THE REGENERATION POTENTIAL OF *THEMEDA TRIANDRA* IN THE MIDDELBURG DISTRICT OF THE EASTERN CAPE

By

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DECLARATION

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

SUMMARY

A common topographical feature of the Nama-Karoo are mesas, commonly known as "platkoppies", that provide an interesting source of landscape heterogeneity to an otherwise flat landscape. Although these isolated mesas are geologically and edaphically distinct from the surrounding flats, many species are shared between these habitats. These include palatable species such as *Themeda triandra*. A question asked by the broad umbrella project under which this project falls was: to what extent do mesas provide refuges for palatable species that are under pressure from heavy overstocking on the surrounding flats?

A study on the regeneration potential of *T triandra* on and off the Tafelberg Mesa in the Middelburg district of the Eastern Cape, South Africa, was undertaken within the context of a broader umbrella project "Restoration of degraded Nama-Karoo: role of conservation islands". The Nama-Karoo has had centuries of heavy commercial livestock production and it is considered to have been transformed from a relatively (by arid ecosystems) productive system to one dominated by shrubs and somewhat less productive species. *Themeda triandra* is one of the preferred grass species for livestock production. Although *T. triandra* is a preferred grass species, relatively, little is known about its ability to produce viable seed and the establishment of seedlings particularly in restoration and rehabilitation programmes. This study examines the pattern of seed production and seedling survival, seed dispersal, seed germination, and the morphological and ecophysiological variability of *T. triandra*, a species with great potential for restoration of degraded Nama-Karoo sites, particularly those in the Eastern Cape.

Themeda triandra was found to be one of the dominant species on summit of the Tafelberg Mesa. In comparison, it occurred in small isolated populations on the flats surrounding the mesa. The flats and slopes are grazed more intensely by domestic livestock than the summit of the mesa. This is due to the inaccessibility to livestock due to a steeper topography and the lack of water at the higher altitudes.

Annual seed production of *T. triandra* per plant and per m^2 was highest for the populations on the flats despite these populations being grazed most intensively. Rainfall

had an effect on annual seed production, which was monitored over two years. Rainfall increased from less than 20mm in November 1999 to 125, 110, 50 and 135mm in December 1999, January 2000, February 2000 and March 2000 respectively. With the increased rainfall prior to the May 2000 sampling period, more seeds were produced per plant and per m^2 for the flats and slopes habitats of the Tafelberg Mesa. The opposite trend occurred on the summit of the mesa, where seed production actually decreased. This could be attributed to increased competition or to lower grazing intensities. Increase in rainfall also had a positive effect on the cover of other grasses (excluding *T. triandra*) and *T. triandra* itself. Despite higher levels of seed production in populations of *T. triandra* on the flats, seedling survival was clearly low whereas seedlings on the slopes and summit had significantly higher seedling survivorship. This negative impact could be explained due to the trampling effect of domestic herbivores.

The results of a seed dispersal experiment clearly suggest that the seed dispersal distance of *T. triandra* to "safe" microsites is short distance (majority of seeds disperse up to 60cm) and that the dispersal agent is wind. Microsites for re-establishment was found to be open or rocky sites.

In a controlled experiment, seed emergence of *T. triandra* indicated that optimal sowing depths varied with soil type. Maximum germination was achieved at sowing depth 2cm and 3cm in soil collected from the flats surrounding the Tafelberg Mesa. The soil texture of the flats was found to be more sandy loam clay. The flats had slightly higher content (%) of stone, clay, silt and sand compared to the soils collected from the summit and slopes. *Themeda triandra* is clearly not limited in its expansion onto the flats in the Middelburg district due to soil conditions at the germination/recruitment phase. This study also revealed that *T. triandra* germinates best under summer conditions when the probability of rainfall is at its highest. Results with *T. triandra* seed did not convincingly suggest that smoke water is of adaptive significance to boost germination in restoration attempts in the Middelburg district of the Eastern Cape.

In a controlled greenhouse experiment, individuals of *T. triandra* taken from the summit of Tafelberg Mesa showed no differences in photosynthesis, stomatal conductance or transpiration rates to individuals occurring on the flatland areas surrounding the mesa. *Themeda triandra* appears to be relatively adaptable to a range of temperature conditions. These findings suggest that there should be no problem using seed from mesa summits in restoration programmes on the surrounding flats.

This study revealed no conclusive evidence, indicating that the populations on the summit of the mesa were a source of *T. triandra* seed for the flats surrounding the Tafelberg Mesa. However, this two year long investigation found that *T. triandra* has the potential to be used in restoration and rehabilitation programmes. If released from grazing pressures, and assuming favourable climatic conditions, the density of *T. triandra* on the flats can be increased and can be used as a suitable species for the restoration of heavily degraded patches in the Nama-Karoo Region.

OPSOMMING

`n Algemene topografiese kenmerk van die Nama-Karoo is mesas, plaaslik bekend as "platkoppies", wat `n interessante bron van landskap ongelyksoortigheid voorsien aan `n andersins vlakte landskap. Alhoewel hierdie geisoleerde mesas geologies en biofisies verskillend is van die omliggende vlaktes, word baie plant spesies gedeel tussen hierdie habitats. Hierdie sluit in smaaklike spesies soos *Themeda triandra*. `n Vraag gevra deur die groter restorasieekologieprojek waaronder hierdie navorsingsprojek resorteer was: tot watter mate dien mesas as `n hawe aan vreetbare spesies wat onder druk is van swaar oorbeweiding in die omliggende vlaktes?

`n Studie van die regenerasie potensiaal van *T. triandra* op-en-vanaf die Tafelberg Mesa in die Middelburg distrik van die Oos-Kaap, Suid-Afrika, was onderneem binne die verband van die wyer herstelekologieprojek "Herstel van oorbeweide Nama-Karoo weiveld: die rol van bewaringseilande". Die Nama-Karoo was vir honderde jare al blootgestel aan swaar kommersiële lewende hawe produksie en is klaarblyklik verander van `n relatiewe produktiewe sisteem na 'n ekosisteem gedomineerd deur struike en enigsins minder produktiewe spesies. Alhoewel dit `n verkiesde grasspesie is bo ander inheemse grasse as weigras, is min bekend oor die fertiliteit van *T. triandra* sade of oor die vestiging van saailinge, veral in veldrehabilitasie programme. Hierdie studie ondersoek die patrone van saadproduksie, saadverspreiding, saadontkieming, en die morfologiese en ekofisiologiese veranderlikheid van *T. triandra*, `n spesie met groot potensiaal vir die herstel van oorbeweide Nama-Karoo terriene van veral die Oos-Kaap.

Themeda triandra was een van die dominante spesies op die kruin van die Tafelberg Mesa. Dit kom voor in klein geïsoleerde populasies op die uitgestrekte vlaktes rondom die mesa. Die vlaktes en hange van die mesa word op groot skaal oorbewei deur lewende hawe in vergelyking met op die kruin van die mesa. Dit is te wyte aan die onbereikbaarheid van die mesa vanweë `n steiler topografie, asook die gebrek aan standhoudende water op die mesa's self.

Jaarlikse saad produksie van *T. triandra* per plant en per m^2 was die hoogste vir die populasies op die vlaktes, ten spyte daarvan dat hierdie populasies intensief bewei

word. Reënval het `n effek op jaarlikse saad produksie gehad wat oor twee jaar gekontroleer was. Met die vermeerdering van reënval voor die Mei 2000 proeftydperk, was meer sade geproduseer per plant en per m^2 op die vlaktes en hange van die Tafelberg Mesa. Die teenoorgestelde patroon het voor gekom op die kruin van die mesa, waar saadproduksie afgeneem het. Laasgenoemde kan toegeskryf word aan die toename in kompetisie. Toename in reënval het ook `n positiewe effek gehad op die bedekking van *T. triandra* self sowel as van ander grasse. Ten spyte van hoër vlakke van saadproduksie, is saailing oorlewing in *T. triandra* populasies op die vlaktes duidelik negatief terwyl saailinge op die hange en kruin `n betekenisvolle hoër saailing oorlewingsskap gehad het. Die negatiewe impak kan verduidelik word deur die vertrappings-effek van lewende hawe.

Die resultate van die saadvespreidingeksperiment toon dat die saadverspreiding afstand van *T. triandra* na 'veilige' mikroterreine kort is (die meerderheid van die sade is tot minder as 60cm versprei). Wind is die verspreidingsagent. Dit is gevind dat oop of klipperige terreine gunstige mikroterreine vir hervestiging van *T. triandra* is.

In die gekontroleerde-eksperiment het saadverskyning van *T. triandra* aangedui dat die optimale saai-diepte wissel met grondsoort. Maksimum ontkieming is behaal by saai-diepte van 2cm en 3cm in die grond versamel in die vlaktes rondom die Tafelberg Mesa. Die grondtekstuur op die vlaktes is `n sanderige leem-klei. Die vlaktes het effens hoër persentasies klip, klei, slik en sand vergelyke met die grond versamel op die kruin en hange. *Themeda triandra* is duidelik nie as gevolg van grondtoestande beperk in sy uitbreiding op vlaktes in die Middelburg distrik by die ontkieming/werwing fase. Gondtoestande tydens die ontkiemingsfase is duidelik niw beperkend op die gigthede van *T. triandra* op die vlaktes nie. Hierdie studie maak bekend dat *T. triandra* die beste ontkiem onder somer toestande wanneer die waarskynlikheid van reënval op sy hoogste is. Rookwater het geen effect op die ontkiemingspotensiaal van *T. triandra* in die Middelburg streek van die Oos-Kaap nie. Pogings om *T. triandra* saad se ontkieming met rookwaterekstrak te bevorder was onsuksesvol.

In die gekontroleerde eksperiment het individue van *T. triandra* op die kruin van Tafelberg Mesa geen verskil getoon in fotosintese, huidmondjie begeleiding en transpirasie tempo nie in vergelyking met individue wat voorkom op die vlaktes rondom die mesa. *Themeda triandra* blyk relatief aanpasbaar te wees aan `n wye reeks van temperatuur toestande. Hierdie bevindings dui aan dat daar geen probleem hoef te wees om sade van die kruin van die mesa te gebruik in hervestigig-programme in die omliggende vlaktes nie.

Hierdie studie verskaf geen bewyse wat aandui dat die *T. triandra* bevolkings op die kruin van die mesa as `n bron van saad vir die vlaktes rondom die Tafelberg Mesa dien nie. Hierdie twee-jaar ondersoek vind dat *T. triandra* ‘n potensiaal het om gebruik te word in herstel en rehabilitasie programme. As dit aan ligter weidingsruk onderwerp is en gunstige klimaatstoestande heers, kan *T. triandra* hervestig word op die vlaktes en gebruik word as `n plantspesie om erg beskadigde areas in die Nama-Karoo streek te herstel.

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Inspirational thought by Chantal May: *"Don't let life discourage you, everyone who got where he is had to begin where he was"*

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Chapter one

Introduction to a study on *Themeda triandra* in the Middelburg district, Eastern Cape

1.1 Context of this study

Rangelands are characterized by vegetation which is dominantly comprised of grasses, grass like plants, forbs and/or shrubs that are grazed by herbivores. It is by far the single largest land category in the world (43 %), which exceeds forest land (18 %), cropland (10 %), industrial-residential (4 %), and non-productive areas such as glaciers and mountain peaks (15 %) (Lewis 1969). Rangelands are primarily associated with grazing of domestic livestock, wildlife habitat, recreation and mineral production. Rangelands also have scientific and aesthetic value. However, rangelands can be diverse and complex just as the products and benefits they provide. Today, rangelands worldwide are faced with many biological and ecological issues that threaten their existence. One such threat is land degradation.

Land degradation is defined as the reduction or loss of the biological or economic productivity of vegetation and soil. This is especially problematic in arid and semi-arid environments. This process is caused by various factors, such as climate variations and human activities (UNEP 1994). For example, leading causes of land degradation in north-western Jordan were primarily improper farming practices (such as failure to use contour plowing), overgrazing, rangeland conversion to croplands and the uncontrolled expansion of urban and rural settlement at the cost of cultivable land (Khresat *et al.* 1998). It is the removal of vegetation by overgrazing and trampling with subsequent soil erosion that is believed to be responsible for land degradation in South Africa (Hoffman *et al.* 1999). Overgrazing is defined as the repeated utilisation of vegetation until reserve nutrients in the roots are exhausted. Plants thus struggle to absorb water effectively and later die off. It would be interesting to know whether a particular level of dysfunction in a degraded ecosystem can be reversed by simply removing the cause of degradation, or by interrupting it as it develops. This however would require a much more detailed investigation due to the various factors involved in the degradation process.

South African reviews and official investigations in the past concluded that it is people and their land use practices, and not climate, that should be blamed for the state of the environment (Acocks 1953; Wilcocks 1977). Prolonged droughts may form a catalyst for desertification (Tyson 1986). However, whether or not degraded rangelands can recover rapidly by themselves is still a contentious issue among range scientists (Ludwig *et al.* 1996).

The Nama-Karoo is a rangeland located on the central plateau of the Cape Province, the south-western Orange Free State and the southern interior of Namibia (Rutherford and Westfall 1986). The extensive arid and semi-arid areas of the south-western part of southern Africa encompass a high diversity of climates, landforms, soil and vegetation. The arid zone has been divided into three biomes, viz the Nama-Karoo, Succulent-Karoo and Desert (Rutherford and Westfall 1986). The Desert Biome is confined to the coastal forelands of Namibia and southern Angola, while the Succulent Karoo and Nama-Karoo Biomes are within South Africa (Cowling 1986). The Middelburg district in the Eastern Cape, where this research project was based, falls within the Nama-Karoo. The Nama-Karoo Biome covers 607 235 km^2 of South Africa (Palmer and Hoffman 1997) and occupies 28% of South Africa. Dwarf shrublands and arid grasslands are characteristic vegetation types of this biome. Within the biome, the overall increase in grass cover from west to east is correlated with an overall increase in rainfall and a declining proportion of winter rain (Acocks 1953; Werger 1978).

Poor land management and excessive exploitation of this semi rangeland has resulted in widespread loss of palatable vegetation in this biome (Hoffman *et al.* 1999). We also know that semi-arid grasslands are slow to respond to sustainable management because of low rainfall and extreme temperatures (Tainton 1999). The frequency of droughts in these regions contributes to the need for appropriate management strategies.

While withdrawal of grazing may result in recovery of the vegetation (Danckwerts and Stuart-Hill 1988), badly impacted areas might not recover within an economically viable time frame. In these situations, active intervention (e.g. restoration) would be required. This thesis focuses on the biology of one particular species, *Themeda triandra*, which is a good potential candidate for restoration efforts in the eastern parts of the Nama-Karoo.

From a farmer`s perspective, *Themeda triandra* is an important plant species. *Themeda triandra* is a palatable perennial grass that flowers between September and June and can reach a height of between 300 - 1500 mm. It is found dominantly in the Eastern parts of Southern Africa (Figure 1.1) (Gibbs Russell *et al.* 1990) and along the western part of Namibia in higher latitude areas. Besides the African continent, *T. triandra* also occurs on two other continents, namely, Asia and Australia. Morphologically, it is extremely variable and the different ecotypes vary according the environment in which they grow (Gibbs Russell *et al.* 1991). Grazing by domestic livestock over the past century has resulted in significant changes in the botanical composition of natural grasslands and it is believed that the current distribution of *T. triandra* has been significantly reduced in historical times due to the effects of grazing and climate change. The decline of this species with grazing is mainly influenced by plant responses to defoliation, life-form attributes (seed bank dynamics and morphology), herbivore selection for a species and foraging behaviour such as patch grazing (Ash and McIvor 1998) and fire regime. Lunt (1995) stated that many grassland remnants dominated by *T. triandra* require regular burning, grazing or slashing to promote regeneration, flower and seed production.

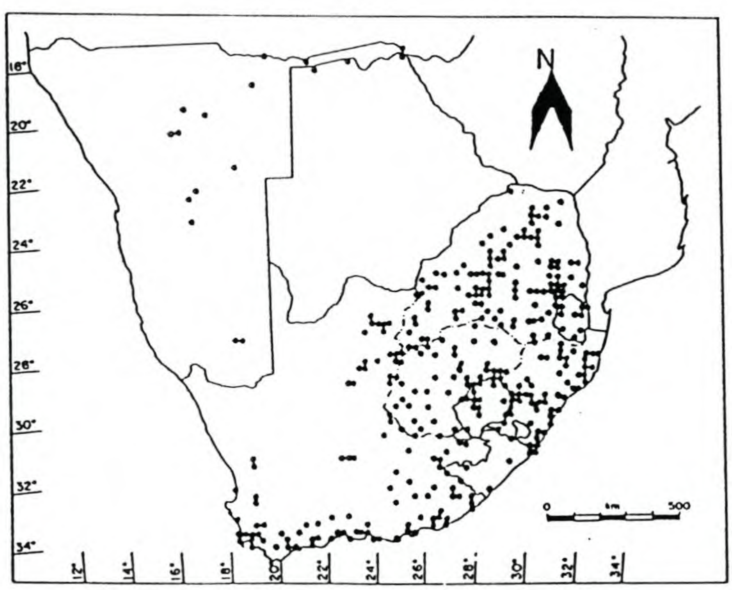


Figure 1.1 Distribution map of *Themeda triandra* in southern Africa (Gibbs Russell and Spies, 1988). • = locality records.

Although *T. triandra* is very variable and a lot is known about it in general (Gibbs Russell *et al.* 1991; Lunt 1995; Ash and McIvor 1998), this thesis focuses on the less understood aspects relating to the restoration potential of *T. triandra* in the Middelburg district.

Mesas are one of the common topographic features in the Nama-Karoo (King 1942) and may act as habitat islands for palatable species that may be locally extinct on the flats. Flats in this region are described as relatively flat landscapes with drainage lines, number of seasonal streambeds, flooded areas and ephemeral seeps. *Themeda triandra* is common on the slopes and summits of mesas in the Middelburg district, but only occurs as isolated patches on the flats. *Themeda triandra* was not recorded on the flats during a related study in this area (Pienaar 2000), because of its exceptionally patchy distribution (pers. obs.). Domestic livestock and indigenous animals do graze on mesas, normally moving up the slopes until gradients become too steep or unstable and therefore become unreachable. The summit of Tafelberg Mesa is being used by indigenous animals and not by domestic livestock. Joubert (1997) suggested in his study of grazing gradients that steeper slopes are more likely to be used than the flatter slopes.

1.2 Justification for Research

Mesas are a common topographical feature in the Nama-Karoo region. Vegetation composition of the mesas in the karoo has the potential to be in a less degraded state than the vegetation on the flats surrounding these mesas. Thus, mesas may provide us with clues as to what the vegetation composition of the karoo used to be like 100-200 years before present, and before the introduction of domestic livestock.

Themeda triandra is a preferred plant species for grazing and is of extreme importance to domestic livestock. Because of high grazing pressure in this region, the population biology of this species has been severely impacted. This study investigates *T. triandra* which occurs in populations on the summit of and off (in protected areas) the mesas in the Middelburg district.

This study provides background data on the regeneration potential of *T. triandra.* This includes aspects of seed production in the various populations, its potential for dispersal, germination behaviour and seedling survival.

1.3 Collaboration with broad umbrella project

This study is a component of a broader project funded by the European Union and National Research Foundation that focuses on the "Restoration of degraded Nama-Karoo: the role of conservation islands". Five partners were involved in this umbrella project with Dr. Esler as my team leader (Table 1.1). The aim of the umbrella project was to assess the value of mesas in the area as conservation islands and their potential use in restoration attempts. This component of the umbrella project provides data on key biological attributes (seed production and seedling survival; seed dispersal; seed germination; and key ecophysiological characteristics) of *Themeda triandra* for the Middelburg district of the Eastern Cape, South Africa. After the initial survey, it became evident that this grass species could play an important role for restoration in the Middelburg district. It was then decided to build a generalised model focussing on the restoration potential of plant species on the local scale using *Themeda triandra* as starting point. This model was developed (Dirk Eisinger, Ph.D. student, partner 3) with the missing data collected (Noel Hendricks, M.Sc. student, partner 1) and incorporated into the model.

Table 1.1: Partners in the integrated umbrella project " The restoration of degraded Nama-Karoo: the role of conservation islands". (NK = Nama-Karoo Biome)

PARTNERS	ZONE OF STUDY	RESEARCH FIELD	INSTITUTION
Dr. K.J. Esler (partner 1 & co-ordinator)	E. Cape- NK/ Grassland ecotone	Plant Ecology	University of Stellenbosch
Prof.M. Samways (partner 2)	E. Cape- NK/ Grassland ecotone	Entomology	University of Natal
Prof.Dr. C. Wissel (partner 3)	E. Cape and Namibian NK	Modelling	Umweltforshungens-Zentrum, Germany
Dr. F. Gilbert (partner 4)	E. Cape and Namibian NK	Entomology	University of Nottingham, Great Britain
Dr. P. Barnard (partner 5) with Dr. A. Burke	Namibia- NK/ Arid zone ecotone	Plant Ecology	Directorate of Envir. Affairs, Namibia

1.4 Research objectives

The main aim of this study was to predict whether *T. triandra* has the potential to be used in restoration and rehabilitation programmes in areas that have been severely degraded. Certain key biological attributes of this grass species is under investigation in order to obtain insights important to these programs. The primary objective of this study is therefore:

> **to investigate selected biological attributes of *Themeda triandra* (seed production, seed dispersal, seed germination, seedling survivorship and ecophysiology) to determine its potential for use in restoration programmess.**

In order to achieve this objective, the following goals were addressed:

1. To determine seed production and seedling survival of *Themeda triandra* on and off the Tafelberg Mesa;

2. to determine seed dispersal distance of *T. triandra* in different vegetation densities (dense vs sparse);

3. to determine the germination potential of *T. triandra* seeds in (i) soil type and with soil depth (ii) under dark and light treatments (iii) and with smoke water concentrations and;

4. to measure key ecophysiological characteristics of *T. triandra* individuals obtained from populations on and off Tafelberg Mesa and grown in controlled conditions (temperature and light intensity responses)

The effect of grazing, using trampling effects, has been considered in this study, because grazing is an important factor influencing the existence of populations of *T. triandra*.

1.4 Key questions and hypotheses

Distribution:

1) How is *T. triandra* distributed over the landscape and in what habitats does it occur? (Chapter 2)

An understanding of the distribution of this species is required to evaluate its restoration potential. For example, if this species is found on the flats, then it is clear that further re-establishment is feasible on suitable habitats. Farmers believe that *T. triandra* is one of the most valuable forage species for livestock. According to them, *T. triandra* was more abundant on the flats in the Middelburg district, but due probably to bad land use management and climate change, this species has been negatively impacted and its abundance has declined considerably over time. Stratified sampling in selected habitats (flats, slopes, summit) did not sample *T. triandra* on the flats (Pienaar 2002) but we are aware of small isolated patches occurring on the flats (Table 2.1). These isolated populations were selected for further study (chapter 2).

Hypothesis: "*T. triandra* occurs in all three habitats (flats, slopes, summit) in the Middelburg district".

Seed production and seedling survivorship:

2) The following questions were addressed in order to gain a better understanding of seed production and seedling behaviour on and off the mesa: (i) Is seed production of *T. triandra* variable over the landscape i.e. could the populations on the mesa be considered to be source populations for the slopes and flats populations? (ii) In what habitats is seedling survival potentially restricted and if so why (chapter 3)?

It is of value to know if mesas provide a source of seeds to the surrounding degraded flats. A source population is found in a habitat where the reproductive success of the population is greater than local mortality and a sink population is the opposite. By studying seed production and seedling survivorship, one can build up a picture as to the potential of different populations as source or sink populations. In addition to this information, one would need to know whether the seeds of *T. triandra* have the potential to disperse from the source to populations on the slopes and flats (addressed in key question 3). If source/sink dynamics do occur within this area, then protection of source populations would be crucial to maintaining the species in the area. The restoration potential of this species on the flats would also be questionable since "sink" populations are by definition declining without input from the source.

Source-sink dynamics

Most of the work investigated concentrated on the importance of dispersal for persistence of populations inhabiting spatially and temporally heterogeneous environments (Venable and Brown 1993). It has been suggested that the so-called source-sink concept is one of the most interesting consequences of the coupling between habitat heterogeneity and dispersal (Shmida and Ellner 1984; Diffendorfer 1998). Dias (1996) presents a detailed review of the source-sink concept and associated assumptions. A common feature of all source-sink models is that differences between habitats are extreme, so that in the source populations, individuals have an average fitness greater than one and a positive rate of increase. Sink populations are poor in that individuals have an average fitness less than one. The persistence of such sink populations depends upon immigration of individuals from neighbouring source habitats where local reproduction exceeds mortality (Kadmon and Tielbörger 1999). Without immigration, sink populations will decline towards the point of extinction.

