AN ASSESSMENT OF THE POTENTIAL FOR UTILISATION OF SOIL-STORED SEED, FROM ON- AND OFF "CONSERVATION ISLANDS" (ISOLATED MOUNTAINS), AS AN INDICATOR OF RESTORATION POTENTIAL OF DEGRADED SITES IN SEMI-ARID KAROO AREAS.

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Declaration

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

THESIS SUMMARY

The composition and state of soil-stored seed banks on- and off the mesa Tafelberg, in the Nama Karoo rangelands of the Eastern Cape, South Africa, were investigated within the context of a broader restoration ecology project "Restoration of degraded Nama Karoo rangelands: the role of conservation islands"[1].

The premise for this seed bank study was that restoration of degraded semi-arid rangelands is possible through applied management programs based on the methodology and practice of ecological restoration. Broadly acknowledged properties of non-equilibrium environments (e.g. unpredictable climates and varying degrees of disturbance) and soil-stored seed banks (e.g. spatial and temporal distributions) formed the basis for investigating the general environment and the properties of existing seed banks in the Tafelberg locality. The potential role of hills as refugia for palatable plant species was an under-lying element of the investigation.

Following a brief investigation, of historical and contemporary research and policy on rangeland degradation in semi-arid regions of the world, the fundamental need for comprehensive and applied seed bank research in the Nama Karoo is emphasised.

Within the framework of the umbrella project, the seed bank study examined local environmental criteria commencing with an investigation into seed bank- and vegetation habitats. Chemical and physical properties of soils from twenty two sites on- and off Tafelberg were described. Substantial soil habitat variation, between the top, the north west slopes and plains and the south east slopes and plains of Tafelberg, was identified. Micro-site variation between open-canopy (interplant spaces) and closed-canopy (under plant cover) micro-habitats was found to be significant. Primary soil habitat differences were linked to soil organic matter content which was found to be low on the plains relative to the top and slopes; and, low in open-canopy micro-sites relative to closed-canopy sites. Soil texture and nutrient composition on- and off Tafelberg was found to be highly variable with significant differences between the top and the plains as well as between the north west and south east plains. The slopes were found to be intermediate (showing some level of gradient) between the top and the plains.

Soil nutrient variation was interpreted as a function of textural and parent-material properties of soils. Anthropogenic factors for accelerated erosion, deposition, leaching and salt-crust formation were also considered. It was concluded that while properties of soils on- and off Tafelberg are inherently related to parent soils, changes to textural and nutrient properties may be occurring and these changes may have been exacerbated by high levels of grazing.

An investigation (focusing on small shrubs) of plant phenological response, in relation to rainfall and grazing gradients, identified trends of peak budding- and flowering seasons following rainfall during summer and autumn respectively. A continuum of seeding activity,

[1] The umbrella project seeks to investigate a variety of aspects of semi-arid rangeland degradation and restoration through identifying challenges to - and opportunities for - the restoration of biological diversity and production potential.

with peaks in late autumn and early winter, was construed from quarterly data. Flush vegetative growth was noted for most small shrubs during spring, autumn and summer surveys. Since some form of activity related to reproductive output (flush growth, budding, flowering or seeding) was apparent at almost all times of the year, it is argued that high intensity disturbance (including grazing) might impact negatively on plant survival, leading to reduced reproductive input (i.e. seeds) into future generations.

Plant communities on the top and plains are described noting significant differences between vegetation on top of Tafelberg (comprising primarily high production, palatable grass and shrub species) and that on the plains (comprising mainly spinescent, ephemeral, toxic and low production species). Given the high grazing pressure on the plains (relative to the less utilised slopes and top of Tafelberg), differences in vegetation composition are discussed in relation to studies elsewhere that describe degraded rangelands. It is concluded firstly that the plains surrounding Tafelberg are degraded, secondly that long term over-utilisation has altered vegetation composition and finally that inter-grazing rest periods of three- or six months alone may not restore vegetation diversity nor desirable plant species to the plains.

Results of germination trials (investigating soil-stored seed banks) from two sampling episodes (spring and autumn 1998) revealed that seed banks in soils removed from the plains, slopes and top of Tafelberg followed distribution patterns observed in above-ground vegetation. Species-specific data was not finalised for this thesis since not all seedlings matured and flowered within given time constraints. In order to compare seedling emergence data, plant categories were developed that distinguished ephemerals versus persistent (perennial) species and dicotyledonous species versus grasses and other monocotyledonous plants.

Samples from the top and the middle to upper slopes showed a high percentage of palatable and persistent grass and shrub species present in soil-stored seed banks while over two-thirds of plants germinating from plains' soil samples were ephemeral species and most of these were both tiny (<5cm) and short-lived (<3 months). Most of the perennial species germinating from plains' samples were seedlings of *Pentzia incana*, *Chrysocoma ciliata* and succulents (mostly Mesembryanthemaceae) but few perennial grasses were present. On the other hand, roughly 94% of seedlings germinating from samples from the top and 63% of seedlings germinating from two slopes of Tafelberg respectively were persistent- grass or shrubby species. Roughly 89% of ephemeral species recorded from slopes' samples germinated from the lowest footslope sites.

Seed densities were closely linked to micro-habitats with roughly three-fold differences between open- (lower seed density) and closed-canopy (higher seed density) micro-sites. Multivariate analysis of variance (MANOVA) indicated that most of the variation in seed density data was explained at the micro-habitat level. Seasonality played a secondary role with significant two-way interaction between the two effects. It is concluded that both factors must be considered when developing restoration programmes that aim to improve both overall plant cover and improved plant species diversity.

While the original or "pristine" state of vegetation composition and seed banks on the plains is unknown, concerns were raised regarding the apparently degraded state of total above- and below-ground plant diversity on these plains. A likely consequence of habitat degradation is that species with specific soil-, nutrient ratio-, aspect- and altitudinal requirements from the top and slopes of Tafelberg (as well as from nearby plains' refugia) may not be able to establish in degraded habitats on the plains. The identification of pioneer plant species (tolerant of habitat degradation) that allow increased vegetation cover and safe-sites for seedling germination of desirable plant species is recommended. Restoration programmes will need to be coupled with strict grazing management principles that allow seedling germination, establishment and successful reproductive output of desirable plants for future rangeland regeneration.

Common and salient features of the soil habitat, plant phenological response and germination trial studies are brought together in an examination of habitats and related seed bank diversity on- and off Tafelberg. Acknowledging the brevity of this research study, but utilising case studies from elsewhere and integrating both lines of questioning, the conclusion is again reached that the plains surrounding Tafelberg are degraded through decades and probably centuries of grazing by domestic livestock. It is considered crucial that restoration through improvement (or rehabilitation) of habitats and increased seedling safe-sites be considered.

Both climate and grazing management appear to play an irrevocably linked role in shaping vegetation composition in rangelands. While rangelands are intrinsically adapted to surviving extremes of climatic variability found in non-equilibrium regions it is argued that the impacts of grazing, particularly during times of drought and climate change, are slowly reducing the intrinsic "buffer-capacity" of rangelands to withstand these changes and extremes.

It seems apparent from research elsewhere that restoration through passive management is slow and probably not economically achievable within a viable time frame. The institution and promotion of integrated and strategic programmes that identify and address issues of land degradation and land use change in semi-arid rangelands is recommended. The input and endeavours of different authorities, ministries and a broad public participation incentive are encouraged in these proposed programmes in order to ensure broadly-based input into long term sustainability and conservation of the considerable biological diversity of these regions.

Seed bank assessment is considered to be a valuable means of indicating restoration potential and rangeland condition with potential for the identification of both degraded and conservation-worthy areas.

Finally, some limitations and challenges of this study are examined through a process of firstly identifying alternative approaches to research methodologies and secondly through proposing recommendations for future research projects. While alternative methods could have been applied for the purposes of accomplishing this study it is concluded that, within the given time- and other constraints, the appropriate methods were applied.

TESISOPSOMMING

Die samestelling en toestand van grond-bewaarde saadbanke op en van die mesa Tafelberg af, in die Nama Karoo weiveld van die Oos-Kaap, Suid-Afrika, is ondersoek binne die konteks van 'n wyer herstelekologieprojek: "Restourasie van oorbeweide Nama Karoo weiveld: die rol van bewaringseilande"[1].

Die uitgangspunt van hierdie saadbankondersoek was dat dit moontlik is om beskadigde semi-droë weiveld te herstel deur middel van toegepaste bestuursprogramme wat gebaseer is op die metodologie en praktyk van ekologiese herstel. Algemeen erkende eienskappe van nie-ekwilibrium-omgewings (byvoorbeeld onvoorspelbare klimate en wisselende mates van versteuring) en grond-bewaarde saadbanke (byvoorbeeld ruimtelike en temporale verspreidings), het die basis gevorm vir die ondersoek van die algemene omgewing en die eienskappe van bestaande saadbanke in die Tafelberg omgewing. Die potensiële rol van heuwels as skuilplek vir aanvaarbare plantspesies was 'n onderliggende element van die ondersoek.

Na 'n kort ondersoek van historiese en kontemporêre navorsing en beleid oor weiveld-beskadiging in semi-droë streke van die wêreld, is die fundamentele behoefte aan omvattende en toegepaste saadbanknavorsing in die Nama Karoo beklemtoon.

Binne die raamwerk van die oorkoepelende projek het die saadbankondersoek plaaslike omgewingskriteria bestudeer, beginnende met 'n ondersoek na saadbank- en plantegroeihabitats. Chemiese en fisiese eienskappe van grond vanaf twee en twintig terreine op en van Tafelberg af is beskryf. Omvattende grondhabitatwisseling tussen die kruin, die noordwestelike hange en die vlaktes en die suidoostelike hange en vlaktes van Tafelberg is geïdentifiseer. Mikroterreinwisseling tussen die oop-dak (tussenplantruimtes) en toe-dak (onderplantdekking) -mikrohabitats is as beduidend bevind. Primêre grondhabitatverskille is gekoppel aan die inhoud van die grond se organiese materiaal, wat op die vlaktes as laag bevind is vergeleke met die kruin en hange; en laag bevind is in oop-dak-mikroterreine vergeleke met toe-dak-terreine. Daar is gevind dat die grondtekstuur en voedingstofsamestelling op en van Tafelberg af aansienlik varieer, met beduidende verskille tussen die kruin en die vlaktes, en ook tussen die noordwestelike en suidoostelike vlaktes. Daar is gevind dat die hange intermediêr is (toon 'n mate van gradiënt) tussen die kruin en die vlaktes.

Die wisseling in grondvoedingstowwe is vertolk as 'n funksie van teksturele en ouer-materiaaleienskappe van grond. Antropogeniese faktore vir versnelde erosie, neerslag, loging en soutkorsvorming is ook oorweeg. Die gevolgtrekking is gemaak dat terwyl die eienskappe van grond op en van Tafelberg af inherent aan ouergrond verwant is, kan veranderinge aan tekstuur en voedingstofeienskappe voorkom, en hierdie veranderinge kon deur hoë vlakke van weiding vererger gewees het.

