manner as many other Increaser grass species (Venter 1968,Tainton 1981, Morris and Tainton 1993) especially regarding resting of veld where *A. junciformis* increases under rest.

2.2 Trial sites

Previously established long term trials (more than 30 years old) were utilized for this study, the primary criterion for selecting suitable experimental sites within these trials was obtaining a broad range of *A. junciformis* density in the sward. The low density sites selected would require a minimum number of *A. junciformis* plants for meaningful comparisons with high density sites. Sites with very few or no *A. junciformis* plants would be excluded.

A second criterion was that the nature and duration of present and past treatments applied to each plot should be known. This would be important in identifying factors which enhance or inhibit *A. junciformis* establishment in the sward.

Consequently the fieldwork component of this study was carried out in Southern Tall Grassveld (Acocks 1975) on the plateau of the University of Natal's research farm 'Ukulinga,' situated southwest of Pietermaritzburg (29°24'E, 30°24'S; 715 m a.s.l.). The mean annual precipitation is 709 mm (Std Dev.=167.5mm; n=38 years) falling in the summer months. Over a 36 year period, the annual mean maximum temperature was 23.6°C, and the annual mean minimum temperature was 13.2°C (Klug, 1989). No further climatic data is available for this site since 1991 (Moodley, pers. com.).

Three established trials on the plateau were investigated for potential experimental sites. The trial sites were located on a shallow Mispah soil form (MacVicar *et al.* 1977) on gently undulating grassland with a slight northerly aspect (slope<5%).

The three trials are described below:

Burning and Mowing Trial

Since the inception of the 'Burning and Mowing' trial at Ukulinga in 1951, grazing by livestock has been excluded (Tainton, Booysen, Bransby and Nash, 1978; Anon, 1986). The trial was initiated on what Tainton *et al.* (1978) reported as pristine veld which had only been used previously for the production of hay. The first treatments were implemented at the start of the 1950/ 1951 growing season i.e. August- October 1950 and have been consistently applied at prescribed intervals since then to the present date. Consequently this trial is one of the oldest of its kind still active in southern Africa if not the world.

The trial consists of all combinations of four summer utilization (whole plot) and 11 aftermath removal (sub-plot) treatments (Tainton *et al.* 1978), in which the vegetative canopy is removed by either burning and/or mowing (Table 2.1). In combination with these removal treatments there are four 'utilization' treatments which prescribe the frequency and timing of the mowing. Each treatment has three replications.

Table 2.1. Defoliation and Utilization treatments of the Burning and Mowing Trial (from Tainton *et al*, 1978).

Utilization treatments
A. Control - no utilization during summer
B. One hay cut early in summer (November or December) of plots
C. One hay cut late in summer (February or March) of plots
D. Two hay cuts - the early summer cut followed by the late summer cut

Defoliation treatments
1. Control - no burn
2. Annual burn first week in August ('dry burn')
3. Annual burn after first spring rains
4. Biennial burn first week in August
5. Biennial burn after first spring rains
6. Biennial burn in autumn
7. Triennial burn first week in August
8. Triennial burn after first spring rains
9. Triennial burn in autumn
10. Annual mow first week in August
11. Annual mow after first spring rains

Notes:

1. The first spring rain is defined as the first rain of 12.5 mm in 24 hours. Spring is normally taken as September while Autumn is generally defined as March to April. Summer is generally defined as October to March.
2. Autumn burn plots (6 and 9) are not utilized in summer in order to accumulate material for the burn. Therefore all autumn burn plots are treated the same as A6 and A9.

Rotational Grazing and Resting of Veld Trial

The second trial in which sites were selected for this study was originally established in 1957 to examine the effects of frequency of grazing and resting of the vegetation (Tainton, 1972; Tainton, *et al.* 1978). By the time of the study reported here, the trial as originally conceived had been discontinued and many of the plots absorbed into other experiments.

In the original trial three stocking rates were applied in conjunction with each grazing treatment, but for the purposes of this study only the four plots of one stocking density were examined. The first plot had been subjected to continuous grazing, the second to rotational grazing, the third to rotational resting and the fourth to no grazing (i.e. the control treatment) (Table 2.2).

Table 2.2. Rotational Grazing and Resting of Veld Trial, grazing management treatments (from Tainton, *et al.* 1978).

1. Continuous grazing - Animals grazed continuously on veld for duration of season while still palatable.
2. Rotational grazing - Animals rotated through a three camp system on a cycle of 14 days in/ 28 days out.
3. Rotational resting - In a three year cycle each camp of a three camp system is deferred from grazing for spring, summer and autumn. When not being deferred, it is grazed continuously.
4. Control - Camp is not grazed but accumulated dry matter from the growing season is removed by cutting in mid-winter.

Note: The season was defined as starting once sufficient herbage for grazing had accumulated in the spring, and continued for eight months.

Days In/ Days Out Trial

The third site examined had formerly been part of a now defunct rotational grazing trial known as the 'Days In/ Days Out Trial.' Plots from this trial in conjunction with some of those remaining from the Burning and Grazing trial described above had been amalgamated at the time of this study into the 'Aristida Trial' in which the effects of combinations of early and late season burning and grazing were being examined for their impact on *A. junciformis* (Morris, Tainton and Hardy, 1992; Morris and Tainton, 1993).

The 'days in' component of the title refers to the numbers of days in which grazing animals, usually sheep were allowed to graze a specified plot. The 'days out' component refers to the number of days the plot was rested before the resumption of the next cycle of grazing. The design included a simulation of all combinations of periods of occupation and absence from 2 to 60 days. For this study, plots which had been at the opposite ends of the grazing intensity spectrum for the same duration but differed in the rest period were measured for possible inclusion in this study.

2.3 Techniques

The initial task was to identify specific plots or treatments within these trials which, when taken together, would provide a range of *A. junciformis* densities suitable for experiments for this study. More intensive methods would be then used to determine differences in plant size distribution and density, basal and canopy cover, and species composition which could be correlated with treatment differences. Where possible, all replications of any particular treatment were measured.

2.3.1 Point Quadrat Method

A modification of the point quadrat method described by Greig-Smith (1964) was used to rapidly quantify the extent of encroachment of *A. junciformis* in the large number of plots compared to more desirable species (from a graziers point of view) such as *T. triandra*. Plants were identified as either *A. junciformis* or 'other species' (all grass species including *T. triandra*) nearest to the point but the distance from the point was not recorded. In each plot of 250 m^2 two hundred points were located using a steel rod to mark the points. In larger areas proportionally more points were used to achieve the same density of coverage as that of the 250 m^2 plots. This was achieved by determining the area by which these plots exceeded 250 m^2 and increasing the number of points accordingly to achieve even coverage.

2.3.2. Results

Burning and Mowing Trial

Within the burning and mowing trial, the results (Figures 2.1 to 2.4), clearly illustrate the importance of disturbance in inhibiting encroachment by *A. junciformis*. In those treatments with high levels of defoliation created either through mowing and/ or burning there was minimal or no *A. junciformis* present and correspondingly high proportions of other grass species.

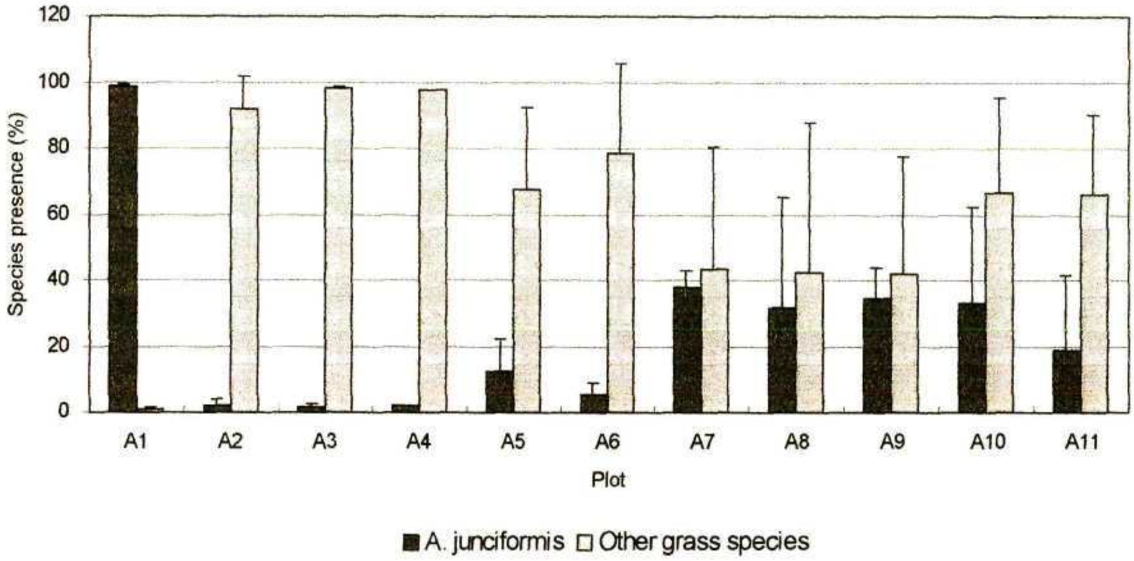


Figure 2.1. Percentage composition of *Aristida junciformis* and other grass species in the no summer utilization (A treatment) plots of the long term Burning and Mowing trial. (Bars indicate Standard Deviation (S.D.)

Mowed treatments with few exceptions exhibited minimal (<10%) or no encroachment by *A. junciformis* and uniformly high abundance of other grass species. The few exceptions measured were the A10, A11, B10 and B11 treatments, encroachment of which appeared to be at similar levels. Starting in the 1968/69 season, Treatments A10 and A11 were mown annually in August, and after the first spring rains respectively, as controls for the B, C and D treatment plots in measuring herbage production. These plots showed that regular disturbance reduced the proportion of *A. junciformis* present but indicated that an annual mow was possibly less effective than annual burning in reducing the encroachment of this species.

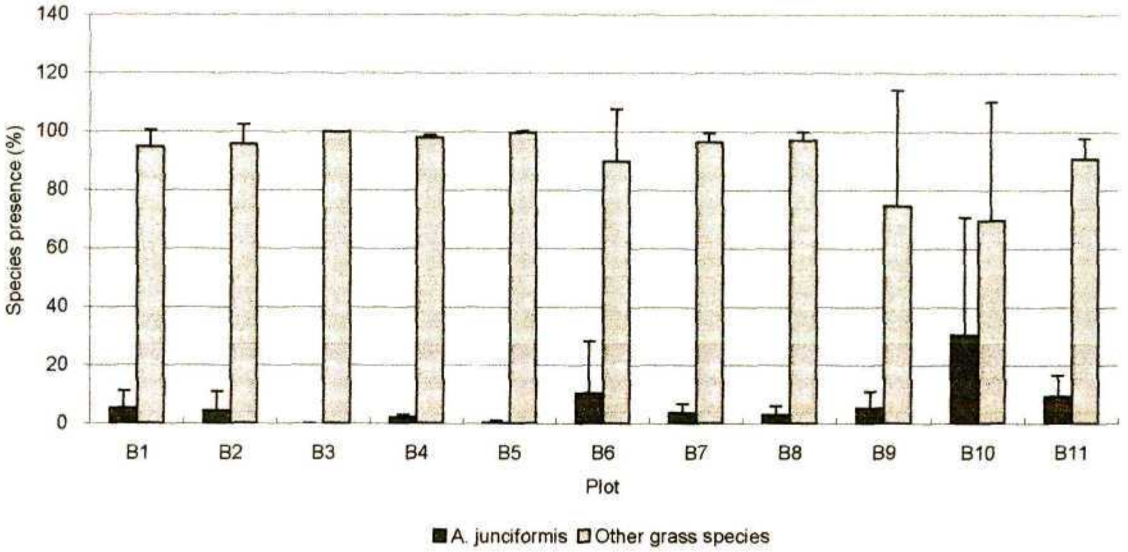


Figure 2.2. Percentage composition of *Aristida junciformis* and other grass species in the hay cut early in summer (B treatment) plots of the long term Burning and Mowing trial. (Bars indicate S.D).

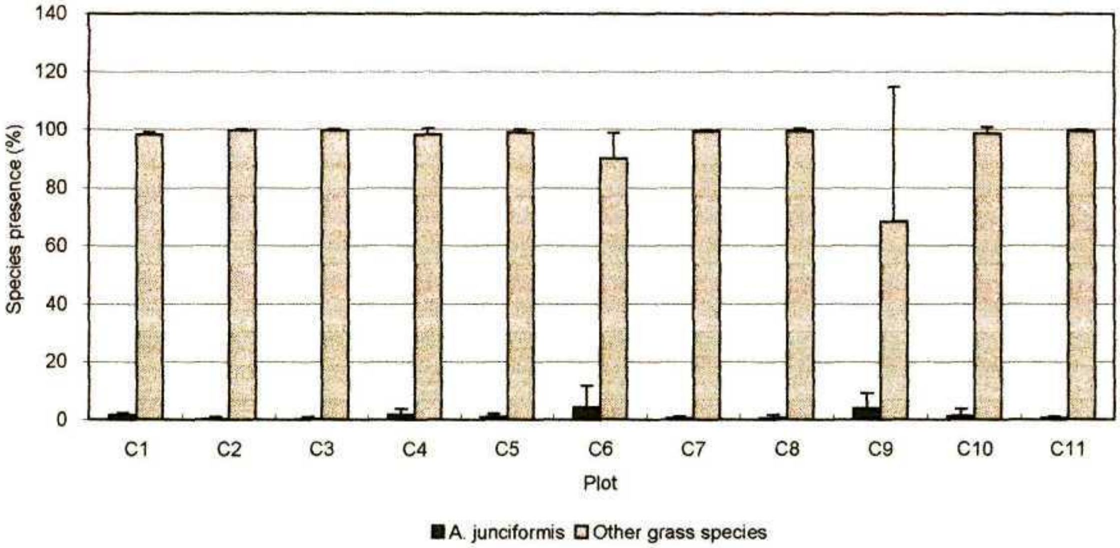


Figure 2.3. Percentage composition of *Aristida junciformis* and other grass species in the hay cut in late in summer treatment) plots of the long term Burning and Mowing trial. (Bars indicate S.D).

Of those treatments which were not mowed but only burnt (A2 to A9) the annual burn treatments (A2 and A3) showed the lowest incidence of *A. junciformis*. With decreasing frequency of burning (treatments A4 to A9) there was increasingly more *A. junciformis* and a proportional decrease in other species.

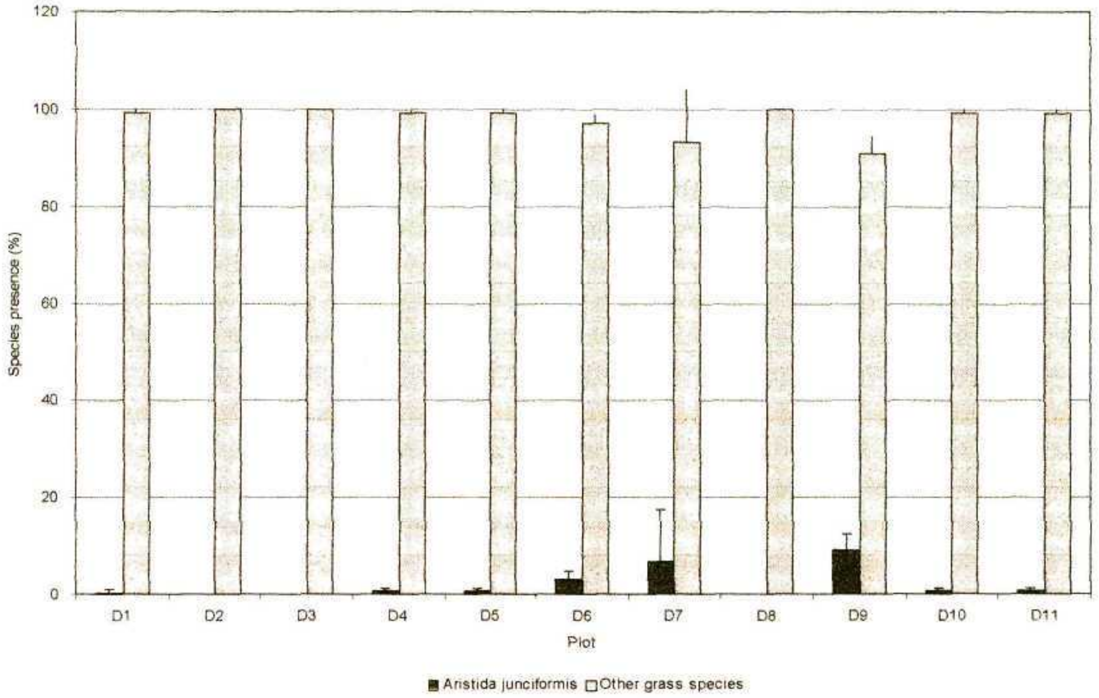


Figure 2.4. Percentage composition of *Aristida junciformis* and other grass species in the two hay cut (D treatment) plots of the long term Burning and Mowing trial. (Bars indicate S.D).

However, the herbaceous component of the no utilisation treatment (A1) was dominated by *A. junciformis* with less than one percent of any other grass species present. The sward in the three replicated plots had been subjected to periodic disturbance in the form of three arson fires, the most recent being in 1985 (Zacharias, pers. com.) since the inception of the trial. Clearly, complete resting of the sward where *A. junciformis* is present even in small amounts for long enough leads to complete domination of the sward by this species. An internal report on the burning and grazing trial (Anon, 1986) indicated that *A. junciformis* was not recorded in the area when the trial was established though it was "probably present in small quantities." In view of the results obtained for this trial, the A treatment plots (no summer utilization) were selected for more intensive data collection.

Rotational Grazing and Resting of Veld Trial

The no grazing (control) and rotational grazing treatments were dominated by *T. triandra* with *A. junciformis* marginally present (Figure 2.5). The rotational resting and continuous grazing treatments were heavily encroached by *A. junciformis*, probably as a result of long rest periods (c. 9 months) allowing the expansion of this species. In view of these results, one replication each of the rotational grazing, rotational resting, and continuous grazing treatments were chosen for more intensive investigation.

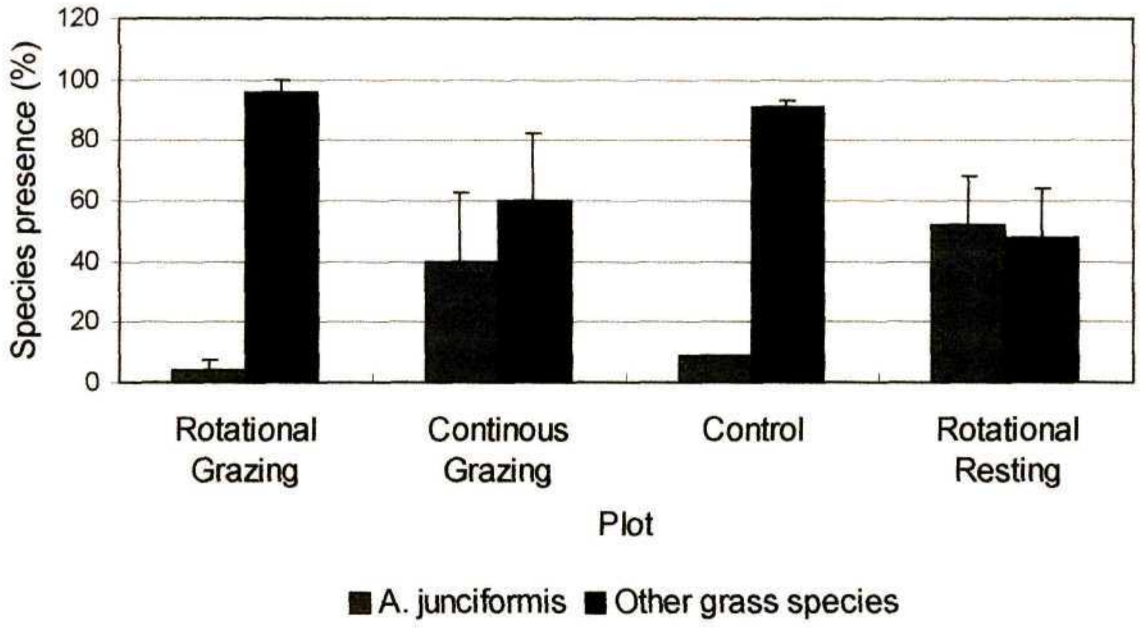


Figure 2.5. Percentage composition of *Aristida junciformis* and other grass species in the Rotational Grazing and Resting of Veld' Trial. (Bars indicate S.D).

Days In/ Days Out Trial

The results were less clear for this trial (Figure 2.6), but plots in which long grazing periods were followed by long rest periods showed the highest encroachment by *A. junciformis*. From this trial a single replication of the 2 days in/ 20 days out and the 2 days in/ 60 days out treatment plots were selected for further experimental work as these sites appeared to be in the initial stages of encroachment.

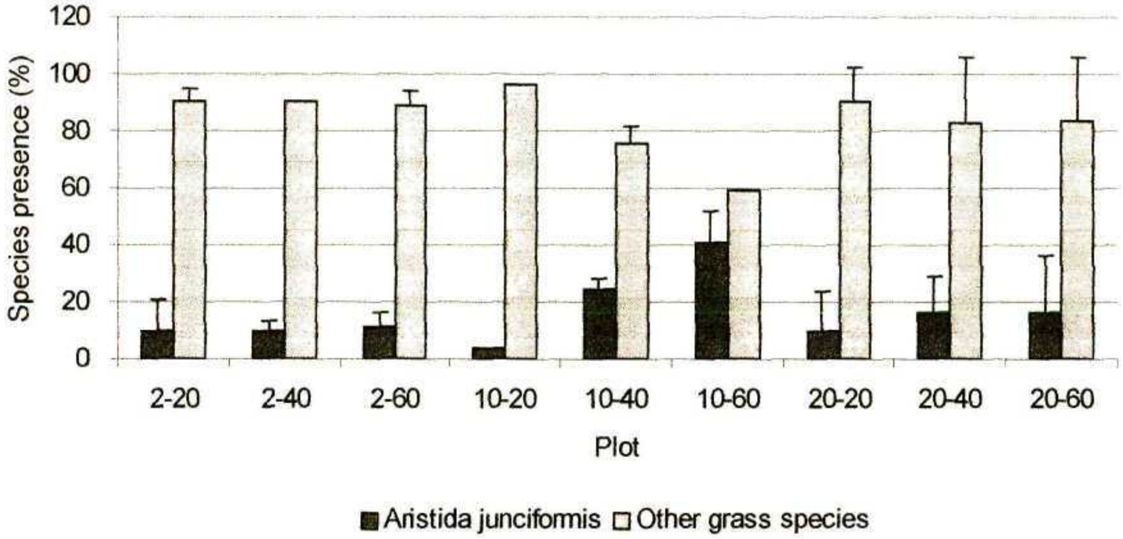


Figure 2.6. Percentage composition of *Aristida junciformis* and other grass species in the 'Days In/Days Out' trials. (Bars indicate S.D).

2.4. Line ellipse-intercept method

2.4.1. Introduction

In order to collect basal cover, canopy cover, species composition, plant density and plant size distribution data the ellipse-intercept method of Stokes and Yeaton (1994) was used. The usefulness of this method lies in the large amount of information that is generated for the sampling effort required.

The method provides three measures of plant abundance (percentage cover, density, and intercept cover) and also provides plant size distributions but requires no more effort than the line intercept method. The technique is based on interceptions between a sampling line and an ellipse associated with the plant that has the same area and similar shape to the plant's canopy or base.

2.4.2. Method

In each of the plots selected from the point quadrat results; five, 10 m line-transects were used to sample the sward. A transect line was laid down in the vegetation, and for each basal area of a grass tuft intercepted by the line, the two perpendicular axes of the ellipse described by the grass plant canopy and the plant species were recorded. Both canopy and basal perpendicular axes of the grass tuft were measured. Analysis of these data involved calculating the cover and density contribution of each intercepted plant based on the width of transect that would equivalently sample that plant.

2.4.3. Results

The results are presented in Tables 2.3 and 2.4. Basal diameters were compared statistically using a one-way ANOVA with Tukeys studentised range test for differences between means applied to a logarithmic transformation of these data (Steel and Torrie, 1980). The logarithmic transformation was applied as some of these data were not normally distributed. Tukeys studentised range test was used throughout the study when using ANOVA as it is the least sensitive of the various range tests and as such is the most suitable for biological analysis which is often subject to a lot of 'noise' in data. The canopy cover data, though included in Tables 2.3 and 2.4 was discarded for further analysis due to the variability of the data primarily as a result of the difficulty of distinguishing the canopy of any particular plant particularly of *A. junciformis*.

Table 2.3. The effect of defoliation frequency on *Aristida junciformis*.

Treatment	Canopy cover (%)	Basal cover (%)	Modal basal diameter ±S.E. (cm)	Composition (%)	Density (plants m^2)
Burning and Mowing Trial					
No burn or mow (control)	78.8	31.5	11.0±0.6	92.2	6.2±0.3
Annual burn (August)	0.5	0.4	0.6±0.3	0.6	0.6±0.2
Annual burn (spring)	0.8	0.4	0.5±0.8	0.9	1.1±0.2
Biennial burn (August)	3.6	0.9	1.0±1.1	4.7	5.7±0.2
Biennial burn (spring)	9.3	3.8	5.5±0.6	9.5	5.7±0.3
Biennial burn (autumn)	11.8	2.9	5.0±0.9	13.9	3.9±0.6
Triennial burn (August)	25.5	9.4	11.0±1.0	25.8	4.4±0.5
Triennial burn (spring)	21.1	5.8	11.5±1.0	22.6	1.9±0.2
Triennial burn (autumn)	38.4	12.4	19.0±0.9	40.2	5.6±0.3
Annual mow (August)	25.1	4	3.0±0.7	28.9	3.4±0.2
Annual mow (spring)	68.7	6.8	15.0±0.8	69	3.7±0.3
Rotational Grazing and Resting of Veld Trial					
Rotational grazing	0.3	0.4	3.6±2.8	0.3	1.9±0.1
Continuous grazing	8.8	14.6	2.5±0.2	9.2	1.2±0.1
Rotational resting	20	24.2	5.0±0.3	20	6.4±0.4
Days In/ Days Out Trial					
Two days graze/ 20 days rest	7.9	1.2	6.2±0.4	9.1	2.4±0.2
Two days graze/ 60 days rest	2.4	0.5	6.0±0.3	3	6.1±0.5

Table 2.4. The effect of defoliation frequency on *Themeda triandra*.

Treatment	Canopy cover (%)	Basal cover (%)	Modal basal diameter ±S.E. (cm)	Composition (%)	Density (plants m^2)
Burning and Mowing Trial					
No burn or mow (control)	0.5	0.1	4.5±0.4	0.6	0.1±0.0
Annual burn (August)	9.2	24.7	1.5±0.8	83.8	57.1±1.1
Annual burn (spring)	32.8	13.1	0.5±0.2	37.9	144.4±1.9
Biennial burn (August)	32.0	11.7	4.0±0.5	41.7	37.9±0.9
Biennial burn (spring)	7.6	11.8	4.5±0.6	42.5	37.9±0.7
Biennial burn (autumn)	43.4	14.9	6.5±0.9	51.2	16.2±0.6
Triennial burn (August)	2.3	0.8	12.5±0.7	2.3	1.9±0.3
Triennial burn (spring)	3.1	1.4	6.0±0.6	3.3	4.0±0.6
Triennial burn (autumn)	3.6	1.4	5.0±0.5	3.8	4.3±0.5
Annual mow (August)	82.0	17.9	2.5±0.6	64.3	57.0±2.1
Annual mow (spring)	19.7	3.0	2.5±0.4	19.8	8.6±1.3
Rotational Grazing and Resting of Veld Trial					
Rotational grazing	24.8	45.0	8.0±0.5	24.8	91.8±3.7
Continuous grazing	29.7	35.8	2.5±0.3	31.1	54.0±3.1
Rotational resting	36.0	24.5	7.0±0.2	36.2	26.1±1.5
Days In/ Days Out Trial					
Two days grazing/ 20 resting	13.4	26.3	7.5±0.4	15.4	22.0±1.1
2 days grazing/ 60 days resting	27.8	50.8	7.0±0.7	35.1	20.3±1.2

Long term Burning and Mowing Trial

All replicates of the control treatment A1 (no burning or mowing) were completely dominated by *A. junciformis* which on average accounted for 92% of the grass species found in the sward, the highest proportion found in any of the treatments of any of the trials. There was also prominent establishment of dicotyledonous shrubs and trees, both indigenous and exotic, including *Acacia* species, *Rhus dentata* and *Melia azedarach* (Figure 2.7).