Pullian and Danielson (1991) demonstrated that population size in a source-sink landscape can be affected by a landscape's composition. When sink habitats are abundant and dispersers are limited in their searching ability, it might happen that not enough source habitats will be found to maintain the same population size. Species with limited dispersal abilities may not exist at all in landscapes where source habitats are severely diluted in a sea of sink habitats. Perhaps, Kadmon and Shmida (1990), who examined populations of a desert grass have provided the best example of a source-sink population, *Stipa capensis*, which grew in two adjacent habitats. They found that grass populations in a relatively rich wadi habitat produced sufficient seed to be a source population compared to the smaller populations found in a surrounding slope habitat sink population. Seed production in the slope habitat was apparently augmented by dispersal of seeds from nearby wadi habitat patches. Thus, population size in the sink habitat may depend on the distance between the sink habitat and the closest source.

Themeda triandra is dominant on the summit of the Tafelberg Mesa, but occurs in very small isolated patches on the flats surrounding the mesa. It is of critical importance to know whether the populations on the summit and flats act as source and sink populations respectively.

Hypothesis: In the absence of grazing, populations on the flats are potential source populations. i.e it is predicted that without grazing there is no difference in seed and flower production of the populations on/off the mesas but in the presence of grazing, populations on the flats are sink populations.

Dispersal:

3) (i) Is *T. triandra* capable of long distance dispersal, or does the species conform to the pattern of many xeric species in being a short distance disperser (mother site theory) (Ellner and Shmida 1981)? (ii) How variable are dispersal distances in different vegetation densities (chapter 4)?

An understanding of the dispersal distances of *T. triandra* will assist in predicting how far this species can travel over the landscape. If this species conforms to the mother site theory (topochory), then active intervention will be required to re-introduce the species into areas where it has become locally extinct.

Hypothesis: Seeds of *T. triandra* are not adapted to long-distance dispersal. Vegetation density would influence dispersal distance. Consequently, seeds of *T. triandra* will travel shorter distances in dense vegetation than in sparse vegetation.

Seed germination:

4) The questions asked are as follows: (i) at what sowing depth (cm) and in which soil type can maximum germination be expected, (ii) under which treatment (dark vs light) will maximum germination occur using three day/night temperature regimes, (iii) what smoke water concentrations will ensure maximum germination under three day/night temperature regimes (chapter 5). This information will be use in potential restoration programmess.

Hypothesis: Germination of seeds of *T. triandra* will not be influenced by i) burial depth, ii) light treatment conditions and iii) higher smoke water solutions.

Ecotypes:

5) Is the morphological and physiological variability of the species an indication that these are ecotypes or does *T. triandra* simply have variable growth forms in relation to the microhabitats in which it grows (chapter 6)?

Themeda triandra is a variable grass species and visually individuals occurring on and off the mesas seems to be different in form. Certain parameters such as: photosynthetic rate, water use efficiency and temperature response curves, distinguish one plant form from the other. If the forms are indeed ecotypes, then this will have an impact in decision making with respect to the general suitability of the mesa form for restoration on the flats.

Hypothesis: *Themeda triandra* growing on the summit of the Tafelberg Mesa is not morphologically or physiologically different from the form occurring off the mesa.

1.5 Structural outline of thesis

Chapter one: An introduction to a study on the regeneration potential of *T. triandra*. In this chapter I focus on issues facing rangelands in general; issues facing the Nama-Karoo; and issues specific to this project. I justify why this research is necessary which is followed up with the objectives for this study. Key questions and hypothesis are also addressed in this chapter.

Chapter two: This chapter deals specifically with the study area, general methodology and species studied. I describe the location of the study area with its topography, geology, climate and vegetation. I also addressed the current land use status. I have done a literature review about the general state of knowledge of *T. triandra* in South Africa. I also look at the distribution of *T. triandra* through the study area.

Chapter three: This chapter specifically addresses patterns of seed production and seedling survival of *T. triandra* populations on and off Tafelberg Mesa in the Middelburg district, Eastern Cape. All three habitats were used (flats, slopes and summit) were used for the seed production seedling survival experiments. Data were recorded from permanent study sites during May 1999 and May 2000 sampling periods for three habitats. Natural Neighbourhood Analysis was used to determine the nearest neighbouring plants from an individual *T. triandra* plant from both the flats and the summit habitats. This analysis also indicated the intensity of grazing.

Chapter four: This chapter focusses on seed dispersal of *T. triandra* in the Middelburg district, Eastern Cape. Seed dispersal experiments were carried out in a sparse and dense vegetation site. Data were collected over a 34-hour and a 58-hour experimental period of time. These experiments were carried out on the flats.

Chapter five: This chapter specifically addressed seed germination of *T. triandra*. Three experiments were carried out at Stellenbosch University: 1) Germination in soil collected from the study sites using four sowing depths, 2) germination using three alternating day/night temperature regimes and, 3) germination using smoke water. Soil was used from Middelburg in experiment one. A potting mixture was also used in experiment one. The germination of seeds were not tested using a combination of smoke water and different soils.

Chapter six: This chapter focussed on certain morphological and ecophysiological variability of *T. triandra* populations on and off the Tafelberg Mesa in the Middelburg district, Eastern Cape. Only populations from the summit were compared to populations from the flats. After approximately 16 months of growth in a greenhouse, measurements of photosynthetic light and temperature responses were taken using the PP-system, CIRAS 1.

Chapter seven: The concluding remarks on the findings of the goals set out in the introductory chapter.

Chapter two

Study site

2.1 Study area

2.1.1 Locality

This study was undertaken in the Middelburg district where the topographic variation of the region is quite diverse. In particular, the locality was selected because of the presence of several flat-topped mesas. This thesis focusses primarily on and around one such mesa, Tafelberg which is situated 25 km south-east of Middelburg (Eastern Cape) east of the national road (R32) between latitudes 31°30`S and 31°40`S and between longitudes 25°05`E and 25°15`E (Figure 2.1).

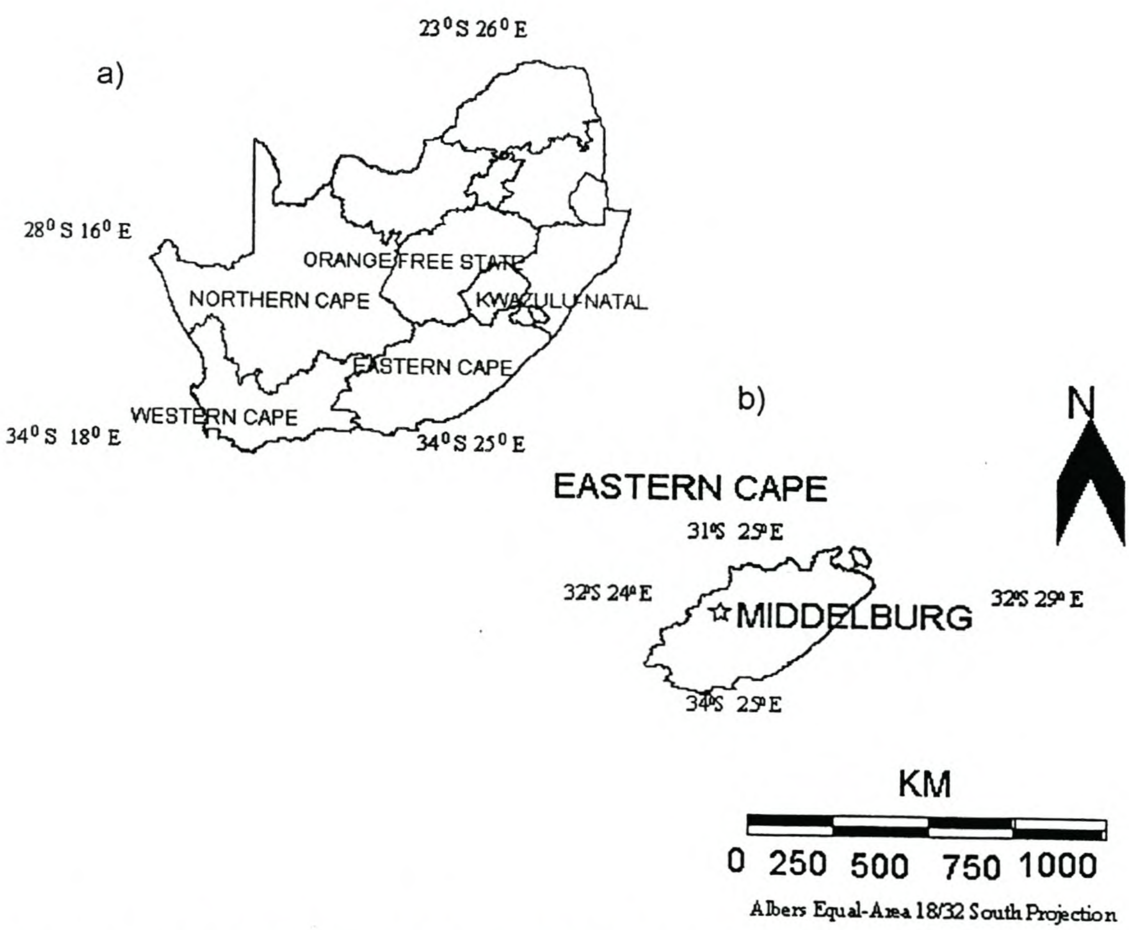


Figure 2.1: Map showing the location of the Middelburg district of the Eastern Cape. a) Map of South Africa indicating location of Eastern Cape; b) location of Middelburg within the Eastern Cape. Adapted from Jones (2000).

2.1.2 Topography and geology

The general study area consists of a mixture of different landforms typical of the karoo which include isolated mesas, low ridges, mountain ranges and extensive flats (Rutherford and Westfall 1994). The flat-topped Tafelberg Mesa together with the surrounding flats was selected for the study, because it is related to other studies (Jones 2000, Pienaar 2002, Hendrick pers. com.). This mesa has a resistant cap, composed mainly of dolerite. Two other mesas, Folminkskop and Buffelskop contribute to an archipelago of hills in the area. Both Tafelberg and Folminkskop are capped with dolerite, however Buffelskop, is a sandstone mesa. The flats surrounding these mesas are composed of alluvial and colluvial material (Geological Survey Map 1996).

The large variety of parent materials contribute to the various geomorphological characteristics in the area. According to Cowling *et al.* (1986), prominent arenaceous zones represent the environment of the Middelburg district. This group, however has been intruded extensively by dolerites which influence both the structure and lithology of the area.

2.1.3 Climate

The maintenance of vegetation in this district is absolutely dependent on both the rainfall and temperature (Hoffman *et al.* 1990). Mean annual rainfall across the Nama-Karoo varies between 60-400mm (Palmer and Hoffman 1997). The Middelburg district receives an average rainfall of approximately 360mm per annum with 15% falling as rain during spring, 30% falling during summer, 50% during autumn and 5% in winter. Most of this falls in the months of December, January and February with dry conditions in June, July and August. Severe droughts are of frequent occurrence in arid and semi-arid environments (Venter *et al.* 1986). The annual median precipitation for the region is 369mm. The average maximum temperature for the district during February is 30 °C and in June the temperature is 0 °C (Figure 2.2).

According to Cowling (1986), the incidence of frost is highest at high altitude areas such as Sutherland (180 days per years) (Venter *et al.* 1986) and the Upper Karoo, while low altitude areas in the south and west are relatively frost-free. Middelburg has an average of 43 days a year with temperatures of 0 °C and below. Frost occurs from late April and early May to the end of September.

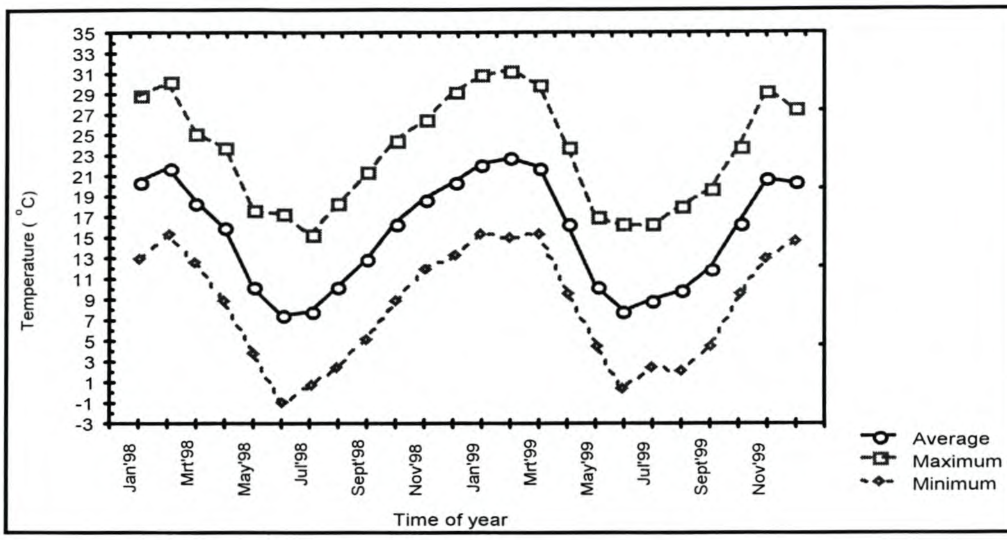


Figure 2.2: Average, maximum and minimum temperatures (°C) for the Middelburg district from January 1998 to December 1999. Data were obtained from the South African Weather Bureau. The weather station is Noupoort.

Wind is an important feature of the Nama-Karoo climatic regime (Desmet and Cowling 1999). Wind may have profound effects on dispersal phases of plant life cycles and probably explains the reason why nearly 50% of the plant species in the karoo are mainly wind dispersed (Hoffman and Cowling 1987). During December to June, the prevailing winds in Middelburg are from the southeast. From July to November the wind changes into a north westerly direction.

2.1.4 Vegetation

According to Acocks (1988), the vegetation of the Middelburg district is a mixture of sweet/sour grassveld Karoo. It is described by Acocks (1953) as "False Upper Karoo" (Veld Type 36). Hoffman *et al.* (1990) classified the district as "Eastern mixed Nama-Karoo" with perennial grass, dwarf shrubs, ephemeral herbs and grass cover varying depending on rainfall seasonality and temperature. The primary study site falls within the " False Upper Karoo" (Veld Type 36) but also lies very close to the "False Karroid Broken Veld" (Veld Type 37) (Acocks 1953).

The flats surrounding the Tafelberg Mesa consist of patches of vegetation interspersed with patches of bare ground that might be an indication of impacted veld (Hendricks pers. com.). According to local farmers, grasses and shrubs desirable to livestock have declined over years to the point where unpalatable ephemeral or low-production species have increased. At present, the shrub, *Chrysocoma ciliata* (bitterbos) is abundant on the flats in the study area, which is of great concern to farmers since this shrub causes mortality in lambs. Pienaar (2002) found that more thorny plant species occurred on the flats compared to the populations on the summit of the mesa. The study site presently consists of a mixture of grasses and shrubs (pers. obs.).

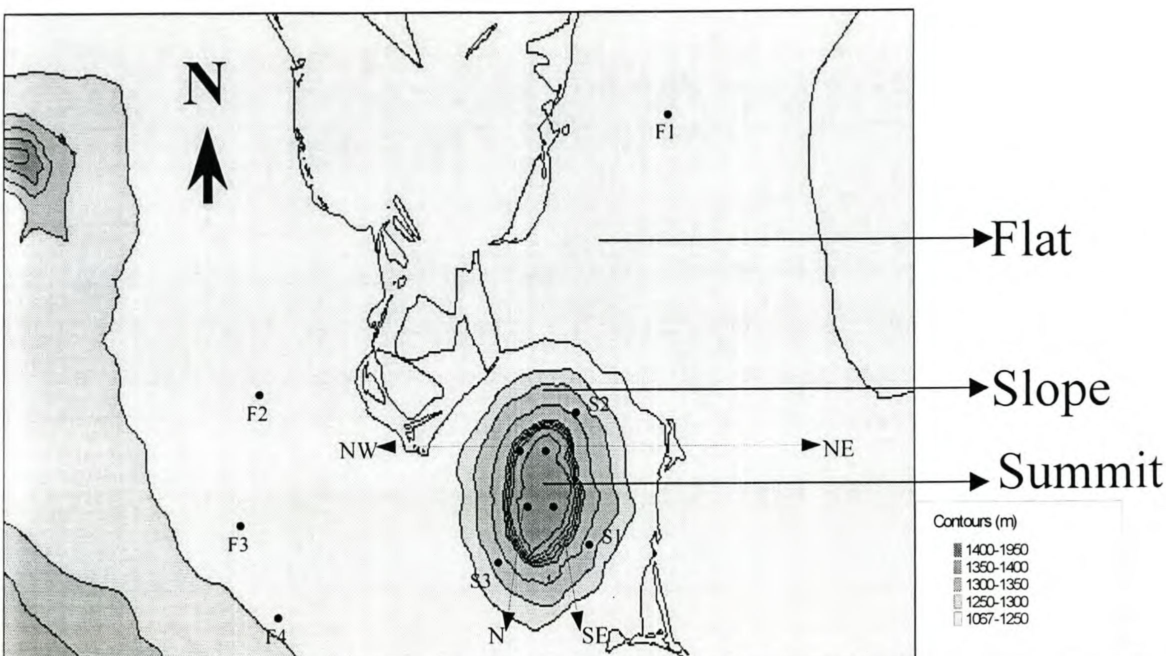
2.1.5 Land use

The farmers in the Middelburg district focus primarily on agricultural practices as a means of land use. Land is predominantly utilized as rangeland for sheep farming. However, small herds of cattle, horses, goats and some ostriches are also present in the area. Farmers cultivate stands of lucerne and dryland fodder crops for their livestock since long periods of droughts are a common phenomenon in this area. The Middelburg district has an average farm size of 5 000 ha. At the end of 1998, the owner of Thorn Springs (R. Gilfillan) introduced small herds of Nguni cattle on his land in place of sheep herds. Game-ranching with indigenous animals, such as Springbuck, Kudu, Reedbuck, etc., has also started to emerge in this region. At the study site, leasing of grazing camps by certain farmers also takes place.

2.2 General methodology

The Tafelberg Mesa is situated on three farms, namely "Thorn Springs (ex "Stradbroke"), "The Mimosas" and "Tafelberg Hall" in the Middelburg district of the Eastern Cape, South Africa. This mesa rises to approximately 445 m above the average height of the surrounding flats and is 1652.9 m above sea level. The smaller mesas in this area, rise between 130 m and 230 m above the surrounding flats. *Themeda triandra* is a very abundant grass species on top of Tafelberg Mesa and decreases considerably in abundance with decreasing altitude. This grass species occurs only as small, isolated patches on the surrounding flats.

A year prior to this study, April and June 1998, 30 m by 5 m permanent sites were established on the summit, slopes and flats of the Tafelberg Mesa (Pienaar 2002). Six of these sites were set up on the summit (Northwest, Southeast, Central South, Central North, Southwest and Northeast); three were on each of the four slope gradients (Northwest, Southeast, Southwest and Northeast); one on the foot slope (start of slope) and four on each of the surrounding flats of the Tafelberg Mesa (Northwest, Southeast, Southwest and Northeast). All six sites on top, one on each slope, called the upper slope (three quarters up the slope) were in used to collect data on seed production (chapter 3), seed germination (chapter 5), seedling survival and general distribution (chapter 3) of *T. triandra* (Figure 2.3).



Grid reference of each study site			
Habitat	**Codes and names**	**Longitude**	**Latitude**
Summit	SE	25.168685670	-31.647201000
Summit	NE	25.168217670	-31.643119170
Summit	NW	25.165063170	-31.643751170
Summit	N	25.166329330	-31.643205000
Slope	SE = S1	25.251716503	-31.648620170
Slope	NE = S2	25.174611543	-31.640178788
Slope	SW = S3	25.163961887	-31.651571571
Flat	FL1 = FL1	25.069369550	-31.492430404
Flat	FL2 = FL2	25.069537238	-31.492495780
Flat	FL3 = FL3	25.068194700	-31.492733236
Flat	FL4 = FL4	25.066996081	-31.492909039

Figure 2.3: Schematic map showing the Tafelberg Mesa study area with surrounding flats. Black dots indicate the study sites. Table also provides the grid references for each study site.

T. triandra was not present in the existing permanent study sites on the flats and four new 30 m by 5 m permanent sites had to be established in places where small populations of *T. triandra* were present (F1-F4).

2.3 Study species: *Themeda triandra*

2.3.1 General literature review on the state of knowledge about *Themeda triandra* in South Africa

Grasses are among the world`s most important agricultural plants, because of the stabilization they provide to various environments (Chapman and Peat 1992). Almost all farm animals and many antelope species, birds, rodents and insects are dependent on grass as a source of food. South African grasslands are essentially composed of a single layered, herbaceous community of perennial grasses. The grasses tend to have shallow, fibrous root systems enabling them to respond rapidly to rainfall and to utilize small rainfall events which usually moisten only the top 10 mm of soil. However, a combination of overgrazing and climate change has apparently altered and in some areas destroyed vegetation cover that absorb water and prevent erosion. With expanding human populations, the semi-arid land was ploughed that should have been left as grazing land (Chase 1959). One grass species that is particularly desirable to farmers in the Middelburg district is *T. triandra,* because livestock prefer this species.

Themeda triandra occurs on three continents (Africa, Asia and Australia) in a diversity of habitats (Clayton and Renvoize 1986), and is one of the most widely distributed grasses in southern Africa. It is a palatable grass species and as stated by Acocks "is by far the most generally important of our grasses". *Themeda triandra* is a decreaser species (Tainton 1972), which normally decreases in abundance as veld declines in condition due to overgrazing. Grazing by domestic livestock over the past century has resulted in significant changes in the botanical composition of natural grasslands and it is believed that the current distribution of *T. triandra* has been significantly reduced in historical times due to the effects of grazing and climate change. According to Wilcocks (1977), the state of arid and semi-arid environments should be blamed on people and their land use practises and not climate, although this is a subject of intense debate. The decline of *T. triandra* with grazing is mainly influenced by plant responses to defoliation, life-form attributes (seed bank dynamics and morphology), herbivore selection for a species and foraging behaviour such as patch grazing (Ash and McIvor 1998). *Themeda triandra* is very sensitive to overgrazing (Ndawula-Senyimba 1972), and is unable to tolerate frequent within-season defoliation (Coughenour *et al.* 1985). Lunt (1995) stated that many grassland remnants dominated by *T. triandra* require regular burning, grazing or slashing to promote regeneration, flower and seed production. Fire is not a frequent phenomenon on mesas in the Middelburg district, but farmers have reported occasional fires on the top of the Tafelberg Mesa.

Themeda triandra is a re-seerder, producing a few large diaspores that are poorly dispersed (less than one meter) (Van Rheede van Oudtshoorn and Van Rooyen 1999). Seeds persist no more than 2-3 years in a state of dormancy, and are subjected to predators such as rodents and other granivores. Such grasses are vulnerable to local extinction in regions that experience both variable rainfall and sustained heavy grazing. Because grasslands have been subjected to varying agricultural practices in the past and present, most, if not all, have undergone radical change. For example, the *T. triandra* grasslands of Natal Midlands have been transformed to *Aristida adscensionis* (steekgras) grasslands due to cultivation. In the Eastern Cape, grazing by cattle in the season following an intense drought, which caused severe tuft mortality, suppressed the recovery of *T. triandra* (Danckwerts and Stuart-Hill 1988). This mechanism could have been responsible for the decline of the perennial grass component over much of the Eastern Nama-Karoo Biome, which experienced heavy stocking by domestic livestock during the second half of the nineteenth century (Acocks 1953).

An understanding of the survivorship of grass seedlings is becoming considerably more important with the growing emphasis on land management and evidence of diminishing native grass resources. More emphasis should be placed on maximising germination and seedling establishment of *T. triandra*. In South Africa, the restoration of native species in impacted grasslands is highly desirable as productivity for subsistence and commercial farming activities needs to be increased. Reasons for *T. triandra* not re-establishing itself are still unclear. It is possible that the original large-scale establishment of *T. triandra* was due to a particular set of weather patterns that no longer occurs in southern Africa (Tainton 1981). The re-establishment of *T. triandra* from seed largely depends on its seed biology characteristics, particularly seed production, dispersal and germination, topics that are dealt with in this thesis (see Chapters 3, 4 and 5).

2.3.2 Distribution of *Themeda triandra* through study area

Themeda triandra is a desirable grass species to livestock. According to farmers in the Middelburg district this species was found predominantly on the extending flats of the Tafelberg Mesa in the past, but has declined in abundance and is now found in very small isolated populations. The botanical study by Pienaar (2002) does not record *T. triandra* on the flats of the Tafelberg Mesa (Table 2.1), however, small isolated populations were found to be present away from the permanent study sites. This decline is suggested to be caused by overgrazing (Acocks, 1953) and variation in rainfall and temperature (Hoffman *et al.* 1990). *Themeda triandra* also occurs from the upper slopes to the summit of the Tafelberg Mesa. This species is regularly grazed by smaller herds of kudu and reedbuck that migrate daily from the slopes where they spend the days, to the flats where they graze nocturnally. *Themeda triandra* is very dominant on the summit of the Tafelberg (Table 2.1 and Figure 2.4). The summit is used to a lesser extent by domestic livestock than the slopes or flats and is mainly grazed by rock dassie, red rock rabbit, duiker and steenbuck. The summit of the mesa is relatively inaccessible to domestic livestock due to the inaccessible topography and/or because of the lack of water at this altitude.