'n Ondersoek (wat op klein struike gefokus het) van plantfenologiese reaksie met betrekking tot reënval en weidingsgradiënte het tendense van piekbot- en blomseisoene na reënval gedurende die somer en herfs onderskeidelik geïdentifiseer. 'n Kontinuum van saadskietaktiwiteit, met piektye in laat herfs en vroeë winter, is van kwartaallikse data saamgestel. Groeistuwing is vir die meeste klein struike waargeneem gedurende lente-, herfs- en someropnames. Aangesien

die een of ander vorm van aktiwiteit met betrekking tot voortplantingsgroei (groeistuwing, bot, blom of saadskiet) op feitlik al die tye van die jaar sigbaar was, word daar geredeneer dat hoë-intensiteitversteuring (ook weiding) 'n negatiewe impak op plantoorlewing kan hê, wat sal lei tot verminderde voortplantingsinset (m.a.w. sade) in toekomstige geslagte.

Plantgemeenskappe op die kruin en vlaktes word beskryf met beduidende verskille tussen plantegroei op die kruin van Tafelberg (wat hoofsaaklik bestaan uit hoëproduksie, smaaklike gras- en struikspesies) en dié op die vlaktes (wat bestaan uit hoofsaaklik doringagtige, efemere, toksiese en laeproduksie-spesies). Gegee die hoë weidingsdruk op die vlaktes (vergeleke met die minder benutte hange en kruin van Tafelberg), word verskille in die samestelling van plantegroei bespreek met betrekking tot studies elders wat beskadigde weiveld beskryf. Die gevolgtrekking word eerstens gemaak dat die vlaktes om Tafelberg beskadig is, tweedens dat langtermyn-oorbenutting die samestelling van die plantegroei verander het, en laastens dat interweiding-rusperiodes van drie tot ses maande alleen dalk nie die diversiteit van plantegroei of die verlangde plantspesies op die vlaktes kan herstel nie.

Die uitslae van kiemingstoetse (wat ondersoek ingestel het na grond-bewaarde saadbanke) van twee steekproefepisodes (lente en herfs 1998) het getoon dat saadbanke in grond wat van die vlaktes, hange en kruin van Tafelberg verwyder is, die verspreidingspatrone volg wat in bogrondse plantegroei waargeneem is. Spesie-spesifieke data is nie vir hierdie tesis gefinaliseer nie, aangesien nie alle saailinge binne die gegewe tydsbeperkinge gegroei en geblom het nie. Ten einde saailing-verskyningsdata te vergelyk, is plantkategorieë ontwikkel wat efemere en langdurige (meerjarige) spesies en dikotiele spesies en grassoorte en ander monokotiele plante onderskei.

Steekproewe van die kruin en teen die middelste en boonste hange het 'n hoë persentasie van aanvaarbare en standhoudende gras- en struikspesies getoon wat in grond-bewaarde saadbanke teenwoordig is, terwyl meer as twee derdes van plante wat in die vlaktes se grondmonsters ontkiem het, efemere spesies was, en die meeste daarvan was klein (<5cm) en met 'n kort leeftyd (<3 maande). Die meeste van die meerjarige spesies wat van die vlaktes se steekproewe kom, was saailinge van *Pentzia incana, Chrysocoma ciliata* en vetplante (hoofsaaklik Mesembryanthemaceae), maar min meerjarige grasse was teenwoordig. Daarenteen was onderskeidelik ongeveer 94% van saailinge wat van monsters van die kruin en 63% van saailinge wat van twee van die hange van Tafelberg ontkiem het, langdurige gras- of struikspesies. Ongeveer 89% van die efemere spesies wat van die hange se steekproewe aangeteken is, het op die laagste voethang-terreine ontkiem.

Saaddigthede toon 'n noue verband met mikrohabitats, met ongeveer drievoudige verskille tussen oop- (laer saaddigtheid) en toe-dak (hoër saaddigtheid) -mikroterreine. 'n Multivariaat-ontleding van variansie (MANOVA) het aangedui dat die meeste van die variasie in saaddigtheidsdata op die mikrohabitat-vlak verduidelik is. Seisoenaliteit het 'n sekondêre rol gespeel, met beduidende tweerigting-interaksie tussen die twee uitwerkings. Die gevolgtrekking word gemaak dat albei faktore oorweeg moet word wanneer herstelprogramme ontwikkel word wat ten doel het om algehele plantbedekking en die diversiteit van verbeterde plantspesies te verhoog.

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[1] Die oorkoepelende projek se doelwit is om 'n verskeidenheid aspekte van semi-droë weiveld-beskadiging en herstel te ondersoek deur uitdagings en geleenthede vir die herstel van biologiese diversiteit en produksiepotensiaal te identifiseer.

Terwyl die oorspronklike of "ongerepte" toestand van die plantegroei se samestelling en saadbanke op die vlaktes onbekend is, is kommer uitgespreek oor die klaarblyklik beskadigde toestand van die totale bo- en ondergrondse plantdiversiteit op hierdie vlaktes. 'n Waarskynlike gevolg van habitatbeskadiging is dat spesies met spesifieke grond-, voedingstofverhouding-, aspek- en seevlak-vereistes van die kruin en hange van Tafelberg (asook van nabygeleë vlakteskuilings) nie in staat sal wees om in beskadigde habitats op die vlaktes te vestig nie. Die identifikasie van pionierplantspesies (verdraagsaam vir habitatbeskadiging) wat verhoogde plantegroeidekking en veilige terreine vir saailingontkieming van verlangde plantspesies toelaat, word aanbeveel. Herstelprogramme sal gekoppel moet word aan streng weidingsbeginsels wat saailingontkieming, die vestiging en suksesvolle voortplantingsproduksie van gewenste plante vir toekomstige weiveldherstel moontlik maak.

Algemene en belangrike eienskappe van die grondhabitat, plantfenologiereaksie en kiemingsproefondersoeke word saamgevoeg in 'n ondersoek van habitats en verwante saadbankdiversiteit op en van Tafelberg af. Met erkenning van die kortstondigheid van hierdie navorsingsondersoek, maar met benutting van gevallestudies van elders en die integrasie van albei vraaglyne, word daar weer tot die slotsom gekom dat die vlaktes om Tafelberg beskadig is deur dekades en waarskynlik eeue se beweiding deur mak lewende hawe. Dit word as uiters belangrik beskou dat herstel deur verbetering (of rehabilitasie) van habitats en 'n groter aantal saailing beveiligingsterreine oorweeg moet word.

Dit lyk asof klimaat sowel as weidingsbestuur 'n onherroeplik gekoppelde rol speel in die vorming van die samestelling van plantegroei op weiveld. Terwyl weiveld intrinsiek aangepas is by die oorlewing van uiterste klimaatswisseling wat in nie-ekwilibriese streke aangetref word, word daar geredeneer dat die impak van beweiding, veral gedurende droogtetye en klimaatsverandering, stadigaan die intrinsieke "buffervermoë" van weiveld verminder om hierdie veranderinge en uiterstes te weerstaan.

Dit blyk uit navorsing elders dat herstel deur passiewe bestuur stadig en waarskynlik nie ekonomies haalbaar is binne 'n lewensvatbare tydsraamwerk nie. Die instelling en bevordering van geïntegreerde en strategiese programme wat kwessies van grondbeskadiging en verandering van grondgebruik in semi-droë gebiede identifiseer en oplos, word aanbeveel. Die insette en pogings van verskillende owerhede en ministeries en deelname deur die breë publiek word aangemoedig in hierdie voorgestelde programme ten einde insette met 'n breë basis in die langtermyn-volhoubaarheid en bewaring van die aansienlike biologiese diversiteit van hierdie streke te verseker.

Saadbankbeoordeling word beskou as 'n waardevolle manier om die herstelpotensiaal en weiveldtoestande met die potensiaal vir die identifisering van beskadigde sowel as bewaringswaardige gebiede aan te dui.

Laastens word 'n paar beperkings en uitdagings van hierdie studie ondersoek deur 'n proses van eerstens die identifisering van alternatiewe benaderings tot navorsingsmetodologieë, en tweedens deur die voorstel van aanbevelings vir toekomstige navorsingsprojekte. Terwyl alternatiewe metodes toegepas kon gewees het ten einde hierdie studie af te handel, is die gevolgtrekking dat die toepaslike metodes binne die gegewe tyds- en ander beperkings toegepas is.

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The Department of Agriculture provided great support for this project and my only regret is that I spent less time than I wanted to in debate and consultation with various officials and researchers from the Department. Mr. Frans van Eeden encouraged and supported my efforts from the word go while Dr. Pierre du Toit supplied unpublished records and other information on the district, answered endless questions and took us on a guided tour of Grootfontein Agricultural College. Mr. Jakkals Roux and Mr. Lehmann Lindeque gave freely of time and energy to aid this project.

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1 The Powrie family come from a long line of French overlords who settled in Scotland and lorded it over the Scottish for some centuries. Since I am part Scot and was a long-standing tenant on her property the title "overlord" seems more appropriate and cosmically satisfying than "landlord".

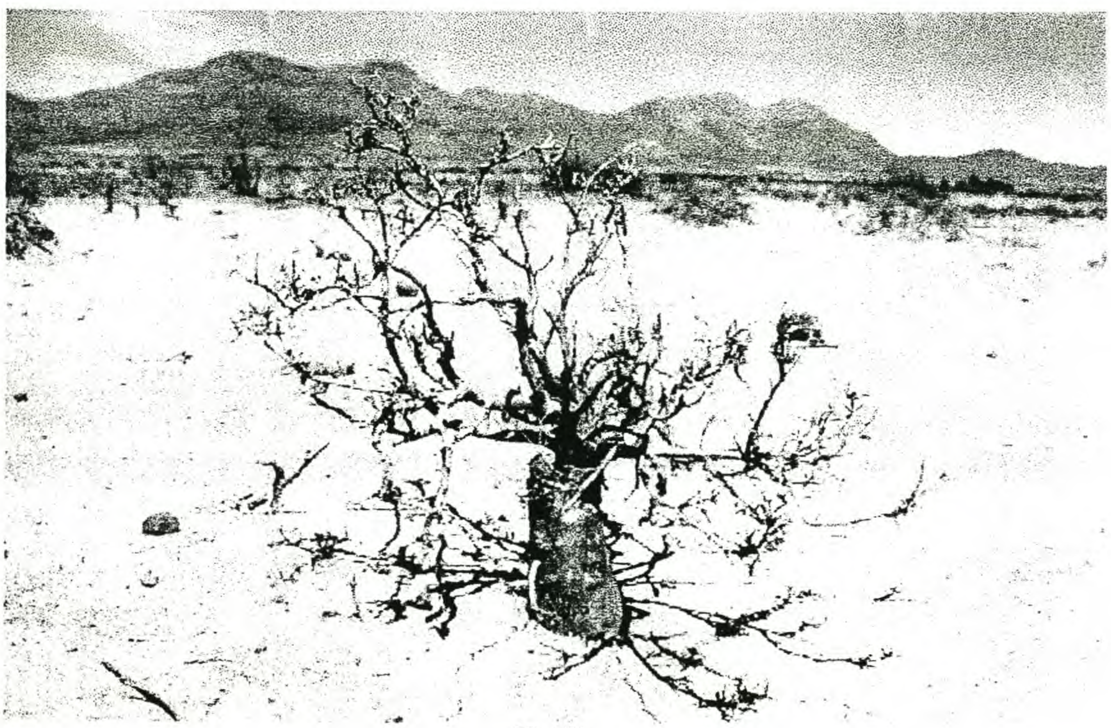
A PARADIGM FOR SUSTAINABILITY

"Many of the agricultural practices followed today by crop and stock farmers are harmful to the environment and are causing a steady decline in the quality of the resource base. Thus soils are eroded, nutrients depleted, rivers pumped dry or polluted by chemicals and many valuable plant and animal species eliminated or replaced by weeds. We need a shift in emphasis from maximizing short-term gains through the use of exploitative practices to approaches that would lead to sustainable productivity over the long term - i.e. a paradigm shift from agribusiness to agro-ecology. This will be achieved only if education changes the attitudes and norms of the farmers. Research should provide alternatives to harmful practices and economic measures be used to reward those farmers who follow ecologically sound practices and penalise those who fail to do so. Not only the biophysical but also the sociological environment should be considered. Ultimately, sustainable agriculture should be a solid building block that supports and interfaces with the social, economic and political structures of a region."