Figure 2.7. One of three A1 (Control) replicates of the Burning and Mowing Trial showing the almost complete dominance of the herbaceous layer by *Aristida junciformis* and the emergence of woody species such as *Melia azedarach* as a result of very long periods of protection from defoliation. Photograph taken in March 1994 on Ukulinga plateau.

Basal cover and sward composition of *A. junciformis* was high but the density of this species was comparatively low due to the majority of tufts being well established and consequently well spaced. Many of these *A. junciformis* plants contained quantities of moribund material within their canopies which eventually decayed and fell to form a thick layer of litter on the soil surface.

The basal diameters of *A. junciformis* in the control (A1) treatments ranged between 9 and 34 cm with a modal diameter of 11 cm. Of the annually mown plots (treatments A10 and A11), A11 was particularly dominated by large *A. junciformis* plants. As previously observed in the point quadrat results there was a clear trend of increasing dominance of *A. junciformis* with decreasing disturbance of the sward. From treatments A1 through to A11 as disturbance either in the form of burning or mowing decreased the proportion of *A. junciformis* increased. Comparing both basal and species composition of annually burnt plots to triennially burnt plots (treatments A2 to A9) there is a concomitant increase in *A. junciformis* (Figure 2.8).

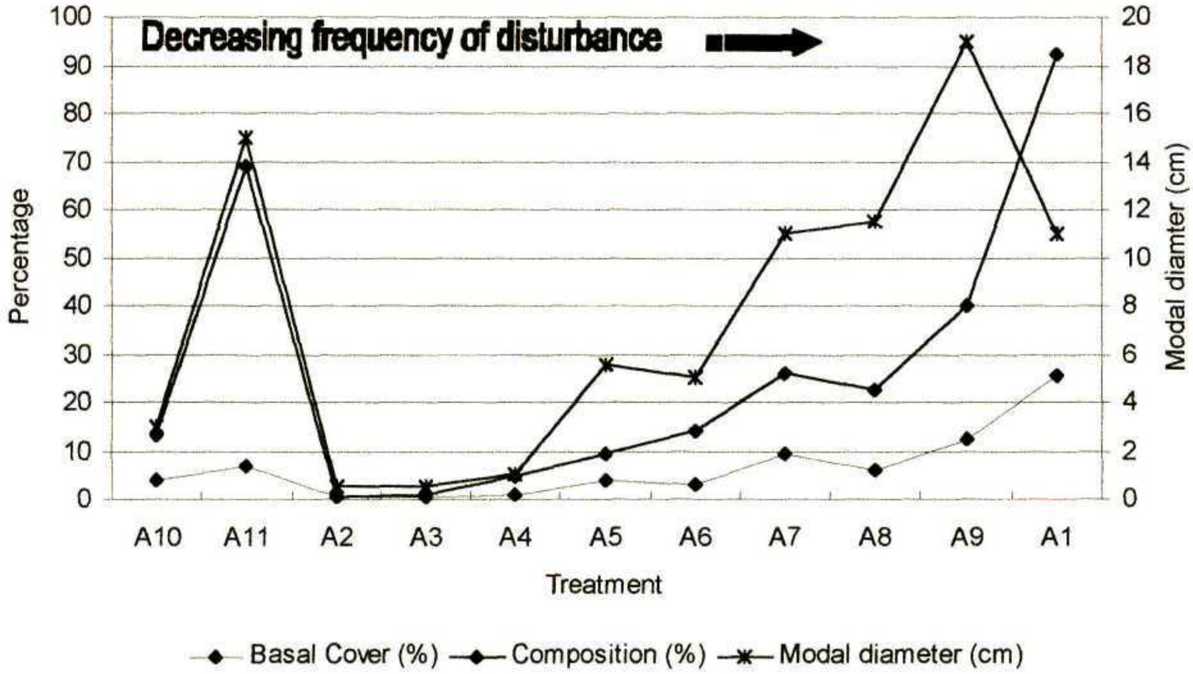


Figure 2.8. Response of *Aristida junciformis* to decreasing frequency of defoliation.

In all three replications of the annual burn/ no mowing treatment (A2) only four *A. junciformis* plants in total were recorded, indicative of the positive effects of regular disturbance on eliminating this species. The frequency of *A. junciformis* in the sward increased rapidly with decreasing defoliation frequency. Coupled with this was the effect of increasing plant size with decreasing disturbance of the plants. The large basal areas of these *A. junciformis* plants resulted in a much lower density in the sward when compared to the density of *T. triandra* (Table 2.4)

The biennial burn treatments (A4 to A6) had increasingly more *A. junciformis* present with *A. junciformis* becoming prominent particularly in the autumn biennial burn plots (A6 treatment). With the triennial burns (Treatments A7 to A9) there was a further increase in *A. junciformis* and a proportional decrease in other grass species.

Statistically there was no difference in the amount of *A. junciformis* in the A1 treatment and the A7, A8, A9 and the A11 treatments while there was a notable difference between A1 and the remainder of the other A treatments (*P*<0.001 for all cases).

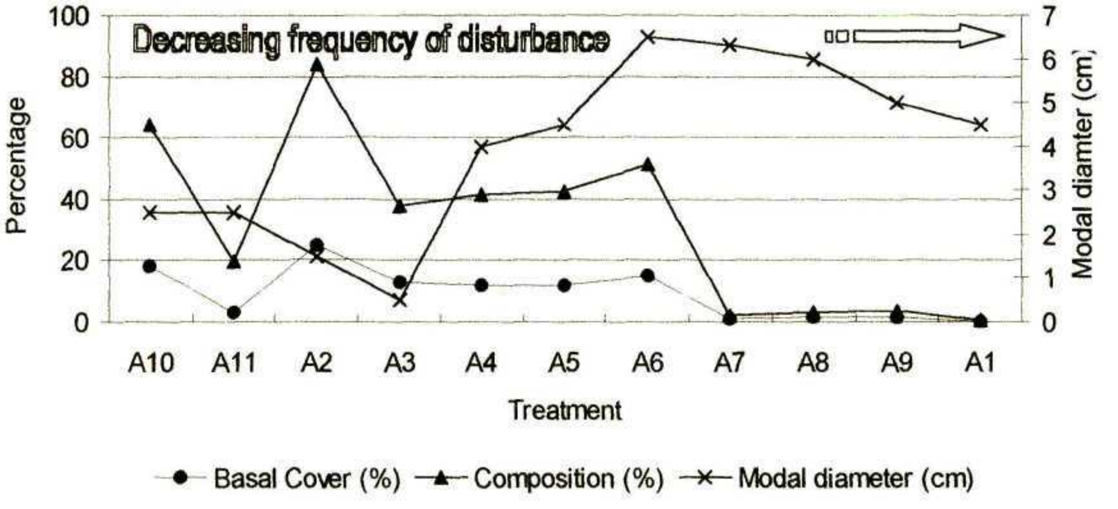


Figure 2.9. Response of *Themeda triandra* to decreasing frequency of defoliation

However differences did occur (*P*<0.0001) in diameter data of *T. triandra* (Table 2.4, Figure 2.9) sampled in the annual burn plots between treatments A2 and A3; and between the biennial burn treatments (A4, A5 and A6) and the triennial burn treatments (A7, A8, and A9), *P*<0.001.

The actual frequency of each tuft diameter encountered in the measured plots in the Burning and Mowing plots are depicted in Figures 2.10 to 2.13 for *A. junciformis* and Figures 2.14 to 2.16 for *T. triandra* respectively.

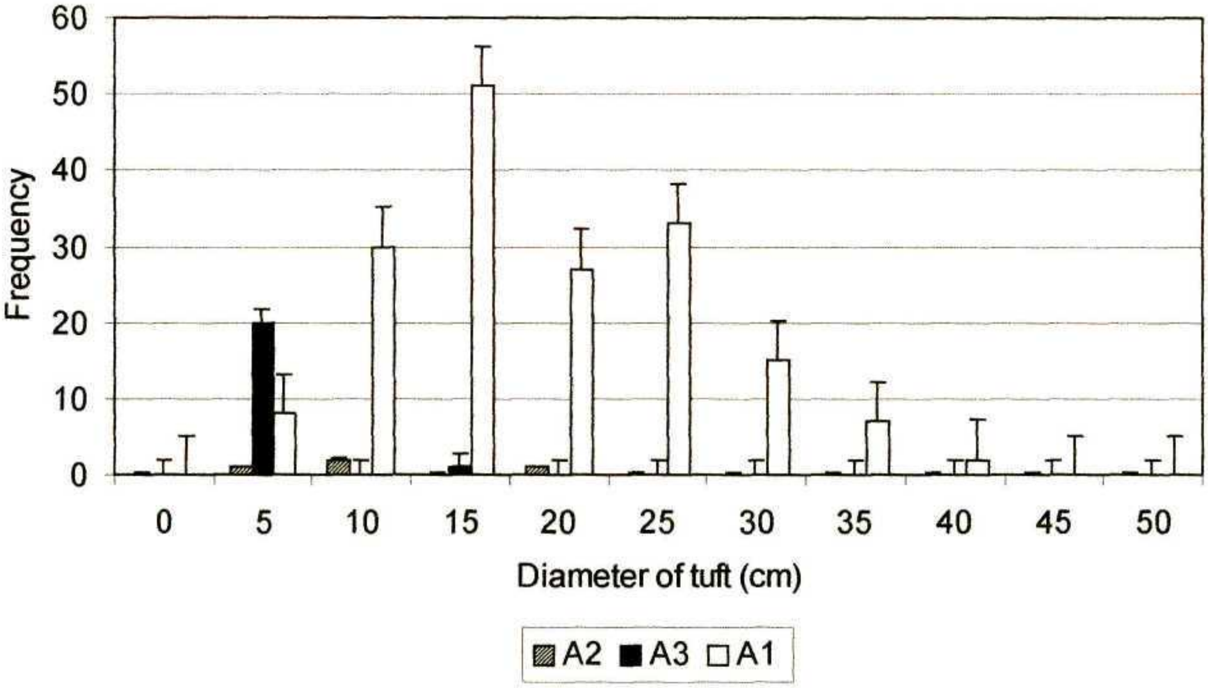


Figure 2.10. The distribution of basal diameters of *Aristida junciformis* measured with ellipse-intercept transects in the annual burn treatments (A2 and A3) compared with the Control treatment (A1) of the Burning and Mowing trial. (Bars indicate S.E).

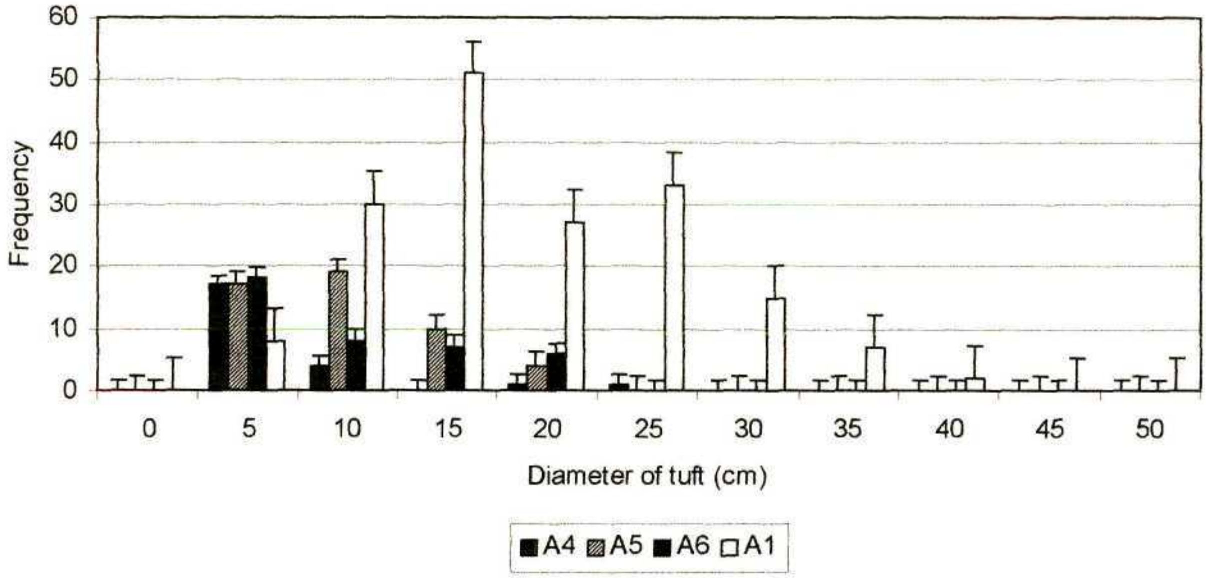


Figure 2.11. The distribution of basal diameters of *Aristida junciformis* measured with ellipse-intercept transects in the biennial burn treatments (A4, A5 and A6) compared with the Control treatment (A1) of the Burning and Mowing trial. (Bars indicate S.E).

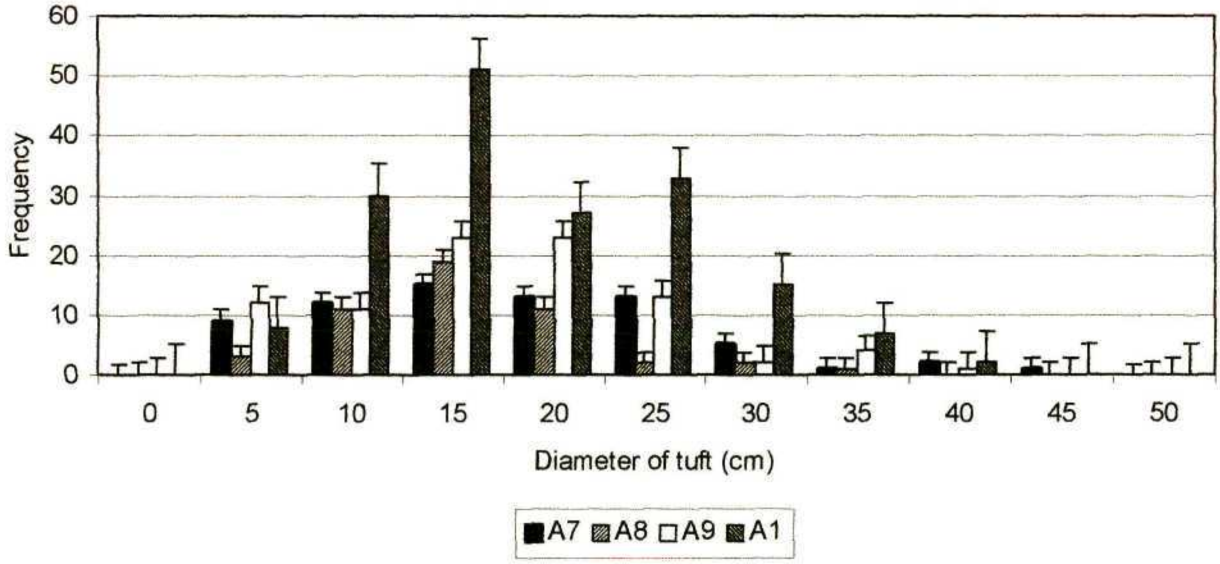


Figure 2.12. The distribution of basal diameters of *Aristida junciformis* measured with ellipse-intercept transects in the triennial burn treatments (A7, A8 and A9) compared with the Control treatment (A1) of the Burning and Mowing trial. (Bars indicate S.E).

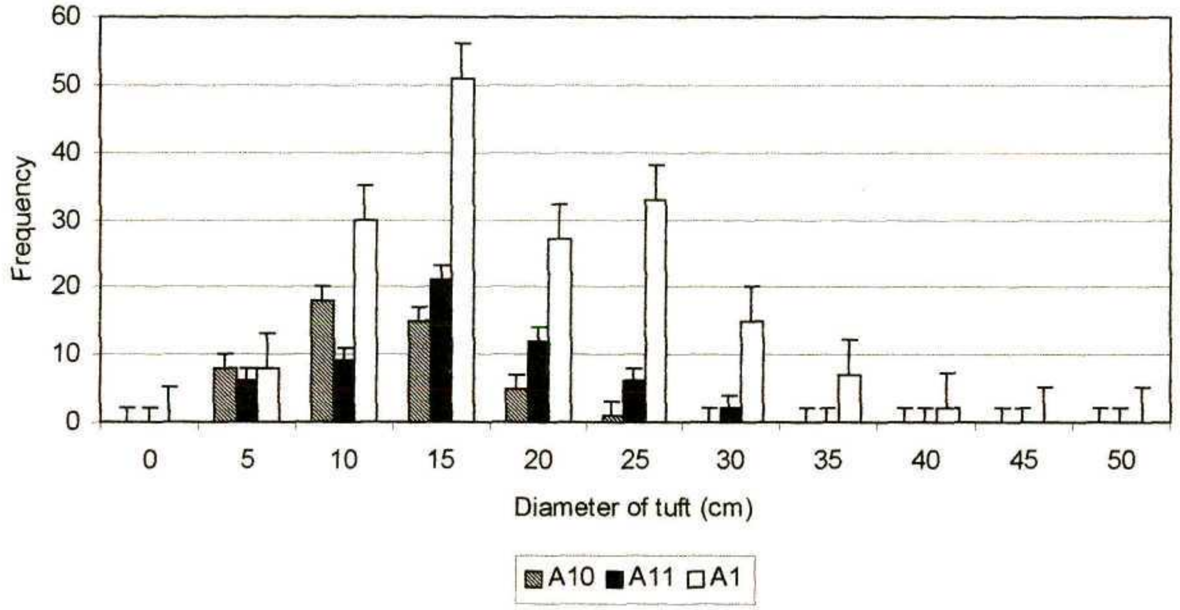


Figure 2.13. The distribution of basal diameters of *Aristida junciformis* measured with ellipse-intercept transects in the annual mow treatments (A10 and A11) compared with the Control treatment (A1) of the Burning and Mowing trial. (Bars indicate S.E).

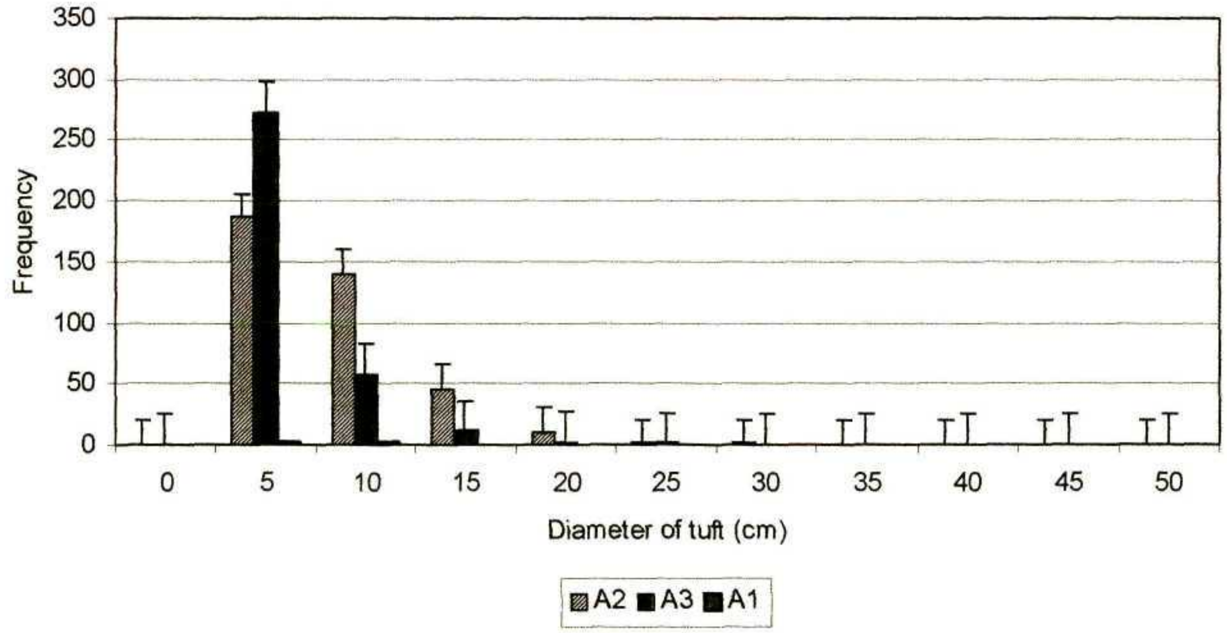


Figure 2.14. The distribution of basal diameters of *Themeda triandra* measured with ellipse-intercept transects in the annual burn treatments (A2 and A3) compared with the Control treatment (A1) of the Burning and Mowing trial. (Bars indicate S.E).

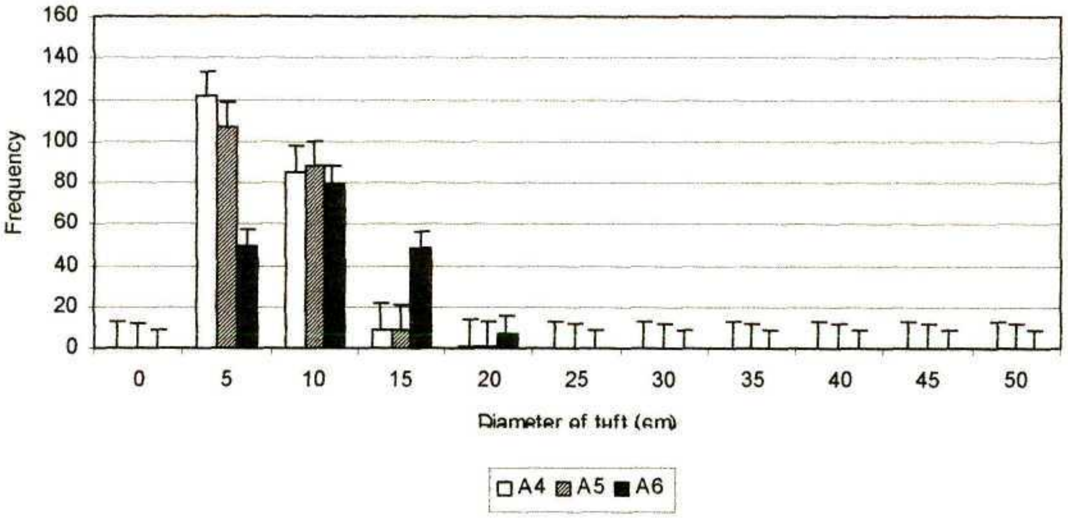


Figure 2.15. The distribution of basal diameters of *Themeda triandra* measured with ellipse-intercept transects in the biennial burn treatments (A4, A5 and A6) of the Burning and Mowing trial. (Bars indicate S.E).

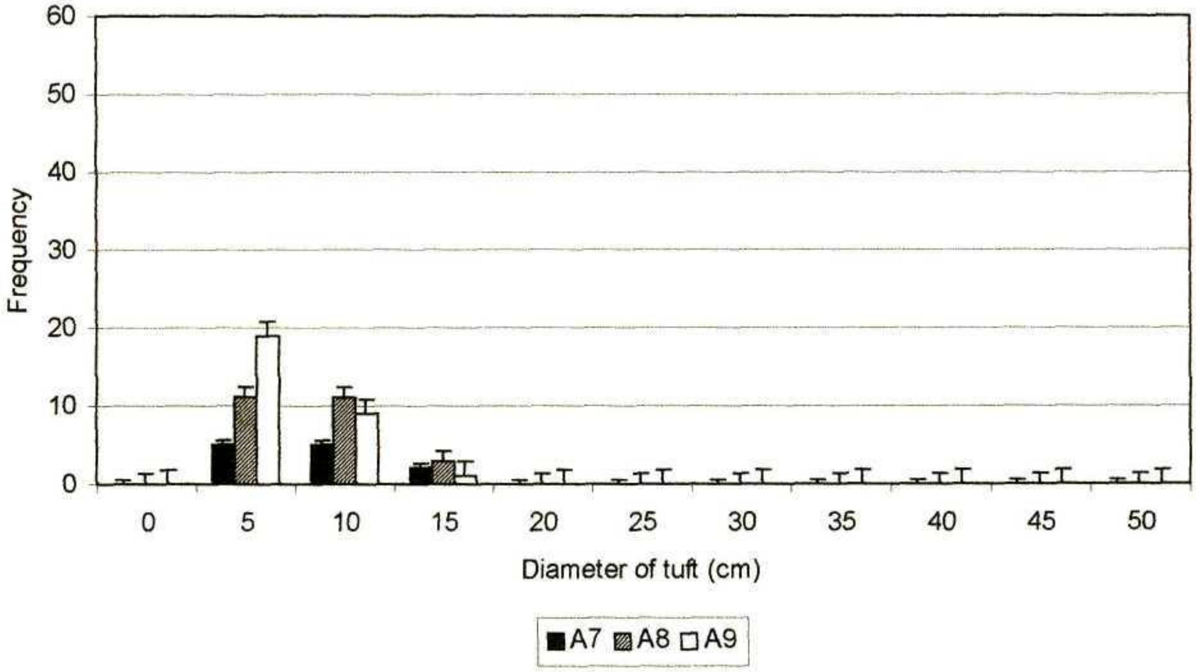


Figure 2.16. The distribution of basal diameters of *Themeda triandra* measured with ellipse-intercept transects in the triennial burn treatments (A7, A8 and A9) of the Burning and Mowing trial. (Bars indicate S.E).

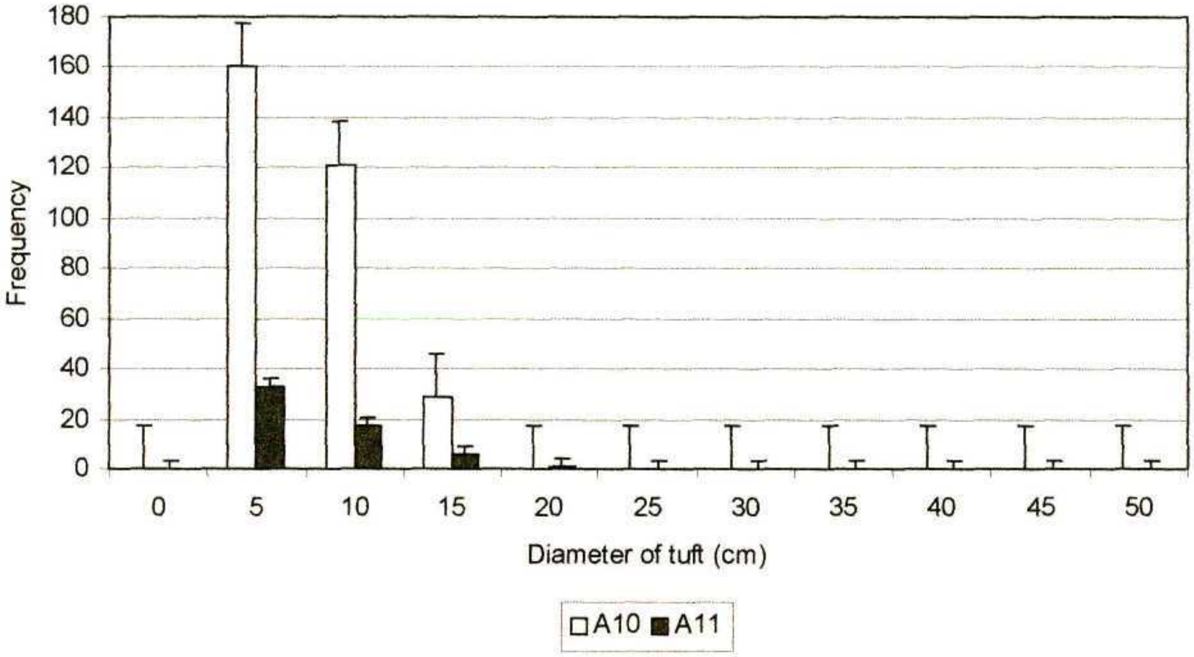


Figure 2.17. The distribution of basal diameters of *Themeda triandra* measured with ellipse-intercept transects in the annual mow treatments (A10 and A11) of the Burning and Mowing trial. (Bars indicate S.E).