Species ↓	Tafelberg			Folminkskop			Buffelskop		
	flat	slope	summit	flat	slope	summit	flat	slope	summit
Aristida adscensionis	5.6 ± 6..1								
Cenchrus cilliarus		2.9 ± 3.1				5.1 ± 4.0			
Cymbopogon plurinodes				4.2 ± 5.0	5.5 ± 3.3				
Enneapogon scoparius							2.9 ± 3.8		
Eragrostis lehmanniana[1]								12 ± 3.4	
Eragrostis obtusa[2]								1.0 ± 1.2	
Sporobolus fimbriatus			2.7 ± 1.4						
Themeda triandra	0.0 ± 0.0	0.1 ± 0.2	16.0 ± 7.4	0.0 ± 0.0	1.5 ± 2.5	4.8 ± 3.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

Table 2.1: Cover of *Themeda triandra* and selected grass species in three habitats (flats, slopes and summit) for three mesas, Tafelberg, Folminkskop and Buffelskop in the Middelburg district of the Eastern Cape. Data are expressed as mean percentage cover ± standard deviation, per m^{-2}. Data were obtained from Pienaar (2002) and only represent the plots from the SW flats, up and over the mesa to the SE flats.

(A)

(B)

Figure 2.4: Photograph indicating the dominance of *T. triandra* on the (A) summit and (B) a small patch on the flats of the Tafelberg Mesa in the Middelburg district of the Eastern Cape. Photograph A was taken from the central north study site and photograph B was taken approximately 2 km southwest from the mesa.

Chapter three

Patterns of seed production and seedling survival of *Themeda triandra* populations on and off Tafelberg Mesa in the Middelburg district, Eastern Cape

3.1 Abstract

Seed production and seedling survival is an important factor in determining the population persistence in arid and semi-arid environments. These parameters as well as evidence of grazing and percent cover were measured for *Themeda triandra* populations occurring on and off the Tafelberg Mesa in the Middelburg district, Eastern Cape. *Themeda triandra* was relatively dominant on the upper slopes and summit of the mesa, compared to small isolated populations found on the flats surrounding the mesa. Populations on the flats were grazed to a greater extent compared to populations on the slopes and summit. The mean percentage cover for *T. triandra* increased slightly from May 1999 to May 2000 in all three habitats. The increased cover for other grasses co-occurring (excluding *T. triandra*) from May 1999 to May 2000 were slightly higher with a significant difference between the habitats of the slopes and summit of the mesa. These increases in cover explained a decrease in the mean percentage cover of bare ground and were explained by higher rainfall recorded prior to May 2000. From May 1999 to May 2000, seed production per plant and per m^{-2} increased for both the flats and slopes populations but decreased for the summit of the mesa. The increased rainfall prior to the May 2000 sampling period had a positive effect on seed production for the flats and slopes. The potential for expansion of populations of *T. triandra* on the flats can be considered since the flats populations do produce seeds under favourable conditions. However, despite the increased percentage cover and seed production of *T. triandra* on the flats, trampling by livestock combined with drought still seem to be responsible for the high rates of seedling mortality. Populations on the flats indicated a lower percentage seedling survival rate, which was significantly different from the slopes and summit.

3.2 Introduction

The processes influencing both seed production and seedling survival of *T. triandra* in the semi-arid eastern Karoo are of fundamental importance in the understanding of establishment and maintenance of this palatable grass species, especially in areas that have been impacted by grazing in the past (i.e. highly accessible flats). Seed production and seedling survival are two of a number of processes, which can influence the turnover of individuals and therefore the potential for the persistence of the population. Factors such as intensive grazing and variation in rainfall may have profound effects on the establishment of grasses in semi-arid environments. The impact of such factors could lead to large compositional changes in the vegetation (Bosch 1989).

Seed-reproducing grasses are often the main constituents of many of the world`s savannas and grasslands (Huntley and Walker 1982). *Themeda triandra* is possibly the most economically important grass species in South Africa (Acocks 1988). Drought and grazing conditions could have an enormous negative impact on population establishment of this species, because the rate of seedling recruitment cannot match the attrition of the established population (Acocks 1988). Other factors that may decrease seedling recruitment of grasses include: seed availability (Orr 1991); available moisture (Lodge 1981); and competition of established vegetation for space and other resources (Samuel and Hurt 1992). O`Connor (1996) found that available moisture had a beneficial effect on both the emergence and seedling survival under shading (shadowed) conditions. This evidence was strongly supported by Lodge (1981) and Orr (1991).

According to Shmida and Ellner (1984), the source-sink concept is related to the interaction between habitat heterogeneity and dispersal. It is well known that source populations are characterized by a higher survival rate of individuals than the mortality rate (Diffendorfer 1998). However the opposite is the case for the sink populations. This is due to the immigration process of individuals from the source populations to the sink populations. Without this immigration process, sink populations will decline to the point of extinction. In source-sink models, dispersal can be constrained by either unidirectional dispersal from source habitats, or by fixed rates of dispersal between patches. The source-sink concept has not been previously tested on this study site, but seed production and seedling survival data for the study species, *T. triandra*, may provide some evidence of source-sink activity for populations found on and off the Tafelberg Mesa.

Themeda triandra is found mainly on the summit of the Tafelberg Mesa but occurs in very small isolated patches on the flats surrounding the mesa. Do populations on the summit of the Tafelberg Mesa have the potential to act as source populations to the surrounding flats? This is despite the constraint due to the distance that the seeds have to travel down the slopes to reach the flats (Zacharias 1990).

In this study, we examined populations of *T. triandra* in three habitats (flats, slopes and summit) of the Tafelberg Mesa. I focused primarily on (i) seed production and (ii) seedling survival. The following questions were addressed in this chapter: (i) Is seed production of *T. triandra* variable over the landscape and can populations occurring on the mesa be considered as source populations? (ii) In what habitats is seedling survival potentially restricted and if so why? It was hypothesized that: (i) In absence of grazing activity, populations on the flats are a potential source population. i.e. without grazing there is a difference in seed production of the populations on and off the mesa. (ii) Seedling survival will fare the worst on the flats due to animal activity. The study on seed dispersal and seed germination is dealt with in chapter 4 and 5 respectively.

3.3 Materials and methods

Study site and layout of plots

This study was conducted on the Tafelberg Mesa in the Middelburg district of the Eastern Cape, between latitudes 31°30'S and 31°40'S and longitudes 25°05'E and 25°15'E. Permanent study sites were set up by collaborating researchers (Chapter 1, section 1.3) on and off the Tafelberg Mesa. During their fieldtrips in April and June 1998

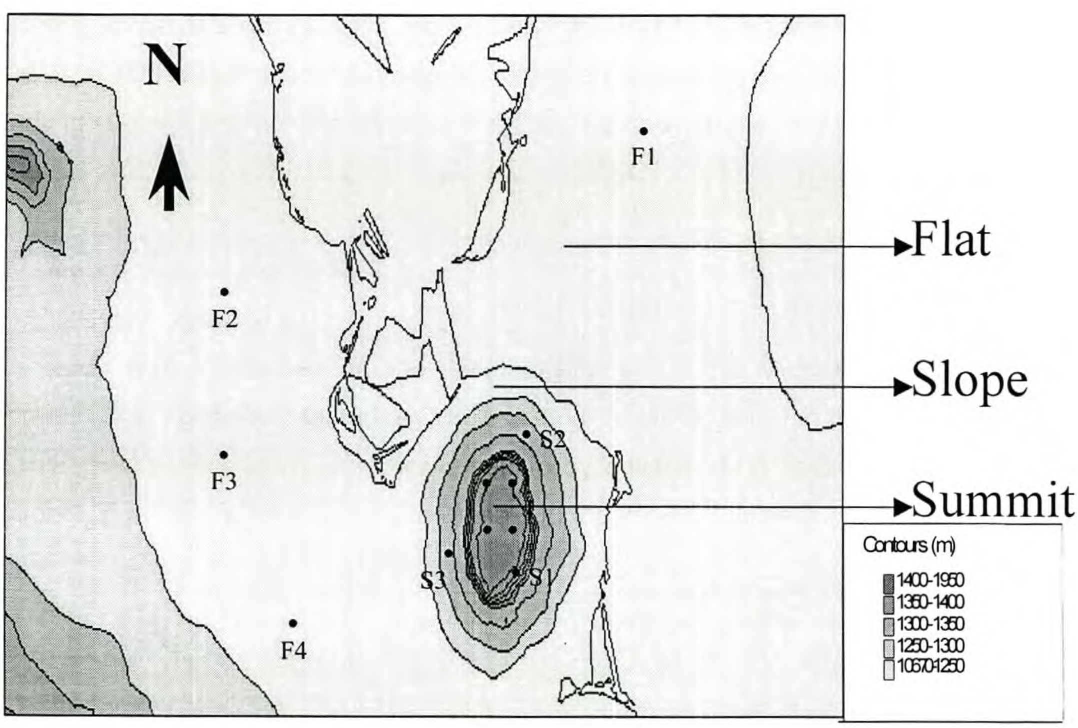


Figure 3.1: Schematic map indicating the study area. Black dots indicate the study sites (30m by 5m) at three habitats (flats, slopes and summit). See Chapter 2, Figure 2.3 for grid references of each study site.

six sites on four slopes (Northwestern, Northeastern, Southwestern, Southeastern) and four sites on each of the four flats (Northwestern, Northeastern, Southwestern, Southeastern) surrounding Tafelberg were established and marked with metal poles (Jones 2000). Each study site was 30m by 5m. One site on each of the Southeastern, Northeastern, and Southwestern slopes was used. The north western slope was omitted in this study, due to the virtual absence of *T. triandra* on it. These study sites were established three quarters up the slopes. Since *T. triandra* occurred in small patches on the flats, four new 30m by 5m study sites had to be established during May 1999 in areas where *T. triandra* occurred. Only the Southeastern, Northeastern, and Southwestern study sites were in use for both the seed production and seedling survival observations (Figure 3.1).

Seed production

Primary flowering time of *T. triandra* in the Middelburg district starts from April and seeds are shed between May and June (pers. Obs.). Seed production measurements were obtained in early May 1999 and repeated in early May 2000. Six, 1x1 m quadrats at 5m intervals were placed out in each study site for all three habitats (flats, slopes and summit). In each quadrat the percentage cover of *T. triandra*, rock, bare ground, other grasses (excluding *T. triandra*) and other vegetation (shrubs) were estimated. Within each 1x1 m quadrat, the basal diameter of each *T. triandra* plant (if present) was measured (cm), and the number of seeds present on the plant estimated by counting the number of seed awns. Each seed has a single awn.

Seedling survival

Well established juvenile *T. triandra* seedlings at a height of approximately 25 mm were selected on and off the Tafelberg Mesa during early May 1999. Seedling characters such as: flat stem; hairy stem and leaves; leaf formation; and leaf colour were used to identify the *T. triandra* seedlings. One hundred seedlings were marked with numbered metal tags in each habitat (i.e. flat= 1-100; slope= 101-200; summit= 201-300). The metal tags were placed on the soil beside the seedlings. A 6cm nail was drilled through the metal tag and hammered into the soil to avoid any tag losses. Some of the seedlings were marked outside the boarders of the study site (within a 2m range). Percentage seedling survival was recorded in May 1999, September 1999, November 1999 and May 2000. Trampling activity was also recorded by observing physical damage to the tags or hoof activity on the soil adjacent to the seedlings in an approximately 0-3cm surrounded area. The distance (cm) to the nearest grass and shrub neighbour was recorded for each seedling to identify its nearest potential competitor.

Nearest Neighbour Analysis

During October 2000, sampling points were located using a sub-meter real time differential GPS (Global Positioning System) in order to investigate the distance of neighbouring *T. triandra*; neighbouring grasses (excluding *T. triandra*) and neighbouring shrubs from an original point which in this case was a *T. triandra* individual. I also looked at the grazing intensity (none, moderate and heavy) of the *T. triandra* and the height of the leaves and flowers above ground level. The data was downloaded as Arcview shape files and converted into MapInfo tab files. In order to translate points into a continous surface model, I used a triangular network (Tin model). This allows estimates of values to be extrapolated from the known sampling points to any unknown position. A nearest neighbour territory around each point was also defined using voronoi polygons. The area associated with each voronoi polygon could be determined and shaded by area sizes into classes. The smaller the size of the polygon, the closer together the samples and the more optimal the habitat. These neighbourhood patterns were related to the continuous surface models generated for the data sampled. This investigation would prove if this technique could explain potential neighbouring competitors.

An Anova and a T-test, using the package Statistica, were calculated with the use of a Microsoft®-Windows application (STATISTICA©, 1999) to test significant differences between habitats. Means and standard deviations were also used to describe populations at each of the sites. Seed viability was not tested and was a constraint of this experiment.

3.4 Results

A one-way Anova analysis indicated a difference in the mean distance between grasses and shrubs to the *T. triandra* seedlings for each habitat (Table 3.1). The distance between both grasses and shrubs were more or less the same in the different habitats. The flats indicated a greater distance between both grasses (10.86cm) and shrubs (57.60cm) compared to the slopes and summit. Neighbourhood maps also indicated that the distances of *T. triandra* to nearest *T. triandra* plants were further apart on the flats surrounding the Tafelberg Mesa than the slopes and summit (Figure 3.2). Figure 3.3 revealed that the distance of other grasses on the summit were closer to nearest *T. triandra* plants compare to the slopes and summit of the mesa. Figure 3.4 showed that the distance of shrubs to nearest *T. triandra* plants were more or less the same for all three habitats.

A slight increase in the mean percentage cover of *T. triandra* from May 1999 to May 2000 was recorded for all three habitats but no significant differences were found (Figure 3.5a). Between May 1999 and May 2000, a significant difference was found between the mean percentage cover of other grasses for both the slopes ($F = 7.394$; df = 1, 14; $p<0.05$) and summit ($F = 2.976$; df = 1, 15; $p<0.05$) whereas the flats showed a slight increase in cover but were not significantly different (Figure 3.5b). The mean percentage shrub cover between May 1999 and May 2000 was more or less the same for all three habitats (Figure 3.5c). The mean percentage rock cover on the flats was significantly different from the slopes ($F = 144.69$; df = 1, 45; $p<0.001$) and summit ($F = 155.29$; df = 1, 45; $p<0.001$) of the mesa (Figure 3.5d). Percentage bare ground was found to be higher on the flats and lower on the slopes and summit of the mesa (Figure 3.5e).

Neighbourhood schematic maps indicated that *T. triandra* at three of the study sites on the flats were more heavily grazed than populations on the summit of the mesa (Figure 3.6). Personal observations also indicated that grazing was more concentrated on the leaves than on the flower parts of the plant in all three habitats.

Although not significantly different, the mean number of seed produced per m^2 increased from 12 in May 1999 to 12.17 in May 2000 for the flatlands surrounding Tafelberg (Table 3.2a). An increase of 2.5 seeds (May 1999) to 5 per m^2 (May 2000) was also found on the slopes of Tafelberg whereas a decrease in seed production on the summit of the mesa occurred. The flats were significantly different ($F = 25.885$; df = 1, 41; $p>0.001$) in seed production during May 1999 compared to populations on the slopes and summit in the same year. In May 2000, a significant difference ($F = 46.359$; df = 1, 37; $p<0.001$) in seed production was found between all three habitats. On an individual plant basis, seed production in May 1999 on both flats and slopes increased from 11.91 and 2.36 to 12.76 and 4.06 in May 2000 respectively (Table 3.2b). Generally, the results showed that the flats produced the most seeds followed by the slopes and summit of the mesa. The significant differences found in seed production may be due to the increased rain between December 1999 to March 2000 recorded at the Tafelberg Hall farm (Figure 3.7). During May 1999, seeds on the flats were mainly produced by plant individuals with basal diameters between 8-16cm and 27cm (Figure 3.8a). In May 2000, seed production on the flats shifted to individuals in smaller diameter classes (Figure 3.8b). The diameter range of seed production for the slopes and summit during May 1999 and May 2000 were more or less the same.

All habitats showed a decline in seedling numbers between May 1999 and May 2000. The decline continued into November 2000 on the flats (slopes and summit habitats were not recorded). Clear trends existed between habitats, with the highest levels of seedling survival being recorded on the summit of Tafelberg (%) and the lowest on the flats (%) (Figure 3.9). Trampling of seedlings was inversely related to seedling survival (Table 3.3) with the highest levels of trampling recorded on the flats and the lowest levels on the summit of Tafelberg.

Table 3.1: Mean (± standard deviation) distance (cm) of *T. triandra* seedlings to nearest neighbours (grass or shrub) in three habitats (flats, slopes and summit) on and around Tafelberg. Sample size refers to the number of seedlings measured.

Habitat	Grasses	Shrubs	Sample size(n)
Flats	10.86 ± 7.85	57.60 ± 107.55	103
Slopes	9.73 ± 4.82	49.36 ± 30.65	89
Summit	9.35 ± 4.96	40.17 ± 23.40	88

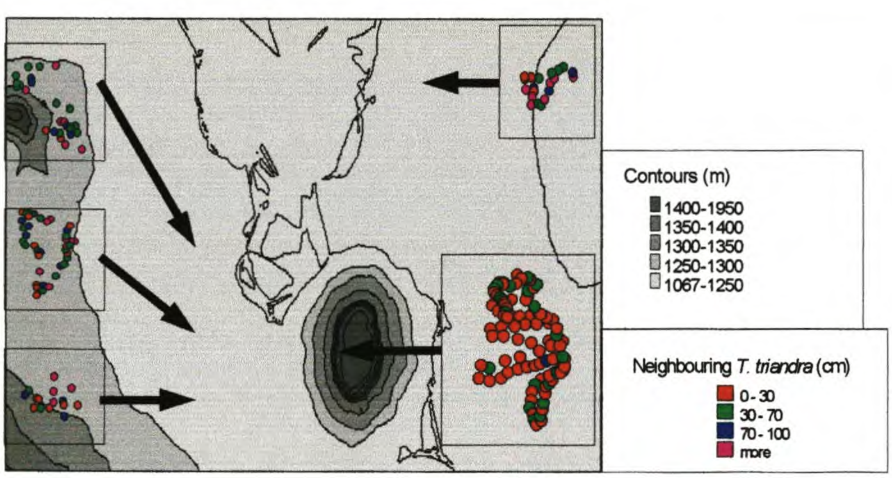


Figure 3.2: Schematic map indicating the distance of neighbouring *T. triandra* to an individual *T. triandra* plant on the summit and flats of the Tafelberg Mesa. The distance (cm) between the neighbouring plants is represented by the coloured circles (legend). Arrows points to position of sites in the landscape.

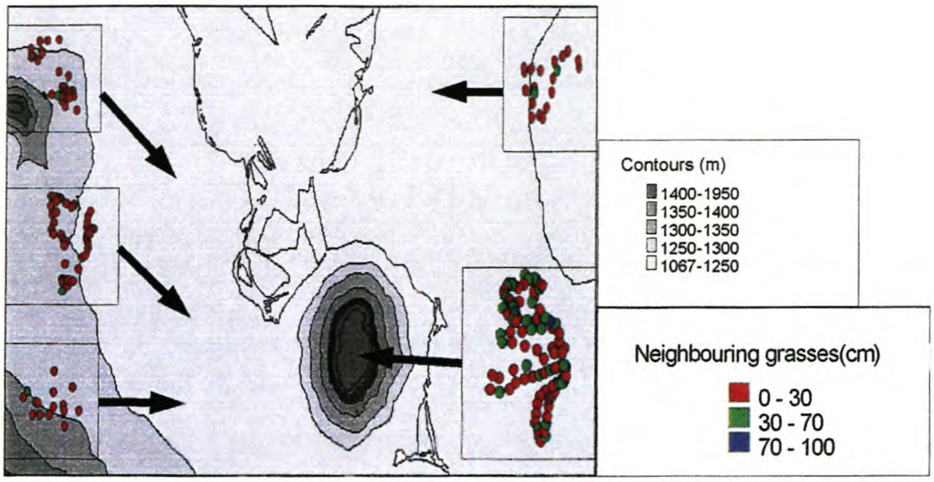


Figure 3.3: Schematic map indicating *T. triandra* individual to neighbouring grass species (excluding *T. triandra*) on the summit and flats of the Tafelberg Mesa. The distance (cm) of the neighbouring grass is represented by the coloured circles (legend). Arrows points to position of sites in the landscape.

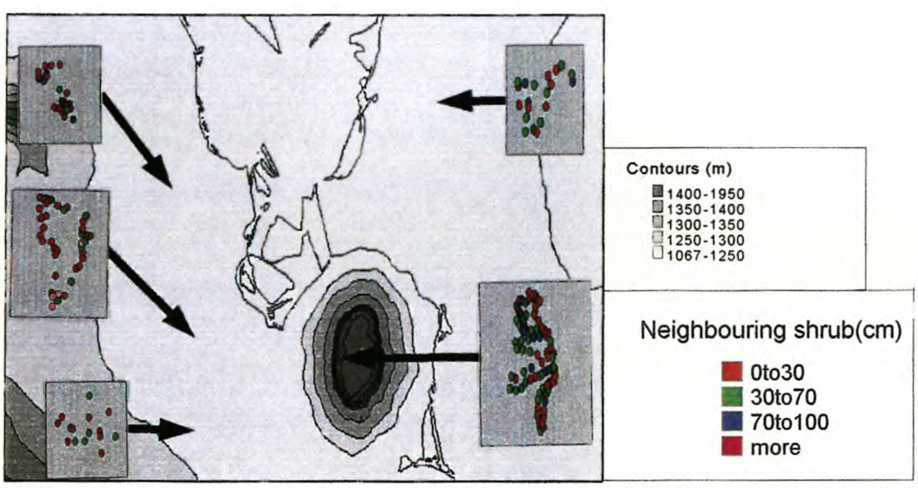
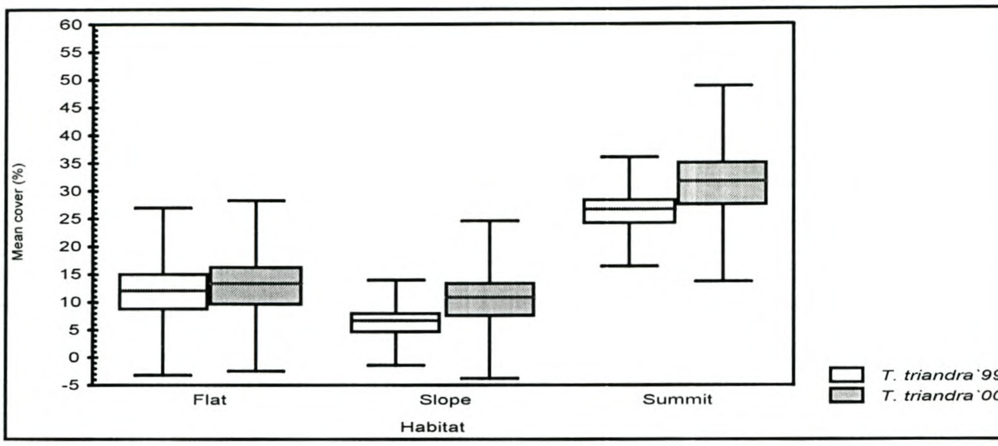
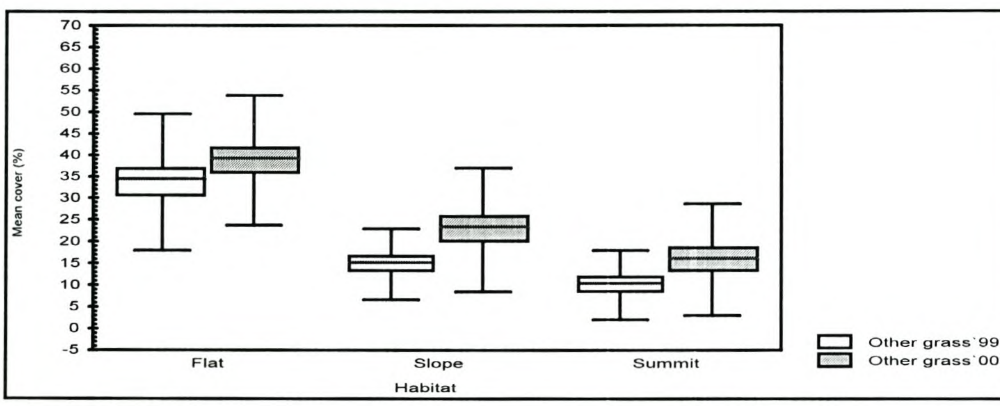


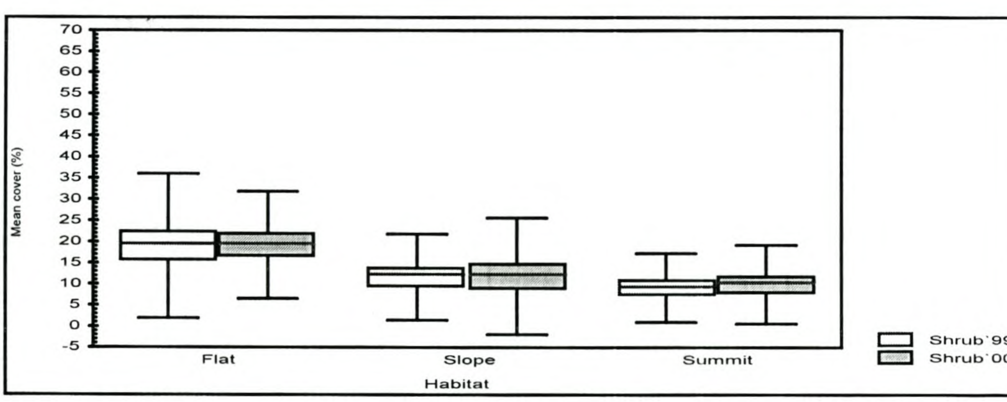
Figure 3.4: Schematic map indicating the *T. triandra* individual to neighbouring shrubs on the summit and flats of the Tafelberg Mesa. The distance of the neighbouring shrubs is represented by the coloured circles (legend). Arrows point to position of sites in the landscape.