Giliomee, J.H. (1992). Agriculture. In: Fuggle, R.F. and Rabie, M.A. (Eds). *Environmental Management in South Africa.* Juta, Cape Town. 739 - 747.

"Sustainable development must ensure that our developing economy proceeds from unrestrained growth and insensitive development to environmental sustainability. This is characterised by a stable state economy that addresses the needs of society in an equitable fashion while remaining in balance with ecological cycles."

DEAT (1997), *Environmental Management White Paper*. Government Printers, Pretoria, South Africa



Drosanthemum sp. on the north west plains of Tafelberg looking toward the Sneeuberg

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1.1 Context of this study

1.1.1 Setting the international and national scene on semi-arid rangelands

Degradation of semi-arid grasslands is an issue of international concern (Jordan *et al*, 1988; Dean and Milton, 1994; Milton and Hoffman, 1994) and national significance (Danckwerts and King, 1984; Bosch, 1988; Novellie, 1988; Danckwerts and Stuart-Hill, 1988; Hoffman and Cowling, 1990; Milton and Dean, 1995; Hoffman *et al*, 1999a; Roux, 1999; DEAT, 1999a) since these areas support vast and biologically diverse natural pastures (rangelands) which in turn maintain a variety of domestic stock and indigenous fauna.

Southern Africa has one of the highest species densities in the world (Gibbs Russell, 1985; Cowling *et al,* 1989) and among areas of comparable size, the richest flora, including both temperate and tropical regions (Gibbs Russell, 1985). South Africa justifiably signed the International Convention on Biological Diversity (CBD) (UNCED, 1992) in June 1993 and ratified the CBD on 2 November 1995 (DEAT, 1997a). The CBD aims to improve international co-operation in the quest for conservation of biological diversity and to promote sustainable use of global natural resources (Glowka *et al*, 1994, DEAT, 1997b). In January 1995, South Africa signed the Convention to Combat Desertification (CCD) (UNCED, 1994) and ratified the CCD on 29 August 1997 (DEAT, 1997a). This convention seeks to combat desertification in those countries experiencing serious drought and/or desertification, particularly in Africa.

Some 85% of the total surface area of South Africa consists of rangelands and 65% of these rangelands receive mean annual rainfall of less than 500mm *per annum* (Snyman, 1991). A significant proportion of this surface area falls within the Nama Karoo Biome (*sensu* Rutherford and Westfall, 1986), the second largest biome in southern Africa after the Savanna Biome (Cowling *et al*, 1986, Rutherford and Westfall, 1986, Low and Rebelo, 1996). Since relatively inadequate data are available on the flora of the Nama Karoo Biome (Cowling and Hilton-Taylor, 1999) and less than 1% of the biome is formally conserved (Cowling *et al*, 1986, Rutherford and Westfall, 1986, Low and Rebelo, 1996) there exists an urgent need for accurate assessment, of both the past- and present state and composition of these rangelands, as well as for strategic planning to improve their plight. These needs are thus not only a national priority but are also international obligations required under both the CBD and CCD and enforced by promulgation of the National Environmental Management Act (NEMA) (DEAT, 1999b).

Research and incentives for improving the quality, and ensuring sustainability, of these semi-arid regions have therefore a consequential political, economic and ecological rationale. Several South African government schemes including the "National Grazing Strategy" (Anonymous, 1985) and the "Stock Reduction Scheme" evaluated by Baard (1978) (both described by Du Toit *et al* (1991)) have attempted to address issues of rangeland degradation. More recently, efforts to catalogue and describe the situation have been undertaken by partnerships that have included national and international participants (e.g. Hoffman *et al*, 1999a; refer 1.2.1).

1.1.2 Issues facing semi-arid rangelands in the Nama Karoo

The Nama Karoo biome (Rutherford and Westfall, 1986) covers 607 235km of southern Africa (Palmer and Hoffman, 1997) and occupies 346 107km^2 or roughly 28.35% of the total area of South Africa (Hilton-Taylor and Le Roux, 1989). Of 21 Veld Types (Acocks, 1953) in the Nama Karoo, eight are classified as "False Karoo" types. These correspond with those areas, with relatively high rainfall, that were formerly grassland but which through grazing pressures have been transformed to karroid shrubland (Hilton-Taylor and Le Roux, 1989).

Poor land management and excessive exploitation of semi-arid rangelands (veld) have led to reduction of natural resources (Bombridge, 1986; Snyman and Van Rensburg, 1986) through loss of desirable vegetation and accelerated erosion of top soil (Snyman, 1997). Globally (and in the Nama Karoo) the sheer extent of semi-arid areas that are degraded, through unsustainable agricultural practices and poor land management, have led to doubts whether restoration at the landscape scale is possible (Jordan *et al*, 1988; Hobbs, 1993). There is widespread understanding however, that both habitat reconstruction as well as restoration of degraded ecosystems have an important role to play in the international quest for conservation of biological diversity (Hobbs, 1993).

Veld condition is intrinsic to profitability of veld per hectare (Danckwerts and King, 1984) thus issues of rangeland degradation are important with respect to loss of economic potential; loss of ecological function; and, concomitant loss of biological diversity in an economically significant agricultural production region. Degraded semi-arid grasslands in the Nama Karoo are slow to respond even with sustainable management, owing to low rainfall and extremes of temperature, since they are highly susceptible to drought (Skinner, 1981, Snyman and Van Rensburg, 1986; Danckwerts and Stuart-Hill, 1988; Hoffman *et al*, 1990; Milton *et al*, 1995) and soils are often shallow and inherently prone to degradation (Ellis, 1988; Watkeys, 1999).

While species composition may recover after drought if grazing is withdrawn, the longer grass-veld is rested after drought the more likely it is that overall grazing capacity will be restored (Danckwerts and Stuart-Hill; 1988). There is however a rising concern that if inappropriate management strategies continue for too long, veld condition may become severely degraded (Wiegand and Milton, 1996) to a point after which it is held that the degraded veld may never be able to recover without active intervention and probably not within an economically appropriate or viable time frame (Wiegand and Milton, 1996; Jeltsch *et al*, 1999).

Long term veld degradation through inappropriate management strategies has resulted in a reduction of palatable species and an increase in unpalatable and other undesirable species (Acocks, 1953; Milton and Hoffman, 1994). These latter include alien invasive species such as *Atriplex semibaccata*, which may increase soil salinity levels to the detriment of indigenous species (Milton *et al*, 1999), as well as invasives such as *Salsola kali* and *Opuntia* spp.; thorny indigenous species such as *Rhigozum trichotomum*; and, otherwise unpalatable or undesirable indigenous species such *Chrysocoma ciliata* and *Gnidia polycephala* (Le Roux *et al*, 1994). Further, soil-stored seed banks of desirable plant species may have become depleted over a period of time through excessive grazing of plant material prior to flowering or successful seed set; loss of seed through seed predation; loss of germinated seedlings during drought following brief rainfall events; and, through natural loss of seed viability (Parker *et al*, 1989; Louda, 1989).

The historical lack of integration of scientific disciplines (for example the schism between "pure sciences", such as ecology and systematics; and technical, or applied, sciences such as grass-land science) resulted in a division of problems and challenges (Bosch, 1988). The ensuing dispersed effort has not led to resolution of complex problems such as vegetation deterioration. Bosch (1988) contends that this lack of integrated research and problem solving may have led to data being collected with little interpretation nor detailed understanding of the fundamental causes of change, nor of the processes and mechanisms involved in these changes.

1.2 Motivation for this study

The contribution to the gross domestic product (GDP) and particularly to the local economy of South Africa through (amongst other) wool and mutton production provides significant economic grounds for greater comprehension of how Karoo ecosystems work (Cowling 1986; Meadows and Sugden, 1988; Milton and Dean, 1995) and a need for sustainable land management in the Nama Karoo. Apparent degradation of veld condition throughout the Nama Karoo (Acocks, 1953; Hoffman, 1996), owing to previously exhaustive land use practices that encouraged economic gain over long term sustainability, has thus led to renewed interest in the potential for restoration of the biodiversity and production capacity of this region.

This study set out to address some key aspects of this historical exploitation of renewable resources, especially the vegetation of the Nama Karoo Biome, through an investigation of the availability of viable soil-stored seed for recruitment events as permitted by favourable precipitation and temperatures. Logically, the availability of viable seeds within a plant community determines the potential future composition of the vegetation (Acocks, 1953; Baker, 1989; Parker *et al*, 1989; Gross, 1990; Palmer *et al*, 1999). The alteration over time in vegetation composition[1] has been correlated to a degree with reduced fruiting and seed production of palatable species through herbivory (Acocks, 1953; Milton and Dean, 1990; Milton, 1995; Milton *et al*, 1999) as well as to variances in rainfall (Hoffman *et al*, 1990; Milton, 1992; Milton, 1994; Midgley and Van der Heyden, 1999).

There is a dearth of seed bank data and subsequent analysis of the importance of such data in the Nama Karoo. Kemp (1989) notes that knowledge of seed banks globally in arid environments is sparse. Several seed bank studies (e.g. Henrici, 1935; Henrici, 1939; Van Rooyen and Grobbelaar, 1982, Dean and Milton, 1991; Dean and Yeaton, 1992; Esler, 1993; De Villiers *et al*, 1994)[2] have previously been undertaken, attempting to define aspects of the condition and ecology of seed banks in semi-arid regions of southern Africa. Several of these are examined in greater detail in Chapter 5, however the need does exist for a deeper understanding of seed bank ecology within semi-arid zones, especially within the scantily assessed Nama Karoo (Esler, 1999), in order to provide background data regarding veld condition and to assess potential for restoration of degraded rangelands.

1.2.1 Hypothetical conservation islands in the Nama Karoo Biome

The assessment of seed banks on isolated hills or mesas and the surrounding plains in the Nama Karoo Biome (this study) is a component of a broader umbrella project with national and international partnerships (Table 1.1) namely "Restoration of degraded Nama Karoo rangelands: the role of conservation islands". The integrated project aims to assess the potential role and value of isolated hills[3] as conservation islands for both flora and fauna in a semi-arid region, the Nama Karoo.