Grazing and Resting of Veld trial

The Rotational Grazing treatment showed minimal presence of *A. junciformis*, the Continuous Grazing treatment an intermediate level of encroachment, and the Rotational Resting treatment substantial encroachment. Similar results were obtained regarding basal cover and plant density (Table 2.3). These results illustrate again the result of allowing *A. junciformis* to germinate and grow without disturbance for sufficient time, particularly in the rotational resting treatment, which allowed the plants to grow out and become unpalatable before re-exposure to grazing animals.

There were considerable differences in the basal diameter of tufts of *A. junciformis* between the rotational and continuous grazing treatments ($P<0.01$). This was due to the very low occurrence of this species in the Rotational Grazing treatment. There were no prominent differences

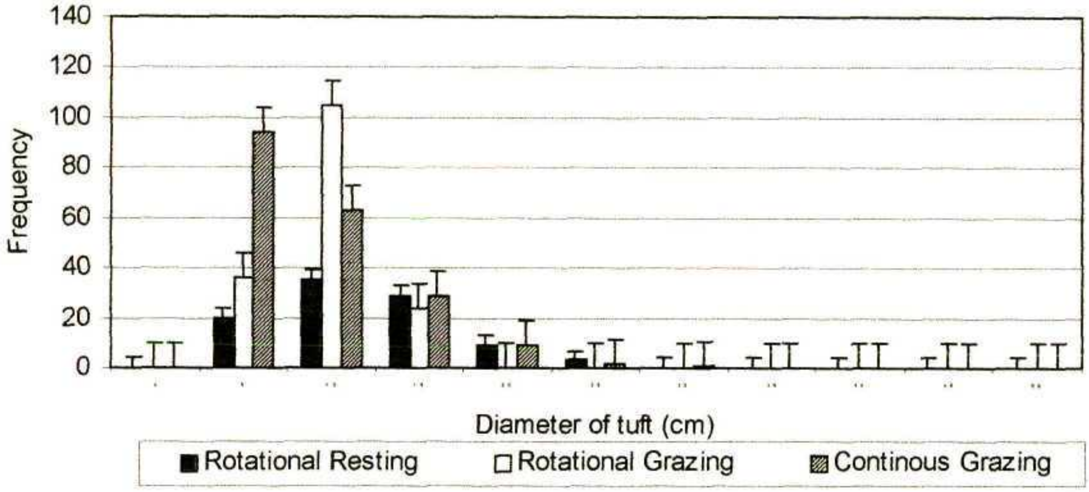


Figure 2.18. The distribution of basal diameters of *Aristida junciformis* measured with ellipse-intercept transects in the Grazing and Resting of Veld trial. (Bars indicate S.E).

between the continuous and rotational resting treatments though the average basal diameter was larger in the rotational resting treatment compared to the continuous grazing treatment. The actual frequency of each basal area encountered in the measured plots in this trial are depicted in Figures 2.18 and 2.19 for *A. junciformis* and *T. triandra* respectively.

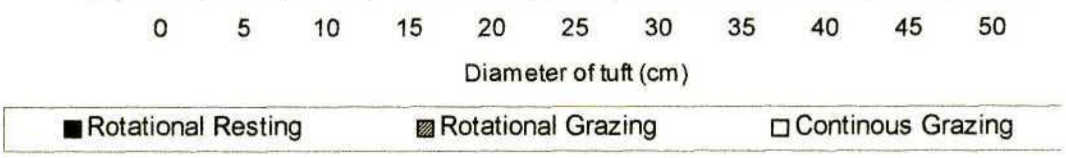


Figure 2.19. The distribution of basal diameters of *Themeda triandra* measured with ellipse-intercept transects in the Grazing and Resting of Veld trial. (Bars indicate S.E).

Days in/ days out trial

A similar pattern to the one described above was repeated in the treatments examined in this trial. The two days in (grazing period) and sixty days out (resting period) maintained the competitive advantage of the climax grass species such as *T. triandra* while the two days in (grazing) and 20 days out (resting period) treatment placed more pressure on the decreaser species and moved the competitive balance towards increaser species such as *A. junciformis*. The actual frequency of each basal area encountered in the measured plots in this trial is depicted in Figure 2.20 for both *A. junciformis* and *T. triandra* respectively.

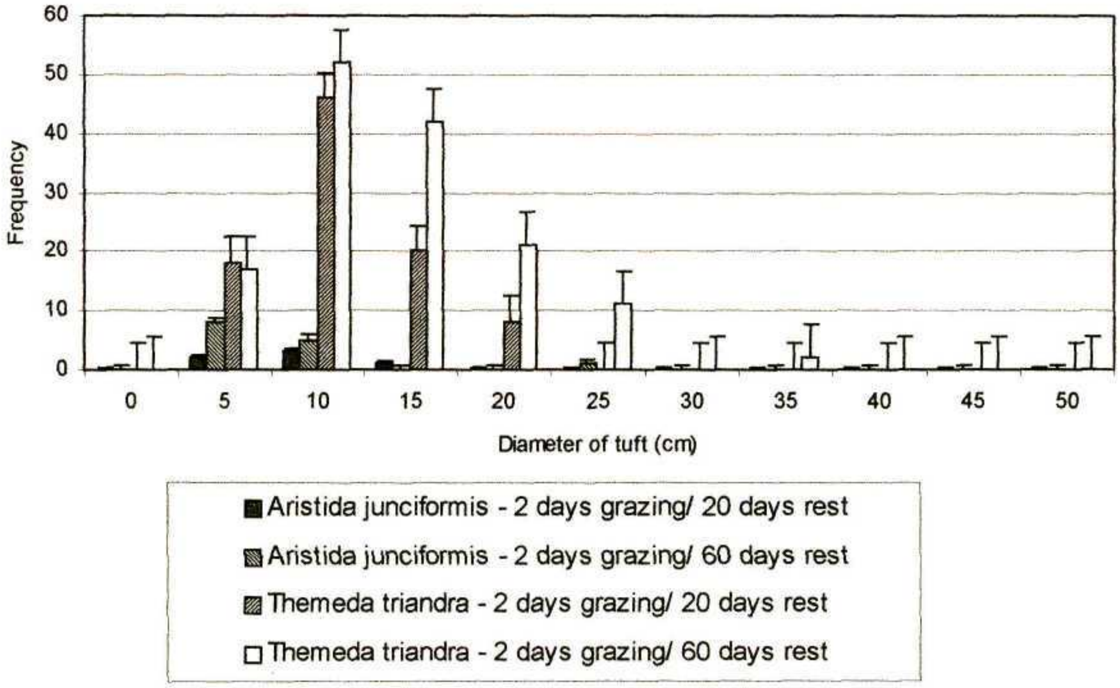


Figure 2.20. The distribution of basal diameters of both *Aristida junciformis* and *Themeda triandra* measured with ellipse-intercept transects in the in the 'Days In/ Days Out' trial. (Bars indicate S.E).

2.4.4.. Discussion

The potential for encroachment of Southern Tall Grassveld by *A. junciformis* appears dependant on the frequency of either burning, mowing, grazing or rest to which the grass component is subjected. As the abundance of *A. junciformis* increases, veld deterioration gradually accelerates as grazing pressure on the remaining palatable species increases. These palatable species are then slowly replaced by *A. junciformis* and less palatable species such as *Sporobolus africanus* (Tainton, 1972).

Frequent mowing and burning prevents *A. junciformis* dominating a sward, is effective in reducing the ability of *A. junciformis* to compete for resources with more desirable species thereby diminishing its' competitive ability. An exception appears to be mowing in spring which appears to strongly alter the competitive balance in favour of *A. junciformis* . Possibly *A. junciformis* is less effected by mowing and is able to gain a competitive advantage as a result of decreaser species such as *T. triandra* having to draw heavily on root-stored reserves to produce new tillers at the expense of root volume and consequently competitive ability.

Rethman and Booysen (1968), in a clipping experiment to examine the effects of time of defoliation, found a progressive decrease in regrowth potential with lateness of defoliation from September to August in the previous season. It also appeared that plants cut before the end of March showed a considerably better growth response than those clipped during late autumn and winter. In terms of regrowth potential, Rethman and Booysen (1968) suggested that winter cutting (particularly early winter cutting) appears to be more harmful than summer cutting. These authors concluded that the veld has a greater susceptibility to defoliation in winter than in summer as early winter cutting prevented translocation in winter and resulted in a long period of exposure to cold. Data collected in this study indicates that winter cutting (Treatment A10) is more effective in promoting *T. triandra* and thereby restraining *A. junciformis* encroachment than cutting in spring. An early spring mow (Treatment A11) appears to be the most detrimental to *T. triandra* and other decreaser species and consequently benefits *A. junciformis* as seen in the relatively high incidence of *A. junciformis* in this treatment.

Time of burning is also important. An early spring burn appears to be the most detrimental to *T. triandra* and consequently benefits *A. junciformis*. Drewes and Tainton (1981) reported comparable results when they stated that early spring defoliation brought about the greatest setback to *T. triandra* in particular. They ascribed this to the young lateral growth being removed at a time when the plants were still replenishing food reserves and subsequent growth would therefore be required to develop from less mature laterals and so reduced plant reserves. Where *A. junciformis* becomes prominent is often ascribed to long rest periods provided in any specific grazing system. Tainton (1972) noted that spring rests in particular allowed *A. junciformis* a period of undisturbed establishment when it may have otherwise been grazed at a vulnerable stage of development.

CHAPTER THREE

COMPETITION AND SEEDLING SURVIVAL

3.1 Introduction

Competition has a major impact on the composition of plant communities. It can be defined as a process which occurs when one organism withdraws a resource needed by another, such as water, nutrients and space, from their common environment (Heady and Child, 1994). Competition is therefore an inevitable consequence of increasing density of plant communities, when some or all of the individuals in a community may receive an insufficient quantity of a limiting resource to fulfil their needs. The factors for which competition occurs are numerous, but those for which it is generally most intense include light, moisture and nutrients. All of these are deficient in South African environments, at least at some time during the year.

3.2. Experimental Sites

The majority of the field experiments described below were carried out within a range of experimental sites identified and selected from the treatments discussed in Chapter Two. These sites were selected as representing a clear gradation of *A. junciformis* encroachment. For ease of reference in describing experimental work, these sites were named to reflect the degree of encroachment of *A. junciformis* found within them. The percentage basal cover of *A. junciformis* and *T. triandra* respectively in each site is shown in brackets.

These sites were as follows:

High Encroachment site (32% vs. 0.1%)

Limited Encroachment site (3.8% vs. 11.8%)

Medium Encroachment site (24% vs. 24%)

No Encroachment site (0.5% vs. 51%)

3.3. Nearest Neighbour Analysis

If interspecific competition is taking place within a plant population, unsuccessful competitors should either be small and stunted, or else completely unable to establish themselves. Also the closer two plants are to each other, the more intensely will they compete with one another. The fact that the plants are competing with one other may therefore show itself in two ways; the distance between any plant and its nearest neighbour will be positively correlated with the sum of their sizes, and there may be a lower limit to the distance between any plant and its nearest neighbour i.e. each successful plant may have around it its own territory within which no new colonizers can establish themselves (Pielou, 1962).

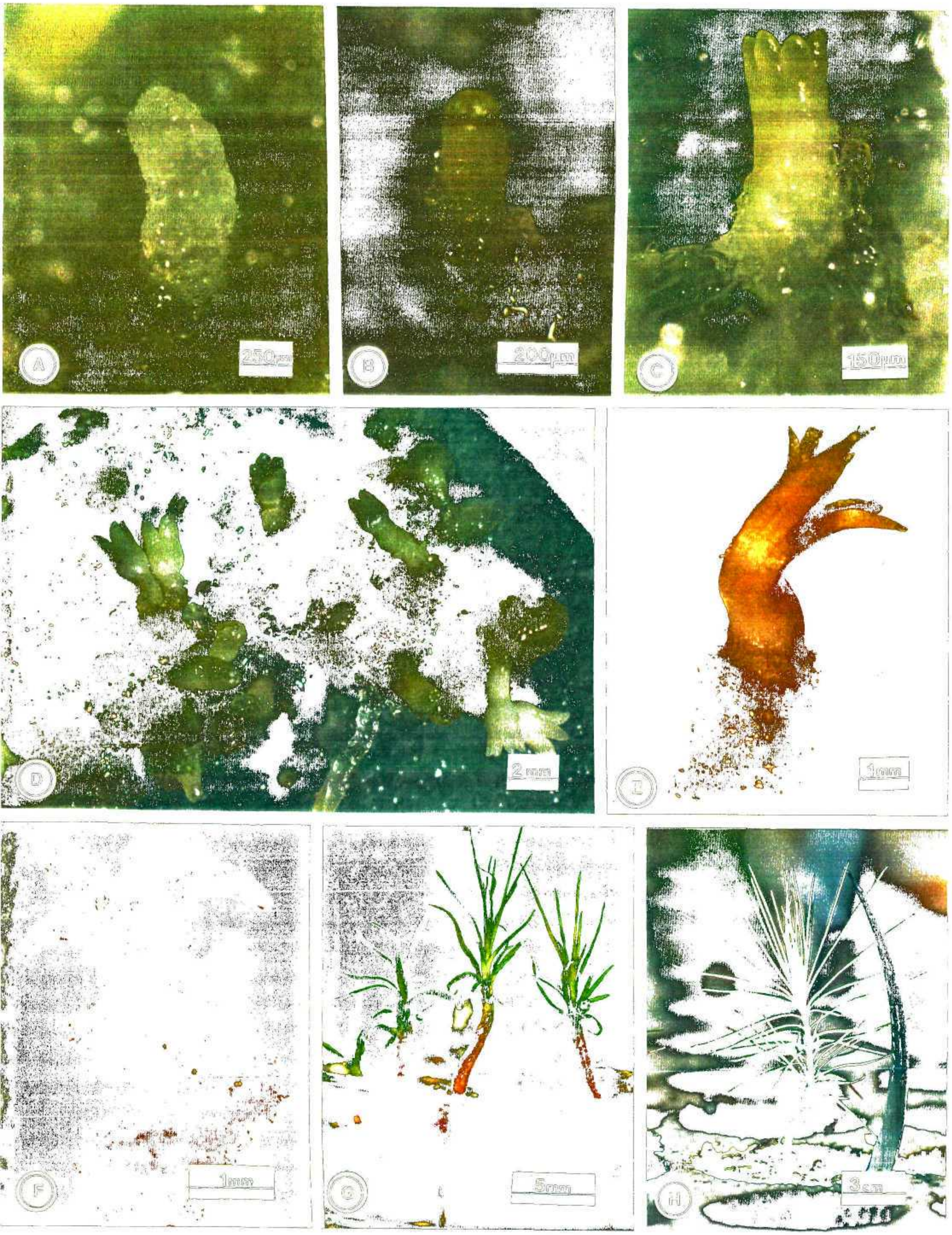
Interspecific plant competition appears to have an important role in encroachment of *A. junciformis* into swards formerly dominated by species such as *T. triandra*. Observations in the field showed that many mature *A. junciformis* plants appeared to have a clear area around their base in which no other species occurred, a possible indication of intense competition. Consequently interactions within and between *Aristida junciformis* and *Themeda triandra* plants in the sward were studied using nearest-neighbour analysis as described by Pielou (1962).

3.3.1. Method

The method followed in actually selecting plants for measurement was that described by Yeaton, 1990. Individuals were randomly selected within the Limited Encroachment site by choosing a point on the horizon and walking towards it within the site. The size of each individual plant intersected during the walk was measured and its species noted. The plants were identified either as *A. junciformis*, *T. triandra* or 'other' grass species.

The size of each individual plant was calculated by using the average of the longest axis of the tuft diameter and the axis at right angles to it. In addition, the identity and size of it's nearest neighbour and the distance between the centres of the two plants was determined. This process continued until a minimum of 100 nearest-neighbour pairs for each possible intra- and interspecific combination (i.e. 300) pairs was obtained following Yeaton (1990).

The distances between nearest-neighbour individuals were regressed against the sum of the sizes of the two neighbours. A positive, linear correlation between the two variables and a slope significantly different from zero suggests a competitive interaction (Pielou, 1962). Whether there were positive or negative associations between the two species, both intra- and interspecifically, was tested by using a square-root transformation on the distance measures and comparing them by a Student's *t*-test following Goodall (1965). The square root transformation was used to normalize the distribution of the small numeric values of the ratios involved (Steel and Torrie 1980).


A
250µm
B
200µm
C
150µm
D
2mm
E
1mm
F
1mm
G
5mm
H
3cm

3.3.2. Results

None of the intra- and interspecific pairings showed any correlations between nearest-neighbour distance and the sum of the sizes of the two neighbours in any of the treatments sampled (Table 3.1).

The distance between individuals of *A. junciformis* and *T. triandra* was greater ($\bar{x}$=45.9 cm, *P*<0.001) than that between individuals of *T. triandra* and *T. triandra* (13.8 cm), but not conspicuously greater than between individuals of *A. junciformis* and *A. junciformis* (37.2 cm, Table 3.1).

Table 3.1. The relationship between nearest-neighbour distance and the sum of plant diameters for *Aristida junciformis* and *Themeda triandra*.

Species Interaction	n	b	r	Distance (cm)
A. junciformis versus *A. junciformis*	204	0.22	+0.5	37.2±1.9
T. triandra versus *T. triandra*	101	0.13	+0.4	13.8±1.4
A. junciformis versus *T. triandra*	164	0.1	+0.3	45.9±4.0

n= number of pairs sampled; b=slope of the regression line; r=correlation coefficient. None of the slopes are significantly greater than zero at P<0.01.

3.3.3. Discussion

Nearest-neighbour analysis failed to demonstrate that competition is taking place between *A. junciformis* and *T. triandra* as there were no conspicuously positive linear correlations between nearest-neighbour distance and the sum of sizes of the two neighbours. This technique has been successfully used in grasslands which are more arid than those at Ukulinga where competition has been shown to be taking place for soil moisture both within and between species (Yeaton and Cody, 1976; Yeaton, 1990). However, it can be inferred from the results, that both *A. junciformis* and *T. triandra* individuals are more tolerant of individuals of their own species rather than individuals of other species. The tolerance of an individual *A. junciformis* plant for a member of it's own species was not substantially different to that of a *T. triandra* plant, suggesting that *A. junciformis* is interacting with *T. triandra* as if they are members of the same species and it can be concluded that the two species are ecologically equivalent (Yeaton, 1990).

3.4. Adult versus seedling competition

3.4.1. Introduction

The lack of discernible competition between *A. junciformis* and a dominant decreaser species such as *T. triandra* at the adult stage raised questions of the effects of competition at the seedling stage of the two species life history's. Competition for resources from adult plants appeared to be an important factor in seedling survival, especially in the ability of *A. junciformis* seedlings to grow and eventually out-compete adult *Themeda triandra* as well as other palatable species in a sward This was exemplified by the apparent lack of seedlings of both species in the experimental plots. The reverse situation would also provide an interesting comparison, namely the ability of *Themeda triandra* seedlings to invade *Aristida junciformis* dominated areas and reestablish in such areas. It was important to establish at what level does this competition take place; is it root competition (for water and/or nutrients), light competition (size of the canopy), or combinations of these factors?

3.4.2. Methods and analysis

The experimental site was situated in an area dominated by *A. junciformis* and *T. triandra* with approximately equal proportions of each species in the sward. Four treatments were used to investigate competition between seedlings and adult plants. Twenty adult (i.e. large tufts that had previously flowered) tufts of both *A. junciformis* and *T. triandra* of uniform diameter were selected. Surrounding each plant four seedlings of the focal species were planted at the cardinal points as close to the base of the associate species as possible. This close proximity was to ensure competitive interactions between the adult plant and the seedlings. For all the treatments all vegetation surrounding tufts up to a diameter of 45 cm were first killed with herbicide and then clipped to eliminate all other possible sources of competition to the seedlings and adult plants.

These seedlings were watered for two weeks at the rate of two litres of water per plant every three days until they were established and up to the first rains fell. Due to the poorly established root systems of such young seedlings, especially *T. triandra,* there was a high mortality rate of the seedlings. Before all the seedlings were established, 48 *T. triandra* and 24 *A. junciformis* seedlings, that had died within days after planting, were replaced by live seedlings grown in the same cohort. Seedlings were grown in 'Speedling' trays and planted into holes of uniform volume excavated with a bucket soil augur. All 320 seedlings of each species used for this experiment were at the one tiller stage of growth when planted.

3.4.3. Description of treatments

The control treatment was adult plants left intact with four seedlings planted on the plant's basal perimeter.

The root competition treatment necessitated the canopy of adult plants being clipped to a 5 cm leaf length. This ensured the seedlings would not be shaded by the adult plant but would still be effected by root competition. The clipped plants were maintained at their initial leaf length through regular clipping for the duration of the experiment.

The light competition treatment entailed the killing of tufts through the use of a herbicide 'Nomix' (active ingredient glyphosate), but leaving the canopy. This would effectively remove root competition but not competition for light. However, it was recognized that the likely response of adult grass plants to frequent defoliation would be the redirection of resources from the roots to the canopy in order to produce new tillers, resulting in a gradual shrinkage in root volume of the adult plant over time. This would have influenced competitive interactions between the adult tuft and surrounding seedlings for the duration of the experiment.

The no competition treatment entailed both the killing and clipping of the adult tufts, effectively removing any competition between the seedling and the adult plant.

3.4.4. Data collection and analysis

The number of tillers produced by seedlings of both species were measured weekly. Differences in tiller production and seedling survival was tested between treatments for both species after a square-root transformation was applied to normalize variables for analysis of variance (ANOVA) (Steel and Torrie 1980). This test was selected as being the most powerful suitable for testing possibly minor differences in tiller production and seedling survival.

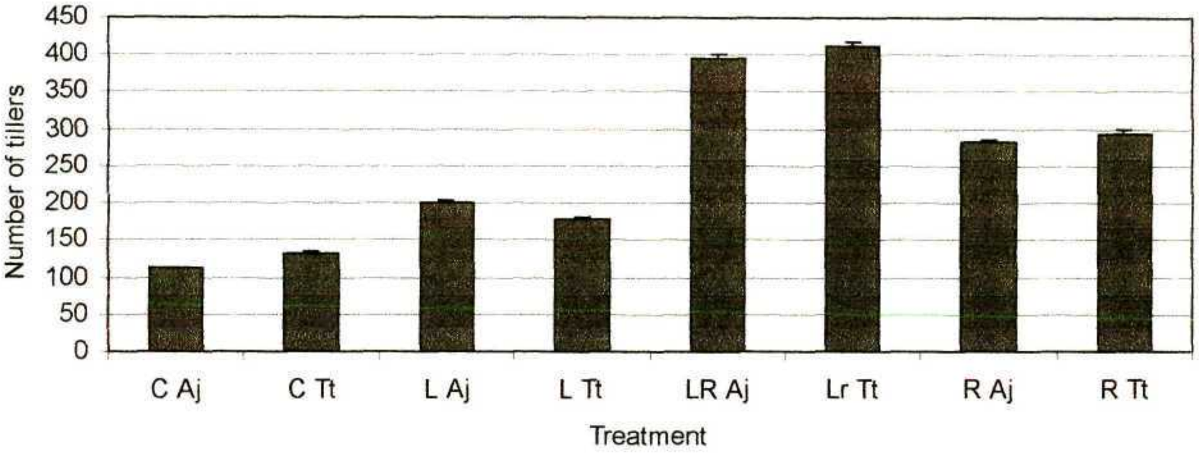


Figure 3.1. Tiller production (±S.E.) of *Themeda triandra* and *Aristida junciformis* seedlings in competition with adult *Aristida junciformis* plants.

Legends
C Aj = Control, both light and root competition; *Aristida* seedlings
C Tt = Control, both light and root competition; *Themeda* seedlings
L Aj = Root competition, no light competition; *Aristida* seedlings
L Tt = Root competition, no light competition; *Themeda* seedlings
LR Aj = No light or root competition; *Aristida* seedlings
LR Tt = No light or root competition; *Themeda* seedlings
R Aj = Light but no root competition; *Aristida* seedlings
R Tt = Light but no root competition; *Themeda* seedlings

3.4.5. Results

The results were important in that the number of tillers produced for seedlings of both *A. junciformis* and *T. triandra* species varied directly in response to the intensity of competition they were exposed to (Figures 3.1 and 3.2 respectively) and Tables 3.2 to 3.5.

For both *A. junciformis* (Figure 3.1) and *T. triandra* (Figure 3.2), the highest tiller production by seedlings occurred where there was no light or root competition. Conversely, the control treatments, in which competition occurred for both light and below ground, showed the lowest

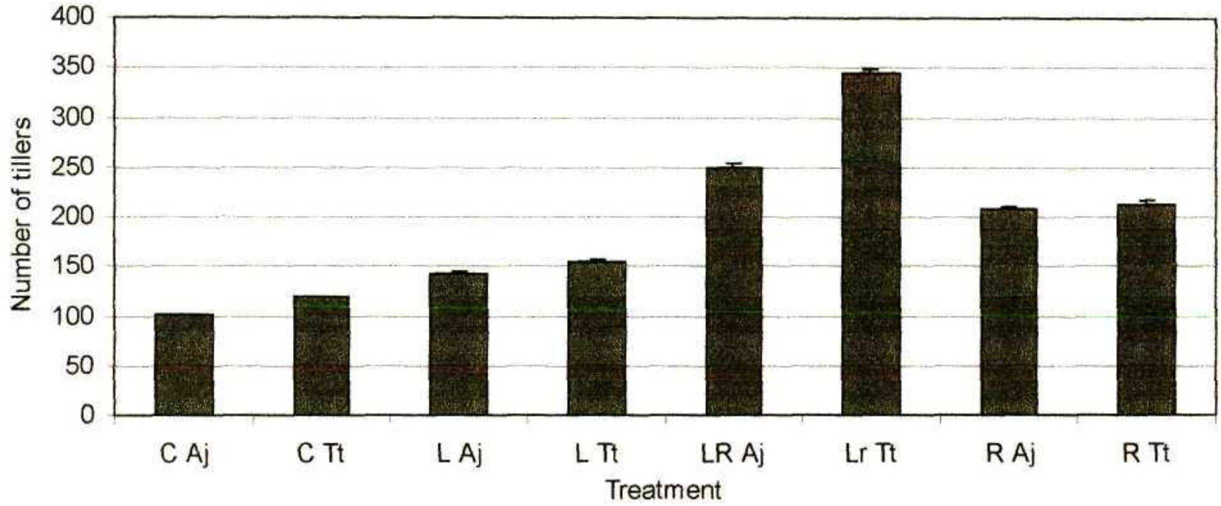


Figure 3.2. Tiller production (±S.E.) of *Themeda triandra* and *Aristida junciformis* seedlings in competition with adult *Themeda triandra* plants. Legends as for Figure 3.1.

production of tillers for both species, an indication of the intense competition.

Furthermore, less tillers, c. 46% ($P<0.01$ for both species), were produced by seedlings subjected only to root competition for both species than those subjected only to light competition. Both of these treatments in turn displayed considerably higher tiller production than the control treatment, demonstrating competition for both below ground and light resources.

However, the higher tiller production found in seedlings subjected to root but not light competition should be viewed with regard to a common response of adult grass plants to frequent defoliation, namely the redirection of resources from the roots to the canopy in order to produce new tillers. This results in a gradual shrinkage in root volume of the adult plant over time and would have ameliorated competitive interactions between the adult tuft and surrounding seedlings for the duration of the experiment.