(A)

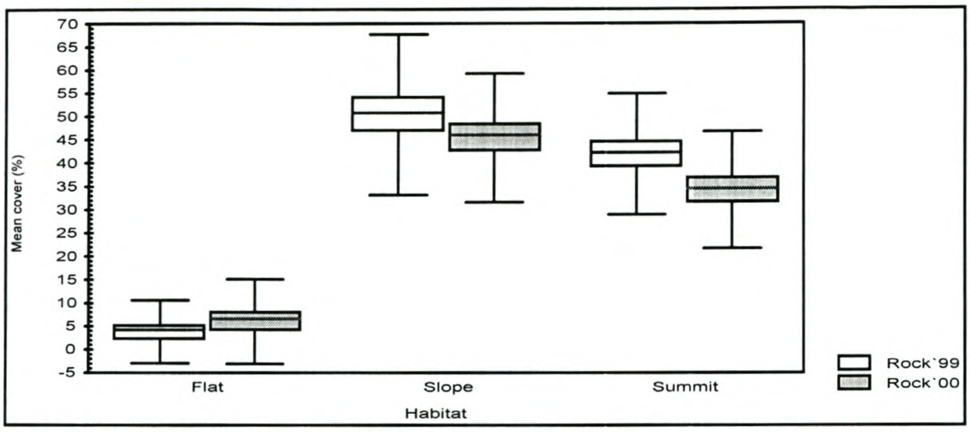


(B)

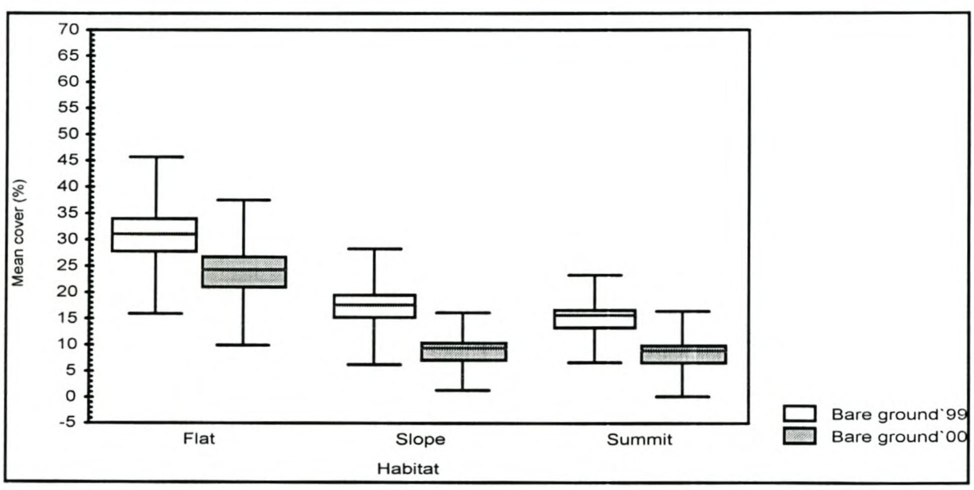


(C)

Figure 3.5: Cover of *T. triandra* (A); other grasses (B) and shrubs (C) for the three habitats (flats, slopes and summit) of the Tafelberg Mesa during May 1999 and May 2000. Data presented are the mean percentage (%) values plus or minus standard deviations.



(D)



(E)

Figure 3.5: (cont) Cover of rock (D) and bare ground (E) for the three habitats (flats, slopes and summit) of the Tafelberg Mesa during May 1999 and May 2000. Data presented are the mean percentage (%) values plus or minus standard deviations.

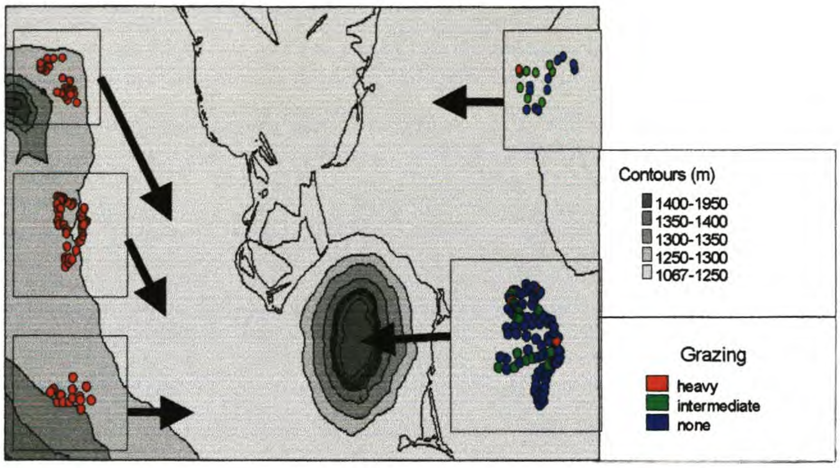


Figure 3.6: Schematic map indicating grazing intensity on the summit and flats of the Tafelberg Mesa. The intensity of grazing was measured as either none, intermediate or heavy and is represented by the coloured circles (legend). Arrows points to position of sites in the landscape.

Table 3.2: Seed production per plant (a) and per m^2 (b) of *T. triandra* in three habitats (flats, slopes and summit) of the Tafelberg Mesa during May 1999 and May 2000. Data presented are means ± standard deviations. Differences were investigated using a t-test.

(a)

Habitat	Seed production/plant		
	May 1999	May 2000	Difference between May'99 and May'00
Flats	11.9 ± 3.49	12.8 ± 6.80	p= 0.734; t= 0.504; N= 24
Slopes	2.36 ± 1.93	4.06 ± 1.83	p< 0.05; t= 2.394; N= 24
Summit	2.04 ± 0.99	0.56 ± 0.20	p< 0.01; t= 2.890; N= 24

(b)

Habitat	Seed production/m^2		
	May 1999	May 2000	Difference between May'99 and May'00
Flats	12 ± 12.58	12.2 ± 16.71	p= 0.616; t= 0.504; N= 24
Slopes	2.5 ± 3.35	5.0 ± 5.47	p< 0.01; t= 3.244; N=24
Summit	2.0 ± 5.60	0.57 ± 1.19	p< 0.01; t= 2.856; N= 24

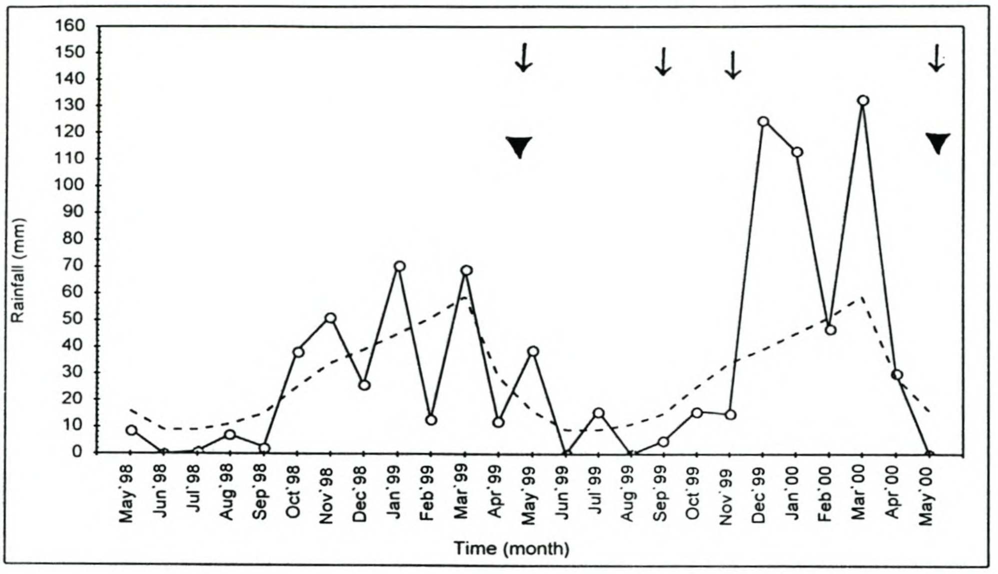
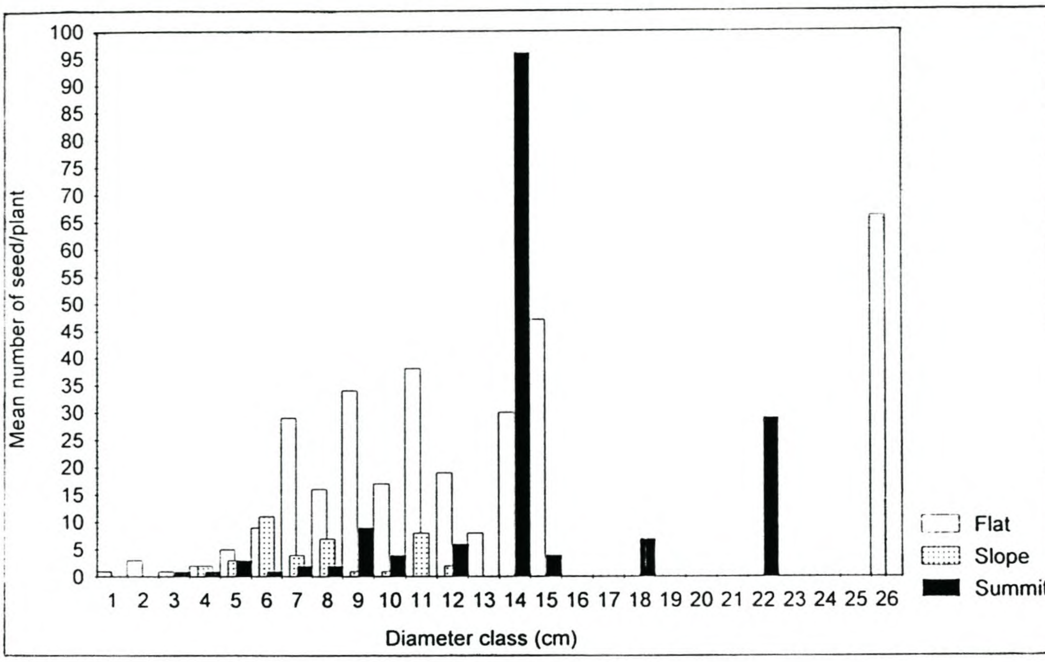


Figure 3.7: Monthly rainfall (mm) from May 1998 to May 2000 recorded at Tafelberg Hall farm, SE of Tafelberg Mesa. Data provided by William Asher. Arrows indicate when seed production was monitored (▼) and when seedling survival (↓) was monitored. Dotted line indicates the monthly average rainfall for the past 100 years (1899-1999).

a)



b)

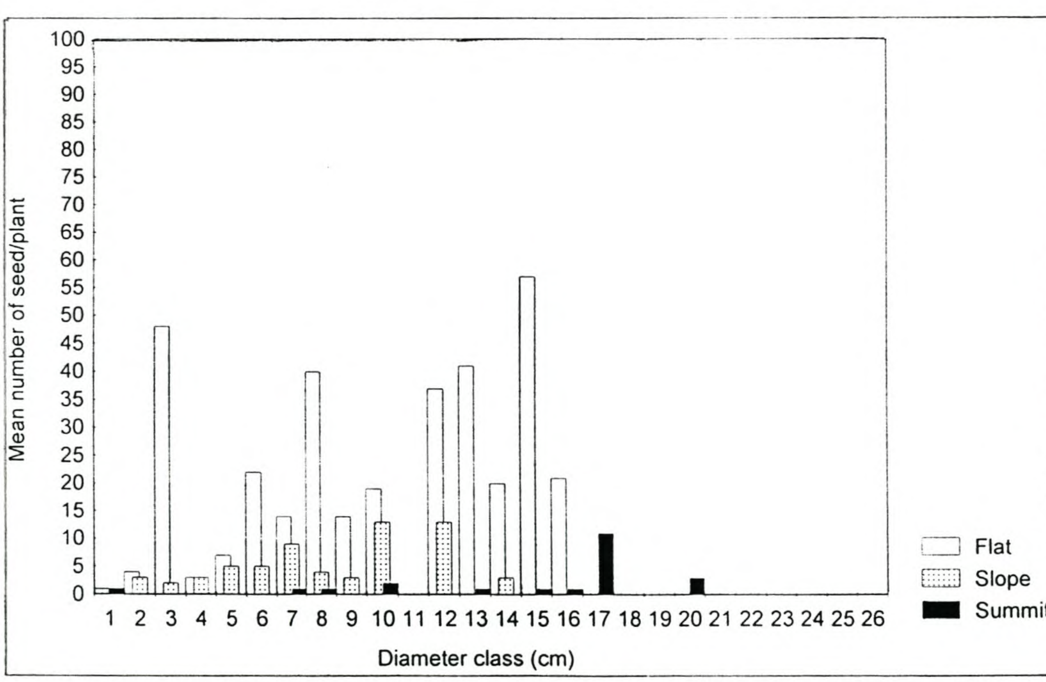


Figure 3.8: The mean number of seeds per plant produced by different basal diameter (cm) size classes of *T. triandra* during a) May 1999 and b) May 2000 (b) in three habitats (flats, slopes and summit) of the Tafelberg Mesa.

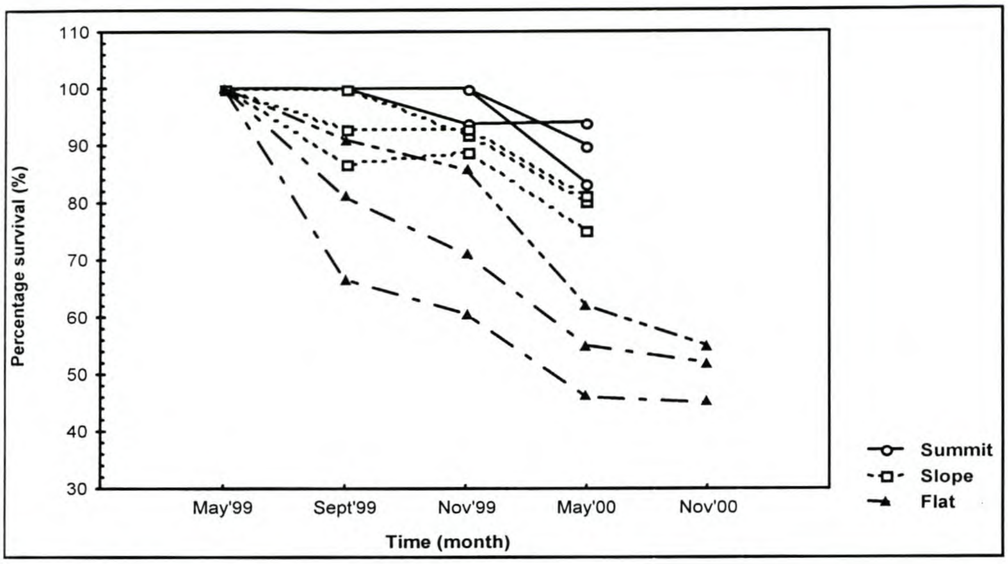


Figure 3.9: The survival (%) of *Themeda triandra* seedlings on three sites in each habitat (flats, slopes and summit) between May 1999 and May 2000 on off the Tafelberg Mesa in the Middelburg district.

Table 3.3: Percentage of seedling survival (survive) and trampling (trample) during the growing period from May 1999 to May 2000 for the three habitats (flats, slopes and summit).

Habitat	**Time (month)**							
	May` 99 (%)		**September` 99 (%)**		**November` 99 (%)**		**May` 00 (%)**	
	survive	**trample**	**survive**	**trample**	**survive**	**trample**	**survive**	**trample**
Flats	100	0	83.4	0	72.4	19	57.8	26
Slopes	100	0	93.2	0	91	3	78.7	6
Summit	100	0	100	0	97.9	0	89	0

3.5 Discussion

Themeda triandra was found to be very rare on the flats surrounding the Tafelberg Mesa. Where present, it occurred in very small patches of approximately 20m radius. Small populations were also found along roadside verges but did not extend beyond the fence lines of grazing camps. There are two possible explanations as to the presence of patches of *T. triandra* on the flats. The one is that in the past, extreme grazing conditions have confined this species to isolated patches or patches protected from grazing. The other explanation is that due to unfavourable rainfall conditions, this species is confined to areas where water availability is greater (e.g. run-off from tarred roads or wetter sites). Both of these explanations could play a role in explaining the current distribution of *T. triandra*, which is at the margins of its distribution range in the Middelburg district. It is interesting to note that in some areas, notably the roadside *T. triandra* populations are confined to areas that could not benefit from run-off (being "higher" than the road) and that they stop abruptly at the fence lines; suggesting that grazing does play a role. *Themeda triandra* is also relatively dominant on the upper slopes and summit of Tafelberg where grazing is less intense (slopes) or absent (summit). These sites also receive more precipitation from run-off and as a consequence of their altitude. This study does not however, address the vexing question of distribution of *T. triandra*, rather, it concentrates on the performance of the populations over the landscape with respect to reproductive attributes.

Despite the patchy distribution of *T. triandra* on the flatlands surrounding Tafelberg, the results showed that the populations on the flats produce the highest number of seeds per plant, despite being the most intensely grazed. Seed counts were conducted during May when the camps under consideration were being rested. Observations later on in the year (September) revealed that the *T. triandra* tufts were grazed to approximately 2-3 cm above ground level. Under heavy grazing conditions, tuft size of *T. triandra* has been shown to decrease significantly (O`Connor and Pickket 1992). They found 163, 65 and 0 seeds per m^2 under light, moderate and heavily grazed sites respectively. This in turn influences seed production, which also declines with increased grazing activity. The contradictory results of this study can possibly be explained by the structure of the population. Individual plants tended to be larger and spacing between plants was greater on the flats (i.e. less intraspecific competition from neighbours) than on the slopes and summit of the Tafelberg Mesa.

Rainfall had a positive effect on seed production. With the increased rainfall prior to the May 2000 sampling period, more seeds on average were produced per plant and per m^2 on the flats than on the slopes of Tafelberg. Interestingly, the opposite trend occurred on the summit of the mesa. With the increased rain, seed production actually declined which could possibly be attributed to greater inter and intra specific competition. Rainfall also had a positive effect on cover of other grass species and to a lesser extent on *T. triandra* itself (most significant change on summit). No significant changes were recorded for shrub cover. During the higher rainfall period (May 2000), seed production shifted to smaller tuft diameter size classes on the flats and slopes populations. Several other studies on grass species have indicated a significant influence of rainfall on seed production (Dye and Walker 1987; Cornelius 1950). Spring and summer rainfall in the Karoo tends to promote the growth of grasses whereas autumn and winter rainfall promotes the growth of dwarf shrubs (Roux 1966; Roux and Vorster 1983; Skinner 1976; Hoffman *et al.* 1990). This study confirms previous observations.

Despite higher levels of seed production in the flats populations of *T. triandra*, Jones (2000) found significantly larger soil-seed banks of *T. triandra* on the summit and upper slopes of Tafelberg and virtually no diaspores on the flats. She did not, however, sample soil close to the isolated populations that were sampled in this study on the flats. O`Connor and Pickett (1992) found larger seed banks of *T. triandra* on lightly or moderately grazed sites. They also recorded more seed production on sites that were slightly grazed. Robinowitz and Rapp (1980) also found that *T. triandra* produces more seeds under conditions of high rainfall and slight or moderate grazing.

Seedling survival was clearly negatively impacted on the flats whereas the slopes and summit had significantly higher seedling survivorship. A possible explanation for the low percentage seedling survival on the flats is due to trampling effects by the livestock. The high trampling effect on the flats might also imply a higher degree of grazing intensity on those seedlings. It seems that the high rock cover on summit of the mesa makes a valuable contribution in terms of protection and water availability to seedlings. The greater seedling survival is also due to the soil climate differences. It is clear that the soils from the summit is organically richer and therefore having better water retention abilities. Another environmental factor that might add to the decrease in seedling survival on the flats is competition.

Competition of seedlings with neighbouring plants for certain resources might also be considered as a factor that contribute to seedling survivorship. In the Mountain Zebra National Park, the importance of surface rock as a factor influencing plant community composition was emphasised by Van der Walt (1980). He suggested that stones help to preserve grass cover by reducing the accessibility of grass seedlings to large herbivores and by increasing moisture availability by concentrating rainfall run-off around their margins. The results of this study also showed that rock cover was more abundant on summit of the mesa than on the flat areas where very little cover of rocks was recorded.

Thus, less grazing activity and greater water availability are reasonable explanations for the dominant occurrence of *T. triandra* on summit of the Tafelberg Mesa. Due to ecological constraints such as grazing, trampling and drought, the populations of *T. triandra* on the flats struggle to maintain existence. We do know that re-establishment of this species on the flat areas is feasible and that it has the potential to be used for restoring degraded patches. A restoration site undertaken by Dr Karen Esler (Stellenbosch University) and Dr Klaus Kelner (Potchefstroom University) shows positive results on germination potential of *T. triandra* on a bare patch (brak kol) of the southeastern flats of the Tafelberg Mesa (Esler and Kellner 2001). *Themeda triandra* can therefore be considered for such restoration programmes.

Chapter four

Seed dispersal of *Themeda triandra* in sparse and dense vegetation of the Middelburg district, Eastern Cape.

4.1 Abstract

Dispersal distance of *Themeda triandra* was investigated in dense and sparse Nama-Karoo vegetation in the Middelburg district, Eastern Cape. Seed dispersal experiments were carried out over a time period of 34 and 58 hours on the north and south-western flats surrounding the Tafelberg Mesa. In both the two time period experiments, the overall percentage recovered seeds in number and weight were (88% ; 71%) and (70.5% ; 56.25%) for dense and sparse vegetation respectively. Results also show a maximum seed dispersal distance of 100cm for the dense vegetation site. In contrast, a small proportion of seeds dispersed to a 400cm radius within the sparse vegetation site. Maximum dispersal distance in the sparse vegetation site was at 60 – 100cm. *T. triandra* were found to be a short distance disperser. Experiments indicated that within both the dense and sparse vegetation sites, the majority of seeds dispersed into sites classified as open. This seed dispersal method (counting and weighing) shows great potential for future use of dispersal experiments of *T. triandra*.

4.2 Introduction

Understanding the nature and strength of demographic impacts of interactions between individuals and communities within which they occur is fundamental to understanding community processes. Wiegand *et al.* (1995) demonstrated this using a grid-based simulation model based on field data from a semi-arid Karoo ecosystem in order to predict future changes in the ecosystem. They found that recruitment and turnover in the system occurred firstly only when timing and amount of rainfall facilitated seed production, seed germination and survival of seedlings and secondly, if safe sites (Harper 1977) were available to the seeds. This chapter explores the theme of seed dispersal and safe sites for *T. triandra*.

Seed dispersal is a phenological stage in a plant`s life history that has the strongest influence on gene flow (Bawa 1995). Fluctuations in climatic conditions means that in good years, species disperse and establish in areas not normally accessible to them. In bad years these species become isolated into small, favourable microhabitats. Dispersal of seeds into distant sites may reduce the likelihood of local extinction because distant sites can be colonized and original sites can be recolonised from these distant sites (Pulliam 1994). The concept of a "safe-site" suggests that the probability of a seed becoming a successful recruit depends on the characteristics of the micro-site or macro-site within which it will emerge, grow and survive (O`Connor 1997). In a xeric vegetation matrix, selective pressures are towards short-distance dispersal and/or seed retention. It has been suggested that this strategy has a selective advantage over long-distance dispersal in arid environments because seedlings have a higher probability of survival close to where the parent plant has survived to reproduction (Ellner and Shmida 1981).

Themeda triandra is a tufted perennial with dark brown awns of about 3-6 cm long. These awns presumably have some dispersal function. It is a palatable plant species and is considered as valuable for grazing animals. *Themeda triandra* is used as indicator of good veld condition (Roberts 1973; Gibbs Russell *et al.* 1990).

Each plant species has its own morphological adaptations to aid in dispersal (Willson *et al.* 1990), and different patterns of dispersal are presumably a consequence of selection for features that increase the chance of the seeds finding a safe site. According to Chippindall (1955), many grass species bear elaborate appendages, such as hygroscopically active awns, that suggest that they are adaptations for wind or animal dispersal. Robinowitz and Rapp (1981) reported that the awns do not play any role in the movement of the seeds over horizontal distances. The role of the awn in the grass species, *Aristida vagans* is simply to orientate the seed during its fall so that it can establish itself near the vicinity of the parent plant (Peart 1981). The awn of *T. triandra* might act in a similar way for successful establishment near the parent plant.