This study was a component of the Plant Ecology research programme (Table 1.1), providing baseline soil composition and seed bank data for the Middelburg district of the Eastern Cape, South Africa. The area was selected for its varied topography that includes hypothetically less-grazed conservation islands in the form of isolated hills. These hills permitted comparative

[1] Specifically the decline in numbers of palatable species and the potential concomitant increase in less palatable species.
[2] Most of these studies were undertaken in the Succulent Karoo or in Namaqualand.
[3] These may be mesas, buttes or spitskop (koppie) types of hills or mountains. For the purposes of this thesis from here onward the term "koppie" may be used occasionally as a generic term meaning any of the three types of isolated hills or mountains. Where specific geological landforms are intended these will be named as mesas, buttes or spitskop formations.

studies on the state and composition of seed banks on the slopes, top and surrounding plains[4]. The data accumulated, on species composition and distribution of soil-stored seed, provide a means of assessment as to whether observed variation in above-ground plant species composition (a study conducted by another member of the Umbrella project, E. Pienaar) on- and off the mesas may be attributed either to the presence or absence of soil-stored seed, and/or to other environmental factors affecting germination. These include the duration and timing of rainfall events as well as variability in habitat.

Table 1.1: Partners in the integrated umbrella project "The Restoration of degraded Nama Karoo: the role of conservation islands".

PARTNERS	ZONE OF STUDY	FIELD OF RESEARCH	RESEARCH INSTITUTION
Dr. K.J. Esler (Co-ordinator)	E. Cape - NK / grassland ecotone	**Plant Ecology** - 5 MSc and 1 PhD student	University of Stellenbosch
Prof. M. Samways	E. Cape - NK / grassland ecotone	**Entomology** - 1 PhD student assisting	University of Natal (Pmb)
Prof. Dr. C. Wissel	E. Cape and Namibian NK	**Modelling** - 1 MSc and 1 PhD student assisting	Umweltforshungens-zentrum Leipzig-Halle GmbH, Germany
Dr. F. Gilbert	E. Cape and Namibian NK	**Entomology** - field assistance	University of Nottingham, Great Britain
Dr. P. Barnard	Namibia - NK / Arid zone ecotone	**Namibian Plant Ecology** - with Dr. A. Burke and student assistance	Directorate of Environment Affairs, Namibia

Through interpretation of results from the seed bank study, the intention is to contribute toward a growing national information source, that will enable managers to conserve and utilise a potentially sustainable rangeland resource (conservation islands and soil-stored seed) for restoration of degraded areas by means of appropriate land management strategies. The proposal is that by striving for rangelands to reach an ecologically desirable and more biologically diverse state, through informed, dynamic and opportunistic management strategies, land management for event-driven, semi-arid rangelands will be improved and overall biodiversity enhanced.

1.3 Research objectives

Objectives of this research study were:

1. to identify broad habitat types through: soil analysis; relative canopy cover; slope and aspect analysis; data collection on seed bank seasonality and composition; and, a brief phenological survey;

[4] More specifically whether seed banks on the apparently heavily utilised plains, surrounding the hills, are degraded in relation to those found on the hills.

2. to analyse data collected in the field and during germination trials to provide key principles regarding seed bank status in the study area; and,
3. to make recommendations as to whether, and by what means, seed banks may be used to restore degraded lands surrounding mesas or koppies (believed to act as conservation islands).

1.4 Key questions and hypotheses

1.4.1 Key questions

Key questions that were investigated during the course of this study included:

1. How does one identify a suitable sampling depth for seed banks that will adequately represent soil depth on the plains, slopes and top of hills?
2. How can seed be encouraged to germinate?
3. Given microhabitat and niche preference by many species, will a representative number of species be found on isolated mountains or hills that also occur naturally on plains?
4. Are seed banks consistent with above-ground (extant and visible) vegetation and do seed banks exhibit firstly temporal and secondly spatial variability?
5. What role do natural events such as wind, flooding and erosion play in determining the nature of the seed bank (depth, size, seed viability, etc.)?

1.4.2 Hypotheses:

This study set out to evaluate the following hypotheses:

Hypothesis 1: The composition of seed banks is strongly correlated to the degree of habitat degradation at both the landscape and micro-habitat scale.

Hypothesis 2: There is a greater floral diversity stored below-ground in degraded areas than currently represented above-ground.

Hypothesis 3: This soil-stored genetic material may be used to re-establish the presence of broader floral biodiversity.

Hypothesis 4: Hills are relatively less degraded than plains, acting as refugia for populations of species that may be used as a source of material for restoration of degraded plains (e.g. for reseeding of the plains).

1.5 Study area

1.5.1 Research locality

The primary study site for the seed bank assessment is a flat-topped mesa, Tafelberg. Tafelberg lies some 25 km south-east of Middelburg, Eastern Cape, east of national road R32, between latitudes 31°30'S and 31°40'S and longitudes 25°05'E and 25°15'E (Figure 1.1). The plains girdling Tafelberg lie at an altitude of roughly 1180 metres above mean sea level (amsl) and the trig survey beacon (ref: 65) at the top of Tafelberg is 1653 metres amsl (Land Affairs, 1990).

Three farms, namely "Thorn Springs" (ex "Stradbroke"), "The Mimosas" and "Tafelberg Hall" encompass the total study site for this seed bank study.

This seed bank study focused on the top, slopes and plains surrounding Tafelberg as a point of departure for research on seed banks in the region.

1.5.2 History

The district for this study (Middelburg District) has been sampled by numerous botanists over the past century including Phillip Burger (Department of Agriculture) who surveyed Tafelberg Hall in 1956 (Du Toit, pers comm) as well as J.P.H. Acocks (1966) who started his "multi-camp" grazing system on "The Mimosas" on the north-eastern slopes of Tafelberg. This system, of camping stock and forcing non-selective grazing (NSG) through high stocking rates followed by long rest periods, was one of two primary fore-runners of various rotational grazing systems now commonly practised by many farmers on rangelands.

A semi-arid region, the natural vegetation is typically characterised by a mix of diverse grasses, Karoo scrub (bushes), succulents and other xerophytes. Over the past three centuries in the Nama Karoo Biome, many farms larger than 10 000 hectares (ha) have been divided into smaller farms (Du Toit, pers comm) and today relatively few farms in the Karoo (less than a quarter) are larger than 6 000 ha with close to half of these commercial enterprises operating on less than 3 000 ha (Hoffman *et al*, 1999b)[5].

These dwindling farm units have been subjected to diverse management practices and land use regimes, primarily ranching, often at unsustainable stocking rates and during times of low average rainfall. Utilisation and drought are fundamentally important in determining rangeland quality (Joubert, 1986; O'Reagain and Turner, 1992; Milton *et al*, 1995) in semi-arid regions.

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[5] Tafelberg Hall, The Mimosas and Thorn Springs (ex Stradbroke) were once part of the same large farm, incidentally the first fenced farm in the Cape (Asher, pers comm).

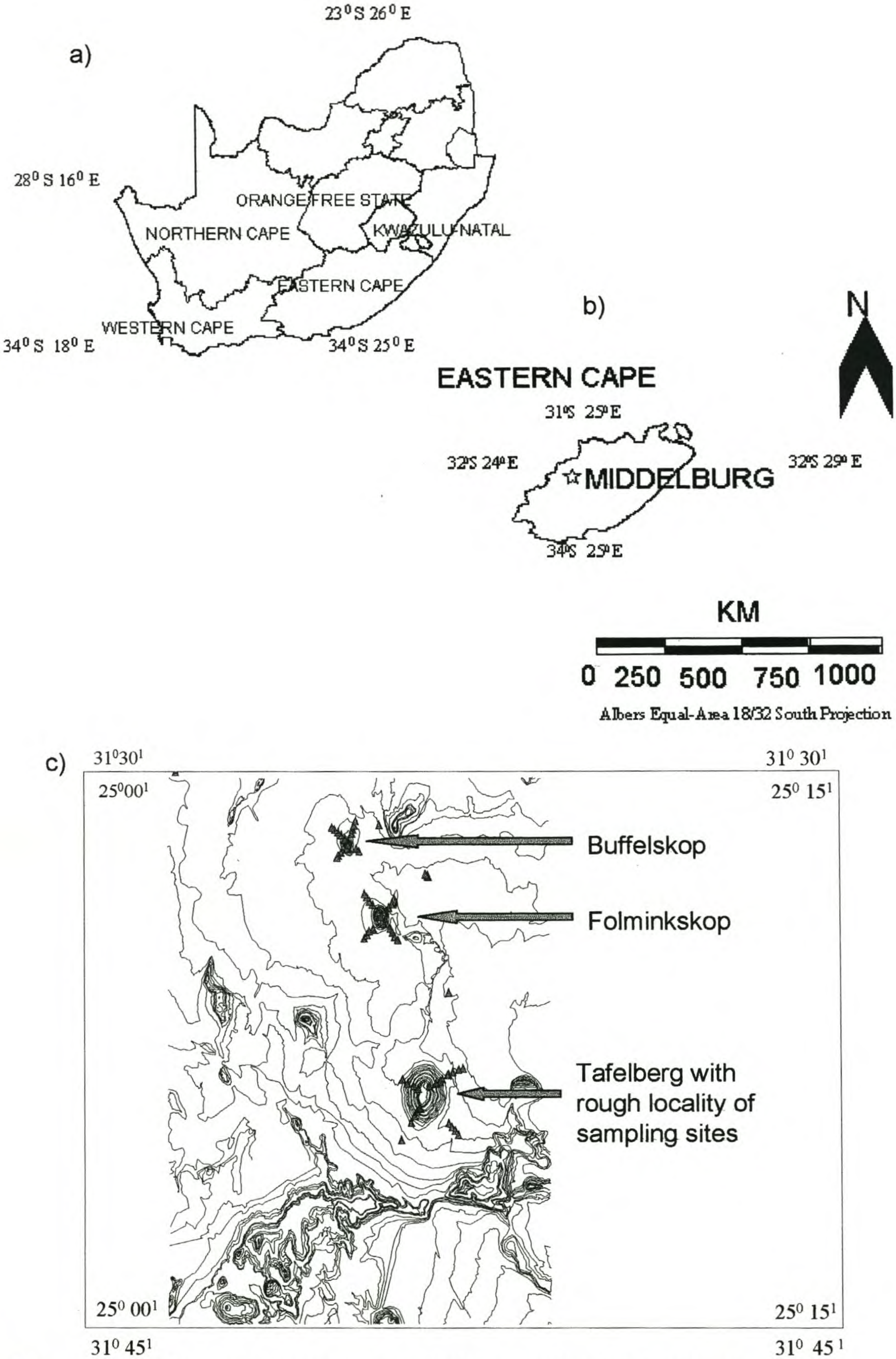

Figure 1.1: Schematic representation of the locality of Tafelberg. a) Map of South Africa indicating location of Eastern Cape Province; b) locality of Middelburg within the Eastern Cape; c) Schematic map of study locale. Adapted from E. Christians (pers comm).

Inappropriate management of live-stock such as ostriches (Gatimu, 1995), sheep and goats, has transformed substantial tracts of the natural rangelands to areas now dominated by unpalatable and spinescent species (Milton 1994). Excessive stocking rates of domestic stock (Danckwerts and King, 1984; Vernon, 1999) and inadequate resting periods for veld, especially after drought (Danckwerts and Stuart-Hill, 1988) are two primary historical causes of rangeland degradation that presently exist in these regions.

The historical perception, or paradigm, provided by conventional equilibrium, or ecological succession, models (Mentis *et al*, 1989; Westoby *et al*, 1989) that guided agricultural authorities and managers with respect to stocking rates and grazing regimes has gradually been replaced by a more dynamic comprehension of the chaotic and "event-driven" nature of semi-arid systems (Mentis *et al*, 1989; Westoby *et al*, 1989; Milton and Hoffman, 1994). This study investigated the future of rangeland management and restoration within the scope of the latter, more contemporary, understanding of the ecology of semi-arid rangeland systems.