Table 3.2. Tiller production of *Aristida junciformis* seedlings in competition with adult *Aristida junciformis* plants.

	Average tillers per plant (±S.E.)	F Ratio (n=40)	*P*
Control vs. light competition	2.2±0.1 4.7±0.5	$F_{1,78}=15.1$	<0.001
Control vs. root competition	2.2±0.1 3.2±0.3	$F_{1,78}=0.2$	<0.01
Control vs. no competition	2.2±0.1 5.2±0.6	$F_{1,78}=25.7$	<0.001
No competition vs. root competition	5.2±0.6 3.2±0.3	$F_{1,78}=0.23$	<0.001
No competition vs. light competition	5.2±0.6 4.7±0.5	$F_{1,78}=1.7$	N.S.
Light competition vs. root competition	4.7±0.5 3.2±0.3	$F_{1,78}=2.6$	<0.001

Table 3.3. Tiller production of *Themeda triandra* seedlings in competition with adult *Aristida junciformis* plants.

	Average tillers per plant (±S.E.)	F Ratio (n=40)	*P*
Control vs. light competition	3.3±0.2 5.9±0.5	$F_{1,78}=6.6$	<0.001
Control vs. root competition	3.3±0.2 4.3±0.3	$F_{1,78}=0.3$	<0.05
Control vs. no competition	3.3±0.2 9.6±0.7	$F_{1,78}=12.2$	<0.001
Light competition vs. root competition	5.9±0.5 4.3±0.3	$F_{1,78}=1.6$	<0.05
No competition vs. root competition	9.6±0.7 4.3±0.3	$F_{1,78}=0.30$	<0.001

Table 3.4. Tiller production of *Aristida junciformis* seedlings in competition with adult *Themeda triandra* plants.

	Average tillers per plant (±S.E.)	F Ratio (n=40)	*P*
Control vs. light competition	2.5±0.2 6.4±0.3	$F_{1,78}$=3.9	<0.001
Control vs. root competition	2.5±0.2 4.6±0.3	$F_{1,78}$=2.0	<0.001
Control vs. no competition	2.5±0.2 8.5±0.9	$F_{1,78}$=30.1	<0.001
No competition vs. light competition	8.5±0.9 6.4±0.3	$F_{1,78}$=2.5	<0.05
No competition vs. root competition	8.5±0.9 4.6±0.3	$F_{1,78}$=0.10	<0.001
Light competition vs. root competition	6.4±0.3 4.6±0.3	$F_{1,78}$=5.8	<0.01

Table 3.5. Tiller production of *Themeda triandra* seedlings in competition with adult *Themeda triandra* plants.

	Average tillers per plant (±S.E.)	F Ratio (n=40)	*P*
Control vs. light competition	3.6±0.2 8.0±0.6	$F_{1,78}$=7.1	<0.001
Control vs. root competition	3.6±0.2 4.9±0.5	$F_{1,78}$=0.2	<0.05
Control vs. no competition	3.6±0.2 11.7±0.8	$F_{1,78}$=9.6	<0.001
No competition vs. light competition	11.7±0.8 8.0±0.6	$F_{1,78}$=0.7	<0.01
No competition vs. root competition	11.7±0.8 4.9±0.5	$F_{1,78}$=0.4	<0.001
Light competition vs. root competition	8.0±0.6 4.9±0.5	$F_{1,78}$=3.2	<0.001

Interspecific competition for both light and root competition treatments appears to be more severe than intraspecific competition between adults and seedlings. Root competition appears to exert a greater effect than competition for light. Overall, *Themeda triandra* appeared less suppressive on seedlings *Aristida junciformis*. Seedling survivorship fluctuated with the level of competition (Table 3.6). A decrease in intensity of competition from full competition (control treatment) to no competition saw enhanced seedling survival. For both *A. junciformis* and *T. triandra* seedlings in competition with adult tufts of either species there were noticeable differences in survival between full competition and no competition ($P<0.001$ for both species). There was also enhanced seedling survival for both species when subjected only to light competition as opposed to full competition.

Table 3.6. Percentage seedling survival in response to the level of intra- and interspecific competition. (Number of seedlings planted for each treatment=40).

	Full (%)	Root only (%)	Light only (%)	None (%)
Adult Aj tufts vs. Aj seedlings	38	68	73	90
Adult Aj tufts vs. Tt seedlings	65	73	88	100
Adult Tt tufts vs. Aj seedlings	73	83	85	95
Adult Tt tufts vs. Tt seedlings	68	73	93	98

Codes:
Aj = *Aristida junciformis*
Tt = *Themeda triandra*

3.4.6. Discussion

Increasing intensity of competition from adult plants correspondingly increased mortality of seedlings and constrained growth of surviving seedlings attempting to establish in the grass sward. Seedlings successfully germinating close to adult plants will struggle to become established unless the canopies of adult plants are severely reduced at regular intervals. This removal of the canopy occurred in many of the experimental sites where continuous selective grazing pressure on species such as *T. triandra* has constantly removed competition for light, and ensured consequent shrinking of root volumes in the plants' efforts to produce new tillers. This leads to a exponential decrease in these species competitive ability if the grazing pressure is maintained and their eventual loss from the sward.

The lack of competition from the formerly dominant species has allowed *A. junciformis* seedlings to establish. Once these seedlings become adult plants they were avoided by grazing animals and the grazing pressure on the remaining palatable species are consequently increased. This allowed the *A. junciformis* plants to attain their maximum basal areas and increase their density in the sward. Once this density was sufficiently high, grass seedlings of either *A. junciformis* or any other more desirable grass species are unable to establish, resulting in a monotypic stand of *A. junciformis*.

The failure of species such as *Themeda triandra* to re-establish in swards being managed so as to encourage the competitive ability of palatable species has led some authors to suggest that the conditions under which these grasslands developed no longer exist (Tainton, 1981) or that *A. junciformis* has increased due to bad veld management in the past and is presently exploiting another set of conditions which are not necessarily directly linked to bad veld management at all. Johnson (1989) has suggested that in becoming dominant in the sward, *A. junciformis* has been able to ameliorate soil conditions to ensure its persistence through mechanisms such as root exudates which alter the availability of cation exchange sites, soil pH, and increases the quantities of available aluminium in the soil. This, in turn, has important implications for the microflora associated with the roots inhibiting the return of formerly dominant species such as *T. triandra*.

The results of this experiment suggest that simpler mechanisms are operating where adult *A. junciformis* plants maintain a perimeter zone in which seedlings of other grass species are unable to establish through direct competition for resources. Those that do manage to establish in a sward are often removed by the selective action of grazers who target the palatable species in preference to *A. junciformis*. Heavily grazed plants sufficiently large enough to avoid being pulled out of the ground by the cropping action of grazing animals are then forced to draw on root reserves to produce new tillers. This results in the shrinkage of root volume and a correspondingly diminished ability of the plant to deal with interspecific plant competition and other environmental stresses to which it is subjected. This ultimately results in it's removal from the sward and the continued dominance of *A. junciformis*.

3.5. Vegetative expansion

3.5.1. Introduction

In examining the life history of any plant species, a fundamental consideration is how that species maintains or perhaps even increases its population numbers in the environment.

Commonly, for many grass species it is through seedling recruitment and/ or vegetative expansion of the existing population. In view of *A. junciformis*' rather unique responses (as compared to other grass species) to conventional veld management practises, it was important to determine the primary mechanism(s) employed by this species in encroaching into a sward. To do this an assessment had to be made of the relative importance of seedling recruitment (described in Chapter 4) as opposed to the basal expansion of existing grass plants on a seasonal basis in swards encroached to varying degrees by *A. junciformis.*

3.5.2. Method

To investigate the importance of vegetative growth to *Aristida junciformis* and, as a comparison, that of *Themeda triandra* and other grass species, 40 quadrats each 1 by 1 m within the four trial sites described in Section 3.2 were established. Five quadrats, permanently marked by steel fencing droppers driven into the ground at the four corners of each quadrat, were placed in each site. The pantograph was set to transcribe a quarter of the quadrat at a time. This entailed the pantograph being placed in sequence at each corner of the quadrat, and used to transcribe both the live and dead basal areas of plant species found within the quadrat onto A4 sized paper. The use of this pantograph reduced from life-size the basal areas of each plant found within the quadrat by a factor of 3.1.

First measurement of the quadrats took place in the summer months of November and December 1993 and the second in the winter months of August and September 1994. Apart from basal areas, seed germination and seedling survival of grass species were also recorded in these quadrats (results from these data are discussed in Chapter 4). An example of the transcribed basal areas is illustrated in Figure 3.3.

Data were analysed with a Kontron Image Analysis (Vidas 2.1; Kontron, Germany) system which measured the transcribed basal areas of *A. junciformis*, *T. triandra*, and other grass species found in the quadrats (the latter grouped together for analysis purposes) from the diagrams produced in the field. This method of measuring the basal areas provided a rapid and accurate means of measuring the 320 field diagrams.

The first step in analysing these data was to adapt an existing software program to measure each area, it's perimeter and maximum and minimum diameters. The program used is listed in Appendix 1. The repeatability of the scans was tested by scanning a diagram of known area five times. These successive determinations of the measured areas were closely correlated with minimal variance generated in these data due to the scanning technique.

Figure 3.3. Example of pantograph transcribed basal areas of species encountered in a 50x50 cm quadrat. Four quadrats of this size encompassed the one metre square quadrat used to sample the various treatments.

Data were summarized for each quadrat for *A. junciformis*, *T. triandra*, and 'other' grass species for both 1993 and 1994. Though these data were normally distributed in some treatments, this was not so for all species. Therefore, the paired t-test was rejected in favour of a distribution free non-parametric test. As the same areas were being compared over time i.e. they were effectively paired treatments, the Wilcoxon Signed Rank Test (Siegal and Castellan, 1988) was used to test for any real changes in basal area.

3.5.3. Results

High Encroachment site

All three replications of this treatment were dominated by *A.junciformis* with very few other grass species being present. The *A. junciformis* plants in these plots are mostly large, mature established plants(average basal diameter 16.2±0.6 cm) with clear interplant distances. In contrast to all the other sites measured, the overall basal area of *A. junciformis* decreased 37% during the period from summer of 1993 to winter 1994 ($P \leq 0.001$). When examining individual plants it appears that the larger plants basal area decreased proportionally more than the smaller plants which exhibited comparatively little decrease.

There was a minor presence of *T. triandra* and other grass species in this treatment. Despite this and the dominance of *A. junciformis*, these species did expand marginally by 3% ($P \leq 0.84$).

Medium Encroachment site

The basal area of *A. junciformis* expanded by 20.3% ($P \leq 0.063$) over the same period in this site.

Themeda triandra also expanded overall by 33.3% (*P*≤0.063). The other herbaceous species exhibited a 6.8% (*P*≤0.920) reduction in basal area.

Limited Encroachment site

At this site, approximately equal proportions of *A. junciformis* and *T. triandra* in terms of basal cover, occurred in 1993 (refer Tables 2.3 and 2.4). In the case of *A. junciformis*, there was an overall increase of 36% (*P*≤0.008) in this species basal area when measured again in 1994. Within the same period, there was a 31% (*P*≤0.004) decrease in basal area of *T. triandra*, and a minor decrease of 3% (*P*≤0.922) of other grass species.

No Encroachment site

At this site, the small areas of *A. junciformis* initially present expanded by 10%(*P*≤0.17), as did *T. triandra* by 7.4% (*P*≤0.06) and 'other grass species' by 2.3% (*P*≤0.63).

Table 3.7. Changes in average basal cover per site of *Aristida junciformis* between November 1993 and September 1994. n.s.=not significant.

Treatment	1993 basal area (cm²)	1994 basal area (cm²)	% change	*P*
No Encroachment	1783	1982	+10 %	≤0.172 n.s.
Limited Encroachment	4321	6766	+36 %	≤0.008
Medium Encroachment	12995	16303	+20 %	≤0.063 n.s.
High Encroachment	25456	16052	-37 %	≤0.001

Table 3.8. Changes in average basal cover per site of *Themeda triandra* between November 1993 and September 1994. n.s.=not significant.

Treatment	1993 basal area (cm²)	1994 basal area (cm²)	% change	*P*
No Encroachment	24778	26762	+7.4 %	≤0.063 n.s.
Limited Encroachment	6401	4445	- 31 %	≤0.004
Medium Encroachment	5336	7998	+33.3 %	≤0.063 n.s.
High Encroachment	0	0		

Table 3.9. Changes in average basal cover per site of other grass species recorded between November 1993 and September 1994. n.s.=not significant.

Treatment	1993 basal area (cm²)	1994 basal area (cm²)	% change	*P*
No Encroachment	8224	8417	+2.3 %	≤0.625 n.s.
Limited Encroachment	6336	6167	- 2.7 %	≤0.922 n.s.
Medium Encroachment	3658	3410	-6.8 %	≤0.920 n.s.
High Encroachment	1329	1365	+3 %	≤0.844 n.s.

3.5.4. Discussion

The results discussed above represent only a brief ‘snapshot’ of ecological interactions taking place in the grass sward monitored, and can be only a limited indication of the complex interactions taking place above and below ground.

The results of this monitoring study though tentative, suggest that, in monotypic swards, large mature *A. junciformis* plants are not static but expand to some physical maximum, beyond which they are constrained by environmental factors such as self shading of tillers, physiological limitations induced by tiller and caryopsis production, and intraspecific competition. Fluxes in the levels of availability of resources and other environmental factors would influence growth and produce an oscillation in basal area in response to these fluxes. The average basal diameter of all *A. junciformis* plants measured was highest in the monospecific High Encroachment site (X=16.2±0.6 cm), and was the only site in which the basal area of this species decreased substantially.

In the other sites monitored, all of which had heterogenous swards, the basal areas of the species measured appear to be responding more to interspecific competition than any other environmental factor. In the Limited Encroachment site, the total basal area of *A. junciformis* increased by 36%, while that of *T. triandra* and other grass species decreased by 31%. In the Medium Encroachment site, both *A. junciformis* and *T. triandra* expanded in basal area whilst other grass species declined marginally.

In the No Encroachment site, the dominance of palatable species such as *T. triandra* has been maintained through regular burning and grazing. This combined with the minimal presence of *A. junciformis*, has strongly maintained the competitive balance in favour of these palatable species and prevented encroachment by *A. junciformis*. Expansion in basal area occurred for all grass species measured and could be considered a natural response to the plants receiving sufficient resources. Conversely it could be regarded as the very early stages of *A. junciformis* encroachment which is taking place despite annual burning and grazing. This could be as a result of the grazing animals actively selecting against the increasingly unpalatable *A. junciformis* plants as the plant grows out, and thereby altering the competitive balance in favour of this species. However, the limited duration of this study mitigates against any definite conclusions in this regard.

Results from the Limited Encroachment site is indicative of the processes occurring in the sward in the initial encroachment of *A. junciformis*. In the time period monitored, the basal cover of *A. junciformis* expanded whilst that of *T. triandra* and the other grass species encountered in the quadrats decreased. This expansion of *A. junciformis* appears to be to the detriment of palatable species such as *T. triandra*, which are diminishing in the sward as *A. junciformis* increases.

The beneficial effect of regular burning for many decreaser species is perhaps illustrated in the Medium Encroachment site, where a substantial increase in basal cover of *A. junciformis* was accompanied by a concomitant increase in the presence of *T. triandra* and a slight decrease in the basal cover of the other grass species encountered. In this site, which is subjected to annual early burns and early grazing by cattle, the new tillers of *A. junciformis* tend to come away before those of *T. triandra* and are heavily selected for by the cattle whilst the new tillers of *T. triandra* remain relatively well protected. Before these tillers become susceptible to grazing, the cattle are removed and the *T. triandra* plants left to grow out and flower; which appears to be according an increasing competitive advantage of *T. triandra* over *A. junciformis* in the sward. This strategy appears more effective when the relatively low initial presence of *T. triandra* in this site is realized. It should be noted that at the time of this study this early burn\early graze treatment was relatively recent (c. two years) and only long term monitoring will confirm or disprove this as a possible strategy.

The limited time span of this study prevents more substantive conclusions being made. What these results do suggest, however, is that *Aristida junciformis* in this area of Southern Tall Grassveld is expanding primarily through vegetative growth via growth of lateral tillers from established plants, and that recruitment from seedling populations does not appear to be an important source of population expansion in this particular system, or at this particular stage of the encroachment process. The importance and role of seedlings in the encroachment process were separately investigated (Chapter 4).

CHAPTER FOUR

SELECTED ASPECTS OF SEED PHYSIOLOGY AND FUNCTION

4.1 Introduction

Availability of propagules (vegetative or seed), dormancy mechanisms, germination and seedling establishment conditions influence which species will be able to occupy available space in the environment (Grubb, 1977). In his concept of the 'regeneration niche,' species-specific requirements for germination and establishment are a major factor in the structuring of communities. Harper (1977) and Grubb (1977) suggested the events determining the fate of individual plants frequently occur during caryopsis dispersal, germination, and seedling establishment. If so, the nature of the environment immediately surrounding a seedling and its effects on that seedling are of critical importance in determining the dynamics of plant populations and the composition of plant communities.

A variety of causes can prevent caryopses in the field from germinating. Diurnal temperature fluctuations are more extreme in gaps than under a closed canopy and caryopses may respond to this (Thompson, Grime, and Mason 1977). Light and substrate conditions can influence germination, while heavy grazing can prevent seedling establishment (Wright and van Dyne 1976; Salihi and Norton 1987 cited in O'Connor 1991).

Understanding the mechanisms controlling the germination of *A. junciformis* seed and the establishment of seedlings in the micro-environment is critical. Consequently the effects of light, temperature, orientation and viability on the germination success of *A. junciformis* seed were experimentally investigated. The production, dispersal, density of caryopses and seedling survivorship in the field were also examined.

4.2 Germination Responses of *Aristida junciformis* to Light and Temperature

4.2.1. Introduction

One of the best known micro-environmental influences is the inhibition of germination under a leaf canopy in species sensitive to light quality (Fenner 1980; Silvertown 1980). As well as altering light quality, gaps in vegetation canopies alter the micro-environment in other ways that are less well understood.

Removal of grass canopies not only increases diurnal temperature fluctuations (Savage, 1980) but also changes the spectral quality and quantity of light reaching the seedbed. Removal of the grass canopy as a result of overgrazing and excessive burning could lead to higher seedling emergence for certain plant species than would occur under intact canopies.

Since green vegetation transmits more far-red (FR) than red (R) light the FR/R ratio is much lower under a green plant canopy than in the open (Smith, 1982). Low red to far-red light ratios or darkness may result in a lack of the correct phytochrome (P_{fr}) for germination. Removal of the plant canopy results in greater exposure to red light and greater temperature fluctuations in the seedbank than under unburnt canopies.

It was hypothesized that the encroachment of overgrazed and frequently burned swards by *A. junciformis* would increase after canopy removal as a result of stimulation of the *A. junciformis* caryopses on the soil surface by increased exposure to red light and widely fluctuating temperatures.

The ecological significance of a requirement for diurnal temperature fluctuations is two-fold. Firstly the more specific a species is in terms of its requirements for temperature alternation, the less likely they are to be satisfied and the more likely dormancy is to be enforced due to unsuitable temperatures. A delay in germination through such enforcement of dormancy could increase the chances of caryopses being incorporated into the soil seed population.

Conversely, a persistent requirement for diurnal temperature alternation may serve as a 'gap-detecting mechanism' enabling caryopses already buried to sense greater temperature alternations created removal of plant cover and creation of a gap in the sward (Thompson, *et al.* 1977). This latter requirement could be one of the primary factors investing *A. junciformis* with its ability to invade overgrazed and burnt swards with such apparent ease.

4.2.2. Methods

Therefore, to test this hypothesis, four experiments were conducted which broadly following the protocols described by Roundy, Taylorson and Sumrall 1992 for their work on seed of *Eragrostis lehmanniana* Nees. This protocol was used as these authors had examined the germination response of an indigenous grass species to darkness, red and far-red light and the importance of phytochrome in the regulation of germination events.

Caryopses used in these experiments was collected while still on the awns of adult *A. junciformis* plants in March 1993 from the Burning and Mowing trial at Ukulinga. The caryopses was sorted, any that were not filled or obviously defective being rejected. Viability of this screened caryopses was determined using the tetrazolium test (Anon, 1985).

Caryopses were placed on filter paper moistened with distilled water in nine centimetre diameter petri dishes. Five replications, each of 20 caryopses, were used per experiment. All experiments except Experiment 4, were run at 25°C as both preliminary germination tests and a search of the literature indicated that this was the optimum temperature for germination experiments with this species. Preliminary germination trials of caryopses under constant light and temperature conditions (25°C) had established that fourteen days was sufficiently long enough for any dormancy mechanisms to be broken and for all viable caropyses to germinate. The emergence of the embryo is often clearly apparent by the eighth day after imbibition. This observation coupled with the rapid reponse of phytochrome to red/ far-red light ratios indicated that a fourteen day period would be sufficient for these experiments. The periods of time that the caryopses was exposed to darkness, and red and far-red light was that as described by Roundy, *et al*, 1992.

Experiment 1

This was carried out to ascertain germination responses to different periods of red light after imbibition in the dark. This was to simulate the situation where caryopses lying dormant in far-red light under a grass canopy is exposed to red light once the canopy is removed through either burning (assuming the caryopses survives the fire), mowing or grazing and to see whether the length of exposure to red light was critical for germination.

Caryopses were imbibed in darkness for 24 hours and then exposed to red light for 0, 1, 5, 20 or 60 minutes before being returned to darkness. The number of germinated caryopses were recorded after 14 days in the incubator. These variable times of exposure to red light (and/or far-red light in the other experiments) were utilized to investigate if the length of exposure to either form of light is important in the germination process.

Experiment 2

This was carried out to determine if red light stimulation of germination was reversible by exposure to far-red light. This was to determine whether *A. junciformis* caryopses is sensitive to the changing ratios of R/FR light exposure experienced in the field.

Caryopses were imbibed in darkness for 24 hours, and then either left in darkness, exposed to red light for five minutes, exposed to red light for five minutes then exposed to far-red light for five minutes, or exposed only to far-red light for five minutes.

After these treatments all the caryopses were returned to darkness and the number germinated recorded after 14 days.

Experiment 3

This was carried out to ascertain the effects of time of imbibition in darkness or far-red light on germination of caryopses subsequently left in darkness or exposed to red light. Caryopses were imbibed in darkness or far-red light for 0, 8, 24, 48, and 72 hours then either exposed to red light for five minutes or not. These are recorded as treatments 1 to 20 in Table 4.2. Germination was recorded after the caryopses had been returned to darkness for 14 days.

This experiment was to simulate the field situation where caryopses lying on or in the soil surface under a dense grass canopy would be exposed to primarily far-red light for varying time periods before exposure to red light initiated germination. This was to duplicate the situation where the caryopsis lay dormant for some time before the canopy was removed and the seed exposed to red light.

The experiment was carried out in a light-tight box with far-red filters in an incubator with a tungsten light source to ensure that sufficient light was provided. The light-tight box was used as the light cabinets used for the other three experiments had a maximum operating time span of 60 minutes and therefore could not expose caryopses to far-red light for longer than this period. The light level in this incubator was 304μ mol m^{-1} s^{-1} as measured by a radiometer equipped with a quantum sensor.

This experiment was then repeated with the dry caryopses first exposed to far-red for either 8, 24, 48 or 72 hours before being imbibed in far-red for the same time period again. These caryopses were therefore exposed to far-red light for twice the time periods used in the first run of the experiment. This was done as a corollary of the field situation where the caryopsis lying on or in the soil surface under a dense grass canopy would be exposed to primarily far-red light for long time periods before suitable germination conditions occurred. These are recorded as treatments 21 to 30 in Table 4.2.

Experiment 4

This was designed to compare germination of caryopses imbibed in darkness or light at constant and alternating temperatures. This was to simulate the field situation where caryopses in open sites would be subject to much widely fluctuating temperatures than caryopses under canopies. Caryopses were imbibed in the dark and in light to simulate caryopses lying under a canopy and caryopses in the open respectively. Four treatments were used in this experiment to determine whether temperature provided a possible germination cue for *A. junciformis* seed. The caryopses were imbibed:

1. In the dark at 25°C
2. In the light at 25°C
3. In the dark at an alternating day temperature of 25°C and a night temperature of 15°C.
4. In the light at an alternating day temperature of 25°C and a night temperature of 15°C.

   (Day temperature 25°C:08:00-18:00; Night temperature 15°C:18:00-08:00)

4.2.3. Data analysis

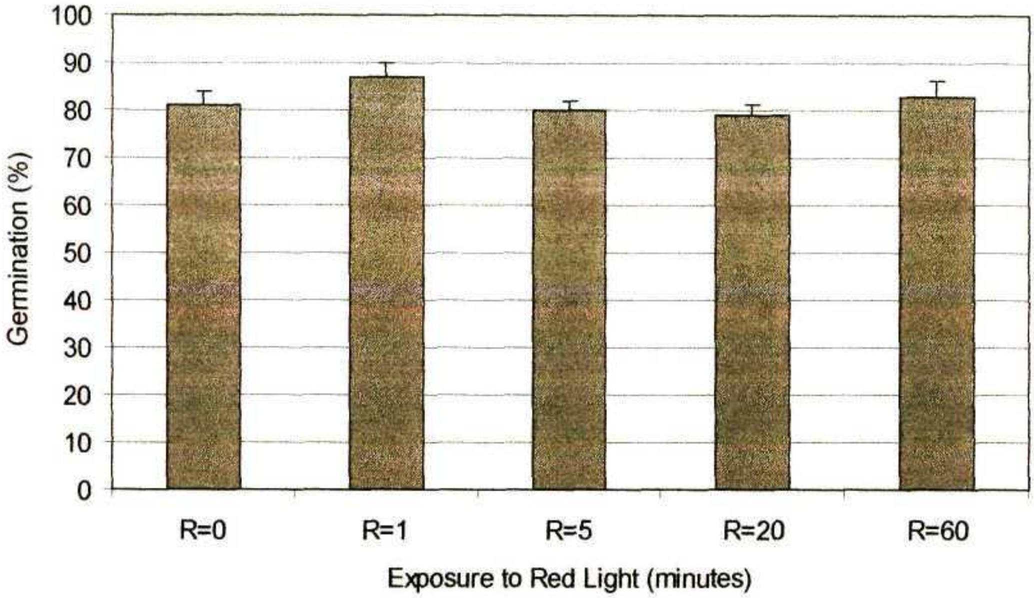
In each experiment, differences among treatments in germination rates were analysed by Chi-square tests (χ^2) (Steel and Torrie 1980) on the contingency tables of treatments versus number germinated and number non-germinated. The distribution free χ^2 test was used as the data collected were in the form of count data grouped either as germinated or non-germinated seed, subject to two variables in each experiment.

4.2.4. Results

Experiment 1

There were no significant differences ($P>0.05$) (Figure 4.1) in seed germination between the five treatments which were all characterized by high germination ranging from 79 to 86%.

Figure 4.1. Percentage germination of *Aristida junciformis* caryopsis after imbibition in the darkness for 24 hours and subsequent exposure to red light (Bars indicate S.D).



Experiment 2

The highest germination occurred in those caryopsis left in the dark after imbibition though this difference was not substantially different ($0.25>P(\chi^2 \geq 6.14)>0.10$) to the other three treatments (Table 4.1; Figure 4.2). There were no meaningful differences between the other three treatments; exposure of the caryopses to red or far-red light for the time periods used did not stimulate or inhibit germination respectively.