Stipa tenacissima (Poaceae) is also a tussock grass with a sharp callus, short bristles and a long awn, which has a spiral structure. The awn rotates with changes in moisture content and assists with penetration into soil and burial of seed (Haase *et al.* 1995).

According to Zohary (1937), each diaspore of *Erodium* species (Geraniaceae) consists of a carpel plus awn which moves by hygroscopic uncoiling of the awn during wetting and recoiling on drying. Stamp (1989) found that within *Erodium* species, the mean distance that diaspores travelled was less than 1m and even with windy conditions, the diaspores were unlikely to move more than 2m.

The seeds of *T. triandra* are relatively large in comparison to other grasses. The role of the seed awn in the dispersal process is still debatable. Adams and Tainton (1990) suggest that the function of the awn is to propel the seed along the soil surface, aided by moisture change. The fine hairs that are found at the tip of the diaspore are thought to aid in the anchoring of the seed in a "safe site" (Harper 1977). Others suggest that the function of the seed awn of *T. triandra* is simply to move the seed along the surface of the soil as a dispersal device to locate a suitable microhabitat for germination and also to ensure maximum water uptake by the diaspores for germination and seedling establishment (Peart 1981; Harper *et al.* 1965; Peart 1979).

In this study, the following questions were addressed in order to understand the dispersal behavior of *T. triandra* seeds: (i) Is *T. triandra* capable of long distance dispersal, or does the species conform to the pattern of many xeric species in being a short distance disperser? (ii) How variable are dispersal distances in different vegetation densities? It was hypothesized that seeds of *T. triandra* are not adapted to long-distance dispersal. Vegetation density would influence dispersal distance. Consequently, seeds of *T. triandra* will travel far shorter distances in dense than in sparse vegetation.

4.3 Materials and methods

This study was conducted on the southeastern flats of the Tafelberg Mesa in the Middelburg district of the Eastern Cape. The average rainfall for this region is 360mm per annum with mean maximum temperatures of 30°C and minimum temperatures of 0°C. Prevailing winds in this area tend to start from the west as light breezes and then pick up to stronger breezes, sometimes ending in gusts that are very strong. On the days of the seed dispersal experiments wind conditions were average for the district (pers. obs.) although actual speed and direction were not recorded. This was a design constraint of the experiment. Figure 4.1 indicates that wind blows primarily from a northwesterly direction in summer and in a southeasterly direction during winter (South African Weather Bureau 1960). The wind did not change direction during the duration of the seed dispersal experiments. The wind direction on per year basis is primarily southeasterly. Personal observations indicated that high velocity wind events such as dust devils and whirlwinds are common to the area.

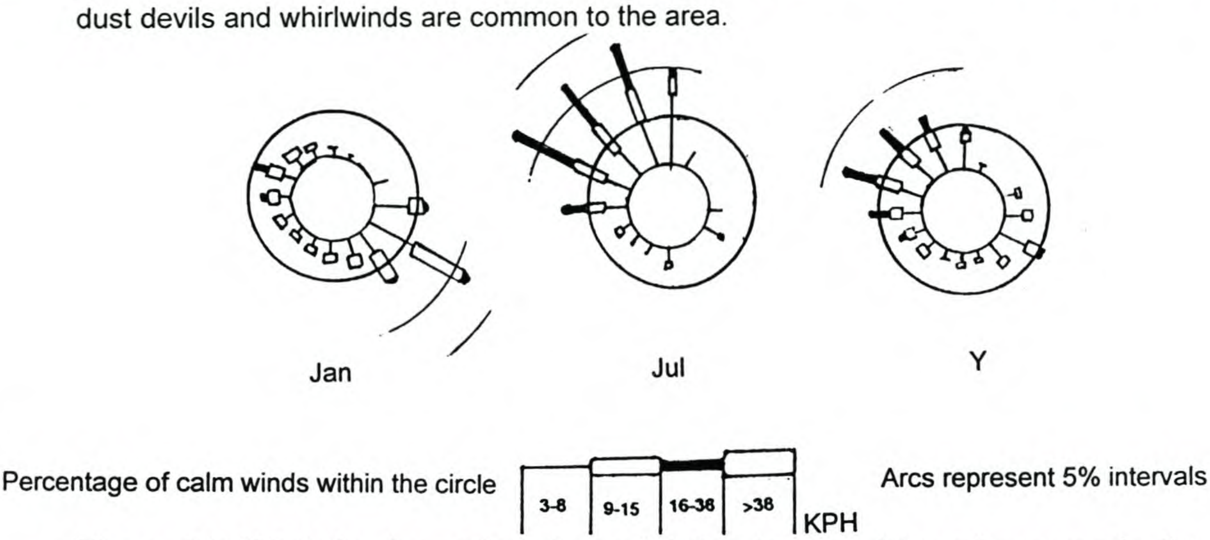


Figure 4.1: Wind direction and wind speed during January, July and per year for the Middelburg district of the Eastern Cape (South African Weather Bureau 1960).

Seeds of *T. triandra* were collected in early May 1999 from populations, approximately 30 km (R58 road, east) outside Middelburg in the Eastern Cape. One hundred seeds were counted out and weighed on a four decimal point, top loaded scale. Eight batches of approximately 100 seeds were made up using weight to estimate number.

Each seed batch was immersed in a Blancophore BBU solution (0.5g dye per 30mL water) for approximately one hour. This solution enables visibility under ultra violet light. Seeds were laid out to dry and exposed to ultra violet light in a dark room to ensure that the dye was present on the seeds in sufficient quantities to make them detectable.

Two replicate seed batches were released into relatively homogenous vegetation sites with densities of 30% shrub; 50% grass and 20% open/rock areas (dense vegetation) and 30% shrub; 30% grass and 40% open/rock areas (sparse vegetation). There were no natural populations of *T. triandra* in the vicinity.

The dominant shrub found at the study sites was *Lycium cinereum*. The dominant grasses were *Aristida adscensionis*, *Cynodon dactylon* and *Tragus koelenoides*. For this study dominance was based on cover abundance rather than frequency of individuals. The dense and sparse vegetation sites were about 15m apart so as to prevent seed mixing as much as possible. The height of vegetation for both sites was approximately 30cm. Replicates in each vegetation site (dense vs sparse) were approximately 20m apart. Seeds were placed in an open area of a 40cm radius between the shrubs and grasses to avoid a windbreak effect.

Seeds were released at 10:00 am on the 5^{th} of October 1999 on the southwestern flatland area. After 10 hours (at 12h00 pm), the movement of the seeds was assessed by using a portable ultra violet light powered by a portable generator. All seeds were counted in consecutive radii (minimum distance = 5cm and maximum distance = 400cm, see also Appendices 1 and 2) with the initial release spot being the center of the circle. Seeds were re-checked after 24 hours. After 34 hours (10h + 24h), all visible seeds were collected (from within each radius).

Two days later with identical climatic conditions, the experiment was repeated with the same initial number of seeds over a period of 58 hours at different sites (northern flats of Tafelberg Mesa) with densities of 35% shrub; 50% grass and 15% open/rock areas (dense vegetation) and 30% shrub; 35% grass and 35% open/rock areas (sparse vegetation).

The objective of this study was to determine what distances (cm) seeds of *Themeda triandra* can travel in two vegetation densities (dense vs sparse) over a period of time (hours).

4.4 Results

The initial mass of 100 seeds weighed in the laboratory was measured at 0.448g. After the 38-hour experiment, the seeds recovery by weight ranged from 88% (0.791g ; 204 seeds) in the dense site to 63.3% (0.567g ; 158 seeds) in the sparse site. For the 58-hour experiment the seed recovery ranged from 54% (0.485g ; 148 seeds) in the dense site to 49% (0.441g ; 124 seeds) in the sparse site. The overall percentage recovered seeds in number and weight, for both experiments, were higher (88% ; 71%) in the dense vegetation sites than in the sparse vegetation sites (70.5% ; 56.25%). Results indicated that the proportion of seeds dispersed was significantly different between the 38-hour and 58-hour experiment (F= 4.006 ; df = 1, 238 ; p< 0.05). For the 38-hour experiment, 267 seeds in total had dispersed while 424 seeds dispersed for the 58-hour experiment. The reason for this difference is likely to be due to the extra time in the latter experiment.

Table 4.1: Counts of seeds dispersed into three microhabitats (open/rock, grass and shrub), data are expressed as means ± standard deviations for both 38-hour and 58-hour experiments.

Microhabitat	Time (hour)	Dense	Sparse
Open/rock	38	4.41 ± 2.49	5.32 ± 0.58
	58	4.95 ± 0.76	5.21 ± 0.73
Grass	38	0.50 ± 0.22	0.73 ± 1.48
	58	3.95 ± 0.26	1.11 ± 2.26
Shrub	38	0.05 ± 0.18	1.65 ± 3.84
	58	1.15 ± 0.70	6.52 ± 0.61

Table 4.1 indicates that within both the dense and sparse vegetation sites, the majority of re-collected seeds had dispersed into sites classified as open sites with the exception of the mean 6.5 seeds that dispersed under shrubs within the sparse vegetation during the 58-hour experiment. Two-way ANOVA shows that the number of seeds dispersed (both experiments) was significantly different between the three micro-habitats (open/rock, grass and shrub) (F= 6.269 ; df = 2, 237 ; p< 0.05). There was, however no significant difference between the number of seeds dispersed into grass and shrub vegetation (F= 0.535 ; df = 1, 158 ; p= 0.466). Both the 34-hour and 58-hour experiment indicated no differences between the proportion of seeds dispersed within the dense and sparse vegetation densities (F= 1.408 ; df = 1, 238 ; p= 0.237).

Combining the two experiments, a significant difference was found between the number of seeds dispersed and the distances the seeds travelled (F= 2.970 ; df = 1, 230 ; p< 0.01). Figure 4.2 and 4.3 shows that seeds in the dense sites dispersed no further than a 100cm radius. In contrast, a small proportion of seeds reached the 400cm radius in the sparse sites (see Appendices 1 and 2). Maximum dispersal of seeds in the sparse vegetation density was at 60–100cm.

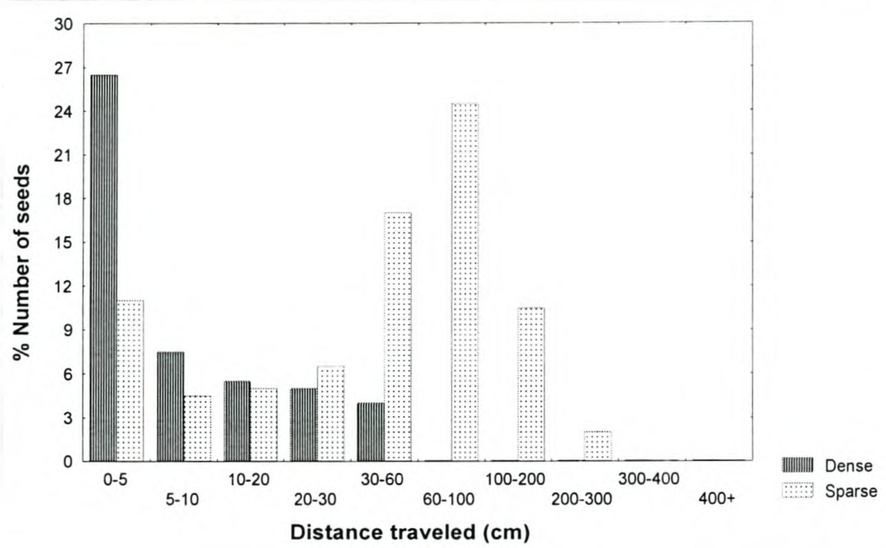


Figure 4.2: Distribution of seeds away from original source after a 38-hour period in two vegetation densities. Data are expressed as the percentage number (%) of seeds dispersed over a distance (cm). Percentage values are presented in Appendix 1.

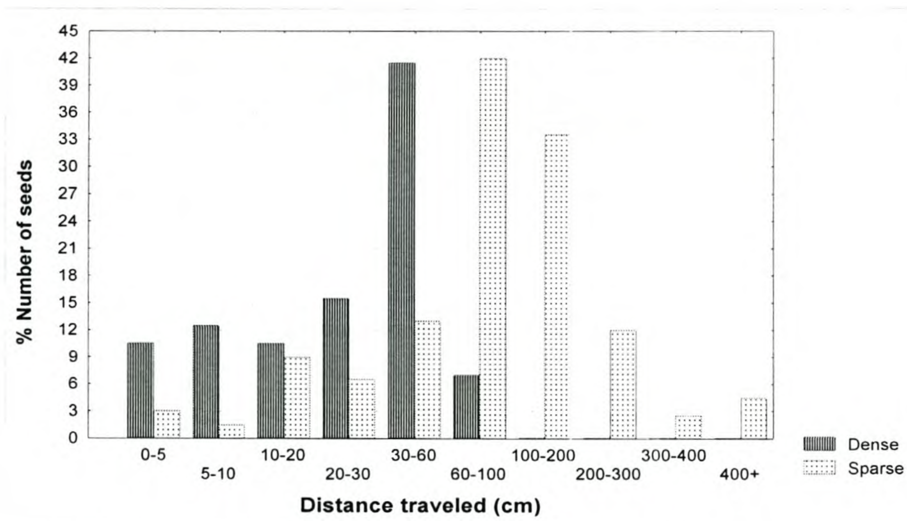


Figure 4.3: Distribution of seeds away from original source after a 58-hour period in two vegetation densities. Data are expressed as the percentage number (%) of seeds dispersed over a distance (cm). Percentage values are presented in Appendix 2.

4.5 Discussion

Both methods used to calculate percentage recovery of *T. triandra* seeds resulted in good recovery figures showing that the dye method has great potential for dispersal studies under similar conditions. Although *T. triandra* seeds are small they luminesced well and are easily detected at night. This is not a time consuming method and all the equipment is easily obtained.

The transport of the generator was one difficulty we encountered but could be overcome by the use of a hand held ultra violet light. The success of this method depends on the time duration for the experiment. If the experiment is carried out over long periods of time, we could run the risk of low recapture numbers. This could be due to the events of dust devils (chance long distance dispersal events) and seed predation, which are common features of arid and semi-arid environments.

Wind generally contributes to the horizontal movement of diaspores in many environments, especially in those where vegetation is sparse or low in structure such as deserts and arid environments (Van Rheede van Oudtshoorn and Van Rooyen 1999). The results of this experiment clearly suggest that within the time period and weather conditions that the seed dispersal distance of *T. triandra* to "safe" microsites is short (majority disperse up to 60cm) and that the dispersal agent is wind, since seeds were dispersed in a clear direction according to the wind direction on the day of the experiments. This information is important for the success of restoration attempts using *T. triandra*. Similar findings have been obtained by Everson (1994) during her study on dispersal distance of *T. triandra* seeds in the mesic grasslands of the Drakensberg where 84% of the seeds fell within the one meter of the parent plant. In this study, results indicated that the maximum number of seeds in the dense vegetation moved only within the 1m mark. These findings imply strong competition between diaspores to locate a favorable microhabitat. Everson`s results indicated a 53% decrease in growth of *T. triandra* seedlings due to intraspecific competition.

O` Connor (1997) stated that the concept of a "safe site" suggests that the probability for a seedling to recruit successfully depends on the characteristics of the micro-site or macro-site within which it will emerge and grow. Soil type may be an important characteristic for a specific microhabitat. It was found that species with hygroscopically active awns are dominant on soils that are well-structured with a relatively high clay content (Peart and Cliffort 1987). These surfaces are either loose and crumbly or crack on drying which is a suitable microhabitat for germination of these diaspores. Since the dispersal mechanism of *Themeda triandra* is poorly developed, seeds generally fall in close vicinity of the parent plant. In sparse Karoo vegetation, 72% of the seeds dispersed up to the 1m mark and 33% dispersed further than 1m. Most of the seeds (52%) in the sparse vegetation dispersed to the open/rock areas. Sindel *et al.* (1993) demonstrated that seeds of *T. triandra* germinate best when on a soil surface in the vicinity of cracks or stones, which allow the seeds to bury themselves by natural means. The main advantage of the sharply pointed seed tip is to facilitate the diaspore to penetrate the soil to maximize the enhancement of water uptake (Van Rheede van Oudtshoorn and Van Rooyen, 1999). According to van Rooyen *et al.* (1990), the diaspore can anchor itself sufficiently to resist surface runoff and to decrease the risk of predation as soon as the diaspore is buried.

A seed predation study undertaken by Capon and O` Connor (1990) indicated that ants consume a considerable number of *T. triandra* seeds, because of the large amount of nutritional endosperm found within the seeds (Gibbs Russell *et al.* 1990). In 1975, Pulliam and Brand stated that ants have difficulties in handling smooth-sided seeds but rather transport awned *Aristida* seeds with ease. It might be suggested that ants contribute to the dispersal of the seed. Although they were present at the time of the experiment, no evidence was recorded on whether ants were responsible for dispersal.

Seed dispersal enables the plant species to migrate to new habitats and is one of the important factors influencing gene flow. The advantage of awned plant species should not be seen in the process of dispersal or distance covered but rather the importance of a anchorage mechanism to increase the success of post dispersal stages i.e. germination and establishment and protection against predators and strong winds (Van Rheede van Outshoorn and Van Rooyen 1999). The activity of seed predation and strong winds were not tested during this experiment. These results confirm within limits that *T. triandra* is a short distance disperser. Thus, supporting the “mother-site theory”, which suggest that most seeds tends to enter the soil very near the parent plant (Cook 1980; Ellner and Shmida 1981; Levin and Kersten 1974; Everson 1994). The results, however also indicate that seeds of this species are capable of dispersing beyond the 1m mark in sparse vegetation densities. This study suggests that *Themeda triandra* is not adapted to long distance dispersal and that vegetation density does influence the dispersal distance.

APPENDIX 1: Table 1 and 2 shows the distance the seeds travelled in dense and sparse vegetation respectively over a period of 38 hours. Seeds dispersed in three vegetation profiles namely: open, grass and shrub. The radius boundaries (i.e 0-5) of the areas of the study site were measured in centimeters. Vegetation for both dense and sparse was ± 30cm in height to reduce the wind brake effect. In sparse, the vegetation were spread about ± 30cm from each other but the vegetation of the dense site were dense to about ±10cm.

	Distance seeds travelled (cm)										Total
	0-5	**5-10**	**10-20**	**20-30**	**30-60**	**60-100**	**100-200**	**200-300**	**300-400**	**>400**	
Open	53	15	11	9							88
Grass				1	7						8
Shrub					1						1
											97

Table 1 indicate the distance seeds dispersed in a dense vegetation site over a period of 38 hours.

	Distance seeds travelled (cm)										Total
	0-5	**5-10**	**10-20**	**20-30**	**30-60**	**60-100**	**100-200**	**200-300**	**300-400**	**>400**	
Open	22	9	7	6	24	20	13	2			103
Grass				7	9	6	2		1		25
Shrub					3	23	6	2	1		35
											163

Table 2 indicate the distance seeds dispersed in a sparse vegetation site over a period of 38 hours

APPENDIX 2: Table 1 and 2 shows the distance the seeds travelled in dense and sparse vegetation respectively over a period of 58 hours. Seeds dispersed in three vegetation profiles namely: open, grass and shrub. The radius boundaries (i.e 0-5) of the areas of the study site were measured in centimeters. Vegetation for both dense and sparse was ±30 cm in height to reduce the wind brake effect. In sparse, the vegetation was spread about ± 30cm from each other but the vegetation of the dense site were dense to about ±10cm.

	Distance seeds travelled (cm)										Total
	0-5	5-10	10-20	20-30	30-60	60-100	100-200	200-300	300-400	>400	
Open	21	25	21	28							95
Grass				3	46	3					52
Shrub					11	11					22
											169

Table 1 indicate the distance seeds dispersed in a dense vegetation site over a period of 58 hours

	Distance seeds travelled (cm)										Total
	0-5	5-10	10-20	20-30	30-60	60-100	100-200	200-300	300-400	>400	
Open	6	3	17	5	16	26	14	11	1	5	104
Grass							8	10		2	20
Shrub			1	8	10	67	45	3	4	2	140
											264

Table 2 indicate the distance seeds dispersed in a sparse vegetation site over a period of 58 hours

Chapter five

Seed germination of *Themeda triandra* in the Middelburg district, Eastern Cape

5.1 Abstract

The seed supply of *Themeda triandra* for restoration and rehabilitation programmes of degraded patches may always be limited given the biological constraints on seed output. Therefore, whenever seed of *T. triandra* is available, it should be used efficiently to maximize population growth. In this study, the germination potential of *T. triandra* is investigated using de-awned seeds. In a greenhouse tunnel, we determined the effect of germination of seeds sown in soil types collected from the flats, slopes and summit of the Tafelberg Mesa and at four sowing depths (0 – 3cm). Soils collected from the flats indicated high mean numbers of seedling emergence from sowing depth 2cm and 3cm, compared to summit with high emergence at sowing depth 0cm. Biomass production stayed more or less the same for all the treatments, except for the below ground structures at sowing depth 0cm and 3cm for the flats and slopes respectively. In germination experiments where temperature and light were varied, high percentages of seed germination were recorded during the light treatment, except for the 15/30 °C temperature regime where germination were more or less the same between the light and dark treatments. Increase in temperature has an increased effect on germination, particularly the light treatments. In an experiment to detect the effects of smoke water, an increased percentage germination was observed as the concentration of smoke water decreased.

5.2 Introduction

Seed germination is usually a critical event in the life history of a species and its relationship to various environmental factors is considered to be important. The relationships between *T. triandra* and environmental factors have been studied and reported variously e.g. Danckwerts and Stuart-Hill (1988); Adams and Tainton (1990); O`Connor (1991b 1994 1996). Not many reports concerning the dormancy and germination of *T. triandra* in Australia are published presumably because it has not been used to any extent in agricultural reseeding programs. Southern Africa considers *T.*

triandra to be one of the best forage grass species and that is why more investigations concerning this species are in progress. *Themeda triandra* has a potential use in rehabilitating and restoration programmes in disturbed sites in highly degraded areas of arid and semi-arid environments. Restoration and rehabilitation of degraded areas involves the re-introduction of locally extinct desirable species or proliferation of desirable species that may have declined in abundance (Adams 1996). According to local farmers in the Middelburg district, *T. triandra* has declined significantly in abundance over the years especially on the flats surrounding the Tafelberg Mesa. Knowledge of recruitment through seed germination and seedling survival may play an important role if rehabilitation and restoration programmes are to be considered for the restoration of degraded areas.

Themeda triandra is a palatable grass species, which is highly desired by local farmers in the Middelburg district simply for its palatability and nutritional value to their livestock. It is common on the slopes and summits of the mesas in the Middelburg district, but only occurs as isolated patches on the flats. Is the absence of this species a consequence of germination/recruitment limitation? Recent research has, however, highlighted the potential to re-establish *T. triandra* artificially from seed (Esler and Kellner 2001), but the artificial re-establishment of this important grass may be limited by factors such as seed availability (Chapter 3), low seed viability and dormant seed (McDougall 1989) or lack of appropriate germination cues. *T. triandra* seeds have a dormancy period of approximately 12 months (West 1951). Indigenous grass seeds generally have to pass through the dormancy period before full germination potential is realized.

Grassland areas, dominated by *T. triandra*, are generally regarded as climax communities subjected to frequent fires (Tainton and Mentis 1984), although fires in the Middelburg district are an infrequent occurrence due to low biomass of communities. It is known that Middelburg is on the edge of *T. triandra* distribution (Acocks 1990). In 1948, the vegetation in Middelburg was classified as marginal grassveld (sweet grassveld), but has been invaded by the Eastern Mixed Karoo type (shrubs and grasses) (Tidmarsh 1948). The success of seed production and seed germination of *T. triandra* might be related to the morphological adaptations to fire. This species survives fire by producing an underground rhizome, which bear tiller initials, close to the soil (Tainton and Mentis 1984). A component of this study focused on the germination potential of *T. triandra* seeds under different smoke water concentrations. This smoke water technique was first used by De Lange and Boucher (1990), to investigate seed germination in fynbos species. Very little is known about germination of *T. triandra* seeds using smoke or smoke water as a stimulant. However, the most recent results were obtained by Baxter *et al.* (1994), who used smoke water as a stimulant and found an increase in germination of *T. triandra* seeds.

The effects of depth of sowing, soil type and seed condition (i.e. ranging from complete dispersal unit through to bare caryopsis) and the interactions between these factors on germination and emergence have not been reported in the literature before Sindel *et al.* (1993). It would be of essential to know the germination requirements of *T. triandra* to make recommendations on whether this species has the potential to be used in rehabilitation and restoration programmes.

This study focused on the germination requirements of *T. triandra*. The aims of this investigation were to determine: (i) at what sowing depth (cm) and in which soil type (taken from the major habitat units in this study) can maximum germination be expected, (ii) under which treatment (dark vs light) will maximum germination occur using three day/night temperature regimes, (iii) in which smoke water concentration will maximum germination occur using three day/night temperature regimes.