1.5.3 Geology, topography and soils

Much of the Nama Karoo Biome (and Middelburg District) are characterised by numerous mesas, koppies and buttes of varying altitudes rising from surrounding plains (Rutherford and Westfall, 1994; Hoffman, 1996). The mesas, koppies and buttes are distinguished from neighbouring mountain ranges such as the Sneeuberge and Joubertsberge in that, as discrete entities rising from flat surrounding plains, they are effectively geological, topographical and ecological "islands".

The primary geology of the Middelburg district is one of dolerite, mudstone and sandstone hills surrounded by low-lying flattish plains of alluvial and colluvial material. There are a number of flat-topped mesas, in this region dominantly capped with dolerite and encircled by fine-grained sandstone and red, and green-grey, mudstone slopes (Geological Survey, 1996). These mesas include Tafelberg, the focus of this study (Plate 1.1a), as well as Folminkskop and Buffelskop (Plate 1.1b) which are being investigated by other members of the umbrella project. The three mesas are part of an archipelago of hills, extending northward from the Joubertsberge, jutting out across an otherwise relatively flat landscape.

Calcrete is present on plains to the north, north-east and south of Tafelberg. Outcrops of black shale as well as other types of mud- and sandstone are present in the area (Geological Survey, 1996). Soils on the plains, slopes and top of Tafelberg are relatively shallow as described for the Karoo region by Watkeys (1999) and as observed during field trials. Chapter 3 contains a detailed description of analyses and qualities of soil and soil habitat types in the study site.

a)

b)

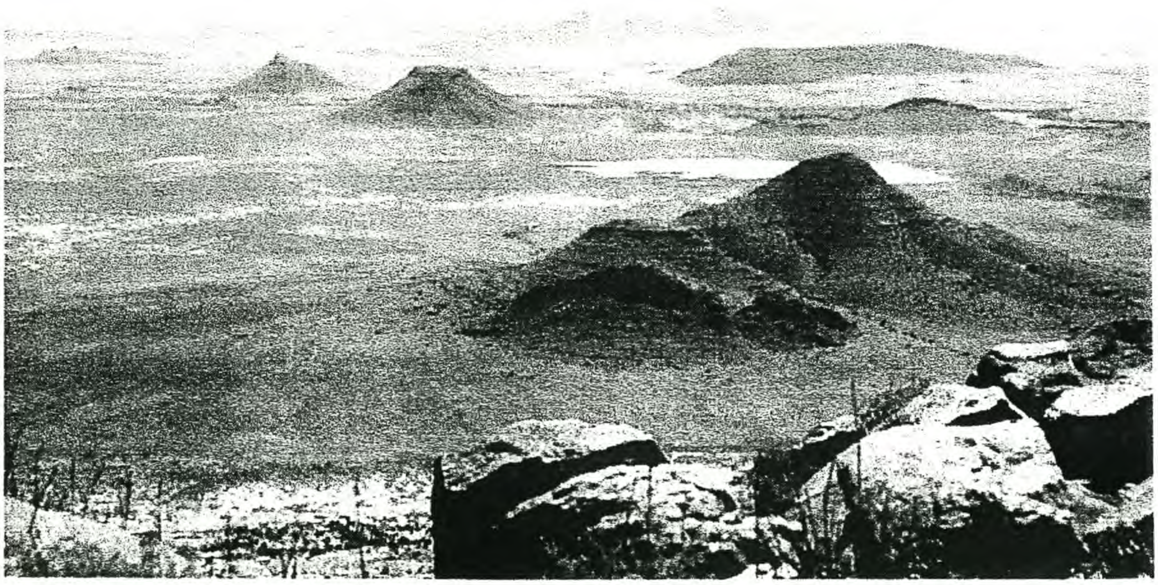

Plate 1.1 Photographs of the mesas in the study locale. Photo (a) shows Tafelberg from the north west aspect while photo (b) shows the archipelago of hills with Spitskop (foreground) and two adjacent mesas, Folminkskop (middle) and Buffelskop (far left background) taken from the north west aspect on top of Tafelberg.

The flat top of Tafelberg is some 950m long (north to south orientation) and 450m wide (east to west). The dolerite cap rises as sheer, but eroded, 20 to 40 metre high cliffs above most of the upper slopes (Plate 1.1). Several small ravines allow access to the top and both the top and slopes are rocky, littered with surface rock rubble.

Drainage lines are conspicuous throughout the study locale and a number of seasonal stream beds, flood plains and ephemeral seeps are visible, particularly on the plains. The study site forms part of the main catchment of the Klein-Brak River (Land Affairs, 1990), which drains southwards and is a tributary of the Great Fish River (Ellis, 1988). On top of Tafelberg, a fresh water spring ceased flowing during the 1960's after attempts to increase its flow with the use of explosives (Asher, pers comm).

1.5.4 Vegetation

The Middelburg district lies within the False Upper Karoo (vegetation type 36) (Acocks, 1953). The primary study site (Tafelberg and surrounding plains) lies close to a tongue of False Karroid Broken Veld (vegetation type 37) extending northwards from the Cradock area. Acocks (1953) noted that the spread of *Acacia karroo* into the upper plateau of the False Karoo would result in False Karroid Broken Veld. Bush encroachment by *A. karroo* on farms surrounding Tafelberg[6] is prevalent (Gilfillan, pers comm).

Vegetation in the Middelburg District is a mix of sweet grassveld karoo (Acocks, 1988), described by Edwards (1983) as a grassy, dwarf shrubland (Rutherford and Westfall, 1994) that in places on the plains has degraded to the point where vegetation cover is sparse and the eroded surface resembles a clay tennis court (personal observation). Described by Acocks (1953) as "False Upper Karoo" (vegetation type 36), he noted that degradation of this veld type could only be termed a "national disaster" as it is dominated in more recent years by less palatable grasses (*Aristida* spp. (steekgras) and *Eragrostis lehmanniana*) owing to heavy grazing. This trend is certainly evident in the vegetation on the plains surrounding Tafelberg.

Hoffman (1996) described the vegetation type of the region as "Eastern Mixed Nama Karoo (52)" comprising both "False Upper Karoo" and "False Karroid Broken Veld" (*sensu* Acocks, 1953). Hoffman (1996) documented that Eastern Mixed Nama Karoo comprises an ecotone between the Grassland and Nama Karoo Biomes that is relatively sensitive to grazing pressure, particularly in times of drought. Palmer and Hoffman (1997) defined the vegetation type of the study area as "Grassy dwarf shrubland". Hoffman (1996) noted that the vegetation

[6] Whether this bush encroachment is as a result of climate change or through pressures from grazing and soil erosion remains unclear at the time of writing.

type is poorly conserved and he confirmed that Acocks (1988) considered this to be the most degraded vegetation type in South Africa.

In the study locale, many previously occurrent palatable and desirable grass and bush species have been grazed out to the advantage of unpalatable, ephemeral or low-production species which are increasing (Asher, pers comm; Gilfillan, pers comm; du Toit, pers comm; J. Roux, pers comm). The pioneer of False Karoo (36), *Chrysocoma ciliata* (bitterbos), is abundant in the area and can cause "kaalsiekte" in lambs of ewes that graze on the flowers (Le Roux *et al*, 1994). The presence of *C. ciliata* indicates veld deterioration and karoo encroachment (Le Roux *et al*, 1994). Various other unpalatable species including *Geigeria ornativa* (vermeerbos), *Gnidia polycephala* (Januariebos) and *Barleria rigida* (scorpion thistle), found in the study locale during site visits, are indicative of unsustainable land management (Le Roux *et al*, 1994).

There is noticeable mixing of grasses and shrubs in the study locale. In discussion with several managers and land owners in the area, during farmers' association meetings and in one-to-one discourse, perceptions and concerns were raised regarding undesirable and unpalatable bush encroachment into the grassveld leading to decreasingly productive veld.

Few comparatively natural vegetation remnants persist in the locality and none that are pristine were observed during this study. The majority of the more species-diverse natural remnants are on top of hills that are relatively inaccessible to livestock because of their topography and/or because of the lack of water at these altitudes.

According to anecdotal evidence (Asher, pers comm; Gilfillan, pers comm; J. Roux, pers comm) hills are seldom grazed to the same extent as surrounding plains owing to various factors including a lack of natural water and formal water points; reluctance of most livestock breeds to climb high for forage; and, the terrain which is rocky and inhospitable for domestic livestock. Hence the hypothesis that hills act as refugia, harbouring populations of species that may be used as a seed or propagule source for restoration of overgrazed plains.

Owing to interrupted water supply (1.5.3, above), the top of Tafelberg has not been grazed by domestic stock for over three decades. Regularly grazed by small herds of *Tragelaphus strepsiceros* (Kudu) and *Pelea capreolus* (Grey Rhebok), the former migrate daily from the slopes where they spend the days, to the plains where they graze nocturnally. The top is utilised by smaller herbivores such as *Procavia capensis* (Rock Dassie), *Pronolagus rupestris* (Smith's Red Rock Rabbit), *Sylvicapra grimmia* (common Duiker) and *Raphistrus campestris* (Steenbok). *Papio ursinus* (Chacma Baboons) frequent the slopes and top and at least one troop appears to trek between the Joubertsberge and Tafelberg often spending several days on Tafelberg (personal observation).

1.5.5 Land use

The primary land use of the Middelburg District is agriculture. Predominantly utilised as rangeland for sheep farming, there are nonetheless small herds of cattle, horses, ostriches and goats in the area. Few cultivated crops are evident except for stands of lucerne in floodplains and dryland drought-fodder crops of *Agave* (sisal) and *Opuntia* (prickly pear). Average farm size in the Middelburg District is less than 6 000 ha (Du Toit, pers comm) which is considerably smaller than the average farm size (11 000 ha) for the district at the turn of the century (J. Roux, pers comm).

A trend toward game ranching is emerging in the district and is developing on one of the three farms (Thorn Springs) studied. The owner of Thorn Springs (R. Gilfillan) has recently started to stock Nguni cattle in place of sheep herds.

Land-ownership of the study site has not been directly correlated to land-use patterns in the past decades since Mr. Ayliffe, farmer of "The Mimosas", leased several camps (mainly on the south east and south west plains surrounding Tafelberg) from Mr. Gilfillan of Thorn Springs. The lease-hold of these camps has recently been allowed to expire at the request of Mr. Gilfillan who intends to significantly reduce the stocking rate in these camps out of concern that they have become degraded over an extended time period.[7]

1.5.6 Climate

Mean winter and summer temperatures for this region appear to be mild but often unpredictable timing and duration of events such as herbivory, heat waves, rainfall and frost do substantiate from the outset that systems are "event driven" rather than regular (or stable) for various cycles (Mentis *et al*, 1989; Westoby *et al*, 1989). The Summer Aridity Index (SAI) (Rutherford and Westfall, 1986) for the Nama Karoo Biome varies between an extreme low of 3.1 up to 5.1[8].

1.5.6.1 Temperature

Average temperature of the district for January is 20.9° C while the average July temperature is 7.9°C (Du Toit, 1996). Frost is a regular event with roughly 180 frost free days per annum between mid-October to mid-April (Du Toit, 1996).