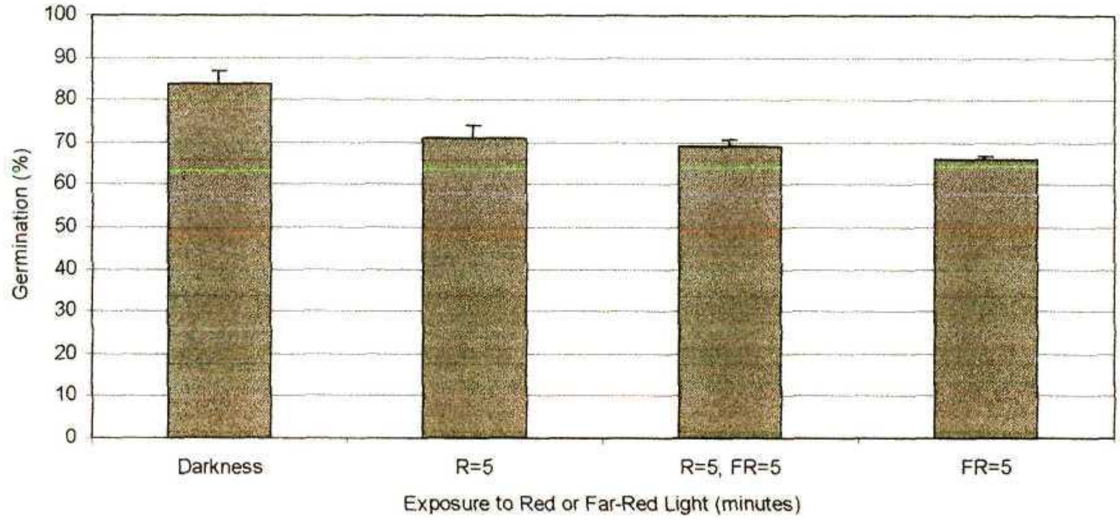


Figure 4.2. Percentage germination of *Aristida junciformis* caryopses after imbibition in the dark for 24 hours followed by exposure for five minutes either to red light, far-red light, both or neither. (Bars indicate S.D).

Table 4.1. Percentage germination of *Aristida junciformis* caryopses after imbibition in the dark for 24 hours followed by exposure to red light, far-red light, or both. R= red light; FR= far-red light. For *P*=0.05, χ^2= 7.81; ns= not significant.

Treatment	Percentage germination	χ^2 (*df*=3)
Dark= 24 hr	84	χ^2= 6.14 ns
Dark= 24 hr, R= 5 min	71	χ^2= 0.21 ns
Dark= 24 hr, R= 5 min; FR= 5 min	70	χ^2= 0.46 ns
Dark= 24 hr, FR= 5 min	67	χ^2= 1.8 ns

Experiment 3

The results are listed in Tables 4.2, 4.3 and 4.4. Uniformly high germination occurred in most treatments except 15 and 25 (Table 4.2) which were both much lower than the other treatments (P<0.005). Caryopses in treatment 15 were imbibed in far-red light for 72 hours with no subsequent exposure to red light. Caryopses in treatment 25 were exposed to far-red light for 72 hours prior to imbibition for a further 72 hours in far-red light with no subsequent exposure to red light. Interestingly treatment 24 in which the caryopses were effectively exposed to 72 hours of far-red light also exhibited depressed germination [0.25>P($\chi^2 \geq$ 12.0)>0.10)].

On a scale of increasing germination (Table 4.4), caryopses exposed to long periods of far-red light with no subsequent red light exposure exhibited the lowest germination. Caryopses in the dark for up to 72 hours with no subsequent exposure to red light, or exposed to long periods of far-red light (>72 hours) with subsequent exposure to red light exhibited much higher germination.

Caryopses imbibed in the dark exhibited high germination whether exposed to red light on not, whilst the highest average germination occurred in those caryopses exposed to red light for up to 72 hours and then exposed to red light for 5 minutes. There were no large differences in average germination of the control treatments the majority of which exhibited a high germination rate ranging between 65 to 83%.

Table 4.2. Average and total germination of *Aristida junciformis* caryopses after imbibition in the dark or far-red light and subsequently left in the dark or exposed to red light after 14 days. FR=Far red light; R=Red light; Wet + FR= imbibed in far-red light for stated time period; Dry + FR= dry caryopses exposed to far-red light.

Treatment	Mean caryopses germinated per replication (±S.E.)	Percentage germination
1. Dark=0hr, No R	13.0±.03	65
2. Dark=8hr, No R	16.4±0.5	82
3. Dark=24hr, No R	13.0±0.3	65
4. Dark=48hr, No R	15.0±0.3	75
5. Dark=72hr, No R	16.2±0.2	81
6. Dark=0hr, R=5 min	14.0±0.0	70
7. Dark=8hr, R=5 min	16.0±0.0	80
8. Dark=24hr, R=5 min	16.4±0.4	82
9. Dark=48hr, R=5 min	13.4±0.2	67
10. Dark=72hr, R=5 min	16.2±0.8	81
11. FR=0hr, No R	16.6±1.4	83
12. FR=8hr, No R	17.8±0.5	71
13. FR=24hr, No R	16.8±0.8	84
14. FR=48hr, No R	19.0±0.8	77
15. FR=72hr, No R	10.2±0.9	51
16. FR=0hr, R=5 min	16.0±0.0	80
17. FR=8hr, R=5 min	17.0±0.5	85
18. FR=24hr, R=5 min	15.8±0.3	79
19. FR=48hr, R=5 min	18.5±0.3	93
20. FR=72hr, R=5 min	18.3±1.3	73
21. Dry+FR=0hr, Wet+FR=0hr,No R	16.5±1.3	82
22. Dry+FR=8hr, Wet+FR=8,No R	15.8±0.3	77
23. Dry+FR=24hr,Wet+FR=24hr,No R	15.2±0.9	76
24. Dry+FR=48hr,Wet+FR=48hr,No R	12.0±0.9	60
25. Dry+FR=72hr,Wet+FR=72hr,No R	10.6±0.5	53
26. Dry+FR=0hr,Wet+FR=0hr,R=5 min	16.2±0.4	81
27. Dry+FR=8hr,Wet+FR=8hr,R=5 min	14.6±1.0	73
28. Dry+FR=24hr,Wet+FR=24hr,R=5 min	19.3±0.0	76
29. Dry+FR=48hr,Wet+FR=48hr,R=5 min	17.4±0.5	87
30. Dry+FR=72hr,Wet+FR=72hr,R=5 min	15.0±0.8	75

Table 4.3. Percentage germination of *Aristida junciformis* caryopses after imbibition in the dark or far-red light and subsequently left in the dark or exposed to red light after 14 days. For $P=0.05$, $\chi^2= 16.9$; ns= not significant; ** = $P<0.005$.

Treatment	Percentage germination	χ^2 (*df=9*)
1. Dark=0hr, No R	65	$\chi^2=5.3$ ns
2. Dark=8hr, No R	82	$\chi^2=2.6$ ns
3. Dark=24hr, No R	65	$\chi^2=5.3$ ns
4. Dark=48hr, No R	75	$\chi^2=0.1$ ns
5. Dark=72hr, No R	81	$\chi^2=1.9$ ns
6. Dark=0hr, R=5 min	70	$\chi^2=1.3$ ns
7. Dark=8hr, R=5 min	80	$\chi^2=2.3$ ns
8. Dark=24hr, R=5 min	82	$\chi^2=2.6$ ns
9. Dark=48hr, R=5 min	67	$\chi^2=3.4$ ns
10. Dark=72hr, R=5 min	81	$\chi^2=1.9$ ns
11. FR=0hr, No R	83	$\chi^2=3.4$ ns
12. FR=8hr, No R	71	$\chi^2=0.9$ ns
13. FR=24hr, No R	84	$\chi^2=4.3$ ns
14. FR=48hr, No R	77	$\chi^2=0.2$ ns
15. FR=72hr, No R	51	$\chi^2=30.7$**
16. FR=0hr, R=5 min	80	$\chi^2=2.3$ ns
17. FR=8hr, R=5 min	85	$\chi^2=5.3$ ns
18. FR=24hr, R=5 min	79	$\chi^2=0.9$ ns
19. FR=48hr, R=5 min	90	$\chi^2=12.0$ ns
20. FR=72hr, R=5 min	73	$\chi^2=0.2$ ns
21. Dry+FR=0hr, Wet+FR=0hr,No R	82	$\chi^2=2.6$ ns
22. Dry+FR=8hr, Wet+FR=8,No R	77	$\chi^2=0.2$ ns
23. Dry+FR=24hr,Wet+FR=24hr,No R	76	$\chi^2=0.5$ ns
24. Dry+FR=48hr,Wet+FR=48hr,No R	60	$\chi^2=12.0$ ns
25. Dry+FR=72hr,Wet+FR=72hr,No R	53	$\chi^2=25.8$**
26. Dry+FR=0hr,Wet+FR=0hr,R=5 min	81	$\chi^2=1.9$ ns
27. Dry+FR=8hr,Wet+FR=8hr,R=5 min	73	$\chi^2=0.2$ ns
28. Dry+FR=24hr,Wet+FR=24hr,R=5 min	76	$\chi^2=0.1$ ns
29. Dry+FR=48hr,Wet+FR=48hr,R=5 min	87	$\chi^2=7.7$ ns
30. Dry+FR=72hr,Wet+FR=72hr,R=5 min	75	$\chi^2=0.1$ ns

FR=Far red light; R=Red light; Wet + FR= imbibed in far-red light for stated time period; Dry + FR= dry caryopses exposed to far-red light.

Table 4.4. Average germination of *Aristida junciformis* caryopses after 14 days as grouped by treatment.

Treatment	Treatment numbers (from Table 4.2)	Average germination (%)
Dry + imbibition in FR, no R	22 to 25	67
Exposure to FR ≤ 72 hrs, no R	12 to 15	70
Imbibition in dark, no R	2 to 5	76
Imbibition in dark, r=5 min	7 to 10	78
Dry + imbibition in FR, R=5	27 to 30	78
Exposure to FR, R=5	17 to 20	82
Controls	1,6,11,16,21,26	77

Experiment 4

The highest germination occurred in the treatment where caryopses were imbibed in the dark at a constant 25°C, but the results (Table 4.5) were not substantially different from the other three treatments. Caryopses imbibed in the light at an alternating temperature showed the next highest germination and was not conspicuously different from the last two treatments.

Table 4.5. Germination of *Aristida junciformis* caryopses imbibed in darkness or light at constant and alternating temperatures (for P=0.05, df=3; ns= not significant).

Treatment	Mean caryopses germinated per replication (±S.E.)	Percentage germinated
Light, 25°C	14.6±0.2	73 (χ^2=1.2, ns)
Dark, 25°C	17.0±0.0	85 (χ^2=3.2, ns)
Light, alternating temperature	15.8±0.2	79 (χ^2=0.1, ns)
Dark, alternating temperature	14.6±0.2	73 (χ^2=1.2, ns)

4.2.5. Discussion

Germination and the Effect of Light Quality

The results of these experiments suggest that germination of *A. junciformis* seed is inhibited by prolonged exposure to far-red light and stimulated by exposure to red light. It should be recognized, however, that even with far-red light inhibition the percentage germination obtained in these experiments were still relatively high. Coupled with the high caryopsis production of *A. junciformis* the possible role of far-red light in controlling germination is probably neglible in many field situations, but may form a component of a suite of factors controlling germination.

Fenner (1979) recorded similar results in field experiments and concluded that *Aristida adscensionis* seed was not sensitive to shading and germination was not inhibited by the quality of light being filtered through the plant canopy.

The spectral quality of light does appear to effect some C_4 species. Roundy *et al.* (1992) found in their study of *E. lehmanniana* that seed germination was inhibited by exposure to predominantly far-red light and by a lack of red light. After imbibition in the dark for a short time (24 hours) germination of younger caryopses (1-2 years) after exposure to a short period of red light was greatly stimulated. Germination was low for caryopses imbibed in darkness or far-red light only. They found that exposure of caryopses to red light after far-red light exposure did not increase germination of younger caryopses and only slightly increased germination of older caryopses (greater than three years old).

Light quality also appears to have an inhibitory or stimulatory effect on C_3 species. Williams (1983) found that in four out of five northern hemisphere grass species tested (*Agrostis capillaris* L., *Holcus lanatus* L., *Poa trivialis* L., *Festuca rubra* L., and *Cynosurus cristatus* L.) germination was inhibited by far-red light, which even appeared to induce dormancy. Stimulation of germination by red light also appeared to operate in some of the species. Williams (1983) found that caryopses of species which required the greatest alternation of temperature required to germinate were the most susceptible to the effects of far-red light, suggesting that gap detection in the plant canopy probably involves a suite of correlated responses.

From the results of this study it can be concluded that light quality does not play a major role in the inhibition or stimulation of germination of *A. junciformis* seed. Exposure to far-red light failed to inhibit germination to any substantial degree whilst exposure to red light did not stimulate germination notably. The alteration of light quality through the removal of grass canopies of palatable grass species through either overgrazing and/or burning for example, does not appear to be a important factor in inducing mass germination of *A. junciformis* seed in such exposed grass swards.

Germination and Dormancy

Mature caryopses collected while still on the awns appeared to have an initial dormancy period of approximately 14 days which was not broken by any temperature or light regime applied. Other workers (Mott, 1972; Harradine and Whalley, 1980) found a similar phenomenon for *Aristida contorta* F. Muell. and *Aristida ramosa* R.Br. seed respectively. In northern New South

Wales most samples of seed Harradine and Whalley (1980) collected were dormant at harvest and typically a sample would not give any germination after three months laboratory storage but would achieve 100 % germination after nine months.

Mott (1972) also found a dormancy period in *A. contorta* and only successfully germinated seed after a four month period of storage. Caryopses collected in spring gave low germination for the first two months of storage rising to 40% of germination after this period. Seed collected in summer gave higher germination and germinated immediately on collection.

However, Fowler (1986) found that after-ripening of *Aristida longiseta* Steud. on the Edwards Plateau of central Texas did not improve germination and that freshly shed caryopses germinated as well as those stored at room temperature for several months.

Germination and Temperature

Harradine and Whalley (1980), examining reproductive development and seedling recruitment, found that the major period of reproduction activity of *A. ramosa* in northern New South Wales was during the summer months with the peak of tiller initiation occurring in January followed at roughly one month intervals by the peaks of anthesis and seed maturation. This agrees closely with the behaviour of *A. junciformis* at Ukulinga which also peaks in reproductive tiller production in January with seed maturing from March onwards.

Fowler (1986) found that germination was unaffected by moderate differences in temperature, a temperature of 27°C (day) and 21°C (night) was only slightly better for germination than one of 21°C (day) and (16°C (night). She found that germination was 90-100% within two weeks. Harradine and Whalley (1980) found that the optimum temperature range of *A. ramosa* was 20-30°C and some germination would occur over the range 15-40°C at constant temperatures.

Mott (1972) found maximum germination at 30°C with much less and slower germination at lower temperatures. Rate of germination at the optimum temperature reached 50% of maximum germination after 24 hours. Mott also found that the caryopses of *A. contorta* had an obligate requirement for light over the entire temperature range.

Williams (1983) found that relatively small variations in temperature had a very large influence on the germination of caryopses of the indigenous grass species examined. Germination of all species (*Agrostis capillaris, Holcus lanatus, Poa trivialis, Cynosurus cristatus* and *Festuca rubra*) was greatest when a temperature of 20°C was alternated with a temperature of 10°C. Lowest germination of two of the species (*A. capillaris* and *H. lanatus*) occurred at a constant 20°C.

The results of the above authors' work suggest that there is likely to be a requirement for diurnal temperature fluctuations for maximum germination of *A. junciformis* seed though this was not established in this study. Use of differently aged seed populations, greater cognisance of field conditions such as soil surface temperatures, and a wider experimental temperature range could be used in laboratory experiments similar to those done by Mott (1972) in which caryopses stored in the dark at either a constant 70°C or at a diurnal alternation between 15°C and 70°C (parallelling the situation found at the soil surface by Mott (1972) in the summer months at the at his study site in Western Australia) gave much higher germination than storage under laboratory conditions (15°C and 25°C).

The ecological significance of a requirement for diurnal temperature fluctuations is two-fold. Firstly the more specific a species is in terms of its requirements for temperature alternation, the less likely they are to be satisfied and the more likely dormancy is to be enforced due to unsuitable temperatures. A delay in germination through such enforcement of dormancy could increase the chances of caryopses being incorporated into the soil seed population. Conversely, a persistent requirement for diurnal temperature alternation may serve as a 'gap-detecting mechanism' enabling caryopses already buried to sense greater temperature alternations created by removal of plant cover and creation of a gap in the sward (Thompson, *et al.* 1977). This latter ability could be one of the major factors in the apparent ease with which *A. junciformis* invades overgrazed and burnt swards.

4.3. Caryopsis Orientation

4.3.1. Introduction

Little variation occurs in flower structure amongst members of the Poaceae but, family members demonstrate an interesting array of adaptive variations in seed morphology. The seed is always enclosed in hard, protective structures formed by one or more of the sterile parts of the spikelet. Further appendages, produced by or from other parts of the spikelet or even other structures of the inflorescence, may then also be formed. A grass caryopsis will often bear one or more appendages, such as hygroscopically active or rigid passive awn, long or short hairs distributed in varying patterns over the surface of the awn, and often a hard, pointed base called the callus.

The callus is frequently covered in stiff, backwardly-directed (antrorse) bristles.

Seed morphology has been interpreted in terms of adaptations for dispersal, placing the seed in a position that ensures maximum water uptake for germination, and for locating suitable sites on the soil surface for establishment of the seedling (Bews, 1929; Harper, *et al.* 1965; cited in Peart, 1981).

Aristida junciformis bears three rigid awns and an antrosely barbed callus (Figure 1.2.). The majority of *A. junciformis* caryopses examined in the field was orientated vertically on the soil surface with the awns uppermost. This suggested that the three awns of the caryopsis act as stabilizing 'fins' and ensure correct orientation of the seed for germination on its descent from the parent tiller to the soil surface.

It was also frequently observed that caryopsis was either buried in the soil with only the awns visible, lodged in cracks in the soil, or embedded in the surface of the soil in a vertical position. This lodging in a vertical orientation appeared to be aided by the antrorse bristles of the callus of *A. junciformis* caryopsis. Quantities of caryopses were also found lying in a near horizontal position on the surface of the soil with the awns and the callus holding the seed off the soil surface.

A pot experiment was therefore carried out to investigate the importance of seed orientation and the role of the callus and awns in micro-site location, germination and establishment of seedlings. Treatments involved both varying orientations of caryopses and/or the alteration of caryopsis morphology through the excision of the awns to certain lengths for example.

4.3.2. Method

Twenty centimetre diameter plastic pots were filled to within one centimetre of the rim of the pot with soil collected from Ukulinga. This soil was first sieved using a two millimetre Endicott's sieve in order to achieve a uniform growing medium. Filled pots were placed in water tight trays in which a constant water table was maintained. This was done in order not to disturb the caryopses placed on the soil surface when watering. Three replications, each of 50 *A. junciformis* caryopses per pot, were used for 15 different treatments (Table 5.5), the pots being placed in a random plot design in a wet-wall equipped polycarbonate greenhouse set at 35°C day-light maximum temperature. Minimum temperatures at night varied between 13-15°C.

Caryopses used for these and the following experiments were collected from caryopsis heads harvested at Ukulinga and then placed on expanded wire screens in the greenhouse to air dry for eight weeks after which all the caryopses that had fallen through the screens was collected. Only this mature seed was used with seed from both species being stored in brown paper packets at room temperature (23°C ±2°C).

Two basic orientations of the seed were used with the seed standing either vertically or lying horizontally. Variations of these orientations were used with vertical caryopses in both a normal position and inverted, with awns and/or glumes removed and the caryopses horizontal with awns intact and excised. Intact caryopses normally orientated were also placed in artificially induced cracks in the soil, litter or buried partially or completely up to the awns in the soil. The cracked soil treatments were created by soaking the sieved soil in the pots and then letting it dry. This resulted in a smooth, hard surface with cracks up to 5 mm in width and 10 mm in depth.

Table 4.6. Treatments and orientations of *Aristida junciformis* caryopses.

Treatment	Caryopsis Orientation	Caryopsis Microsite
1	Vertical	Caryopsis tip only buried in soil
2	Vertical	Caryopsis buried to half caryopsis length
3	Vertical	Awns buried to half caryopsis length
4	Vertical	Inverted on awns
5	Horizontal	Lying on soil surface
6	Horizontal	Awns excised
7	Horizontal	Lying in litter
8	Vertical	In cracks in the soil
9	Vertical	Awns lowermost with awns buried
10	Horizontal	Awns partially excised
11	Horizontal	Caryopsis callus barbs removed
12	Vertical	Caryopsis buried
13	Vertical	Glumes removed
14	Vertical	Glumes removed, seed reversed
15	Horizontal	Glumes removed

Germination was initially monitored on a daily basis for seven days and thereafter every second day. Germination was recorded as number of seed germinated over time and total germination for each treatment sown. Germination was defined as the emergence of any part of the embryo (coleorhiza, epiblast or radicle).

4.3.3. Data Analysis

The number of germinated caryopses was expressed as a percentage (X) of the sown caryopses. As these percentages covered a wide range of values the inverse sine transformation was used in order that the transformed data were approximately normally distributed (Steel and Torrie, 1980) in order to apply the statistically powerful parametric Analysis of variance (Anova) test to the arcsin-transformed values $X'=\sin^{-1}\sqrt{X}$. Zero percentages were substituted by $0.25/n$ giving a small positive value (Bartlett, 1947; quoted in Steel and Torrie, 1980). The figures have been plotted using untransformed data.

4.3.4. Results

The results (Table 4.7) clearly show the importance of orientation in the germination of *A. junciformis* seed. Those orientations which ensured good contact between the soil and the callus end of the caryopsis resulted in high germination.

There were considerable differences ($P<0.001$) in the germination of caryopses orientated normally to those inverted. An inverted position always resulted in minimal germination of the seed, regardless of the amount of contact with the soil. Germination was also poorer ($P<0.001$) in those caryopses held off the soil surface by litter or their awns.

The awns had no effect ($P>0.05$) in re-orientating caryopses on the soil surface into the vertical position. Only 3% of intact caryopses placed horizontally on the soil surface were pushed up into the vertical position, whilst 5% of those caryopses with the callus removed also achieved this.

Table 4.7. Germination of *Aristida junciformis* caryopses depending on orientation and treatment for the duration of the 30 day experiment.

Treatment	Average number of caryopses germinated per pot over 30 days (±S.E.)	Total number of caryopses germinated	Percentage caryopses germinated after 30 days
1	33.7±11.8	101	67
2	23.0±3.0	69	46
3	0.7±0.3	2.0	1.0
4	0.0	0	0
5	17.7±2.7	53	35
6	33.0±3.1	99	66
7	0.0	0	0
8	15.7±5.9	47	31
9	1.0±0.0	3.0	2.0
10	16.7±3.2	50	33
11	26.3±0.3	79	53
12	25.7±1.3	77	51
13	40.7±2.0	122	81
14	0.3±0.3	1.0	0.7
15	35.3±1.3	106	71

The results also illustrate the importance of the caryopsis glumes in the germination process. In both vertically or horizontally orientated seeds without glumes, total germination was high and extremely rapid, compared to intact caryopses. Once again however, inverted seeds with glumes removed also exhibited minimal germination ($P<0.001$).

Caryopses buried under the soil surface exhibited lower germination than those with the caryopsis tip in the soil (*P*>0.05). There was also no important difference in overall germination for caryopses partially buried in the soil or that lying on the soil surface. Caryopses in soil cracks exhibited lower germination than normally positioned caryopses (*P*<0.07). Removal of the awns or callus barbs had no meaningful effect on total germination (*P*>0.05).

4.3.5. Germination Rates

The germination rates of intact caryopses correlated to orientation are illustrated in Figures 4.3 and 4.4. The germination rate of caryopses orientated as normally found in the field, i.e. vertically orientated with the tip buried in the soil surface, was faster (P<0.01) than caryopses lying horizontally on the soil surface. This vertically orientated caryopses also germinated faster than caryopses buried under the soil surface (*P*<0.001). Complete burial of the caryopses led to the majority of seed in this treatment germinating approximately 15 days after sowing as compared to the majority of the other treatments. This was likely due to the time taken for the coleoptile to elongate towards, and the shoot to emerge through the soil surface. Vertical caryopses buried to half it's length did not germinate notably slower than the tip buried caryopses.

Vertical caryopses as well as caryopses lying horizontally also germinated faster (*P*<0.001) than caryopses with awns partially removed. Caryopses with awns totally excised exhibited both a high and rapid germination. Excision of the awns appears to have removed the inhibition of the glumes to some extent.

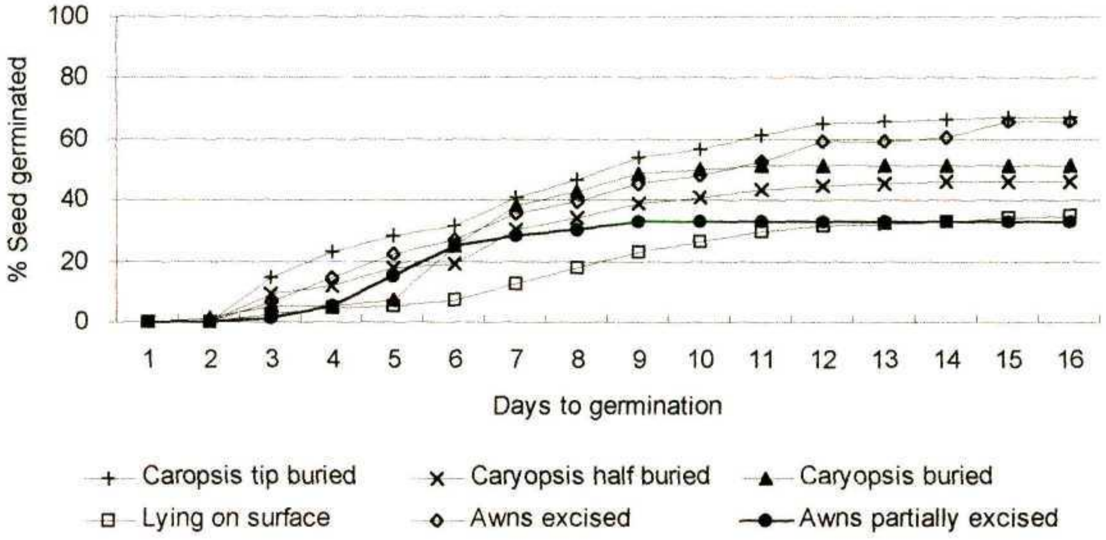


Figure 4.3. Germination rates of *Aristida junciformis* caryopses with glumes intact.

Examination of the results depicted in Figure 4.5 highlight the importance of the caryopses's glumes in the germination process; the highest and fastest germination of seed occurred in those treatments where the glumes were removed. The onset of germination in seeds without glumes was on average six days earlier than comparable treatments with intact caryopses and the rate was startlingly rapid; particularly in vertically orientated caryopses. There was no important difference in germination rates or final germination between vertically and horizontally orientated seed without glumes. Once again however, even with glumes removed, inversion of caryopses inhibited germination ($P<0.001$).

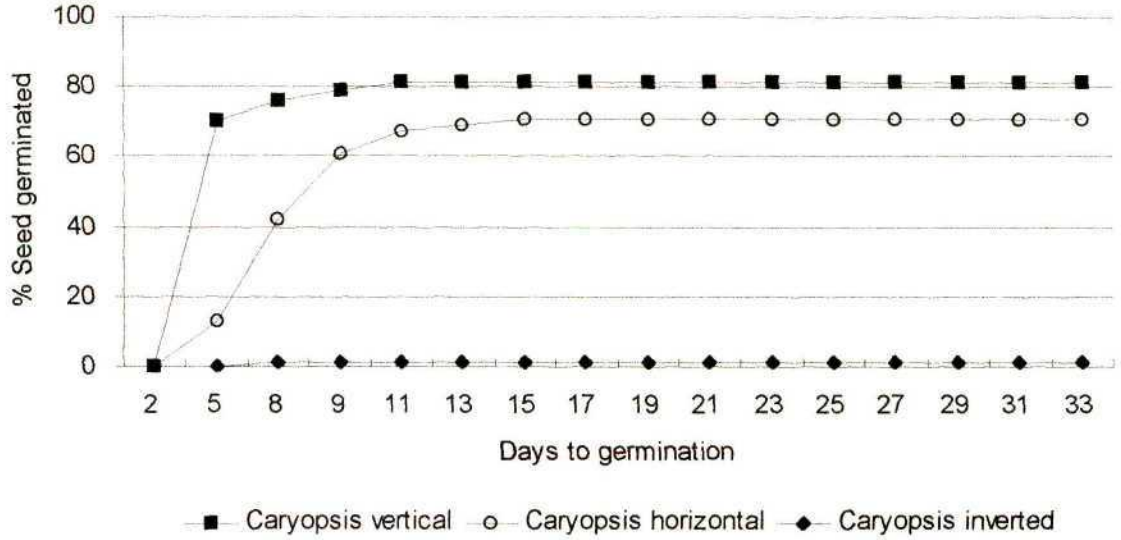


Figure 4.4. Germination rates of intact *Aristida junciformis* caryopses inverted and in soil cracks.