5.3 Methods and Materials

Seeds of *T. triandra* were collected in May 1999 from a roadside, approximately 30 km (R58 road, east) outside Middelburg in the Eastern Cape. The seeds were then stored at room temperature (23-27 ^{0}C) to reduce the risk of inducing seed dormancy. Seed viability was not tested and was a constraint of these experiments. Before the start of the experiments, seeds were placed in a bleach (Jik) solution (100mL distilled water and 5mL jik) to reduce the possibility of fungal infection during the germination trials.

5.3.1 *Experiment one: Sowing depth*

The aim of this experiment was to determine the germination potential of *T. triandra* seeds at four sowing depths (cm) in four soil types. The effect of soil type and sowing depth on germination was determined by sowing *T. triandra* seeds in plastic trays (16 x

23 x 5cm) in June 2000 and placing them in a greenhouse tunnel with day/night temperatures of 35-45 °C/18-25 °C. Only firm, presumably viable seeds (viability determined by visual means) were used for sowing and the non-viable seeds (dispersal units which were not dark brown or firm) were rejected before sowing.

Soils from the flats, slopes and summit of the Tafelberg Mesa were used in this experiment. All three soil types were sieved and well watered before the start of the experiment. A potting mixture (general) was obtained from NBI, Kirstenbosch, Cape Town, and included as the fourth soil type in this test. Trays were separately filled by these four soil types. Seeds were sown at depths of 0, 1, 2, and 3cm below the soil surface. The depths were applied to all the four soil types and three replicates were used for each sowing depth. All treatment combinations were completely randomized.

For each replicate, three furrows were made by pushing a 4mm thick wooden board onto the edge into the moist soil to the required depth. Eight seeds were laid at the bottom of each furrow, then re-filled with moist soil up to the surface level and firmed down. Thus, 24 seeds in total were used per replicate. For the 0cm treatment, the seeds were placed in a shallow (1-2mm deep) furrow with no soil covering. Each tray was well watered at sowing using a fine spray, with follow-up irrigation during the mornings on every second day.

Seedling emergence for all treatment combinations was determined daily for 32 days. The dead and living leaves per seedling were counted 32 days after sowing (DAS). Above and below ground biomass was harvested at 32 DAS. Root/leaf material was then bulked for each replicate, oven dried at 80 °C, and weighed.

Soils from four study sites respectively on the summit (North, Northwest, Northeast and Southwest) and flats (Flat 1, 2, 3 and 4) of the Tafelberg Mesa were sampled for texture analysis. Small (roughly 125mm^2) soil samples were taken at approximately 2.5m intervals, about 1m outside the perimeter of each study site (30m by 5m) and bulked. After air-drying, these samples were sent to the Soil Analysis Laboratories at Elsenburg (Department of Agriculture) to determine the percentage composition of stone, clay, silt and coarse sand.

5.3.2 *Experiment two: Temperature/Light treatments*

The aim of this experiment was to determine the germination potential of *T. triandra* under controlled environmental conditions and under two treatments (light vs dark) using three alternating day/night temperature regimes. Twenty viable de-awned seeds were placed in each of three (replicates) 9.0cm petri dishes containing four filter papers (Watman No 1) and 7mL of distilled water. The same was done for the dark treatments, but each petri dish was covered with aluminium foil. Dark treatments were opened only under weak green light (lens of flashlight covered with green cellophane paper). Petri-dishes were assessed at three alternating day/night regimes of 5/15 ^{0}C, 15/20 ^{0}C, 20/30 ^{0}C. Each temperature regime had a light photoperiod of 16 hours and a dark period of 8 hours. After week one, a fungus was detected in the petri dishes and they were immediately sprayed with the fungicide Captan (2g of Captan diluted in 1L of distilled water). The duration of the experiment was 36 days.

5.3.3 *Experiment three: Smoke water treatment*

The general aim of this experiment was to determine the germination potential at three smoke water concentrations using three alternating day/night temperature regimes. At the same time as experiment two, five viable de-awned seeds (because of seed limitation), representing one of three replicates, were placed in a through-flow germination box (Appendix 3). A description of the through-flow germination boxes is on page 67. Three replicates plus a control for each replicate (pure distilled water) were used for each of the three temperature regimes. In the box, the seeds were laid on glass micro fibre filter paper. The three smoke solution dilutions were made up from 3 delb (Meets 2000) smoke water as follows: i) 1:150 (0.05 L smoke water diluted in 2.45 L distilled water), ii) 1:200 (0.04 L smoke water diluted in 2.46 L distilled water) and iii) 1:250 (0.03 L smoke water diluted in 2.47 L distilled water). Each smoke solution was applied to each replicate for the three temperature regimes. The smoke solution was poured into the reservoir (Appendix 3) and filtered up through the glass micro fibre filter paper. Smoke solutions were added when ever levels were low to ensure continuous up filtering. The duration of this experiment was 36 days.

In experiments two and three, a seed was considered germinated when both the radicle and the plumule had emerged. For all three experiments, germination was recorded on every second day.

Mean and standard deviations were determined. Statistical analyses were done with the use of a Microsoft®-Windows application (STATISTICA©, 1999) to determine significant differences.

5.4 Results

5.4.1 *Experiment one: Sowing depth*

Soil analysis indicated that the flats had more of a sandy loam clay soil texture, being slightly higher in stone, silt and clay content (%) than soils collected from the Summit (Figure 5.1). The texture of the Summit soils was found to be more sandy loam because of the higher sand content (%).

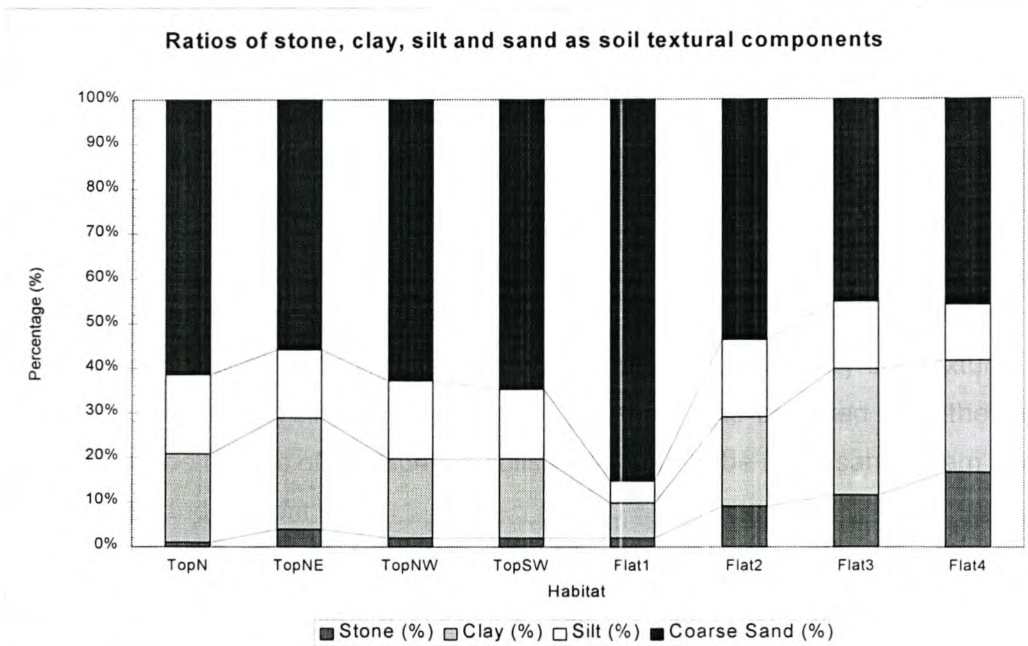


Figure 5.1: Soil texture composition ratios for four sites on the summit of Tafelberg (North, Northeast, Northwest and Southwest) and, four on the surrounding flats (Flat 1, 2, 3 and 4) were compared. Summit is referred to as top.

Soils collected from the flats and the potting mixture had the lowest seedling emergence at a sowing depth of 0cm, whereas the soils from the summit of the Tafelberg showed the highest emergence of 68% seedlings (Table 5.1). A significant difference ($F=3.352$; $df= 1, 44$; $p<0.005$) was found between seedling emergence and soil depth, 0cm and

3cm. However, at sowing depths of 2cm and 3cm, a high emergence of 76% and 68% was recorded respectively from soil collected on the flats with no significant differences between the 2cm and 3cm sowing depths (Table 5.1). Seedling emergence was more consistent at all depths (0-3cm) in the soils collected from the summit than on the slopes and flats. Emergence declined the greatest as sowing depth decreased in the flats soils (Table 5.1). The results showed no significant differences ($F= 0.083$; $df= 1, 44$; $p=0.969$) between seedling emergence and soil type.

No consistent trend was observed in leaf numbers per seedling for the four soil types and four sowing depths (Table 5.2).

Biomass production for the below ground structures (roots) was not significantly different for the different sowing depths with soil types being a co-variate ($F=0.666$; $df= 1, 43$; $p=0.578$). However, variation in biomass was found between the flats and slopes at sowing depths 0cm and 3cm respectively (Figure 5.2A and C). Variation was more at 0cm then at 3cm sowing depth. Higher biomass production was recorded on the flats at the 0cm soil depth (Figure 5.2A). Generally, biomass production stayed more or less the same for the other treatments. No significant differences were obtained for biomass production of the above ground structures (leaves + stems) in the four sowing depths with soil type being a co-variate ($F=0.740$; $df= 1, 43$; $p=0.534$).

Moisture content in the below ground structures was not significantly different for the different sowing depths with soil type being the co-variate ($F=0.901$; $df= 1, 43$; $p=0.449$). However, the results show a slight difference in moisture content in the below ground structures in the potting mixture at sowing depth 0, 2 and 3cm (Figure 5.3A, C and D). The moisture content of the above ground structures was significantly different ($p>0.05$) between the sowing depths 0cm and 3cm, and between 1cm and 3cm with soil type being a co-variate (Figure 5.3A, B and D).

5.4.2 *Experiment two: Temperature and light treatment*

Germination of *T. triandra* seeds was highest in the light treatments at all temperatures. As treatments increased in day/night temperatures, an increase in germination was recorded. The lowest mean percentage germination of 42% was recorded at the 5/15 °C temperature treatment and the highest of 62% at a 15/30 °C alternating temperature regime (Figure 5.4). Under the dark treatment, the lowest percentage germination of 27% and 28% were recorded at the 5/15 °C and 10/20 °C respectively, with the highest of 63% germination at the 15/30 °C temperature regime (Figure 5.4). Under light conditions, germination started from day 2-10; 6-16 and 12-32 for the 5/20; 10/20 and 15/30 °C temperature regimes respectively (Figure 5.5a, b and c). Under dark conditions the trend was approximately the same.

5.3.3 *Experiment three: Smoke water treatment*

In all temperature treatments there was an increase in percentage germination as the concentration of smoke water decreased, with the best results being obtained in the controls and the 1:250 dilution at 15/30 °C with mean germination of ± 15% (Figure 5.6). Smoke water had no significant differences on seed germination of *T. triandra* seeds.

Table 5.1: Seedling emergence (seed germination in/on soil) and seedling recruitment (seedlings survived till end of experiment) of *T. triandra* at sowing depths of 0, 1, 2, and 3cm in four different soil types (flats, slopes, summit and potting mixture). The duration of the experiment was 32 days after sowing. Data are expressed as percentage means.

Sowing depth (cm)	**Mean emergence (%)**				**Mean recruitment (%)**			
	Flat	**Slope**	**Summit**	**Potting mixture**	**Flat**	**Slope**	**Summit**	**Potting mixture**
0	25	34.6	68	25	22.1	25	66.7	25
1	50	63.8	47.1	61.3	48.8	59.6	45.8	59.6
2	70	50	44.6	68	66.7	47.1	44.6	68
3	68	66.7	62.5	50	63.8	66.7	54.2	47.1

Table 5.2: Number (mean ± standard deviation) of leaves per seedling (mature seedlings) of *T. triandra* at sowing depth 0, 1, 2, and 3 cm in four soil types (flats, slopes, summit and potting mixture). Duration of experiment was 32 days after sowing.

Sowing depth (cm)	Leaf number per seedling			
	Flats	Slope	Summit	Potting mix
0	2.7 ± 0.6	3.4 ± 0.8	2.9 ± 0.5	3.9 ± 0.1
1	2.8 ± 0.6	3.9 ± 0.5	2.3 ± 0.8	2.9 ± 0.3
2	3.5 ± 0.3	3.0 ± 0.5	3.1 ± 0.6	3.8 ± 0.5
3	3.4 ± 0.4	3.3 ± 0.4	2.9 ± 0.7	3.7 ± 0.3

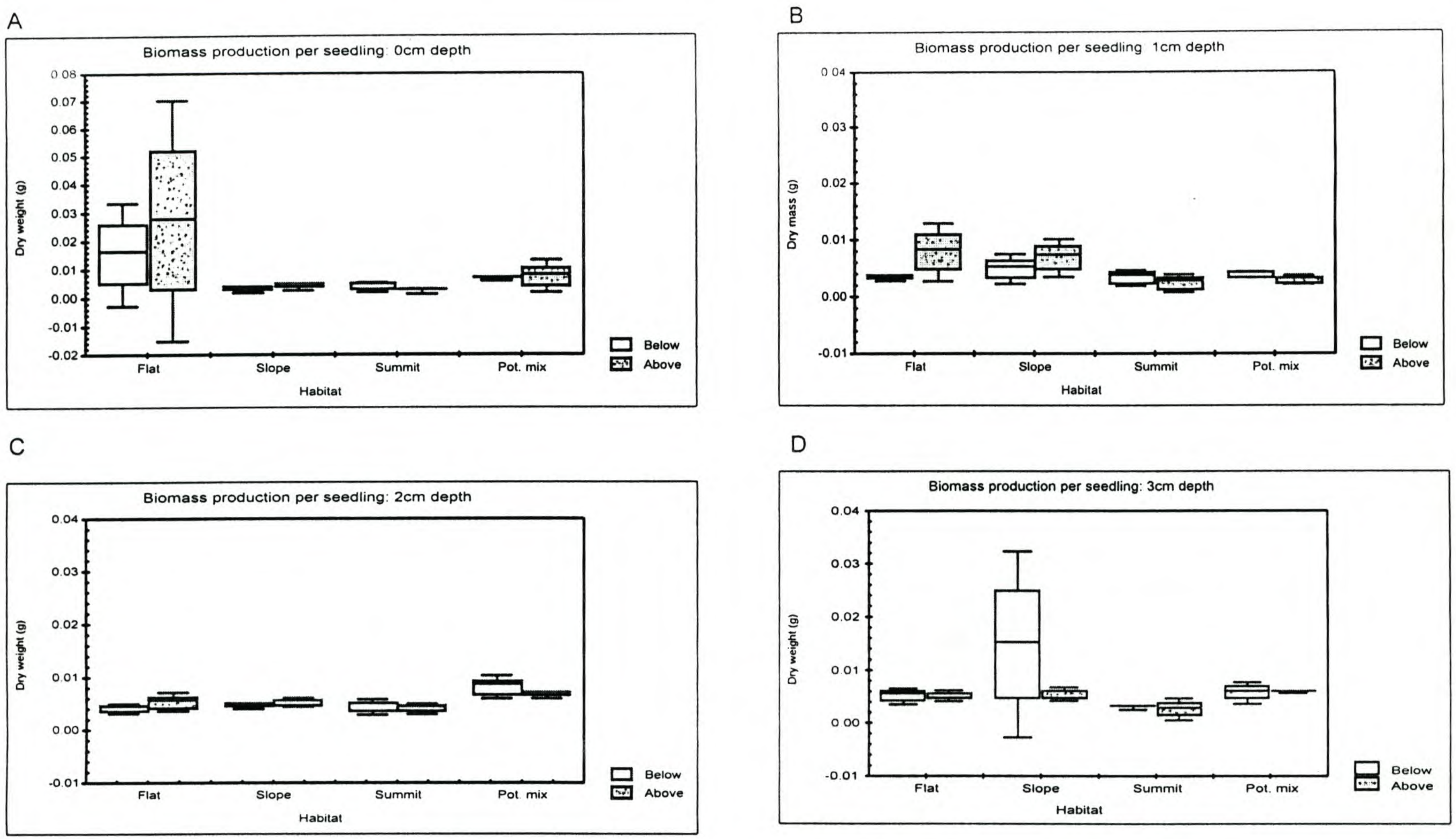


Figure 5.2: Biomass production (gram) per seedling for *T. triandra* at sowing depth 0 cm(A), 1 cm(B), 2 cm(C) and 3 cm(D) in four soil types (flats, slopes, top and potting mixture). Dry weight was recorded for below ground (roots)- and above ground (leaves + stem) structures per seedling. Due to some variation in graph A, the y-axis scale was between –0.01 – 0.08 (g), while graph B, C and D had the same axes between –0.01 – 0.04 (g). Data are presented as means ± standard deviation.

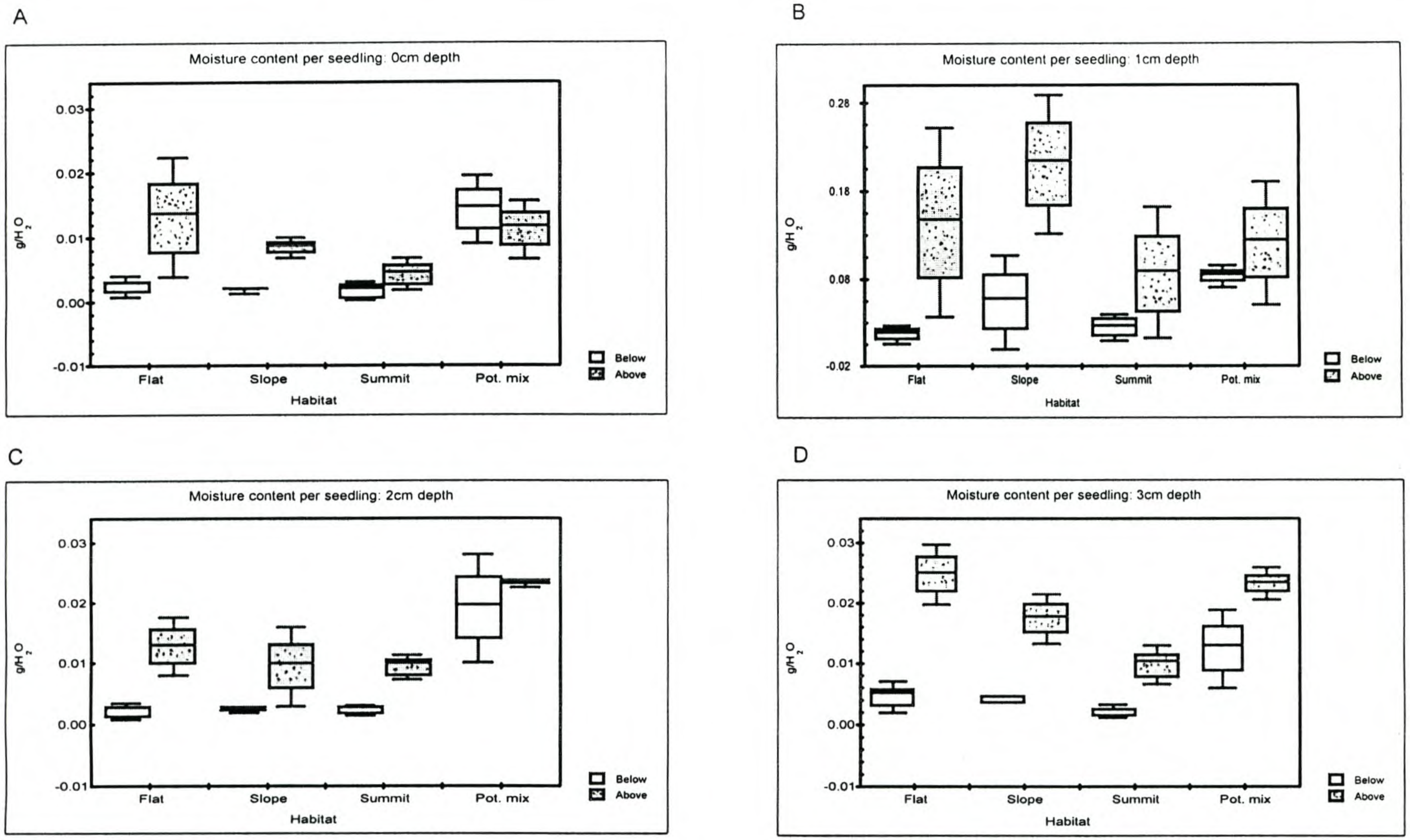


Figure 5.3: Moisture content (g/H_2O) per seedling of *T. triandra* at sowing depth 0 cm(A), 1 cm(B), 2 cm(C) and 3 cm(D) in four soil types (flats, slopes, top and potting mixture). Moisture content was recorded for below ground (roots)- and above ground (leaves + stem) structures per seedling. The y-axes for graph B is between –0.02 – 0.3 (g/H_2O) while graph A, C and D had a scale between 0.001 – 0.034 (g/H_2O). Data are presented as means ± standard deviation.

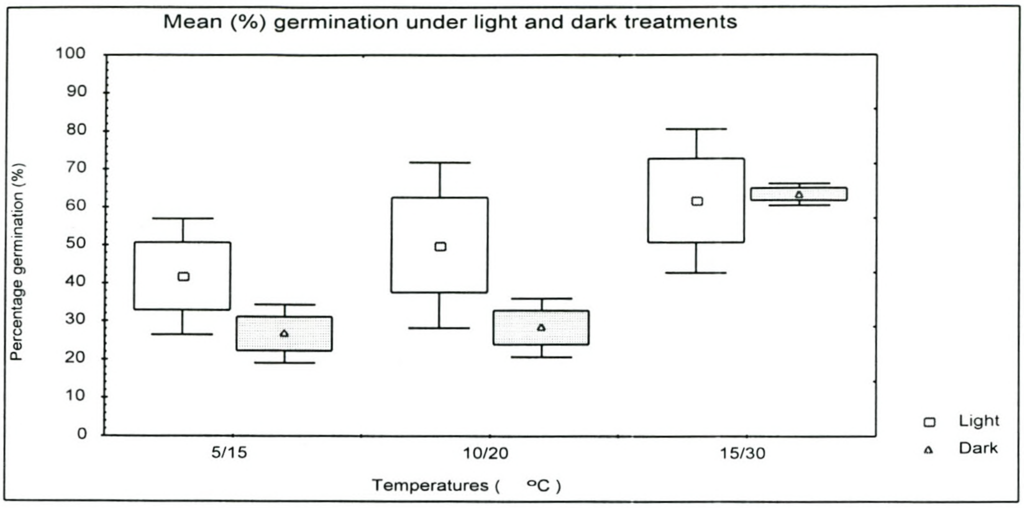


Figure 5.4: Mean (%) germination of *T. triandra* seeds under light and dark treatments for 5/15 °C, 10/20 °C and 15/30 °C alternating day/night temperature regimes. Percentage germination was recorded after 32 days.

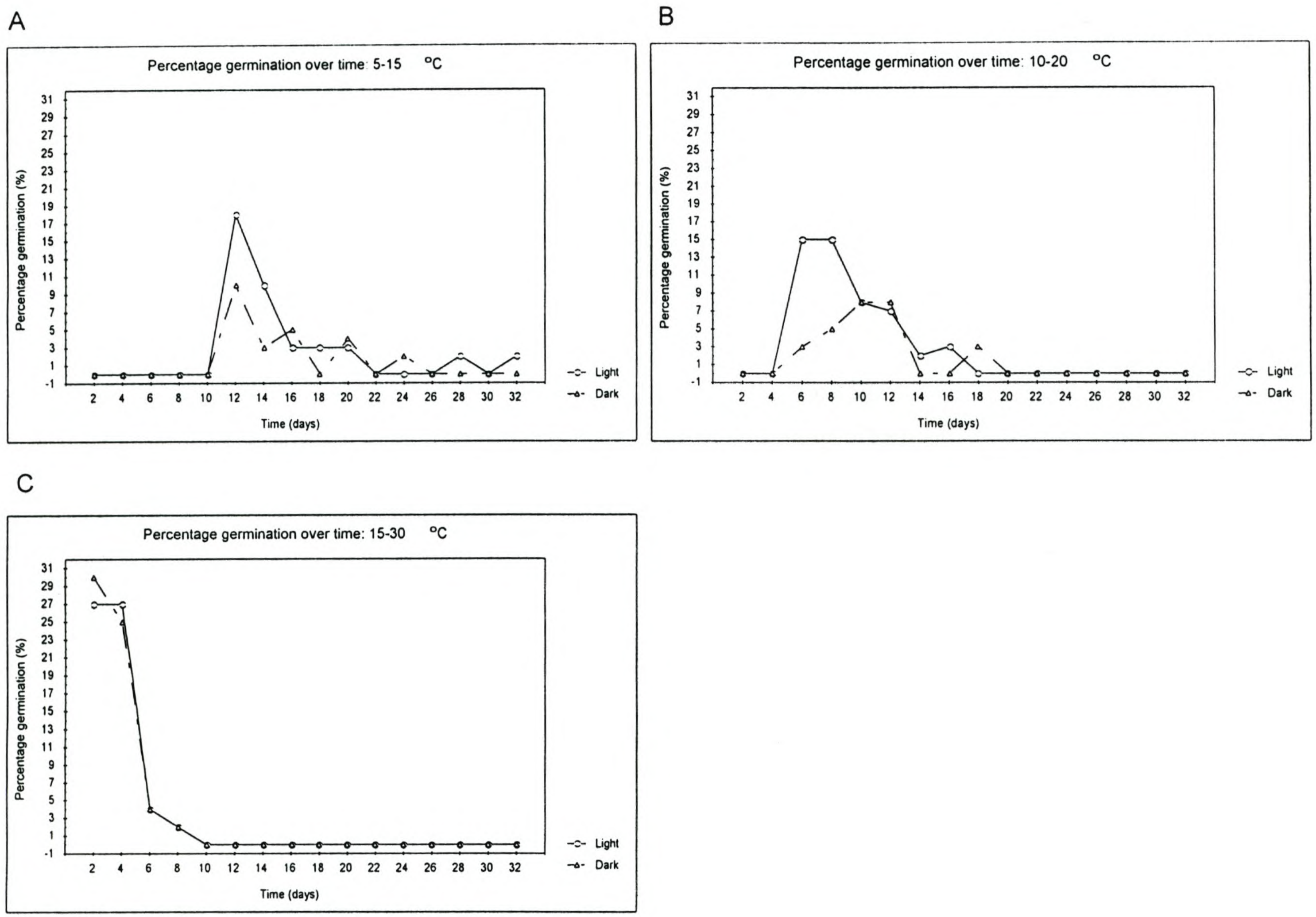


Figure 5.5: Percentage (%) germination recorded over time (days) for *T. triandra* seeds at 5/15 °C, 10/20 °C and 15/30 °C alternating day/night temperature regimes. The duration of the experiment was 32 days.