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[7] There appears to be a common point of view (or at least rural legend) that lease-holders are less concerned about long-term sustainability of land than land-owners although this is not an established rule (personal observation). Long term grazing history and recent rainfall distribution appear to be the main factors in determining species composition (Turner, 1999)

[8] Compared with the SAI for the Succulent Karoo Biome (*sensu* Rutherford & Westfall, 1986) which ranges between 4.8 to roughly 7.5 (Rutherford & Westfall, 1994)

1.5.6.2 Precipitation

The study area lies in the summer rainfall karoo, receiving regular summer rains although timing (and duration) of rainfall may be inconsistent (Hoffman and Cowling, 1987; Cowling and Hilton-Taylor, 1999). Consequences of this irregularity may be as significant as the amount that falls since critical periods such as flowering (Milton, 1992) and germination time (early to late spring) may be adversely affected by insufficient rainfall for adequate recruitment (Esler, 1993; Esler and Phillips, 1994; Milton, 1994).

Mean annual rainfall for Tafelberg Hall is roughly 341mm ± 115mm[9] of which 40% falls during summer (Dec. - Feb.); 8% in winter (Jun. - Aug.); 21% in autumn (Mar. - May) and 31% in spring (Sept. to Nov.). According to P.W. Roux (pers comm) the Middelburg district lies in a "rain-shadow". Rainfall data for Tafelberg Hall over the past century are presented in more detail in Chapter 4. The town of Middelburg relies on ground water, drawn from a *Merxmuellera* wetland to the north west of the town. Some springs in the Tafelberg Hall area have dried up during the past decades (Asher, pers comm).

1.5.6.3 Wind

Prevailing winds for the Middelburg District are north west in winter and south east in summer (Du Toit, pers comm). Wind appears to play an integral role within semi-arid systems and the Karoo is subject to frequent winds (Siegfried, 1999). Wind (and water) erosion on sparsely vegetated plains is prevalent (Rutherford and Westfall, 1994; personal observation) and localised high velocity wind events such as dust-devils and whirlwinds are common (personal observation).

Winds can increase air-borne dust and elevate soil-moisture evaporation as well as depress temperatures during frost events (wind chill) and heighten plant stress during extreme heat events through increased evapo-transpiration (Ennos, 1997). Finally, wind is likely to play a pivotal role in pollination and seed dispersal systems and these aspects will be assessed in detail by other components of the umbrella project.

1.6 Synopsis of the background and rationale for a seed bank study

The state of semi-arid rangelands globally is in crisis. A large percentage of South Africa is covered by semi-arid rangelands that are arguably degraded, ecologically damaged and dysfunctional. This study aimed to assess firstly whether seed banks on an isolated mesa, as

[9] Data supplied by W. Asher (pers comm) comprising 100 years of rainfall data for Tafelberg Hall. Grootfontein Agricultural College in Middelburg records show annual median rainfall of 359mm with 15% falling in spring, 30% in summer, 50% in autumn and 5% during winter months (Du Toit, 1996).

well as on the sparsely vegetated and more heavily grazed surrounding plains in the Nama Karoo, may harbour species that are not presently evident in the above-ground vegetation. Secondly this study set out to evaluate the inherent potential for restoration of degraded areas through allowing these latent seed banks to germinate (should they indeed exist). A third aim of this study was to propose steps and strategies towards identifying economically-viable land management techniques that will enable farm managers to determine a desired future state for their land. It is hoped that this study may add to the pool of information that will empower managers to begin to convert camps on degraded plains and lower slopes to a more biologically diverse state with increasing numbers of palatable and desirable species.

1.7 Achievable results and outcomes

The achievable outcomes of this study were:

1. to provide a record of seed bank data for the study site in a manner that is replicable and in a format that is able to be expanded upon. This included keeping clear records, setting up permanent sites and keeping detailed information of data collection;
2. to provide recommendations that managers may use to identify portions of their land that may be set aside as genetic material stores for potential future restoration thereby conserving and improving biodiversity in the Nama Karoo; and,
3. to contribute to the broad existing knowledge base that enables managers and authorities to formulate dynamic action plans for opportunistic and pragmatic improvement of overall veld condition and biological diversity in the Nama Karoo.

1.8 Thesis outline

Following an overview of methods applied in component studies of the seed bank research project (Chapter two), this thesis explores local environmental criteria beginning with an investigation into seed bank- and vegetation habitats. Chapters 3 and 4 provide contextual and habitat data and discussion for the primary component of this study, the germination trials (Chapter 5). Focusing firstly on the soil medium (Chapter 3), chemical and physical properties of soil samples from twenty two sites on- and off Tafelberg are described. The record of analysis and ensuing discussion are undertaken with reference to both the natural state as well as to possible changes that may have been incurred through long term grazing management and local climatic conditions.

Plant phenological response (of specifically small shrubs) to gradients of rainfall and grazing, is examined in Chapter 4, while results of germination trials from two sampling episodes (spring and autumn) are presented in Chapter 5. Both chapters examine aspects of change in vegetation response and vegetation composition to environmental conditions over time and space and further discuss the impacts that these changes may have had, or may continue to have, on seed banks.

In Chapter 6 common features of all three component studies (soil analyses, plant phenological response and germination trials) are brought together in a consolidated discussion that examines habitat- and plant diversity and distribution (as revealed by the results of the germination trials) on- and off Tafelberg.

Chapter 7 discusses the limitations and challenges of this study through identifying potential alternative approaches to research methodologies used and secondly through proposing recommendations for future research projects.

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1.10 Personal communications

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CHAPTER 2 STUDY DESIGN: METHODS AND MATERIALS

2.1 Introduction

This chapter describes the methods and where relevant the materials used to locate permanent plots; to extract soil for germination trials and soil analyses; for data capture; and, for the component ecological studies and other data analyses that comprised the seed bank study.

2.2 Design and establishment of sampling plots

The criteria, used to place permanent study sites, were predetermined by the umbrella project team (1.2.1, above) in the project planning phase. The design was adjusted during ensuing site visits to adapt to field conditions and constraints.

2.2.1 Location and establishment of sites

Permanent study sites were located on the top, slopes and plains of Tafelberg radiating from the footslopes on to the plains to a distance of no less than one kilometre from the base of Tafelberg (Figure 2.1). The four compass half-points (SE, NE, NW and NE) were used in order to assess ecologically (not anthropically) defined data, since it was assumed that the north west and south east aspects would be the hottest and coolest slopes on Tafelberg respectively.

During two field trips, undertaken during April and June 1998, six sites on top, four sites on each of the four slopes (NW, NE, SW, SE) and four sites on each of the four plains (NW, NE, SW, SE) surrounding Tafelberg were established (Figure 2.1) and marked with metal poles. Of these, only those on the south east and north west plains and slopes, as well as three sites on the top of Tafelberg were sampled for seed bank analysis owing to time constraints[1]. These sites, and those sampled for soil analyses and for the phenology study, are catalogued in Table 2.1 and illustrated in Figure 2.1. Each site was subdivided into six contiguous plots consisting of three above-ground vegetation plots alternating with three seed bank sampling plots.

2.2.2 Permanent plot design, placement and alignment

The surface area, for optimal sampling plot size in the local vegetation, was assessed using species/area curves (Appendix 2.1)[2]. Consistently, on top of Tafelberg and on the plains, a 4x4 metre plot size proved adequate (Pienaar, pers comm). The initial proposal to establish five-by-

[1] During the October sampling, only two sites on top of Tafelberg were sampled owing to inclement weather (thunderstorms and extremely high wind conditions) and the resulting time constraints that these environmental conditions placed on the field trip.

[2] The author and E. Pienaar were informed by Du Toit (pers comm) that plots of 3X3 metres (i.e. $9m^2$) are adequate for sampling in the Middelburg district.

Figure 2.1 Schematic representation of position and layout of permanent sites on- and off Tafelberg (refer Table 2.1 and Figure 1.1) (not to scale).