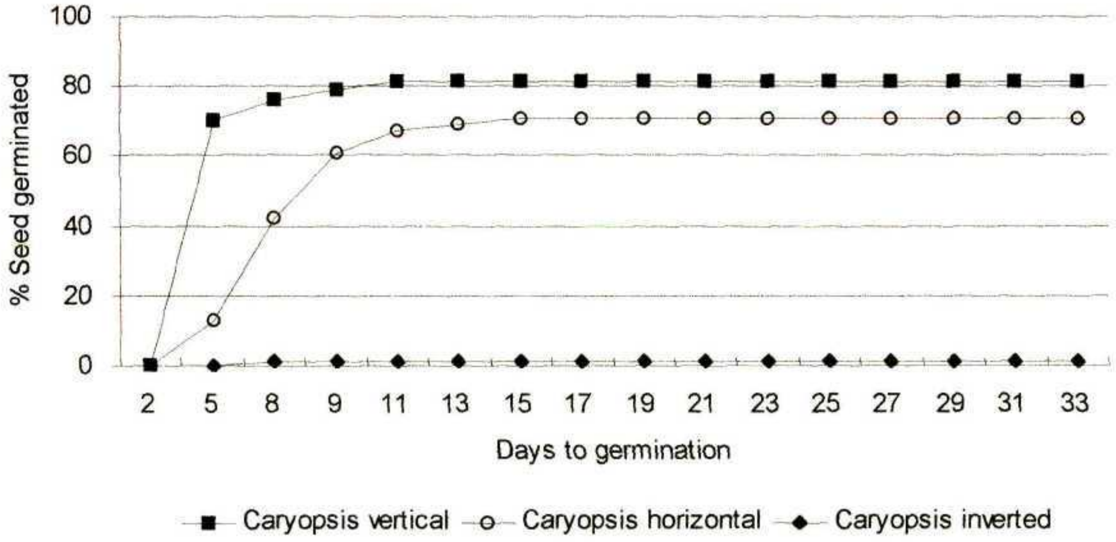


Figure 4.5. Germination rates of *Aristida junciformis* caryopses with glumes removed.

4.3.6. Discussion

Caryopsis morphology has been subject to selection pressures associated with a range of functions, such as dispersal, location of micro sites on the soil surface, orientation for germination, anchorage for establishment, provision of an adequate food supply for establishment of the seedling, and protection from desiccation. The caryopses is therefore not only adapted for dispersal but also for locating specific micro sites on the soil surface and placing the seed in a position which ensures maximum water uptake for germination (Peart, 1979).

At the scale of a caryopsis, the physical environment is extremely heterogenous, the surface of the soil strewn with a variety of different micro sites potentially available for germination and establishment. Differences among species in their requirements for micro sites in which to germinate and grow are one mechanism that has been hypothesized to maintain competing species in a community and make their coexistence possible (Grubb, 1977; Harper, 1977; Silvertown, 1981).

A variety of causes prevent caryopses in the field achieving the high germination percentages often observed in the laboratory. The micro- topography of the soil surface may determine which caryopses and which species germinate and which remain dormant in the soil.

The results obtained in these experiments illustrate the importance of seed orientation for optimum germination. The necessity for vertical orientation in *Aristida* species has also been identified by other workers. Peart (1981) found the rigid awns of *Aristida vagans* Cav. orientated the caryopsis during its fall from the parent plant and thereby increased the chance that it would land with its callused end penetrating the soil surface or cracks. He suggested that the sharp pointed callus helps the caryopsis to penetrate compacted or litter covered surfaces but did not appear to assist in the movement of the caryopsis or in the location of cracks and crevices.

In later work Peart (1984) found a close association between caryopsis orientation and seedling survival for both *A. vagans* and *Aristida queenslandica*; 70% of the seedlings that germinated from standing diaspores established while 70% of seedlings that germinated from horizontally orientated caryopses died before reaching this stage of development.

Peart (1981) found removal of the awns of *A. vagans* greatly reduced the number of standing caryopses regardless of the soil surface or presence or absence of the callus. With the awns intact, however, the removal of the callus lowered the proportion of the standing caryopses regardless of soil surface while in the absence of the awn the excision of the awn had no effect. He also found similar results to this study in that the removal of the callus, awns or both did not substantially affect the germination response of caryopses of *A. vagans*. In the presence of the awn, removal of the callus reduced establishment considerably on a compacted litter free surface. He also found that removal of the callus greatly increased the number of seedlings which exhibited delayed penetration of the soil surface.

Taylor and Gardner (1960) (quoted in Peart 1979) also showed that if the radicle is to penetrate the soil then the diaspore must be anchored. The actual mechanism in *Aristida* is described by Peart (1981) in which the antrorse bristles anchor the diaspore firmly and provide a counter to the force of the radicle pushing into the soil. The callus therefore plays an important role in ensuring rapid radicle penetration for successful germination.

Peart (1984) also suggested that since the small embryo of the grass caryopsis is invariably adjacent to the callused tip of the caryopsis it is not surprising to find burial of the caryopsis with the callus end lowermost results in higher germination percentages than from horizontally lying caryopses in most species examined experimentally.

Those caryopses held off the soil surface by litter showed very poor germination which has also been recorded by Fowler (1986). This is important in the field situation where caryopses landing in a grass tuft is trapped there unable to reach the soil surface, or there is a thick layer of mulch which the radicle is unable to penetrate before the caryopsis dies. The results also illustrate the ability of the glumes to inhibit germination. Mott (1972) found that mechanical damage to the hull of *A. contorta* gave an increase in germination to more than 90% when the closely adhering hull was completely removed, yielding normal, viable plants. *Aristida contorta* normally germinates after summer rain and sets seed in autumn, overwintering before germination in the following summer. Experimental breaking of dormancy by de-hulling, together with the lack of chemical inhibitors to germination in the seed, indicated that the mechanism responsible for dormancy is a mechanical one residing in the glumes. In the field situation, dormancy appears to be initially very important, as the autumn seed of *A. contorta* would remain dormant during the cool winter, before a short period of the high soil-surface temperatures of summer broke dormancy, and allowed germination to take place during the summer rains (Mott, 1972).

Mott (1974) termed the dormancy breaking effects of high temperature the 'primary dormancy' and the after-ripening requirements of the embryo 'long-term' dormancy imposed on the seed by the properties of the seed coat. Mott (1974) found that the primary dormancy could also be broken by the action of GA_3 or thiourea. From his work it appears that primary dormancy in

Aristida species is an after ripening process similar to that found in cereals which can be broken by storage for several months at ambient temperatures or exposure to alternating temperatures for shorter time periods.

Mott (1974a) found that the area of the hull that exerts control over long term dormancy is directly over the embryo. The role of the coat is to restrict oxygen access to the embryo as the hull appears to be an effective oxygen barrier. The oxygen consumption of long-term dormant grains is very low, but on removal of the hull, germination occurs and oxygen consumption increases dramatically.

Mott (1974b) in a description of *A. contorta* seed observed that for both flowers and mature grains, the lemma invests the florets or caryopsis, and the palea is a reduced glume within the lemma, only persisting at the proximal end of the caryopsis. The leaf-like structure of the glumes is clearly apparent at time of anthesis, and by the time the seed has matured the cells composing the glumes have become thickened to form an extremely tough hull. The outer epidermal cells are heavily impregnated with silica, the silica forming a continuous layer over the surface of the glume as well as being apparent in the mesophyll in the form of long rods.

These thickened mesophyll cells also possessed a thin inner layer of lipids (Mott 1974b). This inner layer was intact in all dormant seed examined by this author but fractured in non-dormant seed. Mott (1974b) suggests that this lipid layer in the glumes of *A. contorta* covering the inner epidermis may be of similar ontogeny to the cuticular layer formed on the vegetative leaves of other species and that this cuticular layer in dormant caryopses appears well suited to restricting gas exchange to the embryo. The glumes therefore appear to play an integral role in 'recognizing' when the seed is in a suitable micro- habitat, correctly orientated and environmental conditions are suitable for germination to follow.

4.4. Caryopsis Dispersal

Dispersal in flowering plants can be defined as the removal of the seed and its transport to a new site. Two important factors determining the size of a population of any particular species are the number of viable caryopses available and the efficiency of their dispersal for germination and establishment (Harper, *et al.* 1961).

The seed morphology of the Poaceae has often been interpreted in terms of dispersal by wind or passively by animals. There are some references in the literature to the importance of animal dispersal of *Aristida* seed, primarily to species found in Australia. It is widely known that caryopses of *Aristida* becomes entangled in the coats of sheep (Peart, 1979). This author (Peart, 1979) also makes reference to work done by Norton (1971) in New South Wales, Australia, where *Aristida ramosa* has become a highly undesirable species because of it's low palatability, and the fleece and meat contamination caused by it's caryopses. Harradine and Whalley (1978) quote a personal communication from Hamilton, who states that some 40 % of sheep carcasses received at a certain abattoir have to be downgraded because of *A. ramosa* contamination of the flesh.

What is unclear is if this caryopses tangled in the sheeps' coats would ever be deposited in another site where it could germinate. Sheep are an introduced animal to Australia and could be a factor in the genus's comparatively recent range expansion. However, from the above authors work it appears that most of these caryopses is working it's way through the fleece into the skin and is therefore unlikely to locate a suitable microsite for germination.

The caryopses does not appear to be adapted for dispersal by indigenous animals. Peart (1979) failed to find any awned grass caryopses in the fur of 100 carcasses of wild marsupials in Australia. The cattle present on some of the trial sites at Ukulinga during this study did not appear to have any caryopses in their coats. As no sheep were present for the duration of this trial they were unable to be studied for the presence of *A. junciformis* caryopses.

Examination of available literature revealed that animals have seldom been implicated in spreading caryopses of Aristida and the primary agent of seed dispersal appeared to be wind. Logistically, examination of the role of grazing animals in the dispersal of *A. junciformis* caryopses was beyond the scope of this study and it was decided to concentrate on wind dispersal only.

As the caryopses of *A. junciformis* appeared to be primarily wind dispersed, caryopsis traps were therefore used to test whether the awns of *A. junciformis* caryopses aided the wind dispersal of caryopses by increasing buoyancy in the air (acting as a ‘parachute’) apart from ensuring correct orientation in the caryopses fall from the flowering tiller to the soil surface.

4.4.1. Method

A comparison was made between areas where the sward had been reduced either by mechanical mowing or grazing by cattle and those in which the grass height was unaltered.

Plant tufts selected as caryopses sources were isolated by removing all surrounding flowering tillers within a radius of 10 m. By removing only the flowering part of the tiller from these other tufts the airflow around these plants was altered as little as possible while simultaneously preventing caryopses from distant plants entering the caryopses traps.

The caryopses traps were manufactured from upturned plastic petri dish lids of 9.5 cm diameter glued to wire spikes which were fixed into the ground at distances from immediately beside the parent plant's basal perimeter, to 50 cm, 100 cm, and 200 cm from the tuft periphery along two orthogonal axes which were for each experimental plant orientated true north - south and the second west - east. This required a total of 16 traps per tuft (5 plants), 80 traps per treatment and a total of 160 traps for both treatments.

Once positioned, the petri dishes were smeared with automotive grease and left until the end of the flowering season for *A.junciformis* in May. The caryopses traps were then recovered and the number of trapped caryopses counted.

4.4.2. Data Analysis

The number of caryopses trapped (X) at each set distance from the parent tuft for both open and closed swards was expressed as a percentage of the total number of caryopses captured in the traps overall. These percentage data were inverse sine transformed to ensure that the data were approximately normally distributed (Steel and Torrie, 1980). Statistical analyses were made on the arcsin-transformed values $X'=\sin^{-1}\sqrt{X}$. Figure 4.6 has been plotted using untransformed data.

The number of caryopses trapped for both open and closed swards as effected by wind direction was analysed by χ^2 tests on tables of direction verse number of caryopses trapped as these count data were in a categorical form.

A simple, linear correlation was used to test whether there was a correlation between the height of the parent tuft, its' diameter (and therefore number of caryopses released) and the number of caryopses trapped in the closed sward.

4.4.3. Results

Effect of Sward Density on Caryopses Dispersal Distance

For all four distances tested, there were greater numbers of caryopses trapped in the open sward compared to the closed sward ($F_{7,28}$=12.3, P<0.001). Overall four times more caryopses (765 as compared to 175) were trapped in the open sward than in the closed sward. This equated to a trapped caryopses density of approximately 380 caryopses/m^2 in the open sward and 88 caryopses/m^2 in the closed sward. The numbers of caryopses trapped for each distance are recorded in Table 4.8.

For both types of sward the number of caryopses dispersed declined rapidly with distance demonstrating a characteristic leptokurtic distribution (Figure 4.6). It appeared that a large proportion of the caryopses that was released in the undisturbed sward was trapped in the foliage of surrounding plants

Table 4.8. Average number (±S.E.) of *Aristida junciformis* caryopses trapped in open and closed swards in relation to distance from parent tuft.

	Average number of caryopses trapped		
Distance (cm)	Closed sward	Open sward	P
0	22.0±5.9	70.4±17.8	<0.05
50	13.8±3.6	45.6±9.8	<0.01
100	4.8±1.4	24.6±3.6	<0.001
200	3.3±1.4	12.4±2.4	<0.001

The numbers of caryopses trapped on each orthogonal axis (north, south, east and west) for both open and closed swards are recorded in Table 4.9. Despite the prevailing wind direction at Ukulinga being from the south to southeast and less frequently from the north, there was no meaningful difference between the number of caryopses collected for any one axis though numerically more caryopses were trapped on the north side than any other axis. From these data it is apparent that caryopses density in the sward is not greatly influenced by wind direction.

Table 4.9. Average number (±S.E.) of *Aristida junciformis* caryopses trapped for both open and closed grass swards in relation to wind direction (for P=0.05, df=7); ns = not significant.

	Open sward- average caryopses trapped	Closed sward- average caryopses trapped	Total caryopses trapped- open vs. closed sward	Trapped caryopses density - open vs. closed sward (caryopses/m²)
North	10.3±2.1	4.7±1.2	204/75 χ^2=12.5 ns	408/150
South	11.6±2.2	2.1±0.5	233/33 χ^2=6.9 ns	466/66
East	9.3±2.0	2.3±0.7	185/37 χ^2=0.5 ns	370/74
West	7.1±1.4	1.9±0.5	143/30 χ^2=0.2 ns	286/60
		Average open vs. closed sward = 383 vs.88 caryopses/m²		

Effect of Parent Plant Size and Tiller Height

There was no marked correlation between the height of the parent tuft or its diameter (and therefore number of caryopses released) and the number of caryopses trapped (R^2=25.6%).

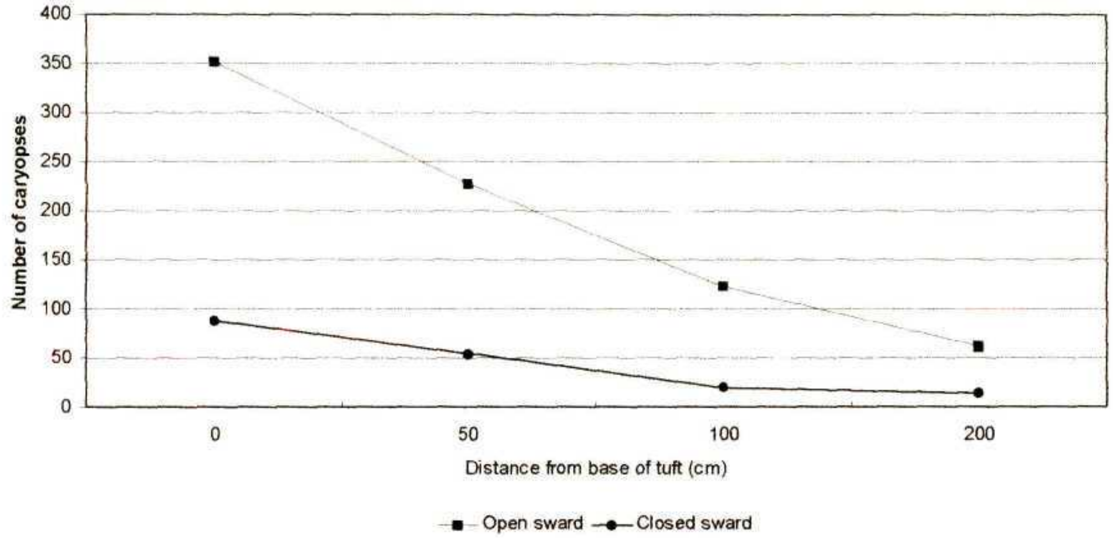


Figure 4.6. Dispersal distances of *Aristida junciformis* caryopses in open and closed swards.

4.4.4. Discussion

The results of this study suggest that a high proportion of the caryopses that is released in an undisturbed sward is trapped in the foliage and surface litter of surrounding plants preventing dispersal any substantial distance from the parent plant and ultimately germination in a suitable microsite. This has also been found by Fowler (1986) in greenhouse experiments who found that caryopses trapped in high levels of litter would germinate before reaching the soil surface and therefore die. The opposite is true of open swards where caryopses appears to have greater opportunity to be blown both aerially and along the ground considerably further distances. This implies that in overgrazed veld where particularly basal areas are small, soil litter minimal, and the areas of bare soil correspondingly high the potential for wind blown caryopses is great.

Despite this, the high density of caryopses trapped close to the basal perimeter of the parent plant whether in a closed or open sward is a strong indication that the primary function of the three awns of *A. junciformis* is correct orientation of the caryopses in its fall from the flowering tiller to the soil surface rather than acting as a 'parachute' to disperse far distances.

Peart (1981) recorded similar results. The majority of *A. vagans* seedlings germinated in the immediate vicinity of the parent plants and dispersal to even moderate distances from the parent plant was the exception rather than the rule. This author also concluded that the primary role of the awns is to orientate the caryopsis during its fall rather than to reduce the rate of fall and enhance dispersal over moderate distances by wind. He recorded terminal velocities in the order of 100-250 cm per second for species of *Aristida*, considerably higher than the 20-25 cm per second recorded by Sheldon and Burrows (1973) for the wind dispersed plumed cypselas of species within the Asteraceae.

For those caryopses which do not immediately locate a microsite for germination, wind dispersal along the soil surface can potentially distribute caryopses large distances. Peart (1981) has observed that movement along the ground is hampered by the antrosely barbed callus of the caryopsis but both Rice, Penfound and Rohrbaugh (1960), and Fowler (1986) have observed that the three stiff, long awns of *Aristida* species, which hold the caryopsis away from the ground, insures that it can be blown along the ground very easily for considerable distances. Fowler (1986), made this observation for *A. longiseta* on the Edwards Plateau in central Texas, whilst Rice, *et. al.* (1960) attributed partial responsibility for the early invasion of abandoned fields by *Aristida oligantha* ('triple awn grass') in central Oklahoma to wind dispersal along the ground. They observed that caryopses and even entire plants of *A. oligantha* were often carried 'fairly long distances' by high velocity wind common in the region.

Results from this study at Ukulinga on *A. junciformis* suggest that caryopses could be blown considerable distances in overgrazed veld, the combined effects of bare soil and reduced height of palatable grass species in the sward enhancing the likelihood of *A. junciformis* caryopses travelling further, and finding, suitable micro sites for germination than those released in a closed lightly defoliated sward. Extrapolating from the results of this study, in swards where there is still good basal cover and herbage accumulation the majority of the caryopses will be trapped in close vicinity to the parent plant and is unlikely to disperse beyond a radius of four metres from the parent plant unless subject to very high wind conditions or similar such natural phenomenon. In this study there were no instances of entire plants being carried over long distances by the wind as that observed by Rice, *et. al.* (1960) in central Texas.

4.5. Caryopsis Density

4.5.1. Introduction

Given the possible role which caryopses plays in the invasive ability of *Aristida junciformis* it was necessary to derive an estimate of the quantity of caryopses that actually reaches the soil surface and which, if viable, is in a position to germinate. (Viability of these caryopses are investigated in Section 4.7 below). Considering that Venter (1968) estimated that a single tuft of *A. junciformis* is capable of producing up to 18 000 viable caryopses each season there is apparently great potential for large numbers of seedlings to emerge if conditions are suitable.

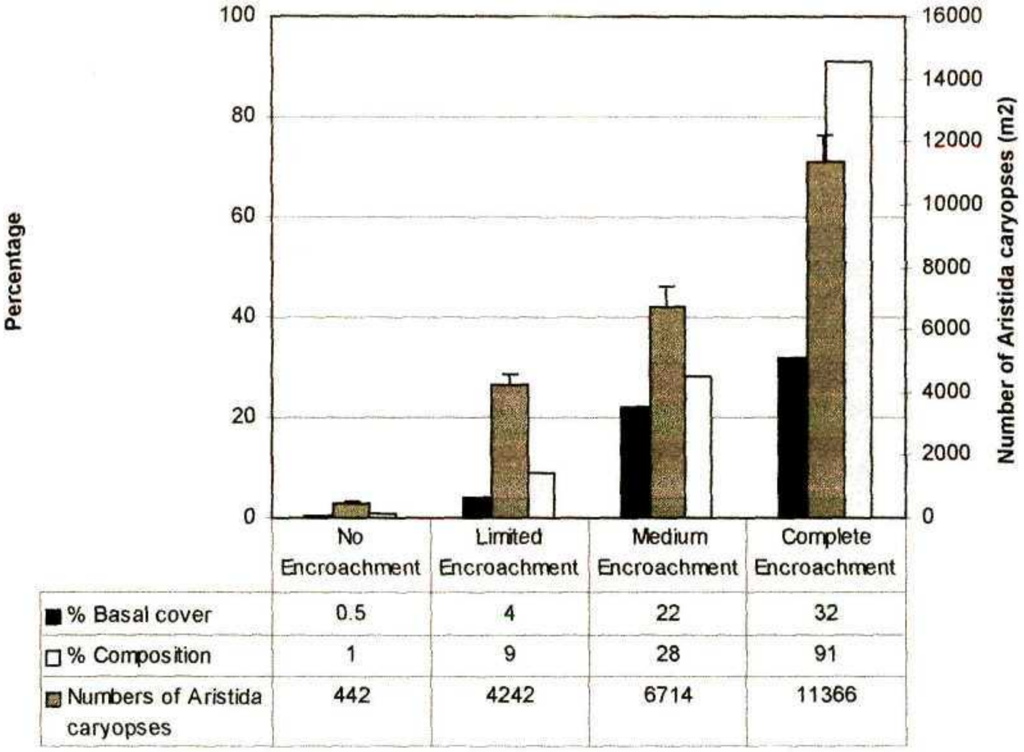
Results from the dispersal distance experiments suggested that the amount of caryopses produced in any particular area would be directly correlated with density of parent tufts in that area. As basal area and plant density data already existed for permanently marked quadrats in several trials, caryopses numbers were counted within the No Encroachment, Limited, Medium and High Encroachment sites.

4.5.2. Method

Within each of five, one metre square quadrats in each selected trial plot, ten 10 x 10 centimetre square quadrats were randomly placed and the number of caryopses within each quadrat counted. This represented a total of 50 quadrats per trial plot. The quadrat size was determined by the high number of caryopses in some trial plots making it difficult to accurately count the number of caryopses if bigger quadrats had been used.

4.5.3. Results and Discussion

Caryopses numbers were collated and averaged for all five quadrats per trial plot measured. These averages were multiplied to express the results on a square metre basis. The results depicted in Figure 4.7 demonstrate that caryopses densities on the soil surface are strongly positively correlated with the density of adult plants in the sward.



	No Encroachment	Limited Encroachment	Medium Encroachment	Complete Encroachment
■ % Basal cover	0.5	4	22	32
□ % Composition	1	9	28	91
▨ Numbers of Aristida caryopses	442	4242	6714	11366

Figure 4.7. Caryopsis density of *Aristida junciformis* found on the soil surface in relation to basal cover and percentage of *Aristida junciformis* found in the sward.

There was a considerable difference in caryopses densities between the areas measured ($F_{3,196}$=325, $P<0.001$). There were important linear and positive correlations between the basal cover of *A. junciformis* and the number of caryopses found on the soil surface; Y=0.29X+1.41, r= 0.91; and percentage composition of *A. junciformis* in the sward and the number of caryopses found within these quadrats; Y=0.11X+2.28, r= 0.89; (*P* for all cases <0.05).

Areas with a high density of *A. junciformis* such as the High Encroachment Site, which had an average composition of 92% for *A. junciformis* when measured in 1993, had a very high caryopses density of approximately eleven and a half thousand caryopses per square metre. In comparison, areas such as the No Encroachment site, which had a very low incidence of approximately 0.5 % *A. junciformis*, had an average caryopses density of 400 caryopses per square metre. The rest of the trial areas measured fell between these extremes.

The distribution of caryopses within the sward is patchy, as the majority of caryopses are found in close proximity to the parent plants and is therefore strongly correlated with their presence or absence in the sward.

4.6. Caryopsis Production

The substantial investment of resources in seed production by adult *Aristida junciformis* plants as evidenced by the high seed production required quantification in relation to plant size and number of caryopses released. Associated with this was the possible effects of intra- and interspecific plant competition on the quantity of the caryopses produced. Does an *Aristida junciformis* plant growing in a monotypic *A. junciformis* sward produce less or more caryopses than a plant growing in a sward dominated primarily by *T. triandra*? *Themeda triandra*, an infinitely more desirable species from a graziers point of view, was used as a comparison species for investigating caryopses production.

Having been defined as an 'Increaser II' species by Tainton (1988), *Aristida junciformis* has a fundamentally different caryopses dispersal strategy to a 'Decreaser' species such as *Themeda triandra*. *Aristida junciformis* disperses large quantities of relatively small caryopses (average caryopsis mass= 0.56±0.025 mg, n=50) into the environment, compared to a species such as *T. triandra*, which releases comparatively fewer but larger caryopses.

4.6.1. Method

The quantity and quality of caryopses produced by *A. junciformis* was compared to that of *T. triandra* before the caryopses reached the soil surface. Immature, flowering tillers of both species were bagged using fine muslin material in the 1993 and 1994 seasons to prevent caryopses escaping from mature inflorescences. For *A. junciformis*, mature flowering tillers were harvested in late March. Flowering tillers were collected from 20 *A. junciformis* plants growing in pure *A. junciformis* swards, and 20 plants growing in those mixed swards with high proportions of *T. triandra* present.

Similarly bagged flowering tillers of *T. triandra* were collected in December from 20 plants growing in a sward dominated by *T. triandra*, and from 20 plants growing in swards dominated by *A. junciformis*, once the caryopses were mature.

For each flowering tiller harvested from *T. triandra* plants, all caryopses present on the tiller were counted. In view of the much higher caryopsis production of *A. junciformis*, a sub-sample of ten flowering tillers for each plant were randomly selected and the number of caryopses on them counted, as was the total number of flowering tillers per plant. The average number of caryopses per tiller was then multiplied by the number of flowering tillers to estimate total caryopsis production per plant. When the tillers were harvested, the plant's basal area was recorded to determine if there was a correlation between basal area and the number of flowering tillers and caryopses produced for both species.

4.6.2. Results

The results are shown in Tables 4.10 and 4.11. For flowering tillers of *T. triandra* harvested in 1993, there was a correlation between the number of flowering tillers and caryopsis production, but no correlation between basal area and flowering tiller production, or between basal area and caryopsis production.