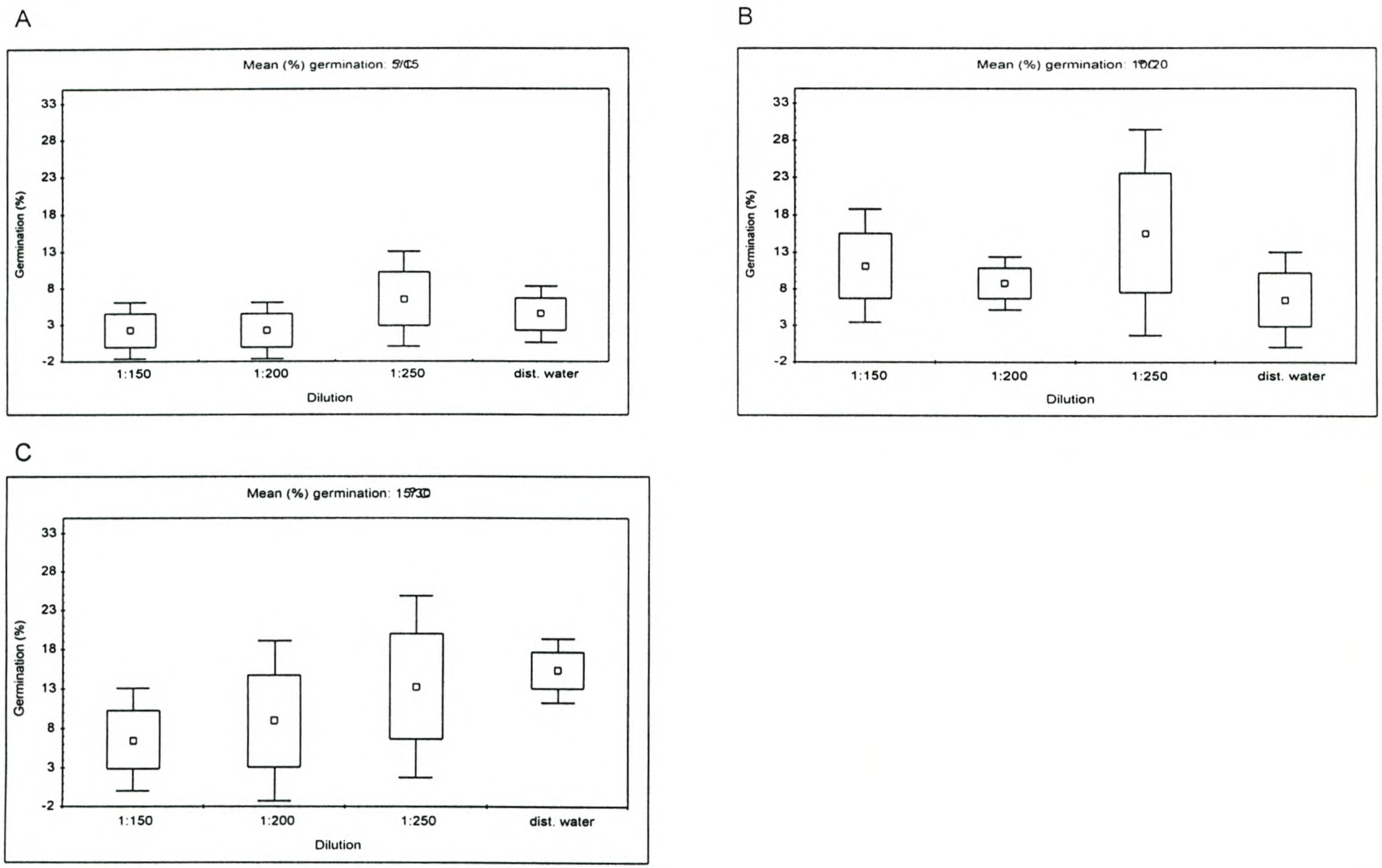


Figure 5.6: Mean percentage (%) germination recorded for *T. triandra* seeds under three smoke water concentrations (1:150, 1:200 and 1:250) at 5/15°C, 10/20°C and 15/30°C alternating temperature regimes. Included was a control, which was pure distilled water. Seeds were placed in Through flow germination boxes (appendix 3) in growth cabinets. The duration of the experiment was 32 days.

5.5 Discussion

It is very typical for *T. triandra* to be found on virtually any soil types but this species particularly favours soils with more clay and stone content (Dannhauser 1985; Hagon and Chan 1977). Soil nutrient status has no effect on seedling emergence, whereas a layer of mulch may improve plant survival by reducing soil moisture loss during establishment (McDougall 1989). De-awned seeds of *T. triandra* sown below the soil surface are likely to give the best results (Sindel *et al.* 1993). The preference for certain soil textures and seed burial depths observed in this study concur with these observations. Maximum germination was achieved at sowing depth 2cm and 3cm in soil collected on the flats around the Tafelberg. Generally, these soils were slightly higher in stone, clay and silt content (%) with the exception of flat 1 compared to the soils of the summit of the Tafelberg Mesa. The higher percentage of coarse sand for Flat 1 could possibly be explained by the location of the site approximately 30m from a dust road. High mean numbers of leaves per seedling were also found at sowing depth 2 cm and 3 cm from soils sampled from the flats.

The implication of these findings is that *T. triandra* is clearly not limited in its expansion onto the flats in the Middelburg area due to soil conditions at the germination/recruitment phase. One possible limitation to current distribution, however, relates to soil compaction. Field observations have indicated that too much compaction of surface soil can dramatically reduce seedling recruitment (Sindel *et al.* 1993). Certainly much hoof action was observed in the vicinity of the small patches of *T. triandra* on the flats (pers. obs.), and this hoof action negatively impacted on seedling survival (Chapter 3).

Full potential of germination of *T. triandra* is only realized when the period of seed dormancy is passed. The seeds collected were stored in paper packets at room temperature for 12 months. This is critical when considering restoration options. The high percentage germination recorded at the 15/30 °C alternating temperature regime is strongly supported by other existing literature (Everson 1994; Groves *et al.* 1982; Hagon 1976). High mean germination (37%) was also obtained by seed subjected to high temperatures (35%) in an alternating dark/light regime (Everson 1994). According to Groves *et al.* (1982), *T. australis* seeds from the study site Alice Spring (250mm rainfall/annum), germinated best at constant temperatures of 35 °C and 40 °C but declined drastically at lower temperatures. This study also noticed a decline in germination for the 5/15 °C temperature regime. Hagon (1976) found that maximum germination occurs at day/night temperature regimes of 30/20 or 35/25 °C. *Themeda triandra* thus germinates best under summer conditions when the probability of rainfall is at its highest. This is consistent with climatic conditions in the Middelburg district, thus the pre-conditions for germination are met and pose no limitation to restoration attempts.

The stimulation of *T. triandra* seed germination by smoke or smoke water at sub-optimal temperatures is of ecological importance and may increase the likelihood of seed germination in the field. According to Brown (1993), smoke and smoke solution acts as a seed germination cue in fynbos species. Studies have also shown that non-fire prone species also respond positively (Pierce *et al.* 1995). Aqueous smoke solutions are also known to have a positive effect on radicle emergence and lateral root development (Taylor and Van Staden 1996). Generally it is known that the increase in seed germination in the presence of smoke or smoke water has something to do with the active compounds present in the smoke or smoke water. However, very little is known about the role of these compounds and researchers are currently investigating the chemical characteristics of these active compounds in smoke or smoke water. Meets (2000) demonstrated that dark inhibition of germination in lettuce seed is alleviated by smoke water solution. In this study, this response was not found with *T. triandra* seeds. The higher concentrations of smoke water (lower dilution levels) had a greater inhibitory effect. Baxter *et al.* (1994) used plant derived smoke to test germination of *T. triandra* seeds and found an increase of 6.0% - 35.8% germination. However results with *T. triandra* seed collected from the Middelburg district did not convincingly suggest that smoke is of adaptive significance for this ecotype. It is not essential to provide smoke pre-treatments to boost germination in restoration attempts.

In order to promote the succession of *T. triandra* into highly degraded patches in arid and semi-arid environments, opportunities for seedling establishment need to be maximized. A knowledge about the germination requirements of *T. triandra* is necessary for the success of rehabilitation and restoration programmes of any disturbed areas (Everson 1994). Despite trends in the data suggesting that the requirements for successful germination (adequate soil texture, temperature and available moisture during the correct time) are present, the percentage germination of seeds still remains low for cost-effective restoration projects. Thus, further research on optimizing germination of *T. triandra*, or alternatively planting seedlings into degraded areas, is therefore required.

APPENDIX 3

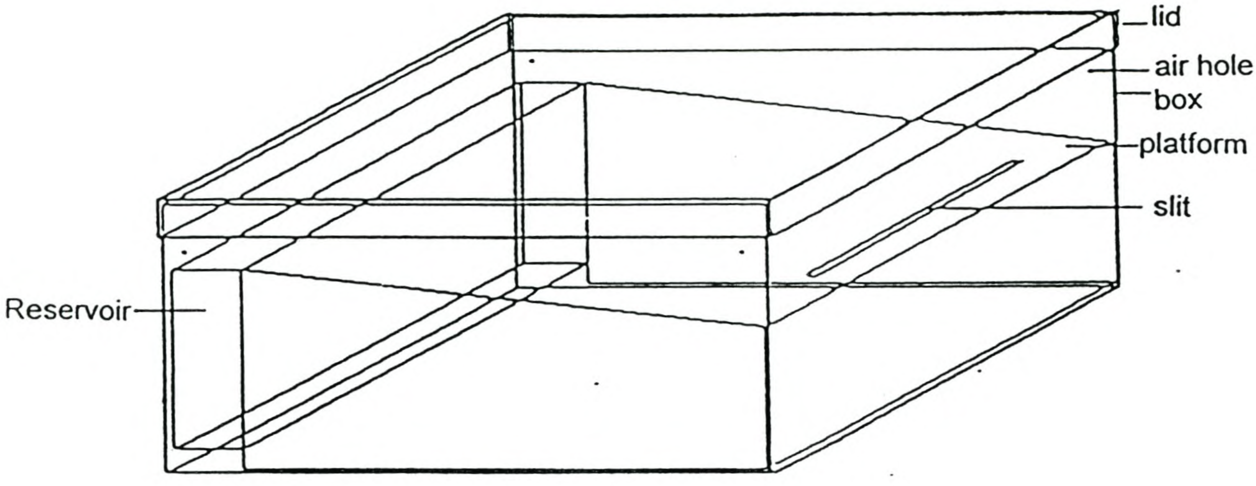


Figure 1: A 3-dimentional view of a germination box

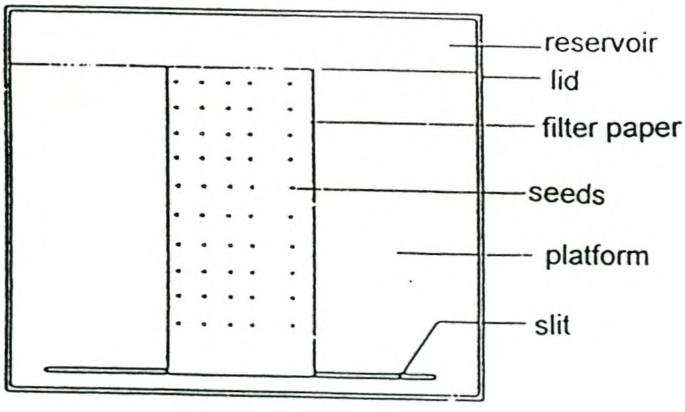


Figure 2: A germination box viewed from above, showing how seeds can be placed on the glass micro filter paper. Extracted from Meets (2000).

APPENDIX 3 (cont)

Through - Flow Germination Boxes (patent pending)

Special germination boxes (Fig. 4.1 & 4.2) were used in this study. These boxes are made of Perspex® and function as and are called the Through-flow System (patent pending). This concept is similar to "slants" (germination paper held at 20° off the vertical) described by Korkmaz & Pill (1999). Some seed (up to one fourth of a given population) of certain herbaceous ornamental plants (Atwater 1980) will germinate readily when moist, but the remainder may have inhibitors that must be leached out before the remaining seed will germinate. The use of the Through-flow System enables any inhibitory excretions from the seed to be removed from the vicinity of the seed. The moisture gradient on the filter paper remains constant throughout. With the through-flow germination boxes, a constant flow of the germination medium, which in this case is aqueous smoke solution, is supplied to the seed. The effect of leaching can also be measured using these germination boxes.

Glass microfibre filterpaper was used, as it is neutral and it does not degenerate, thereby releasing acids, an important consideration when using unbuffered solutions. Use of glass microfibre filterpaper also removed possible germination stimulatory or inhibitory effects from the degradation of cellulose in conventional filterpaper. Furthermore, glass microfibre filterpaper is considered to give a better, more constant flow of the germination solution.

The diagram and basic description of the through-flow germination boxes were obtained from Micheal Meets, Botany Department, University of Stellenbosch (Meets 2000).

Chapter six

Ecophysiological variability of *T. triandra* individuals from populations on and off Tafelberg Mesa in the Middelburg district, Eastern Cape

6.1 Abstract

This study investigates the photosynthetic response of *T. triandra* individuals taken from populations on and off the Tafelberg Mesa. The investigation focussed primarily on whether the populations on the summit and flats of the mesa are ecophysiologically different in order to assess if these populations represent the same or different ecotypes. Plants were grown under controlled conditions inside a greenhouse for approximately 12 months before measurements were taken. Photosynthetic response was determined under different light intensities and temperature regimes. The results revealed no differences in respect of photosynthetic rates, stomatal conductances and transpiration between the populations, suggesting that the populations are representative of the same ecotype. In other words, individuals taken from the summit of Tafelberg could survive on the flats. Photosynthetic rate increased with increased temperature for all the plants with at least two from the summit indicating a T_{optt} of approximately 30 °C. *Themeda triandra* on and off the mesa are adapted to variable temperatures, which is important if the expansion of the populations is to be considered. This also suggest that *T. triandra* might cope with global warming.

6.2 Introduction

Themeda triandra is dominant over a large part of Southern Africa. Its grazing intensity has been well studied (O'Connor 1994), and it is highly preferred as a grazing species. Its relationship to other environmental factors such as temperature and light intensity is also been fairly understood (Wand 1999). In the Middelburg district, it is documented that *T. triandra* was once more widespread and now, after a combination of climate change and grazing mismanagement, it is confined to small isolated populations on the flats and larger populations on selected mesas that have been postulated to have less impact from domestic grazers (e.g. Tafelberg). *Themeda triandra* is known to be highly variable ecologically, with a number of recognized ecotypes in southern Africa having divergent growth forms, chemistry and ecology (Theunissen 1992a). Although this species can justifiably be regarded as one of the most important grass species in southern Africa due to its widespread distribution and dominance in reproductive rangelands, it can by no means represent the diversity of grasses in this region. Over most of the Summer Rainfall Region of South Africa, more than 75% of grass species are C_4 grasses (Vogel *et al.* 1978).

If restoration attempts using *T. triandra* are to be attempted, the role of ecotypes should be understood. In this chapter, I explore possible ecophysiological variation of the species from different habitats in the Middelburg district. Plants have evolved mechanisms for acclimating to different light (Björkman 1981) and temperature (Berry and Björkman 1980) environments, and may optimize survival, reproduction and growth under the prevailing environmental conditions by reallocating resources and/or changing their morphology. The ability of a given genotype to change its photosynthetic characteristics is an adaptive response to changes in environmental conditions such as light, temperature, or water regime (Mooney *et al.* 1978). The key question in this pilot study is: Are the populations of *T. triandra* on the flats and on the summit of the mesa two different ecotypes or are they simply variable growth forms in relation to micro-habitats in which they occur? Potential intra-specific variation in photosynthetic behaviour between plants from the two populations could point to the possibility that two ecophysiologically distinct ecotypes occur in the Middelburg district. On the other hand, if plants behave in a similar manner after acclimitization to similar conditions, there is a greater possibility that restoration attempts on the flats would be successful using mesa populations as a seed source.

Themeda triandra possesses the C_4 photosynthetic pathway. The main feature of C_4 photosynthesis is the CO_2 concentrating mechanism that effectively pumps CO_2 from the mesophyll cells to the vascular bundle sheath cells (Ehleringer and Monson 1993). A study undertaken by Wand (1999) showed, contrary to predictions, that some dominant southern African C_4 grass species are capable of responding positively to increasing atmospheric CO_2 concentrations. Her study indicated that *T. triandra* in particular, is certainly responsive to elevated CO_2 and temperature particularly with regard to gas exchange and leaf area development.

In order to gain a better understanding of the acclimation abilities of *T. triandra* in arid or semi-arid environments, it is important to consider the photosynthetic capacities. In this study, I investigate the effects of light intensity and temperature on *T. triandra* occurring on and off the Tafelberg Mesa. I only focused on the populations from the summit and flats. It is hypothesized that from an ecophysiological perspective, *T. triandra* occurring on and off the Tafelberg Mesa are two different forms.

6.2 Materials and methods

During May 1999, ten mature *T. triandra* plants, together with soil they were growing in, were removed from populations on (summit) and off (flats) the Tafelberg Mesa in the Middelburg district of the Eastern Cape and transported back to Stellenbosch. These plants were then cut back to 12cm in height and potted in 49cm by 9cm growth pots using a standard potting mixture consisting of sandy loam. The plants were grown inside a greenhouse at the Botany Department, University of Stellenbosch, Stellenbosch under the same environmental conditions for approximately sixteen months (end May 1999 to mid October 2000). The plants were watered to field capacity at least three times a week and a nutrient solution (mixture of 3 L water and 5 mL of Nitrosol) was also applied to the plants every second month. After seeding the plants were cut back to approximately 12cm in height to stimulate re-growth. At the end of the growth experiment, only three of the plants on summit and seven of the plants from the flats of Tafelberg Mesa survived. Ecophysiological experiments were conducted on these remaining plants. All gas exchange measurements were performed in mid-October 2000 (the peak of the growing season) on the PP-system, CIRAS 1.

6.3.1 Measurement of photosynthetic light intensity response

Stomatal and photosynthetic responses to variation in light intensity were measured on *T. triandra* plants originally occurring on and off the Tafelberg Mesa. The photon flux densities (PFD) tested were as follows: 0, 20, 40, 60, 80, 100, 140, 180, 250, 350, 500, 700, 1000, 1300 and 1500 $\mu molm^{-2}.s^{-1}$. Measurements were made at an ambient CO_2 concentration of 360 $\mu mol\ mol^{-1}$, leaf temperature of 25 °C and ambient water vapour pressure of 12 mb. The CO_2 concentration in this experiment was kept constant at 360 µmol mol^{-1}. For each measurement, two leaves were placed inside the cuvette. Leaves were allowed to equilibrate at each set of photon flux densities for approximately 8 minutes before the readings were taken. Leaf area inside the cuvette was measured immediately after the completion of each gas exchange measurement. Net CO_2 assimilation rate (A), stomatal conductance (g_s) and transpiration rate (E) were expressed on a leaf area basis.

6.3.2 Measurement of photosynthetic temperature response

The photosynthetic temperature response of *T. triandra* occurring on and off Tafelberg Mesa was studied. Leaf temperature was raised in steps of 2-5 °C from approximately 20-23 °C to 32-35 °C. Leaves were allowed to equilibrate at each temperature for 8 minutes before taking measurements of photosynthetic rate, stomatal conductance and transpiration rates. These gas exchange measurements were all made at a photon flux density of 1 000 µmol m^{-2}s^{-1} and CO_2 concentration of 360 µmol mol^{-1}.

Two leaves of each plant were placed inside the cuvette. Measurements were performed on three plants for each habitat (summit vs flats). Immediately following gas exchange measurements, the area of the leaves inside the cuvette was measured.

Statistical analyses were done with the use of a Microsoft®-Windows application (STATISTICA©, 1999). A t-test for independent variables was used to determine significant differences.

6.4 Results

6.4.1 Measurement of photosynthetic light intensity response

Gas exchange measurements obtained from *T. triandra* plants (summit vs flat) under different light intensities are given in Figure 6.1, 6.2 and 6.3. The results indicated no significant differences in photosynthetic rate (A) between individuals from the summit and flats ($p = 0.11$; $t = 1, 61$; $n = 45$). In figure 6.1 the flats individuals (A1-A3) showed a photosynthetic rate of approximately 8, 8 to 11 µmol CO_2 m^{-2}s^{-1} at a light intensity of 1 000 µmol photon m^{-2}s^{-1}. However, the summit showed the highest photosynthetic rate of more or less 14 μmol CO_2 $m^{-2}s^{-1}$ at a much higher light intensity between 1 300-1 700 μmol photon $m^{-2}s^{-1}$ (Figure 6.1 B1 & 6.1 B3).

Statistical analysis indicated no significant differences in stomatal conductances (g_s) between individuals from the summit and flat ($p = 0.77$; $t = 0.30$; $n = 45$). Figure 6.2 B1 and B2 shows that the summit has a high stomatal conductance of 56 and 81 mol $m^{-2}s^{-1}$ at light intensity of 700 and 1000 μmol photon $m^{-2}s^{-1}$ respectively. Figure 6.2 B2 and B3 shows a stomatal conductance of 52 and 66 mol $m^{-2}s^{-1}$ respectively for individuals from the flats at a lower light intensity of 360 μmol photon $m^{-2}s^{-1}$.

Transpiration rates (E) were also found not to be significantly different between individuals from the summit and flats ($p = 0.40$; $t = 0.85$; $n = 45$). High transpiration rates on the summit (1.6 mmol m^{-2} s^{-1}) were recorded at a light intensity of 1 000 μmol photon $m^{-2}s^{-1}$ (Figure 5.3 B3). The highest transpiration rate (1.29 mmol $m^{-2}s^{-1}$) on the flats was found at a light intensity of 7 000 μmol photon $m^{-2}s^{-1}$ (Figure 6.3 B3).

6.4.2 Measurement of photosynthetic temperature responses

Photosynthetic temperature response curves for the summit and flats are given in Figure 6.4. Statistical analyses showed no significant differences in photosynthetic rate (A) between temperature treatments for both individuals from the summit and flats ($p = 0.25$; $t = 1.17$; $n = 18$). Plants from the flats indicated an increase in photosynthetic rate with increase temperature (Figure 6.4 A1, A2 & A3), thus, making it impossible to indicate the optimal temperature point (T_{opt}). However, the flats showed an approximate photosynthetic rate of 9.9 and 8.9 μmol CO_2 $m^{-2}s^{-1}$ (Figure 6.4 B2 and B3 respectively) at a T_{opt} of 30 °C.