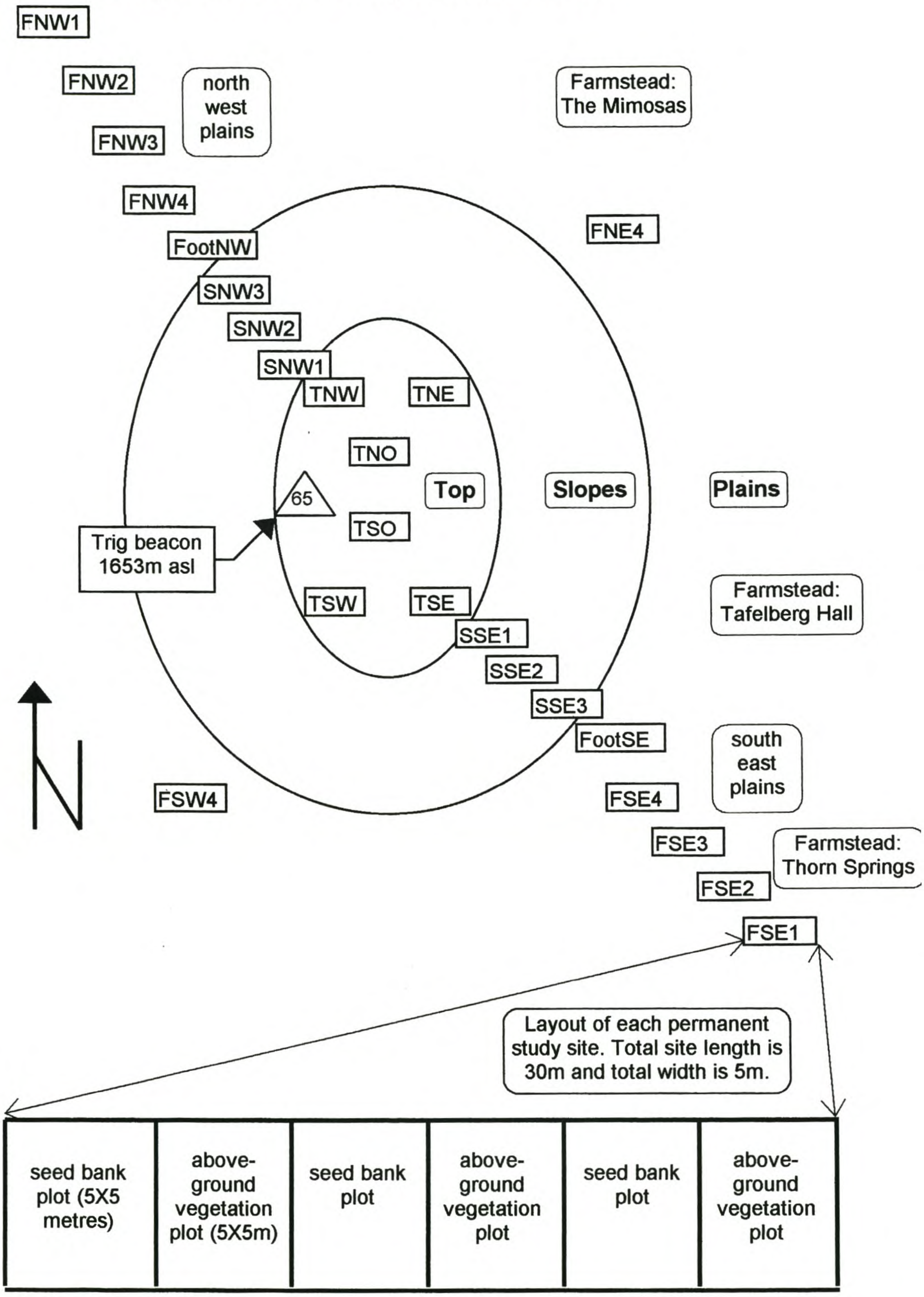


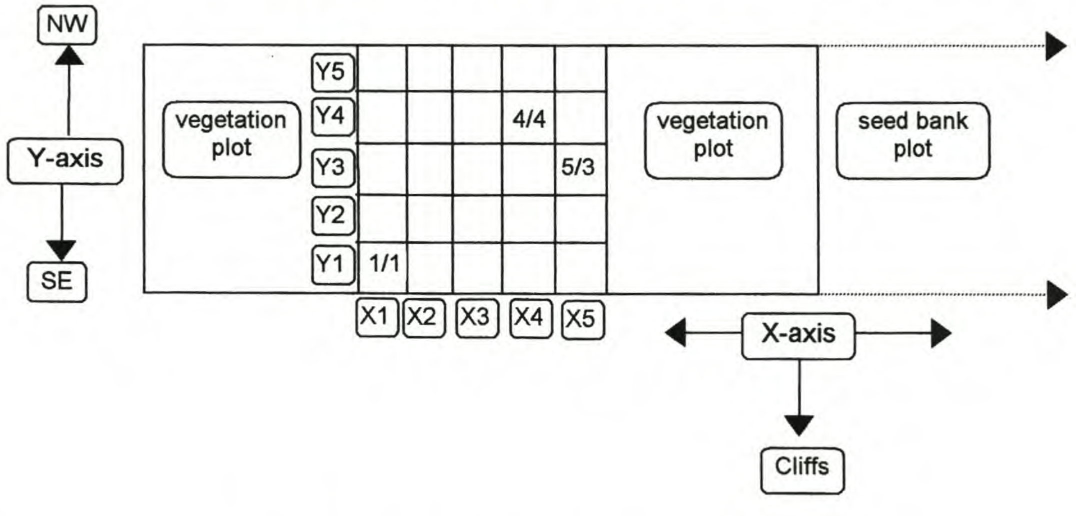
Table 2.1 Geographical Positioning System (GPS) grid references, site codes, sample type and dates of sampling on Tafelberg (refer Figure 2.1) during this study. Preliminary data for GPS readings and altitude supplied by E. Christians (pers comm).

SITE DESCRIPTION	SITE NUMBER	SITE CODE	ASPECT	ALTITUDE	GPS GRID REFERENCE (PRELIMINARY DATA)	PHENOLOGY	SOIL ANALYSIS	SEED BANK ANALYSIS
Plains north west 1	1	FNW1	flat NW	n/avail	31° 38.06 S / 25° 08.65 E		April 99	Oct 98
Plains north west 2	2	FNW2	flat NW	n/avail	31° 38.13 S / 25° 08.86 E		April 99	Oct 98
Plains north west 3	3	FNW3	flat NW	n/avail	31° 38.35 S / 25° 08.90 E		April 99	
Plains north west 4	4	FNW4	flat NW	n/avail	31° 38.44 S / 25° 08.77 E	Jun 98 - Jun 99	April 99	Oct 98
Footslope north west	5	FootNW	NW	n/avail	31° 38.41 S / 25° 09.65 E		April 99	Oct 98
Slope north west 3	6	SNW3	NW	1285m	31° 38.44 S / 25° 09.59 E		April 99	Oct 98
Slope north west 2	7	SNW2	NW	1305m	31° 38.45 S / 25° 09.59 E		April 99	Oct 98
Slope north west 1	8	SNW1	NW	1409m	31° 38.59 S / 25° 09.73 E		April 99	Oct 98
Top north west	9	TNW	level NW	n/avail	not available	Jun 98 - Jun 99	April 98	April 98 & Oct 98
Top north east	10	TNE	level NE	1649m	31° 38.62 S / 25° 10.06 E		April 98	
Top north central	11	TNO	level N	n/avail	31° 38.63 S / 25° 09.97 E		April 98	
Top south central	12	TSO	level S	1599m	31° 38.82 S / 25° 09.98 E	Jun 98 - Jun 99	April 98	April 98
Top south west	13	TSW	level SW	1660m	31° 38.82 S / 25° 09.88 E		April 98	
Top south east	14	TSE	level SE	1592m	31° 39.82 S / 25° 10.12 E	Jun 98 - Jun 99	April 98	April 98 & Oct 98
Slope south east 1	15	SSE1	SE	1476m	31° 38.91 S / 25° 10.32 E		April 99	Oct 98
Slope south east 2	16	SSE2	SE	1450m	31° 39.96 S / 25° 10.47 E		April 99	Oct 98
Slope south east 3	17	SSE3	SE	n/avail	31° 39.02 S / 25° 10.62 E		April 99	Oct 98
Footslope south east	18	FootSE	SE	n/avail	31° 39.31 S / 25° 10.83 E		April 99	Oct 98
Plains south east 4	19	FSE4	flat SE	1192m	31° 39.58 S / 25° 10.88 E	Jun 98 - Jun 99	April 98	April 98 & Oct 98
Plains south east 3	20	FSE3	flat SE	1190m	31° 39.74 S / 25° 10.99 E		April 99	
Plains south east 2	21	FSE2	flat SE	1190m	31° 39.84 S / 25° 11.16 E		April 98	April 98 & Oct 98
Plains south east 1	22	FSE1	flat SE	1189m	31° 39.95 S / 25° 11.25 E		April 98	April 98 & Oct 98
Plains south west 4	n/a	FSW4	flat SW	1213m	31° 40.02 S / 25° 09.05 E	Jun 98 - Jun 99	June 99	
Plains north east 4	n/a	FNE4	flat NE	1197m	31° 38.04 S / 25° 10.59 E	Jun 98 - Jun 99	June 99	

five metre plots was thus determined appropriate to capture vegetation data for above-ground assessment. Werger (1972) regarded optimal plot size to lie between 50-55% of "hectare-information" to ensure adequate data capture and stressed the need for a balance between expended effort and information gained. This author determined that the plot area required to assess 50% of "hectare-information" for scrublands in the False Upper Karoo (dominated by *Chrysocoma tenuifolia*) lay between $25m^2$ and $30m^2$. It was considered too complex to determine species/area curves for the below-ground component and it was decided that removal of several samples from a larger plot size ($25m^2$) would allow adequate data capture for the seed bank study.

The umbrella project has several components that are interlinked (e.g. this seed bank study and above-ground vegetation study) and permanent sites were designed as shown in Figure 2.1. This design improved connectivity and integration between the studies while ensuring that soil-sampling did not disrupt above-ground, plot-based vegetation sampling. The design also allowed replicate sampling from three plots at a distance never greater than 25m across the site. To ensure accurate record-keeping for this and future studies; to facilitate re-sampling in future studies; and, to reduce disturbance of vegetation plots by excavations for seed bank soils, fixed protocols were established. For all sites[3], with one's back to the cliffs, the left-most plot is a vegetation sampling plot. A further protocol, that also enabled random selection of sub-plots for seed bank sampling, was the classification of 25 $1m^2$ sub-plots within each seed bank plot. Arbitrary values of "X" and "Y" were assigned to the axes of the rectangular site. The "X" axis was, in all cases, taken as the long axis and the short axis as the "Y" axis. The sites were aligned so that the long axis is perpendicular to the half compass point that they represent[4]. Sub-plots were classified as shown in Figure 2.2.

Figure 2.2 Numbering and compass orientation of sub-plots for seed bank analysis (e.g. any site on the NW plains or slopes). Sub-plots are allocated an X and Y co-ordinate (e.g. X/Y).



3 Two exceptions, viz. TSO and TNO are viewed from left to right facing due north.
4 The X-axes of TNO and TSO are perpendicular to the north/south axis.

2.3 Field work methods and materials

Soil samples for the seed bank study were collected in April 1998 from six sites on top of Tafelberg and three sites on the south east plains. A second series of soil-sampling for germination trials was undertaken during October 1998 in order to capture seasonal variation. The remainder of sampling for soil analysis (attempting to sample soils during the same season) was completed during April 1999 (Table 2.1).

For all soil removed for germination trials and soil analysis, a stratified-random sampling method outlined by Finney (1980) was used to identify and remove soil samples. Samples were taken from open- and closed-canopy[5] sub-plots using randomly assigned X and Y co-ordinates, for example 1/5 or 3/2 (Figure 2.2).

2.3.1 Estimation of optimum depth for germination trials

Soils on top of Tafelberg are stony and/or rocky and difficult to penetrate to any depth greater than 50mm. Soils on the plains consist of various types of shales and dorbank (known locally as "klip") layers overlain with shallow soils. In other parts, especially near water courses, soils are relatively deeper and sandy (Chapter 3). These field observations concur with descriptions by Ellis (1988) and Watkeys (1999) of soils of this region.

Kemp (1989) notes that, in general, seeds in arid areas (deserts) are distributed near the soil surface and effectively seeds below 7cm in depth are lost to the seed bank owing to various environmental factors (Williams *et al*, 1974). Nonetheless, it was deemed important to investigate whether consequential residual seed banks existed at any depth lower than a desired 5cm sampling depth.

In order to ascertain the possible range of depths for sampling, an 8mm iron bar was hammered with a mallet into the soil until it reached bed-rock. This was repeated at random 25 times in each of the three plains' plots for each site tested. Average maximum soil depth for each plot was calculated (Table 2.2) and was found to be roughly 10cm for two sites and 20cm for the third (FSE4) which is on alluvial soils next to a large but seasonal watercourse. However, this did not represent the reality of the situation. Even though an iron bar could penetrate the klip layer, the author was unable to break through this hard layer without a screw-driver and hammer. Soil removed from these holes utilising this arduous procedure was highly compacted and resembled crumbled shale. A similar procedure attempted on the top of Tafelberg met with similar results but the degree of rock cover and stoniness was greater than on the plains.

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[5] Closed- and open-canopy micro-habitats were respectively defined by the presence or absence of a living plant material canopy as might be seen from a "bird's eye" view.

Table 2.2 Soil depth trial results from three sites on the south east plains of Tafelberg. Data are presented as mean soil depth (cm) ± standard deviation

SITE LOCALE	SITE CODE	PLOT NUMBER	AVE. DEPTH (cm) (n=25) PER PLOT	AVERAGE DEPTH PER SITE
SE Plains (furthest)	FSE1	1	10.76 ± 6.98	9.60 ± 5.83
SE Plains (furthest)	FSE1	2	9.76 ± 5.31	
SE Plains (furthest)	FSE1	3	8.28 ± 4.97	
SE Plains (middle)	FSE2	1	7.88 ± 7.47	9.87 ± 6.87
SE Plains (middle)	FSE2	2	11.88 ± 6.39	
SE Plains (middle)	FSE2	3	9.84 ± 6.36	
SE Plains (closest)	FSE4	1	26.20 ± 2.84	20.69 ± 6.85
SE Plains (closest)	FSE4	2	20.52 ± 6.84	
SE Plains (closest)	FSE4	3	15.36 ± 5.34	

A shale layer (apparently bed-rock) was very close to ground surface level. A depth of 5cm or less was registered from 18% of depth tests and a depth of 10cm or less from 45% of attempts. Only 35% of the attempts were able to reach deeper than 15cm. These however, represent the depth that an iron bar, hammered with a mallet, could be inserted into cracks or fractured rock layers. The reality was very different and for many soil samples the attainable depth was much less than measured by this method (refer Chapter 5, 5.3.1.1 and Table 5.2).