These results were reiterated in the 1994 data for *T. triandra*. Again there was a correlation between the number of flowering tillers and caryopsis production, but no correlation between basal area and tiller production, or basal area and caryopsis production.

A similar trend was apparent in the *A. junciformis* data. For plants harvested in 1993 there was no correlation between basal area and flowering tiller production, or between basal area and caryopsis production. These results were repeated in 1994 for flowering tillers harvested from *A. junciformis* plants.

Table 4.10. Correlation of caryopsis production by *Themeda triandra* in relation to the number of tillers produced and basal area of the plant.

Treatment	r	F Ratio	*P*
Number of tillers versus caryopses produced	0.87 (1993)	$F_{1,18}$=118.7	<0.001
Basal area of plant versus tillers produced	0.28 (1993)		ns
Basal area of plant versus caryopses produced	0.28 (1993)		ns
Number of tillers versus caryopses produced	0.80 (1994)	$F_{1,18}$=103.0	<0.001
Basal area of plant versus tillers produced	0.24 (1994)		ns
Basal area of plant versus caryopses produced	0.30 (1994)		ns

Table 4.11. Correlation of caryopsis production by *Aristida junciformis* in relation to the number of tillers produced and basal area of the plant.

Treatment	r	F - Ratio	*P*
Number of tillers versus caryopses produced	0.79 (1993)	$F_{1,18}$=143.9	<0.001
Basal area of plant versus tillers produced	0.19 (1993)		ns
Basal area of plant versus caryopses produced	0.27 (1993)		ns
Number of tillers versus caryopses produced	0.72 (1994)	$F_{1,18}$=117.8	<0.001
Basal area of plant versus tillers produced	0.24 (1994)		ns
Basal area of plant versus caryopses produced	0.29 (1994)		ns

Caryopsis production of those harvested flowering tillers of the selected *T. triandra* plants in both 1993 and 1994 showed no difference in the amount of caryopses produced between plants growing either in monotypic swards of *T. triandra* or those dominated by *A. junciformis*. *Themeda triandra* plants growing in swards dominated by *A. junciformis* produced an average of 116 caryopses per plant while those growing in monotypic swards of *T. triandra* produced an average 123 caryopses per plant.

This was also true of *A. junciformis* where there was no difference in the number of caryopses produced by *A. junciformis* plants growing in monotypic stands of *A. junciformis* and *A. junciformis* plants growing in swards in which this species was sparse.

The average number of *caryopses* produced by mature individuals of *A. junciformis* was estimated at c. 19 000 caryopses per plant which closely agrees with Venter's (1968) estimate of 18 000 caryopses per plant. Caryopsis production of *A. junciformis* plants with small basal areas such as those found in the No Encroachment Site varied from an average of 4600 caryopses per plant, to a maximum of 18 900 caryopses per plant for those with large basal areas measured in the High Encroachment Site.

4.7. Seed Fill

4.7.1. Introduction

An important aspect of the high caryopses production of *A. junciformis* is the proportion of total caryopses produced that is physically and physiologically competent and able to germinate, and that proportion which is not. In this regard, the effect of intra- and interspecific competition on the quality of the caryopses produced could be very important. If an *A. junciformis* plant is growing in a pure *A. junciformis* sward, does it produce less or more physiologically competent seed than a plant growing in a sward dominated by *T. triandra*?

4.7.2. Method

To quantify this, six replications, each of 20 caryopses, were randomly sampled from the total caryopses collected in the 1993 and 1994 seasons from both *T. triandra* and *A. junciformis* populations, visually examined and subjected to a 'squeeze' test in which each caryopsis was gently squeezed with a pair of forceps where the filled seed would be situated. The lemma of mature caryopses with either reduced seeds or without seeds at all would distinctively collapse when subjected to the pressure of the forceps. This would not occur in properly filled seeds. This seed was then categorized into either filled or not filled purely on this examination, and the differences were tested by x^2 tests. This test was used to test the interaction of two variables namely species and species presence and due to the categorical nature of the data which was in a count form.

4.7.3. Results

No significant ($P>0.05$) differences were detected in the number of *A. junciformis* caryopses filled for both years sampled, either between caryopses collected from plants growing in monotypic stands of *A. junciformis*, or those growing in swards with few *A. junciformis* plants (Table 4.13). There were proportionally more filled caryopses obtained in 1994 from the monotypic stands of *A. junciformis* than from swards dominated by other species though this difference was not significant ($P>0.05$).

These results were similar in the *T. triandra* caryopses collected in both 1993 and 1994. There was proportionally more filled caryopses produced by plants growing in areas dominated by *T.*

triandra than those growing in swards dominated by *A. junciformis* though this was not significant ($P>0.05$).

Table 4.12. Differences in seed fill for *Aristida junciformis* and *Themeda triandra* (for $P=0.05$, $x^2=14.1$, $df=7$).

Species seed	% seed fill	x^2
3. *Aristida junciformis* 1993	59	$x^2=1.69$ ns
4. *Aristida junciformis* 1993	61	$x^2=2.33$ ns
3. *Aristida junciformis* 1994	66	$x^2=5.12$ ns
4. *Aristida junciformis* 1994	62	$x^2=2.88$ ns
1. *Themeda triandra* 1993	47	$x^2=0.18$ ns
2. *Themeda triandra* 1993	32	$x^2=6.48$ ns
1. *Themeda triandra* 1994	43	$x^2=0.98$ ns
2. *Themeda triandra* 1994	26	$x^2=11.71$ ns

Note: 1= high proportion of *Themeda triandra* in sward
2= high proportion of *Aristida junciformis* in sward
3= monotypic sward of *Aristida junciformis*
4= high proportion of species other than *Aristida junciformis*
ns= $P>0.05$

4.8. Seed Viability

4.8.1. Method

From the caryopses that was considered to be filled, six replications, each of 20 caryopses, were randomly drawn for both species and viability assessed using the tetrazolium test for the presence of respiratory activity (Anon, 1985).

For both *A. junciformis* and *T. triandra* caryopses, the glumes were removed and the caryopses pre-imbibed in distilled water for 24 hours, before incubation in a one percent buffered tetrazolium solution for a further 24 hours at 30°C. After this staining period the seed were examined under a dissecting microscope to determine the number of filled caryopses.

4.8.2. Results

These results are characterized for both species by the high positive viability of the seed. All the caryopses appeared physically intact before the test, indicating that filled caryopses have a high probably of germinating if suitable micro sites are located and environmental conditions met. There were no prominent differences in viability between seed of the same species for different years, or between the same species growing in different competitive environments (Table 4.13).

Table 4.13. Results of tetrazolium tests to determine seed viability of *Themeda triandra* and *Aristida junciformis* (for P=0.05, x^2= 14.1, df=7).

Species Seed	% Viable seed	x^2
1. *T. triandra* 1993	83	x^2=0.05
2. *T. triandra* 1993	78	x^2=0.51
1. *T. triandra* 1994	95	x^2=1.34
2. *T. triandra* 1994	87	x^2=0.03
3. *A. junciformis* 1993	80	x^2=0.27
4. *A. junciformis* 1993	96	x^2=1.5
3. *A. junciformis* 1994	89	x^2=0.27
4. *A. junciformis* 1994	69	x^2=3.05

Note: 1= high proportion of *Themeda triandra* in sward
2= high proportion of *Aristida junciformis* in sward
3= monotypic sward of *Aristida junciformis*
4= high proportion of species other than *Aristida junciformis*

4.8.3. Conclusion

Though there is considerable production of infertile seed c. 40% by *A. junciformis*, that proportion of physically intact seed produced will germinate if suitable environmental conditions are met. In the context of this study, it would be interesting to collect data over a number of years, and correlate it with biotic and abiotic factors such as inter- and intraspecific plant competition, rainfall, temperature, soil fertility and frequency of disturbance, to infer the effects of these on seed production and viability.

4.9. Germination and Survival of Seedlings in the Sward

4.9.1. Introduction

A variety of causes prevent caryopses in the field achieving the high germination percentages often observed in the laboratory, whether it is spatial variation in the micro-environment, rainfall or any other combination of biotic and abiotic variables. An important facet of this study therefore, was to quantify actual germination in the field of *A. junciformis* seed.

4.9.2. Data Collection and Analysis

The one metre square quadrats discussed earlier (Chapter 3) that had been intensively sampled to collect basal area data with a pantograph, were monitored to record the number of grass seedlings that germinated in these quadrats. As the initial *A. junciformis* caryopses density of these quadrats had previously been established (see Section 4.6), it was possible to determine the germination of caryopses which germinated and the survival of the seedlings, albeit for a relatively limited time span of this study.

The number of seedlings that emerged were recorded on a two weekly basis. Pins were used to mark germinated seedlings in the quadrats and also marked on the pantograph data sheets so that a specific seedling's survival could be monitored and to prevent double sampling. This process continued up till the end of summer. The quadrats were then examined again the following spring to determine the number of seedlings which had survived the winter. The seedlings that emerged were classified into one of two categories, either *A. junciformis* seedlings or 'other seedlings.' This latter category included seedlings of any grass species apart from *A. junciformis.*

Spearmann rank correlations (Siegal and Castellan, 1988) were used to compare the number of emerged seedlings with the basal area of established plants in the sward for both *A. junciformis* and other grass species. This test was used to test between the two variables of tuft size and seedling survival and the ordinal nature of the data set. Chi-squared tests were used to compare seedling emergence in 1993 and survival in 1994 and between trials in which the quadrats were situated. This test was used due these data not being normally distributed and the categorical nature of the data which was in a count form (Siegal and Castellan, 1988).

4.9.3. Results

Quadrats with high *A. junciformis* caryopses densities showed the highest number of germinated seedlings. Overall, the number of seedlings that germinated, particularly of *A. junciformis* were surprisingly low, considering the high initial caryopses density on the soil surface (Section 4.5). For example, if germination of *A. junciformis* caryopses in the High Encroachment Site is examined, after taking seed fill and viability into account, the actual seed that germinated was only 4.5% of the potential number of seed that could have germinated. This gives an indication of the loss of caryopses due to unsuitable micro sites, unfavourable climatic conditions, incorporation into the soil, amongst other factors. Predation of *A. junciformis* caryopses was not observed in the field during this study, but this possible source of seed mortality was not formally tested in this study.

The overall germination for *A. junciformis* in relation to caryopses density ranged from one to four percent of the total caryopses observed in the quadrat, depending on the initial caryopses density. Caryopsis density of *A. junciformis* was correlated strongly with the basal area of *A. junciformis* plants in the quadrats (r_s=0.788, P<0.001), but there was no correlation between caryopsis density and *A. junciformis* seedling emergence. There was also no correlation between the basal areas of *T. triandra* and associated grass species and the number of seedlings of these species which emerged.

This low germination was exacerbated by the high mortality of seedlings during winter. Of the seedlings counted by the end of November 1993 in 40 1m^2 quadrats, only an average 13% of these seedlings had survived the ensuing dry winter.

Of all the quadrats monitored, the highest number of newly emerged *A. junciformis* seedlings were observed in the High Encroachment Site quadrats. This result was anticipated as the highest density of *A. junciformis* parent plants and caryopses on the soil surface had previously been recorded within these quadrats. A total of 673 seedlings of all species were observed in mid-November 1993, of which 72% were *A. junciformis*. By July 1994 only 13% of the total germinated seedlings had survived, of which 70% were *A. junciformis*.

This low survival was not found in all the treatments. In the No Encroachment Site quadrats which had few adult *A. junciformis* plants, an initial 94 seedlings were recorded, of which 35% were *A. junciformis*. Of these seedlings, 78% survived the winter, of which 88% were *A. junciformis*.

Table 4.14. Seedling survival of *Aristida junciformis*.

Trial	Total number of seedlings	Average seedlings (±S.E.) per m^2	Seedling survival (%)	χ^2
High Encroachment 1993	482	32.0±1.8	15.4	χ^2=0.01 ns
High Encroachment 1994	74	4.9±0.3		
Medium Encroachment 1993	278	55.4±3.3	10.8	χ^2=8.3 ns
Medium Encroachment 1994	30	6.1±0.3		
Limited Encroachment 1993	200	13.3±1.0	16	χ^2=0.4 ns
Limited Encroachment 1994	32	2.1±0.4		
No Encroachment 1993	32	6.4±0.6	78.1	χ^2=5.9 ns
No Encroachment 1994	25	5.4±0.5		

Table 4.15. Seedling survival of *Themeda triandra* and other grass species.

Trial	Total number of seedlings	Average seedlings (±S.E.) per m^2	Seedling survival (%)	χ^2
High Encroachment 1993	87	5.8±0.3	36.8	χ^2=0.54 ns
High Encroachment 1994	32	2.1±0.1		
Medium Encroachment 1993	10	2.0±0.0	120	χ^2=10.9 *P*>0.1
Medium Encroachment 1994	12	2.4±0.2		
Limited Encroachment 1993	114	7.6±0.2	31.6	χ^2=0.3 ns
Limited Encroachment 1994	36	2.4±0.2		
No Encroachment 1993	62.0	12.4±0.9	14.5	χ^2=4.9 ns
No Encroachment 1994	9.0	1.8±0.3		

There were no important differences in seedling emergence or survival between any of the treatments for both *A. junciformis*, *Themeda triandra*, and associated grass species (Tables 4.16 and 4.17). There was proportionally lower germination of *A. junciformis* caryopsis in the biennial spring burn and annual late spring burn treatments, due to the low presence of adult *A. junciformis* plants, but exceptionally high survival of these seedlings in the latter treatment.

4.9.4. Discussion

Despite the large amounts of caryopses produced, dispersed and landing in apparently suitable environment for germination, comparatively few seedlings survived their first winter. The seedlings that did survive and received adequate rainfall the following season had a greatly enhanced chance of long term survival. Nevertheless, from these data, and those in Chapter 3, it appears that the primary method of expansion of *A. junciformis* in the sward is by vegetative expansion rather than seedling recruitment.

Peart (1984) reported similar results for field sites monitored over three years. Of a total of 159 seedlings which he observed germinate, only 20% survived after two years, and only three percent survived to ultimately flower. All of the surviving seedlings were from caryopses that was either standing or buried at the time of germination.

Both Peart (1984) and Fowler (1986) found that germination density increased after rainfall and that lack of rainfall was the primary constraint on seed germination and seedling survival. Fowler (1986), found that in central Texas most of the caryopses had dispersed by May and June, but very little germination occurred until there were major rainfalls (2.5 mm or more) in the summer. The high temperatures of summer appeared to dry out the ground before germination could occur. When normal summer rainfall occurred most seedlings were recorded in the summer or autumn. When rain was not regular the number of seedlings also fluctuated from month to month. During a prolonged dry period the number of germinated seedlings remained consistently low and there was an increase in the frequency of premature deaths among existing seedlings. Harradine and Whalley (1980) recorded a 34% survival rate for seedlings of *A. ramosa* over a two year period at one experimental site, 48% at a second, 19% at a third and zero for a further three sites. The overall survivorship was 11% for all sites. Harradine and Whalley (1980) found an extended period of seed production which coupled with dormancy meant that germinable seed was available in the soil throughout the year. They found the majority of seedlings appeared in the spring and the autumn.

Differences among species in the timing of their germination may provide an important mechanism regulating the composition of the community, or at least the composition of its seedling and juvenile component. Early germination is considered to give an individual a competitive advantage and to be correlated with larger sizes and hence with greater survival and fecundity later in life. Too early germination could be fatal in the unpredictable environment in which these grasses occur, since periods of dry and warm weather may occur in all months of the year. Differing years with varying rainfall, therefore may be expected to favour the establishment of different species.

The requirement of each species for germination and establishment may have a temporal as well as a spatial component; the temporal rather than the spatial aspect of this part of the regeneration niche being the more important with respect to the relative abundance of *A. junciformis* and other grass species and their coexistence.

CHAPTER FIVE

EFFECTS OF HERBIVORY, FIRE AND INTERSPECIFIC COMPETITION ON *ARISTIDA JUNCIFORMIS*

5.1. Effects of Herbivory, Fire and Interspecific Competition

This study on selected aspects of *Aristida junciformis* subsp. *junciformis* Trin. et Rupr. has been carried out within one particular veld type in KwaZulu-Natal in southern Africa - Southern Tall Grassveld (Acocks 1966) and as such any discussion of the autecology of *A. junciformis* is naturally restricted to an extent by these boundaries, both physically and intellectually. This concluding chapter is therefore an attempt to collate information pertinent to this species within this specific ecosystem with some illustrative examples from further afield where these are felt to be relevant.

5.1.1. Herbivory - Selective Grazing

Selective overgrazing by stock, particularly sheep, has been instrumental in degeneration to undesirable species composition changes (Acocks, 1966; Tainton, 1991). Poor grazing management leads to loss of vigour amongst the palatable and normally dominant grasses within the sward whilst having no apparent detrimental effect on *A. junciformis* itself (Edwards *et al.*, 1979; McKenzie, 1982). Management programmes that allow *A. junciformis* to mature in spring appear to be the most detrimental to palatable species (Edwards *et al.*, 1979). Severe defoliation of the palatable species followed by a period of time in which *A. junciformis* seedlings can establish themselves can encourage the encroachment of the species (Tainton, 1972). The unpalatability of *A. junciformis* together with the species' high seed production (Venter, 1968), high germination rate of the seed, and the comparatively deep root system (McKenzie, 1982), appears to give *A. junciformis* a distinct competitive advantage over more palatable species within affected grasslands. Loss of vigour among the palatable species has been attributed to various factors of which excessive stocking rates (inducing increased and more frequent selective grazing); the period of grazing; under grazing (under utilization); damage to apical buds of palatable species (due to burning, trampling or prolonged shading); and the loss of topsoil (through sheet erosion) are considered the most important (Edwards *et al.*, 1979).

Ecological processes typically induced by repeated selective grazing are represented by the results of grazing experiments conducted in Southern Tall Grassveld (Morris and Tainton, 1992). In summer when sheep were introduced into a paddock they concentrated their grazing on selected areas which were grazed short, and to which they repeatedly regrazed whenever sufficient regrowth had accumulated. This repeated grazing of plants in the selected areas resulted in the development of patches of veld which grew slowly relative to the ungrazed veld, even during years when the veld had been rested so that focal points developed for the encroachment of *A. junciformis*.

Once initiated the encroachment of unpalatable species appears to accelerate. As the abundance of *A. junciformis* increased, the grazing pressure on the remaining subclimax species increased and these species were slowly replaced by pioneer grass species of which *Sporobolus africanus* was prominent.

The rate of encroachment of *A. junciformis* also appears to be a function of the length and timing of rest periods provided in seasonal grazing systems. Spring rests in particular allowed

A. junciformis a period of undisturbed establishment when the seedlings are vulnerable (Tainton, 1972). Relatively sudden switches in species dominance occurred in systems of sustained high grazing pressure when the pressure was removed for a period. In one trial the removal of herbivores after 14 years of continuous grazing at a high stocking rate was followed by encroachment of the sward by *A. junciformis*. At the same stocking rate, seasonal rests interspersed between periods of continuous grazing had a similar effect during the grazing phase of the trial.

Apart from the effects of unequal defoliation on palatable and unpalatable species, selective grazing alters the competitive balance in the sward (Briske, 1989). Competition for resources from surrounding plants which remain undefoliated or are lightly grazed accentuate the negative effect of defoliation (Brockett, 1983) and the decline in plant vigour may be distinct and prolonged (Mueggler, 1975). Interspecific competition specifically between *A. junciformis* and desirable species such as *T. triandra* where grazing is highly selective and defoliation severe on palatable plants, results in a decline in vigour of *T. triandra* while *A. junciformis* benefits from the removal of surrounding competition. Work from this study and that reported by Morris and Tainton (1993) have found that the detrimental effects of defoliation on plant vigour were enhanced under the competitive effect of surrounding plants for both *T. triandra* and *A. junciformis*. Reduction of this competition by defoliation of the neighbouring vegetation reduced the influence of defoliation, especially when the plant was severely defoliated. Interestingly the results of Morris and Tainton (1993) showed that *A. junciformis* is more sensitive to the influence of competition when defoliated than *T. triandra* which is not surprising for a species which is resistant to grazing.

The effects of this pattern of grazing and the prolific caryopsis production of *A. junciformis* has also been observed in other species of *Aristida* (O'Connor, 1985). For example *Aristida bipartita* (in study sites in Mphumalanga) maintained relatively prolific caryopsis production even under grazing, while the caryopses of more palatable species such as *Themeda triandra, Setaria incrassata* and *Heteropogon contortus* diminished greatly. The pattern of change observed in the study sites was characterized by the elimination of tall, longer lived, palatable perennial grasses such as *Themeda triandra* and *Heteropogon contortus* accompanied by a marked increase in short, shorter-lived, relatively unpalatable *Aristida bipartita* and the palatable but partially prostrate *Urochloa mosambicensis* and *Sporobolus nitens*.

Further north, studies in Kenya have shown that *Aristida* spp generally increased under heavy grazing (Edroma, 1984; Brown, 1985). The increase in *Aristida* in these areas was partly due to the prolific caryopsis production even under heavy grazing and its consequent representation in the seed bank, a phenomenon also reported for Australian rangelands (Harradine and Whalley, 1980; Brown, 1985).

Incorrect burning management is another major factor believed to be responsible for the increase in *A. junciformis* (Edwards *et al.*, 1979). Staples (1930) and Edwards *et al.* (1979) state that for over 50 years it was advocated that veld burning should be delayed until 12-15 mm of rain had fallen within a 24 hour period in spring. This guideline was proposed in an attempt to eradicate the practice of burning in autumn to obtain a small amount of out of season grazing. Such a long delay in burning has probably been a major contributing factor in increasing the occurrence of *A. junciformis* as the first substantial rainfall in spring is often received long after the veld has started to grow in response to rising temperatures (Staples 1930; Edwards *et al.*, 1979).

Apart from poor grazing and fire management the exact causes of veld degeneration leading to *A. junciformis* domination remain unclear. An increase of *A. junciformis* and the subsequent changes in the species composition of the grassland is often accompanied by detrimental changes in the soil structure caused by increased run off of rain water and sheet erosion of the soil (Bayer, 1955). This in turn makes it difficult for other species to become re-established (Edwards *et al.*, 1979).

In situations where the soil erosion has not appeared to have occurred the failure for species such as *T. triandra* to reestablish is still unexplained. Tainton (1981) suggested that the particular set of conditions such as climate, grazing and fire that *Themeda* veld developed under either no longer exist or do not exist long enough for it to redevelop. O'Connor (1985) contends that an understanding of the mechanisms acting at the sward and individual plant level are needed to explain why *A. junciformis* grassland remains stable under a rest and burning regime where no visible soil degradation has occurred.

Johnson (1989) suggested that physical changes in the soil were responsible for the stability of *A. junciformis* grassland and the lack of reestablishment of palatable species. Johnson (1989) included such agents as excessive burning where the initial effect of burning is to convert all the major nutrients present in plants except nitrogen into oxides. This would temporarily increase the pH (Raison 1979), but on poor or dystrophic soils, the ultimate effect of burning would involve the loss in base status and a subsequent increase in acidification (Raison 1979). Johnson (1989) also found that burning of grasslands leads to an overall export of nutrients from the area, which if not replaced can lead to an imbalance in soil nutrients and a greater dystrophic state. Like burning, grazing also leads to the removal of nutrients from a grassland, this removal being more significant in those areas that are intensively grazed. Johnson (1989) has also argued that acidification of soils and imbalances in soil nutrients can be caused by other agents such as high rainfall (Fey 1981), acid precipitation (Evans 1984; Hall *et al.* 1985), soil disturbance through ploughing, trampling or erosion (Larson, Pierce and Dowdy 1983) among other factors led to a change in the availability of nutrients particularly aluminium which is toxic to most plants (Bennet, Breen and Fey 1985a). Changes in sward composition had altered the nutrient status and pH of the soil therefore were instrumental in ensuring the continued permanence of *A. junciformis*.

Research conducted to test this hypothesis found that *A. junciformis* does indeed have a very high tolerance for soluble aluminium (12 ppm Al) (Fey 1981; Johnson 1989) but the success of *A. junciformis* was probably due more to the poor nutrient status of the soil rather than to the direct effects of the availability or abundance of soluble aluminium (Johnson 1989). The results obtained suggested that low levels of available phosphorus and high percentages of clay, coupled with unusually low total cation counts and nutrient deficiency, may act synergistically with the acid nature of the soils, and the subsequent increased availability of aluminium, to favour *A. junciformis* (Johnson, 1989).

5.1.2. Implications for Veld Productivity

Degeneration in grazing quality due to increasing dominance of *A. junciformis* in previously highly productive grazing lands has occurred at the expense of carrying capacity (Tainton, 1972, 1981). Grasslands are potentially the most productive vegetation types in South Africa, fire climax grasslands in particular being the most productive in terms of animal carrying capacity (0.3 to 0.6 AUha^{-1} per year) (Tainton, 1981).

Most of these fire climax grasslands occur as 'sourveld' which cover approximately 13 million hectares of land in South Africa and support about 1.5 million head of cattle and 6 million sheep (Edwards, 1981). Most of the grasslands in KwaZulu-Natal are fire climax communities where the grasslands have been retained through the restraining effects of fire (Tainton, 1981). Sourveld is characterised by providing palatable material only during the growing season, ability to withstand moderate levels of overgrazing, changes in species composition to more pioneer and less palatable species (rather than a drop in basal cover) when overgrazing and selective grazing is excessive, and extremely slow recovery to more palatable species after degeneration (Tainton, 1981). This implies that any recovery process undertaken to eliminate *A. junciformis* will be a long term process probably in excess of 10 years in which the grazier will have to be extremely careful to protect the palatable species, rigourously avoid overt damage to palatable species such as very hot burns and overgrazing whilst ensuring defoliation of the unpalatable species whenever possible. If economically feasible, regular mowing can be a useful addition to judicious burning to promote the growth of palatable species and restrict *A. junciformis* but is not practical on a field scale or on slopes.

5.1.3. Options for Encroached Grasslands

What is clear is that *A. junciformis* is a species that is unpalatable and therefore escapes grazing (Stuart-Hill and Mentis, 1982). The flowering heads of *A. junciformis* may be utilized to some extent immediately after flowering and in the young seedling stage, when the animals will graze it in the course of grazing the herbage of other species which surround it. Generally however, stock avoid this species once it has become reasonably large (Tainton, 1972).

The overwhelming problem with ngongoni veld is that once it has been dominated by *A. junciformis* it is virtually impossible to eliminate with conventional grazing practices. Attempts at ploughing out severely infested grasslands and reseeding with palatable species of grass such as *T. triandra* have been made. However, these have met with very limited success due mainly to the strong competition from *A. junciformis* and other less palatable species (Venter, 1968; Edwards, 1981; Tainton, 1981).

Farr (1992) cites one case where Ngongoni veld was successfully replaced by being ploughed out, though a cultivated pasture, not the natural grass sward was re-established. The method he advocated was rotovating the ngongoni veld in winter and then leaving it for approximately a month before rotovating again. He noted that *A. junciformis* unlike 'taaipol' (*Eragrostis plana*) is easily destroyed by rotovation. Other management strategies such as spraying with herbicides have been tried to limit the spread of *A. junciformis* into previously unaffected grazing lands and to restore severely affected grazing lands back to a predominately palatable sward. Apart from controlling the spread of the species most of these attempts have been unsuccessful or too expensive and time consuming (Edwards *et al.*, 1979).

At present the only economically feasible management strategies revolve around better veld management. The first of these has been the concept of non-selective grazing which held that palatable species such as *T. triandra* would be favoured as it suffers less under severe defoliation than *A. junciformis* which appears to be more sensitive to the influence of competition when defoliated. This would be enhanced if competition from surrounding plants was also reduced to a minimum.

Unfortunately non-selective grazing remains only a concept as practically it is difficult to achieve complete uniform utilization of the palatable and unpalatable components by selective grazing animals. Attempts to force animals to graze a sward evenly usually result in weight loss, infertility, and occasionally even death. Unpalatable species such as *A. junciformis* are at the most leniently defoliated and often undefoliated while the palatable species are severely utilized (O'Regain and Turner, 1992).