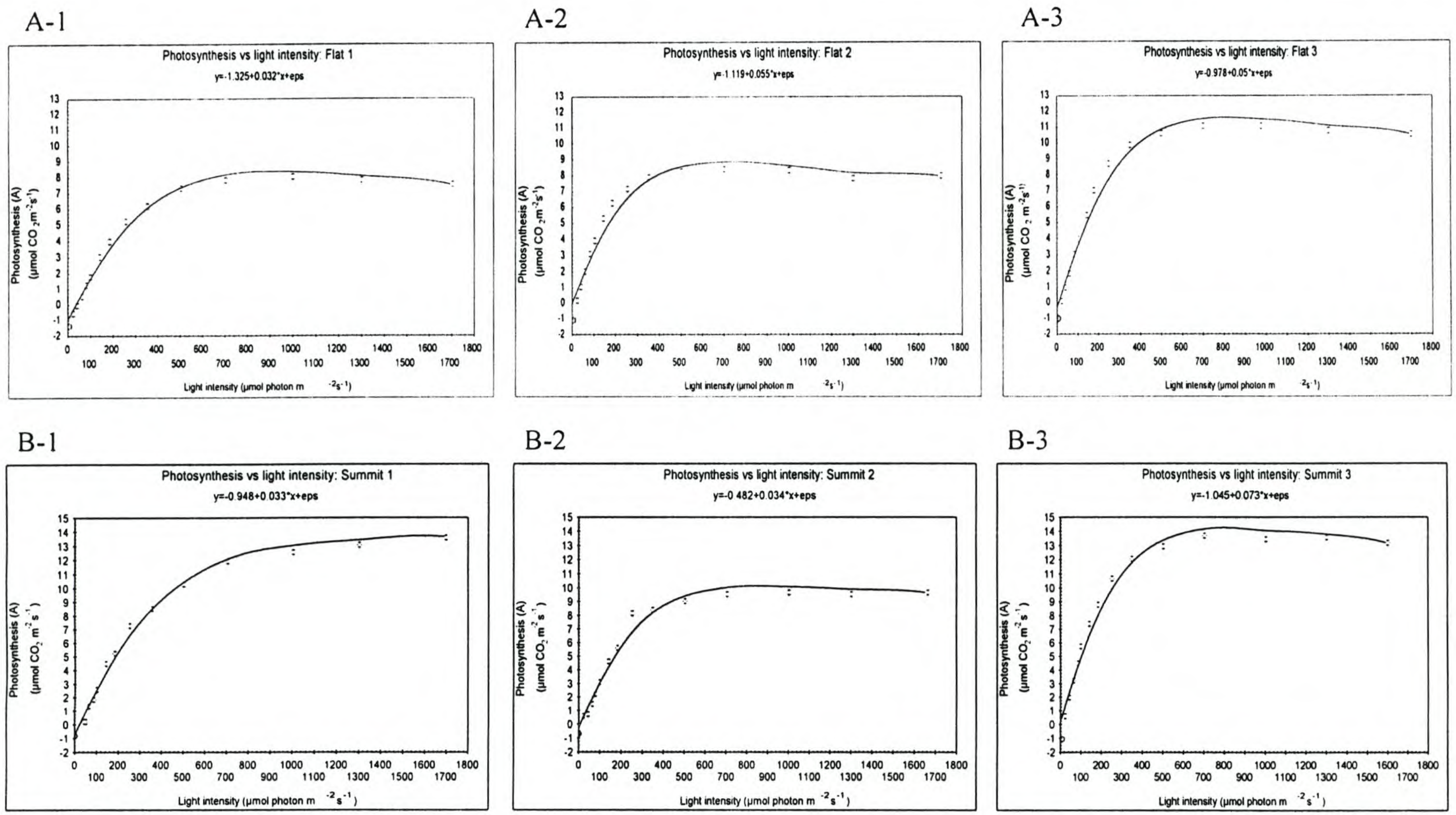


Figure 6.1: Effect of light intensity on photosynthetic responses on *Themeda triandra* occurring on the flats (A1, 2 & 3) and top (B1, 2 & 3) of Tafelberg mesa. Light intensity response curves were obtained for three plants on the flats and top. Before the experiment was carried out the plants were grown for approximately a year in a greenhouse under the same environmental conditions.

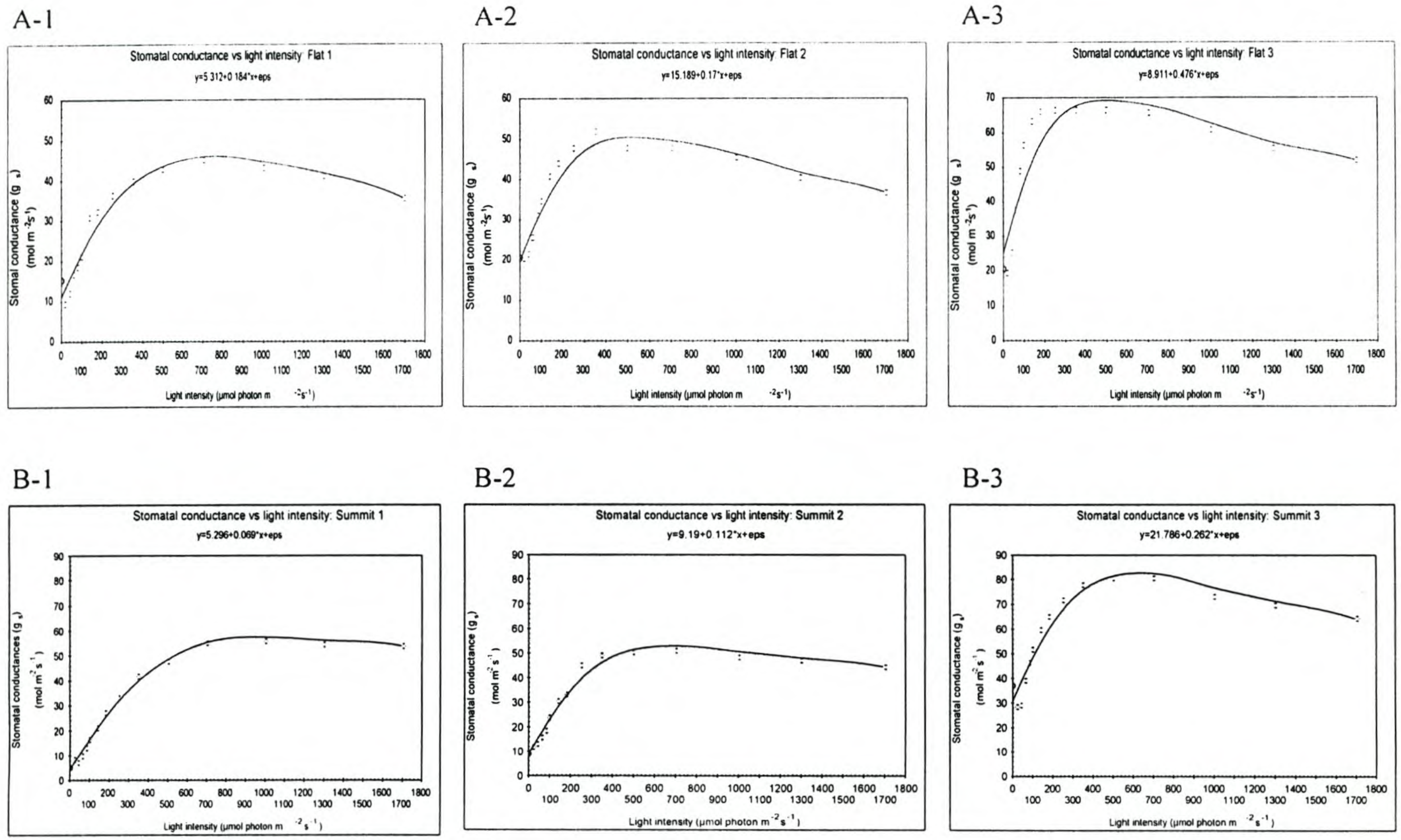


Figure 6.2: Stomatal conductance (g_s) at different light intensities for *Themeda triandra* occurring on the flats (A1, 2 & 3) and top (B1, 2 & 3) of Tafelberg mesa. Response curves were obtained for three plants on the flats and top. Before the experiment was carried out the plants were grown for approximately a year in a greenhouse under the same environmental conditions.

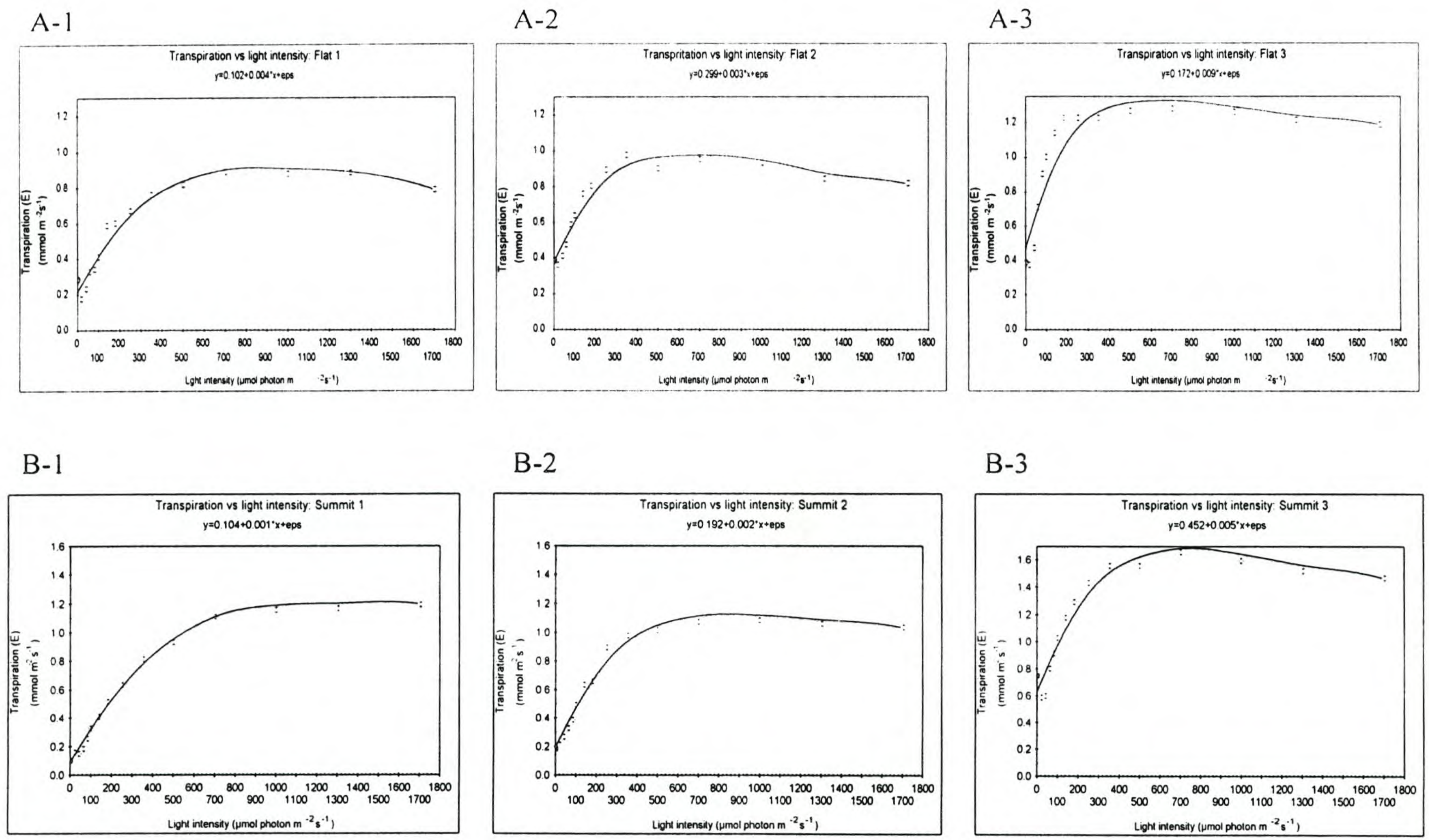


Figure 6.3: Transpiration rate (E) at different light intensities for *Themeda triandra* occurring on the flats (A1, 2 & 3) and top (B1, 2 & 3) of Tafelberg mesa. Response curves were obtained for three plants on the flats and top. Before the experiment was carried out the plants were grown for approximately a year in a greenhouse under the same environmental conditions.

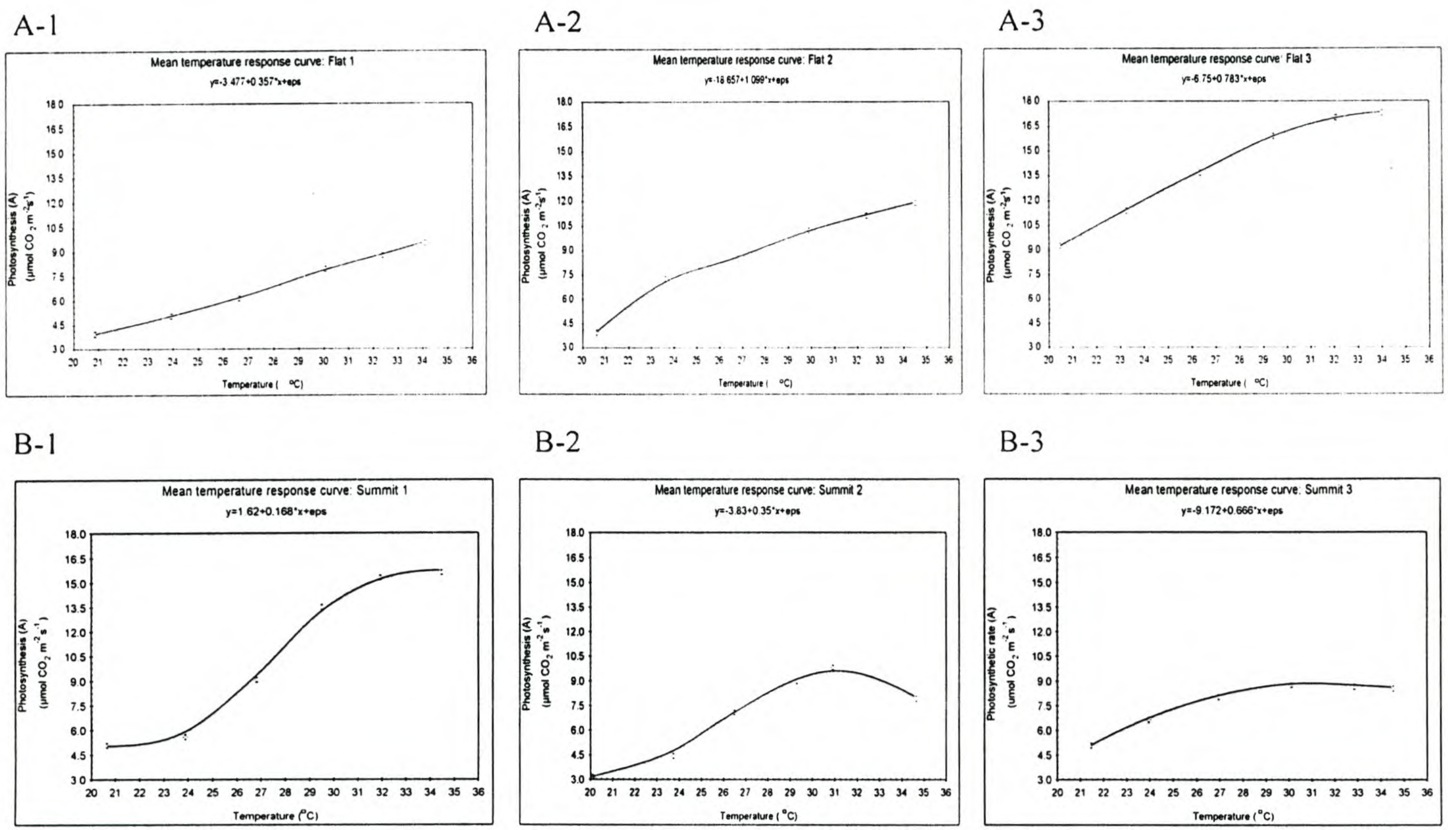


Figure 6.4: Effect of growth temperature regime on photosynthetic temperature responses of *Themeda triandra* occurring on the flats (A1, 2 & 3) and top (B1, 2 & 3) of Tafelberg mesa. Temperature response curves were obtained for three plants on the flats and top. Before the experiment was carried out the plants were grown for approximately a year in a greenhouse under the same environmental conditions.

6.5 Discussion

Themeda triandra individuals from populations on and off the Tafelberg Mesa showed no significant differences in photosynthesis, stomatal conductance and transpiration. This suggests, with respect to the parameters measured, that populations are not representative of two different ecotypes.

Photosynthetic temperature response curves indicated an increase in photosynthetic rate with an increase in temperatures. From these findings it is clear that temperature inhibition did not take place, thus, making it impossible to determine the optimum temperature (T_{opt}) for photosynthesis. However, at least two plants from the Summit indicated a high photosynthetic rate at T_{opt} of more or less 30 °C. Wand (1999), indicated that ambient CO_2-grown plants had a T_{opt} of about 28 – 30 °C, whereas those grown in elevated CO_2 had a T_{opt} of about 37 – 38 °C. During this experiment, the CO_2 concentration was kept constant.

Other studies reveal that C_4 grass species have a T_{opt} between 28 - 38 °C under ambient atmospheric conditions. Botha and Russel (1988) also found that the temperature optima for a range of C_4 grasses from the eastern Cape lay between 30 - 35 °C at comparable photosynthetic rates. C_4 grass species, and *T. triandra* in particular, appear to be highly adaptable to changes in temperature (Downing and Groves 1985). With the predicted 1-2 °C increase in mean temperature over southern Africa, this could be of critical importance to the sustained productivity of grasslands. It was suggested that C_4 grasses are capable of full thermal acclimation while resisting damage to, or inhibition of the photosynthetic system at high temperatures. According to Fitter and Hay (1987), many plant species have the capacity to acclimate to changing air and leaf temperatures, so that their photosynthetic capacities at different temperatures reflect the thermal environment experienced during growth. These differential responses of photosynthesis are partly the reason for the temporal displacement of growth in mixed C_3/C_4 grasslands, with C_3 grasses dominating during the cooler seasons and C_4 grasses dominating during the warmer seasons (Kemp and Williams 1980). Downing and Groves (1985) demonstrated how ecotypes of *T. triandra* originating from cool alpine to hot sub-tropical habitats in southern Africa, were all able to grow and reproduce equally well at temperature up to 36/31 °C.

In conclusion, this pilot study revealed no significant differences in photosynthetic rates between individuals from the summit and flats under different light intensities and temperature regimes. Although, is it impossible from these data to conclusively conclude whether *T. triandra* on the summit is of a different form than the one occurring on the flats of the Tafelberg Mesa, it is likely, however that material collected from the summit of the mesa would have no problem adapting to conditions on the flats if used in restoration and rehabilitation programmes.

A restoration plot set up in November 1999 on a bare patch (150m x 50m), at the base of the Tafelberg Mesa on the southeastern flats, included *T. triandra* in the experiment (Esler and Kellner 2001). Farmers were convinced that this was a positive way of dealing with degraded patches of veld, despite the expressed concern about the financial viability of such initiatives. *Themeda triandra* from the Middelburg area was used in this restoration project and showed great potential for future restoration trials. The generous rains that fell between November 1999 and April 2000 ensured that the response to the treatments was spectacular. During this experiment, *T. triandra* plants responded well indicating that seed from a mountainous population can recruit and survive to produce seeds on the flats, given sufficient rainfall.

Chapter seven

Conclusions

In this thesis an attempt was made to gain a better understanding of the regeneration potential of *Themeda triandra*. This study investigated populations on and off the Tafelberg Mesa in the Middelburg district of the Eastern Cape. The main objective was to determine whether this grass species has the potential to be used in restoration and rehabilitation programmes in the arid and semi-arid environment of the Nama-Kroo. It was also discussed to investigate whether the populations on the summit could potentially act as a source of seed to the small flats surrounding the mesa. This study focussed on key biological attributes such as: Seed production, seed dispersal, seed germination and ecophysiological responses *of T. triandra*. The purpose of this chapter is to review the objectives of this study and to determine the extent to which these objectives were achieved.

7.1 Review of the objectives

In this section, the goals and objectives, as described in Chapter one are reviewed. The overall objective of the study was:

> **to investigate selected biological attributes of *Themeda triandra* (seed production, seed dispersal, seed germination, seedling survivorship and ecophysiology) to determine its potential for use in restoration programmes.**

In doing so, the following goals were specified:

7.1.1 Goal 1: To determine seed production and seedling survival of *Themeda triandra* on and off the Tafelberg Mesa.

This investigation found *T. triandra* to be dominant on the summit of the mesa compared to the small isolated patches on the surrounding flats. Despite this patchy distribution, populations on the flats showed highest seed production levels per individual and per m^2

compared to individuals on the slopes and summit. Seed production was assessed over two years. In May 2000, a slight increase in seed production (per individual and per m^2) was found on the flats and slopes. This increase occurred due to the wetter rainy period prior to the May 2000 sampling period. Rainfall also had a positive effect on the percentage cover of other grasses and to a lesser extent on *T. triandra* and shrubs.

However, despite this increase in cover and seed production, seedling survival on the flats was negatively impacted by livestock. Seedling survival decreased with time in all three habitats, but the greatest declines in seedling survivorship were found in the populations on the flats. Survival appeared to be negatively affected by the trampling effect of livestock. Although grazing activity was not tested, this trampling effect suggests that populations on the flats are limited at the recruitment stage by grazing activity. It also suggests that with the removal of grazing, and with adequate rainfall, populations on the flats could increase in size.

7.1.2 Goal 2: to determine seed dispersal distance of *T. triandra* in different vegetation densities (dense vs sparse).

This study showed that seeds in dense vegetation do not disperse beyond the 1m mark in a 58hr period. Interesting was the 32.5% seeds that dispersed further than the 1m range in the sparse vegetation density. Although wind speed was not measured, wind still suggests a explanation for the distance the seeds travelled. In both vegetation densities, most of the seeds dispersed into open/rock microhabitats. Microhabitats such as cracks and rocks increase the chances of recruitment and germination. Seed dispersal of *T. triandra* is over short distances, supporting the "mother site theory". Morphological factors such as awns and the fine hairs on the tip of the diaspores do play an important role in the movement of the seed to reach a suitable microhabitat for germination. Despite being a short distance disperser, *T. triandra* could still be considered for restoration and rehabilitation programmes because the majority of its seeds have the potential to disperse up to the 1m mark within two days.

7.1.3 Goal: To determine the germination potential of *T. triandra* seeds in (i) soil type and with soil depth (ii) under dark and light treatments (iii) and with smoke water concentrations.

Maximum seed germination was obtained at depths 2cm and 3cm in soils collected from the flats surrounding the Tafelberg Mesa. High mean number of leaves were also found at these sowing depths. *T. triandra* tend to favour soils with a more clay/stone content with nutrient status not effecting the emergence of seedlings. These findings suggest that *T. triandra* is not limited in its expansion onto the flats due to soil characteristics and that re-establishment might be feasible in severely degraded areas.

During experiment 2 (light vs dark), maximum germination was obtained at the 15/30 °C alternating temperature regime. Similar findings were reported by other studies (Everson 1994; Hagon 1976). The 5/15 °C alternating temperature regime had the least effect on germination of *T. triandra* seeds and has been ruled out as a potential temperature regime to obtain maximum germination. It is clear that *T. triandra* seeds germinate best under summer rainfall conditions which are present in the Middelburg district of the Eastern Cape.

Smoke water did not have a significant effect on seed germination of *T. triandra*. There for, the establishment of *T. triandra* in the Middelburg area do not require smoke water as a stimulant for germination. This suggests that fire is not a prerequisite for germination.

7.1.4 Goal: To measure key ecophysiological characteristics of *T. triandra* individuals obtained from populations on and off Tafelberg Mesa and grown in controlled conditions (temperature and light intensity responses).

The summit and flats of the Tafelberg Mesa showed no significant difference in photosynthesis when exposed to different light intensities. An increase in photosynthetic rate with increased temperature was indicated. However, the optimum temperature (T_{opt}) for photosynthesis could not be determined, although the optimum temperature for C_4 grasses in the eastern Cape lay between the range of 30-35 °C. Wand (1999) also found the T_{opt} for *T. triandra* between 28 – 30 °C. This study suggests that with respect to the parameters measured that the populations are representative of the same ecotype. This means that those individuals taken from the summit of the Tafelberg Mesa could survive on the flats.

7.2 Source-sink dynamics

The findings of this study and their implications for source-sink dynamics are inconclusive. The evidence is not strong enough to build an argument as to whether *T. triandra* populations on the summit of the Tafelberg Mesa act as a source to the surrounding populations on the flats. The greater abundance *of T. triandra* populations on the summit does not suggest that the summit act as a source to the surrounding populations on the flats. A much more detailed investigation with appropriate methods for the Tafelberg Mesa is required to gain a clearer and better understanding of the source-sink concept. Required factors such as type and arrangement of habitat patches, resource availability, size of habitat patch and distance between populations etc., need to be considered for a better understanding on the source-sink concept.

7.3 Future research

Opportunities such as seedling establishment needs to be maximized in order to promote the succession of this grass species into highly degraded patches in arid and semi-arid environments. To consider restoration and rehabilitation programmes, it is critical to know as much as possible about the specific requirements of the individual species. For restoration and rehabilitation programmes to succeed, one of the key factors is the availability of seed. Since *T. triandra* has decreased in abundance in rural areas, it is relatively difficult to obtain naturally occurring seed in the areas where it is most needed. Thus, future research on aspects of *T. triandra*`s seed biology (e.g. viability, germination) is required if one is to provide a ready source of seedlings. A restoration attempt on a severely degraded patch at the foot of the Tafelberg Mesa, using *T. triandra* as a potential candidate, has already shown an enormous interest among farmers in the Middelburg district. Such information should be used as a starting point for future attempts. It is critical that farmers in this region should take note of these isolated populations of *T. triandra*, on the flatland areas, and decide on their management strategy (grazing routes/camps) in order to preserve of what is still left.

Chapter eight

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