Jones *et al.* (1967; quoted in Johnson, 1989) compared the botanical composition of Natal Mistbelt Ngongoni Veld over a 13 year period to quantify attempts to prevent selective veld grazing by cattle. They concluded that none of their grazing systems prevented cattle from selectively grazing. They found that in attempting to force the cattle to graze *A. junciformis*, regular and severe defoliation of the palatable species occurred. This was coupled with a decrease in the total basal cover of the sward and a steady increase in *A. junciformis* relative to other non-palatable species. They state that 'the effect of the two systems on the veld was nothing short of disastrous... the deterioration of the veld (being) at least partly a consequence of the attempts made to prevent selective grazing.'

Fire is another management tool that has been applied in an attempt to eliminate *A. junciformis*. Venter (1968) examined the effects of fire and different intensities and times of simulated grazing on Natal Mistbelt Ngongoni Veld over a 10 year period. He found that regardless of what defoliation treatment was used, there was no meaningful improvement in the botanical composition of the veld. He concluded that once established in the veld *A. junciformis* cannot be controlled by normal defoliation practices. However, in later work utilizing a four camp system of veld management for Tall Grassveld, Edwards *et al.* (1979) reported positive results. A stocking rate of one steer equivalent per two hectares was used for the growing season, the stocking density being at a high enough level to keep *A. junciformis* well grazed down from about 6 weeks after the paddock had been burned. From the results achieved they recommended a more intensive grazing system for the Natal Mistbelt Ngongoni Veld, again using a four camp system with each camp divided into three paddocks. Three of the 12 paddocks were to be rested at any one time while the period of stay in the grazed paddocks was never more than 10 days and a period of absence of more than 35 days. In both systems some degree of control was achieved over the spread of *A.junciformis.*

This technique was refined for rehabilitation of veld where *A. junciformis* is dominant and *T. triandra* still present, which involves defoliation of *A. junciformis* in the early growth phase when it is acceptable to stock following a burn (Westoby, Walker, and Noy-Meir 1989). *Aristida junciformis* initiates growth earlier in the season than *T. triandra*, especially in seasons where the spring rains are early and graziers can make use of these opportunities to defoliate only *A. junciformis* (Westoby et al., 1989). *Themeda triandra* is relatively unavailable at this stage and escapes severe defoliation.

Morris and Tainton (1993) have also supported this strategy suggesting that *T. triandra* will be favoured over *A. junciformis* under this treatment. Repeated grazing of *A. junciformis* following a burn until soon after initiation of growth by *T. triandra*, followed by a rest for the remainder of the season, should be continued for a number of years if the competitive balance in the sward is to be shifted in favour of *T. triandra*. However in years where late rains result in a narrow gap between the spring initiation of growth in *A. junciformis* and *T. triandra* the veld should be rested to avoid selection for *T. triandra* which would disadvantage it in the sward (Morris and Tainton, 1993).

Veld rehabilitation by Morris *et al.* (1992) based on this strategy found fire to be a useful management tool. Fire constitutes non selective defoliation and according to the results of their trial appears to favour *T. triandra* over *A. junciformis*. In the Southern Tall Grassveld (the site of the trial), seven years of resting with periodic burning altered the composition of veld that was initially dominated by *A. junciformis* (30%) with hardly any *T. triandra* (4%) to a mixed sward where *T. triandra* and *A. junciformis* were equally well represented (14%).

Fire should, however, be applied when the grass is dormant. Winter burning, judging by the basal cover and species composition of the veld, would seem to be perfectly acceptable, and preferable to burning when the veld has commenced growth in the spring, but autumn burning has proved to be unacceptable, if only because it requires two consecutive summer rests in order to accumulate sufficient flammable fuel to permit burning at this time. Spring burning has generally been found to be as acceptable as winter burning, provided it is applied before spring growth has commenced (Tainton, 1981).

It appears from the evidence available that grasslands subject to some form of impact will cross specific thresholds in which change will continue in those grasslands even if the impact is removed (Noy-Meir and Walker, 1986). If the impact is changed, as it was in Morris *et al.*, (1992) investigations into plant species dynamics in Southern Tall Grassveld, swards that either did not respond or responded very differently to the new impact may be suspected of crossing such a threshold and entering into a different state of vegetative structure (Bosch 1989; Friedal, 1991; Laycock, 1991).

The encroachment of *A. junciformis* in Southern Tall Grassveld (where much of the recent work on this species has taken place) appears to be such an example where a specific threshold has been crossed and a different vegetative structure or species dynamics is operative. The pathways of species change in response to imposed perturbations have not always been along a single, reversible, linear gradient and therefore cannot always be represented using a monogradient model of species change (Foran *et al.*, 1978; Hurt and Hardy, 1989; Morris and Tainton, 1992). It is possible that although 'bad' veld management gave *A. junciformis* the initial impetus to become dominant in the sward, it may be exploiting another set of conditions that gives it an even greater competitive advantage over the palatable species which is not directly linked to sward management (Johnson, 1989). An even more interesting possibility raised by this author is that *A. junciformis* in becoming dominant in the sward has changed some factor or factors which prevent the reestablishment of palatable species and that *A. junciformis* is creating its own permanence. The possibility is raised that *A. junciformis* uses resources in a way that they cannot be released to other species or utilizes mechanisms such as the production of allelochemicals preventing reestablishment. Given the ecological complexity of grasslands both above and below ground as in mycorrhizal relationships for example, these possibilities cannot be ruled out.

Some authors appear to have a rather pessimistic outlook for the future control of *A. junciformis* suggesting that unless present economic conditions change markedly in the future the potentially arable Ngongoni veld infested with *A. junciformis* will be planted to pastures and crops while non-arable veld will be planted to forestry (Edwards *et. al.*, 1979; Tainton, 1981).

The results of this study indicate several options for the management of this species. The key is frequent defoliation. However, under present economic circumstances the use of fire is probably the only economically feasible and logistically practical method for many areas in South Africa. If the fuel load is sufficient the grassland should be burnt annually at least for the time it takes to substantially reduce the basal area of *A. junciformis* in the sward. Another option that can be used either alone or more probably in conjunction with burning is to mow the grassland, especially in the early stages of encroachment. Obviously many areas of grassland do not lend themselves either logistically or financially to this but it appears to have several advantages in that palatable species are not as severely put back as they would be after burning in terms of tiller regeneration, the mulch from these species is not lost and forms a suitable seedbed for species such as *T. triandra*, protects the soil surface from the impact of raindrops and reduces topsoil erosion. The reduction of bare open spaces between plants also reduces the ability of *A. junciformis* caryopses to be blown large distances inhibiting further encroachment. Furthermore, much of the caryopses will be caught in the litter layer and fail to germinate whilst still favouring the establishment of caryopses from *T. triandra* for example. Strict control of grazing animals should then be exercised.

In badly encroached areas grazing should be avoided for as long as possible to enhance the competitive abilities of palatable species by allowing them to increase their resources to optimum levels as rapidly as possible. If grazing is to be allowed, the use of bulk grazers such as cattle is preferable to selective concentrate feeders such as sheep and the length of time they are allowed to graze in a specific area limited to ameliorate the effects of selective grazing, overgrazing, trampling, etc. Preferably badly encroached areas should only be grazed before palatable species such as *T. triandra* 'come away' to enhance to the maximum the competitive abilities of these species and that eradication efforts should focus on reducing the basal area and weakening the *A. junciformis* plants through continual repetitive defoliation.

REFERENCES

Anon, 1985. Biochemical test for viability (the topographical tetrazolium test). *Seed Science and Technology* **13**: 446-483.

Anon. 1986. Burning and mowing of veld, Final report. Typed notes. Department of Grassland Science, University of Natal.

Acocks, J.P.H. 1988. *Veld Types of South Africa*. Botanical Survey Memoirs, No. 57 (3rd Ed.). National Botanical Institute, Pretoria.

Bartlett, M.S. 1947. The use of transformations. *Biometrics* **3**: 39-52.

Bayer, A.W. 1955. The ecology of grasslands. In *The Grasses and Pastures of South Africa*. Ed. D. Meredith. CNA, Johannesburg.

Bennet, R.J., Breen, C.M., and Fey, M.V. 1985a. Aluminium uptake sites in the primary root of *Zea mays* L. *South African Journal of Plant and Soil* **2**: 8-17.

Bosch, O.J.H. 1989. Degradation of the semi-arid grasslands of southern Africa. *Journal of Arid Environments* **16**: 143-147.

Briske, D.D. 1989. Vegetation dynamics in grazed systems: a hierarchial perspective. Proceedings of the XVI International Grassland Congress, October 1989, Nice, France: 1829-1833.

Brockett, G.M. 1983. The effect of defoliation on the persistence of *Elionurus muticus* (Spreng.) Kunth in the Highland Sourveld of Natal. *Proceedings of the Grassland Society of southern Africa* **18**: 81-83.

de Winter, B. 1965. The South African Stipaea and Aristideae (Gramineae): (An anatomical, cytological and taxonomic study). *Bothalia* 8: 234-236.

Drewes, R.H. and Tainton, N.M. 1981. The effect of different winter and early spring removal treatments on *Themeda triandra* in the Tall Grassveld of Natal. *Proceedings of the Grassland Society of southern Africa* **16**: 139-143.

Edroma, E.L. 1984. Effects of burning and grazing on the productivity and number of plants in Queen Elizabeth National Park, Uganda. *African Journal of Ecology* **22**: 165-174.

Edwards, P.J., Jones, R.I. and Tainton, N.M. 1979. *Aristida junciformis* Trin. et Rupr.: a weed of the veld. *Proceedings of the 3rd National Weeds Conference of South Africa*, pp 25-32.

Edwards, P.J. 1981. Sour grassveld. In *Veld and Pasture Management in South Africa*. Ed. N.M. Tainton. Shuter and Shooter, Pietermaritzburg.

Evans, L.S. 1984. Botanical aspects of acidic precipitation. *Botanical Review* **50**:449-490.

Farr, J. *1992. Farmer's Weekly*; September 4, page 32, 1992.

Fenner, M. 1979. Germination tests on 32 East African weed species. *Weed Research* **19**:121-126.

Fenner, M. 1980. The inhibition of germination of *Bidens pilosa* seeds by leaf canopy shade in some natural vegetation types. *New Phytologist*, **84**: 95-101.

Fey, M.V. 1981. Aluminium toxicity. *Arena* **4**: 15-18.

Foran, B.D., Tainton, N.M. and Booysen P. de V. 1978. The development of a method for assessing veld condition in three grassveld types in Natal. *Proceedings of the Grassland Society of southern Africa* **13**: 27-34.

Friedal, M.H. 1991. Range condition assessment and the concept of thresholds: A viewpoint. *Journal of Range Management* **44**: 422-426.

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

Gibbs Russell, G.E., Watson, L., Koekemoer, M., Smook, L., Barker, N.P., Anderson, H.M., and Dallwitz, M.J. 1990. Grasses of southern Africa. Botanical Survey Memoirs, No. 58. Botanical Research Institute, Pretoria.

Goodall, D.W. 1965. Plot-less tests of interspecific association. *Journal of Ecology*, **53**: 197-210.

Greig-Smith, P. 1964. Quantitative plant ecology (2nd edn.). Buttterworths, London.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* **52**: 107-145.

Hall, R.J., Driscoll, C.T., and Likens, G.E. 1985. Physical, chemical, and biological consequences of episodic aluminium additions to a stream. *Limnology and Oceanography* **30**: 212-220.

Harper, J.L. 1977. *Population biology of plants*. Academic Press, London.

Harradine, A.R., and Whalley, R.D.B. 1980. Reproductive development and seedling establishment of *Aristida ramosa* R.Br. in northern New South Wales. *Australian Rangeland Journal* **2**: 124-135.

Heady, H. F., and Child, R. D. 1994. *Rangeland Ecology & Management*. Westview Press, Colorado.

Hurt, C.R. and Hardy, M.B. 1989. A weighted key species method for monitoring changes in species composition of Highland Sourveld. *Journal of the Grassland Society of southern Africa* **6**: 109-113.

Johnson, P.A. 1989. Veld degeneration associated with an increase in *Aristida junciformis* Trin. *et* Rupr. dominant communities. *Investigational Report* No. 39. Institute of Natural Resources, University of Natal, Pietermaritzburg.

Jones, R.J., Theron, E.P. and Venter, A.D. 1967. Final Report, Project N-Ce15. Department of Agricultural Technical Services, Natal Region, Cedara.

Klug, J.R. 1989. Dry Matter Production Patterns in the Southern Tall grassveld of Natal. MSC (Agriculture) thesis, University of Natal, Pietermaritzburg.

Larson, W.E., Pierce, F.J., and Dowdy, R.H. 1983. The threat of soil erosion to long-term crop production. *Science* **219**: 458-465.

Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. *Journal of Range Management* **44**: 427-433.

MacVicar, C.N., de Villiers, J.M., Loxton, R.F., Verster, E., Lambrechts, J. N., Merryweather, R.F., le Roux, J., van Rooyen, T.H., and von Harmarmse, M. 1977. Department of Agricultural Technical Services, Science Bulletin 390, Government Printer, Pretoria.

McKenzie, B. 1982. Resilience and stability of the grasslands of Transkei. *Proceedings of the Grassland Society of southern Africa* **17**: 21-24.

Morris, C.D. and Tainton, N.M. 1993. The effect of defoliation and competition on the regrowth of *Themeda triandra* and *Aristida junciformis* subsp. *junciformis*. *African Journal of Range and Forage Science* **10**: 124-128.

Morris, C.D., Tainton, N.M. and Hardy, M.B. 1992. Plant species dynamics in the Southern Tall Grassveld under grazing, resting and fire. *Journal of the Grassland Society of southern Africa* **9**: 90-95.

Mott, J.J. 1972. Germination studies on some annual species from an arid region of Western Australia. *Journal of Ecology* **60**: 293-304.

Mott, J.J. 1974a. Mechanisms controlling dormancy in the arid zone grass *Aristida contorta*. I Physiology and mechanisms of dormancy. *Australian Journal of Botany* **22**: 635-645.

Mott, J.J. 1974b. Mechanisms controlling dormancy in the arid zone grass *Aristida contorta*. II Anatomy of the hull. *Australian Journal of Botany* **22**: 647-653.

Mueggler, W.F. 1975. Rate and pattern of vigour recovery in Idaho fescue and bluebunch wheatgrass. *Journal of Range Management* **25**: 88-92.

Noy-Meir, I. and Walker, B.H. 1986. Stability and resilience in rangelands. In *Rangelands: a resource under siege*. Eds. P.J. Joss, P.W. Lynch and O.B. Williams. Cambridge University Press, Cambridge.

O'Connor, T.G. 1985. A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa. *South African Natural Science Programmes* report **114**, Council for Scientific and Industrial Research, Pretoria.

O'Connor, T.G. 1991. Patch colonisation in a savanna grassland. *Journal of Vegetation Science* **2**: 245-254.

O'Reagain, P.J. and Turner, J.R. 1992. An evaluation of the empirical basis for grazing management recommendations for rangeland in southern Africa. *Journal of the Grassland Society of southern Africa* **9**: 38-49.

Peart, M.H. 1979. Experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* **67**: 843-863.

Peart, M.H. 1981. Further experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* **69**: 425-436.

Peart, M.P. 1984. The effects of morphology, orientation and position of grass diaspores on seedling survival. *Journal of Ecology* **72**: 437-453.

Pielou, E.C. 1962. The use of plant-to-neighbour distances for the detection of competition. *Journal of Ecology*, **50**: 357-367.

Raison, R.J. 1979. Modifications of the soil environment by vegetation fires with particular reference to nitrogen transformations: a review. *Plant and Soil* **51**: 73-108.

Rethman N.F.G. and Booysen, P. de V. 1968. The influence of time of defoliation on the vigour of a tall grassveld sward in Natal. *Proceedings of the Grassland Society of southern Africa* **7**: 39-43.

Rice, E.L., Penfound, W.T., and Rohrbaugh, L.M. 1960. Seed dispersal and mineral nutrition in succession in abandoned fields in central Oklahoma. *Ecology* **41**: 224-228.

Roundy, B.A., Taylorson, R.B., and Sumrall, L.B. 1992. Germination responses of Lehmann lovegrass to light. *Journal of Range Management* **45**: 81-84.

Savage, M.J. 1980. The effect of fire on the grassland microclimate. *Herbage Abstracts* **50**: 589-603.

Sawer, E.R. 1911. Notes on the botanical and chemical composition of the veld herbage in Natal. Appendix VII. In *Cedara Memoirs on South African Agriculture* **2**: 365-371.

Sheldon, J.C., and Burrows, F.M. 1973. The dispersal effectiveness of the achene pappus units of selected Compositae in steady winds with convection. *New Phytologist* **72**: 665-675.

Siegal, S., and Castellan, N.J. 1988. Nonparametric statistics for the Behavioral Sciences. McGraw-Hill, New York.

Silvertown, J. 1980. Leaf-canopy induced seed dormancy in a grassland flora. *New Phytologist*, **85**: 109-118.

Silvertown, J. 1981. Micro-spatial heterogeneity and seedling demography in species-rich grassland. *New Phytologist* **88**: 117-128.

Smith, H. 1982. Light quality, photoreception, and plant strategy. *Annual Review of Plant Physiology* **33**: 481-518.

Staples, R.R. 1930. Studies in veld management. *Science Bulletin*, No. 91. Department of Agriculture of South Africa, No. 278. Government Printer, Pretoria.

Staples, R.R. and Taylor, A.J. 1929. Studies in pasture management: a preliminary report on the seasonal composition of certain South African pasture grasses in relation to manuring and intensity of grazing. *South African Journal of Science* **26**: 139-153.

Steel, R.G.D., and Torrie, J.H. 1980. *Principles and procedures of statistics.* McGraw-Hill, London.

Stokes, C.J., and Yeaton, R.I. 1994. A line-based vegetation method and its application in succulent karoo. *African Journal of Range and Forage Science* **11 (1)**: 11-17.

Stuart-Hill, G.C. and Mentis, M.T. 1982. Coevolution of African grasses and large herbivores. *Proceedings of the Grassland Society of southern Africa* **17**: 122-128.

Tainton, N.M. 1972. The relative contribution of overstocking and selective grazing to the degeneration of tall grassveld in Natal. *Proceedings of the Grassland Society of southern Africa* **7**: 399-43.

Tainton, N.M., Bransby, D.I. and Booysen, P. de V. 1976. *Common Veld and Pasture Grasses of Natal.* Shuter and Shooter, Pietermaritzburg.

Tainton, N.M., Foran, B.D., and Booysen, P de V. 1978. The veld condition score: an evaluation in situations of known past management. *Proceedings of the Grassland Society of southern Africa* **13**: 35-40.

Tainton, N.M., Booysen, P de V., Bransby, D.I., and Nash, R.C. 1978. Long term effects of burning and mowing on tall grassveld in Natal: Dry matter production. *Proceedings of the Grassland Society of southern Africa* **13**: 41-44.

Tainton, N.M. 1981. The ecology of the main grazing lands of South Africa. In *Veld and Pasture Management in South Africa*. Ed. N.M. Tainton. Shuter and Shooter, Pietermaritzburg.

Tainton, N. M. 1991. Why do we insist on rotational grazing? Bulletin of the Grassland Society of southern Africa Supplement **1**: 2-6.

Taylor, H.M., and Gardner, H.R. 1960. Use of wax substrates in root penetration studies. *Proceedings, Soil Science Society of America* **24**: 79-81.

Theron, E.P. 1966. A study of certain chemical and physical properties of ten indigenous grasses and their relationships to animal preferences. Unpublished Ph.D. Thesis, University of Natal, Pietermaritzburg.

Thompson, K., Grime, J.P., and Mason, G. 1977. Seed germination in response to diurnal fluctuations of temperature. *Nature* **267**: 147-149.

Venter, A.D. 1962. Studies on the Ngongoni veld of the Natal mistbelt. Unpublished M.Sc. Thesis, University of Natal, Pietermaritzburg.

Venter, A.D. 1968. The problems of *Aristida junciformis* encroachment into the veld of Natal. *Proceedings of the Grassland Society of Southern Africa* **3**: 163-165.

Westoby, M., Walker, B., and Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**: 266-274.

Williams, E.D. 1983. Effects of temperature fluctuation, red and far-red light and nitrate on seed germination of five grasses. *Journal of Applied Ecology* **20**: 923-935.

Wright, R.G., and van Dyne, G.M. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *Southwestern Naturalist* **21**: 259-274.

Yeaton, R.I., and Cody, M.L. 1976. Competition and spacing in plant communities: the northern Mohave Desert. *Journal of Ecology* **64**: 689-696.

Yeaton, R.I. 1990. The structure and function of the Namib Dune grasslands: species interactions. *Journal of Arid Environments*, **18**: 343-349.

Zacharias, P.J.K., Tainton, N.M., and Oberholster, C. 1988. The effect of fire on germination in five common veld grasses. *Journal of the Grassland Society of southern Africa* **5:** 229-230.

PERSONAL COMMUNICATIONS

Mr. S. Moodley
Computing Centre for Water Research (CCWR)
University of Natal
Pietermaritzburg
PO Box 375
Pietermaritzburg
3200

Dr P.J.K. Zacharias
Department of Range and Forage Science
University of Natal
PO Box 375
Pietermaritzburg
3200

APPENDIX 1 - PROGRAMME FOR DETERMINING BASAL AREAS OF GRASS SPECIES

```
########################################################################
#1species#Description:
#      # CALCULATION OF VARIOUS SPECIES AREAS FROM A TRACED MAP
#     #
#     # Images                  : Generated (size 512x768)
#     #
#     # Written by              : Barry Dudley & van Zyl
#     #
#     # Stored as         : 1Species. (MCR)
#     #
#     # Date                    : 12/08/94
#     #
#     # System                  : VIDAS 2.1 (Colour or black and white)
#     #
######################################################################

###### initialization ############

alpha
tvchan Channel=2, Syncin=2
measstop
resetpar
resetlim
scalgeom Image=1, Scale=’1:1-scale", Inter=_OFF, List=_OFF
```

```
clearall GreyValue=0
clearallov
setframe Frame="F512"
setimpath ImagePath="f:bamboo.bot”
loadlut File="grey”
ovcolour Mode=6
w=500
for i=1, i<15, i=i+1: write”“
time in seconds for wait
clear message window
####################################################################
#### scale MEASUREMENT ############## (remember to measure go below this)

clearmes
write “start here if you have just started or moved the camera”
write “turn on the camera and press any key to continue.....”
write “”
pause
tvon
write “place the scale-thing-under the micro.”
pause
tvinp Image=1
display Image=1
tvchan Channel=0, Syncin=0
scalgeom Image=1, Scale="1:1-scale”, Inter=_ON, List=_ON
```

```
marker Input=1, UnitX=10, UnitY=10, ClearOv1=_ON, Grid=_ON, Scales=_ON, Font_?=2
pause

############ THIS IS WHERE THE OBJECT MEASURING STARTS. ########

clall
clearmes
tvchan Channel=2, Syncin=2
loadlut File=”grey”
display Image=1
tvon
write “place drawing under camera”
write “do not change zoom or height etc...”
pause
tvinp Image=1
tvchan Channel=0, Syncin=0
display Image=1
clearmes
write “”
write “INTERACTIVE STEP-discriminate using mouse,”
write “aim for continuous green lines”
normim Input=1, Output=2, Threshold=5
write “this requires you to select (green) your objects from the background”
dis2lev Input=2, Outpost=3, LevelLow=64, LevelHigh=191, Binary=_ON, Inter=_ON, Mode_?=1
display Image=3
```

```
75: write "discriminated image displayed"

76: scrap Input=3, Output=4, Select=_OFF, AreaLow=0, AreaHigh=100, BinaryInp=_ON, BinaryOut=ON

77: identify Input=4, Output=4, Conn_8=_ON, RefArea=_OFF

78: cutlink Input=4, Output=4, Auxiliary=5, Thickness=5, Phase=0, Inter=_ON

79: display Image=5

80: fill Input=4, Output=5

81: display Image=5

82: clearmes

83: write "check that all areas have been filled"

84: identframe Input=5, Output=6, Conn_8=_ON, FrMode=1, SizeX=766, SizeY=510, StartX=1, StartY=1, Display=_ON, Inter=_OFF, RefArea=_OFF

85: dispaly Image=6

86: write "This is the check part of the macro - correct the image"

87: cutlink Input=6, Output=1, Auxiliary=5, Thickness=5, Phase=255, Inter=_ON

88: identify Input=1, Output=3, Conn_8=_ON, RefArea=_OFF

89: fill Input=3, Output=3

90: display Image=3

91: identify Input=3, Output=4, Conn_8=_ON, RefArea=_OFF

92: rejectobj Image=4, Aux=6, GreyValue=0

93:

94: # MEASUREMENT

95:

96: clearmes

97: InitObj ACPX, ACPY, AREA, DMAX, DMIN, PERIM
```

```
fvtemp[]=AREA, ACPX, ACPY, DMAX, DMIN, PERIM
DBerase DataBase=”temp”
Dbcreate DataBase=”temp”, Fvector=”fvtemp”
Dbopen DataBase=”temp”, Fvector=”fvtemp”
display Image=4
write “Will measure.......”
measobj Image=4, DataBase=”temp”, Append=_OFF
write “”
write “Write checking measurement - “
write ”“
loadlut File=”grey”
fill Input=4, Output=4
contour Input1=4, Input2=2, Output=6, Shape=7, PhaseCont=128, Overlay=_ON, Inside=_OFF
display Image=6
wait Mseconds=2000

########### entering user value for SPECIES ###########

external AREA, PERIM, DMAX, DMIN
global AREANO
AREANO=0
fvspec3[]= AREA, PERIM, DMAX, DMIN, AREANO
fvspec4[]= AREA, PERIM, DMAX, DMIN, AREANO
Dberase DataBase=”spec4"
Dbcreate Database=”spec4", Fvector=”fvspec4"
```

```
Dbopen DataBase=”spec3", Fvector=”fvspec3"
Dbopen DataBase=”spec4", Fvector=”fvspec4"
Dbopen DataBase=”temp”, Fvector=”fvtemp”
display Image=2

while (1)
Dbread DataBase=”temp”
if (_STATUS) : break
Grectg Image=2, StartX=int(ACPX), StartY=int(ACPY), SizeX=10, SizeY=10, Colour=-1, Mode_?=7
write “THIS AREA= “, AREA
read “ ENTER YOUR SPECIES SPECIFIC VALUE : “, AREANO
Dbappend DataBase=”spec3"
Dbappend DataBase=”spec4"
Gstring Image=2, StartX=int(ACPX+20), StartY=int(ACPY+20), Text=AREANO, Colour=-1, Font_?=1, Mode_?=0
#Gstring 2, int (ACPX), int (ACPY+5), AREA, -1, 1, 0
endwhile

Dbclose DataBase=”temp”
Dbclose DataBase=”spec3"
Dbclose DataBase=”spec4"
outlist DataBase=”spec4", Print=_OFF
#outlist “spec3",_OFF

```

```
write “E”
write “      N”
write “             D”

#########################################################################

stop

printmacro Macro=”library”
printmacro Macro+”1species”

###   IMAGE STORE   ###

clearmes
m=4
bamtxt1=”“
read “The No. of the image you will store :  “,m
read “The NAME of the image you will store :  “, bamtxt1
write “The image, No : “, m, “will be stored as   :   “, bamtxt1
storim File= bamtxt1, Image=m
stop
dos Command=”“
### IMAGE retrieval ###

clearmes
```

```
clovl Image=1
clear Image=1, Phase=0
write “HAVE THE F: DRIVE READY FOR IMAGE RETRIEVAL”
read “The No. Of the image you will to retrieve to : “,m
read “The NAME of the image you want to retrieve : “, bamtext1
getim File=bamtxt1, Image=m
stop

####### the end of the macro 1species. (mcr) #######
```