Replicate soil samples to a depth of up to 15cm (where soil depth allowed) were taken for germination trial testing (2.3.2, below). A detailed account of results from the germination depth trials is provided in Chapter 5, 5.3.1.1.

Based on field observations, as well as on results returned from the germination trials of the depth sampling experiment, a standard depth of 50 mm was taken to be the optimal sampling depth for all sites on the top, slopes and plains of Tafelberg.

2.3.2. Normal soil sampling methods for germination trials

2.3.2.1 Overview of various methodologies used for seed bank estimation

Seed banks have been investigated world-wide in diverse habitats (Chapter 5) in an attempt to derive a closer understanding of the ecological role filled by soil-stored seeds (e.g. Leck *et al*, 1989; Gross, 1990; van Rooyen, 1999). Seed bank studies have an inherently high level of imprecision owing to the nature of both the soil medium as well as the seeds contained therein (Chapter 5). Numerous methods and techniques have been used to attempt to quantify and characterise soil-stored seed banks. These comprise two broad categories of processing samples by means of firstly separating, counting and testing the viability of seed from soil samples (e.g. Thompson and Grime, 1979) or secondly through applied methods such as germination trials (e.g. Roberts, 1981).

Direct counting methods are prone to inaccuracy since separating seeds, especially extremely small seeds, from soil particles is most challenging in both time and complexity (Thompson and Grime, 1979; Gross, 1990). While this method is possible the task of identifying seeds, thus collected and counted, to species level and then determining the viability or non-viability of each seed[6], renders this method time-consuming and not highly effective for a large-scale seed bank study. In the absence of viability testing this method determines the total number of seeds but little is known of seed viability. A major drawback of this method is thus over-estimation of actual seed abundance.

Germination trials have their drawbacks, primarily related to the inexactitude of duplicating the environmental requirements that ensure total germination of all dormant seeds in the samples evaluated (Thompson and Grime, 1979; Gross, 1990). There will inevitably be seeds that remain dormant in the soil medium requiring specific germination cues to break dormancy (Roberts, 1981) and thus these methods are prone to underestimating the total number of seeds in sampled soil. Nonetheless, this method determines species composition, seasonality of germination and seed viability, providing a good estimate of relative abundance and species diversity of soil-stored seed.

While imprecision exists for all known methods of evaluating soil-stored seed banks (Gross, 1990), assessment through germination trials can provide valuable baseline information and provides a valuable estimation of the seed bank component that will germinate readily (Gross, 1990). This is particularly so when conducted over a spatially heterogeneous area during different seasons to capture temporal differences in soil-stored seed banks (Roberts, 1981; Gross, 1990). For these reasons, germination trials were selected as the means to evaluate seed banks at Tafelberg.

2.3.2.2 Seed bank sampling in the vicinity of Tafelberg

For all sites sampled a number of replicates were removed from the field. Each plot was sampled equally and each soil sample was labelled and kept separately. At the outset, it was unknown whether there would be a significant germination rate from the soil samples removed. To ensure meaningful results five open- and five closed-canopy soil samples were removed from each plot (30 samples per site) during the April 1998 sampling. This took into account recommendations by Bigwood and Inouye (1988) that twenty five 10x10cm samples would be required to provide meaningful data for spatial pattern analysis of seed bank data.

During the second sampling field trip (October 1998) the decision was taken to sample more widely (top, slopes and two plains) but to take a smaller number of samples (3 closed- and 3 open-canopy) from each plot (a total of 18 samples per site) for the following reasons:

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6 Viability testing requires the use of diverse methods such as tetrazolium staining (e.g. Gross, 1990) or germination trials to establish viability of each seed.

- germination was relatively good from the April 1998 collection (Chapter 5);
- the time taken to excavate and process 480 samples (16 sites with 30 samples each) as opposed to 288 samples (16 sites, 18 samples each) would have been prohibitive;
- the amount of space available at Kirstenbosch (National Botanical Institute) where germination trials were conducted (2.6, below) was a constraint; and,
- it appeared that statistically significant results could still be gained from a smaller sample number but a larger sample spread.

Methods used for April and October soil-sampling are described in the following paragraphs.

For each plot, randomly chosen co-ordinates were used to predetermine the 1x1m sub-plot locality for each sample (Figure 2.2). Wherever it was impossible to take a sample from a predetermined sub-plot, another randomly chosen sub-plot was used for sampling.

Samples were initiated by measuring and marking the perimeter of the hole. The upper several millimetres of topsoil surrounding the perimeter were scraped away to reduce contamination of the sample. The hole was excavated and all soil placed into tough plastic bags labelled with site-, plot- and sub-plot codes as well as whether it was an open- or closed-canopy sample. All topsoil (including organic matter and small stones in the soil) were included in the sample. Samples measured 50mm deep and 100mm square and should have contained a volume of substrate of 500mm^3. The reality was that many samples contained less soil than this owing to stone and rock content (2.6.1, below).

Soil samples were transported to Stellenbosch for weighing and preparation for germination trials.

2.4 Soil sampling for analysis of chemical and physical attributes

In order to assess congruities and variance between soils on the top, slopes and plains of Tafelberg, soil samples were taken for analysis. After air-drying, these samples were sent to the Soil Analysis laboratories at Elsenburg (Department of Agriculture). A detailed description of the results and implications of this sampling is supplied in Chapter 3.

2.4.1 Field sampling methods for soil analysis

Open- and closed-canopy soil samples[7] were removed for analysis from sites shown in Table 2.1. For both open- and closed-canopy samples, small (roughly 125mm^3) samples were taken at approximately 2.5 metre intervals, roughly 1m outside the perimeter of each site (i.e. 28 small samples from each site) and bulked to give one open- and one closed-canopy sample per site[8].

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[7] Samples taken either from under the plant canopy (closed-canopy) or from inter-plant spaces (open-canopy)
[8] Further soil analysis of other sites in the study area has been undertaken by Hendricks (pers comm).

2.5 Assessment of plant phenological response to environmental gradients

From June 1998 to June 1999, an elementary survey of the phenology of seven sites (three on top of Tafelberg and four on the plains) was conducted (Table 2.1, Chapter 4). These sites were surveyed along a 30m transect every three months. All plants that touched, or were crossed, by the transect (a rope span) were recorded into specific classes of growth form and phenological expression. Relevant data with respect to flowering, seeding and other environmental responses were recorded (Appendix 2.2). Grasses were recorded as a percentage of total canopy cover and dominant grasses noted where recognisable. Flowering and seeding status of these grasses were noted at a low level of detail. Data is provided in Chapter 4 as the proportion of the total number of a specified plant category, for example, in seed or in flower. The estimation of grazing pressure did not take the extent nor the intensity of grazing into account but merely counted the total number of plants of a specified category, along a 30m transect, that showed any physical evidence of having been grazed (Chapter 4, Figure 4.5a).

2.6 Germination trial methods

Methods to assess seed banks were adapted from those detailed by Bigwood & Inouye (1988), various authors in Leck *et al* (1989), Gross (1990) and Esler (pers comm).

Germination trials were conducted at the National Botanical Institute tunnels at Kirstenbosch, Newlands (Cape Town). The facilities are roofed with corrugated PVC but are open to the elements (wind, sun and rain) on all sides (Plate 2.1).

2.6.1 Preparation and handling of soil samples prior to germination trials

Soil samples were air-dried, weighed on a Mettler 2000 scale and the total mass of the sample recorded. All samples that contained a significantly large rock or that could not be excavated to the full depth of 50mm (2.3.2.2, above) and thus did not contain the full volume of soil (500mm^3) were noted during extraction. Samples contained diverse quantities of organic matter and variable stone content, thus providing different sample masses (e.g. 622g ± 115g for April sampling). Stones larger than 8mm diameter (∅) were removed and weighed. The mass obtained from the stone fraction (for each sample) was deducted from the total mass, providing a relative estimate of the mass of soil and stones in each sample. Where samples contained a high number of small stones (<8mm ∅) this was noted but these were not removed. The procedures described above attempted to quantify the number of seeds per unit volume. This information was also relevant for purposes of identifying soil types and relative stoniness as noted during analysis of soil quality (2.4, above; Chapter 3). The data obtained have not been used for this thesis but will be used for future work on the seed bank studies (Chapter 5).

Plate 2.1a Greenhouse facilities used for germination trials at Kirstenbosch.

Plate 2.1b Seedlings marked with pins in tray during germination trials

2.6.2 Seed tray preparation

Seedling trays, 15x23x6.5cm, lined with a single layer of newspaper were filled to a depth of 3cm with a soil medium known as "Kirstenbosch General Mix" (KGM) (Appendix 2.3). KGM is an all-purpose soil medium for propagation and growing-on of plant species from the southern African region and was chosen for this reason. Trays were watered daily for three weeks to allow weedy species contained in the soil mixture to germinate. Few weedy species (roughly five plants in total in over 500 trays) germinated during the three week period prior to insertion of seed bank soils.

Soils from the April 1998 collection were processed (weighed and seedling trays prepared), stored in cool (not cold), dry storage until early spring and sown during August. The delay in sowing was done in order to approximate spring germination time in the Nama Karoo. Soils from the late October collection were air-dried for four weeks, processed (2.6.1 above) and sown in December. Seed bank soil samples were distributed to an average depth of 2cm on top of moistened KGM. Soil in each seedling tray was levelled and trays irrigated (2.6.3, below) with a fine mist spray.

2.6.3 Irrigation, fertilisation and pest control

Trays from the first set of germination trials (April sampling) were initially watered by hand every two days for two months. Irrigation was then done by a microjet system for two minutes twice daily supplemented every third day with hand-watering. This was essential during summer months and was continued throughout the project. On some occasions, during extreme conditions of heat and berg-winds, trays were watered manually every second day to reduce plant stress. During winter 1999, microjet irrigation was discontinued owing to high ambient humidity and hand-watering recommenced once every three days in winter and every second day in warmer conditions. Seed trays were moved around at random every second week firstly to reduce the influence of erratic delivery of irrigation water (mainly through wind movement of the fine spray) and secondly to vary their position and thus access to light in the plant house.

During October 1998 a student employed to water and mark newly emergent seedlings, from the April collection, for an unknown reason did not do any of the required actions. Roughly 20 seedlings died as a result and there was a minor setback in germination rates (Chapter 5).

Kelpak® was applied to seed trays and potted up plants as a 1:250 solution every three weeks to improve soil fertility, stimulate adventitious root formation and reduce transplant shock[9]. No other fertigants were applied during the course of this study.

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[9] Much research has been conducted on Kelpak® and may be viewed on the Internet on www.kelpak.co.za. The product is derived from kelp and contains cytokinins and auxins, the latter stimulating adventitious root formation.

The main pest problems experienced were fungal pathogens (primarily damping-off), guinea fowl and caterpillars. Fungal problems were combated with Captan® applied every three weeks as a mixture at a ratio of 60 ml/10 litres of water. This appeared to reduce fungal infection significantly and few seedling deaths were noted as a result of damping-off.

Caterpillars and snails were removed by hand and while these pests consumed parts of a number of plants, they did not cause significant losses of whole plants. Many of the plants attacked by caterpillars and snails were still identifiable.

Guinea fowls caused some loss of soil through scratching in the seedling trays, removing plants (presumably as food and circumstantially) and may have caused the loss of a number of plants on several occasions. This was difficult to quantify and continued throughout the project.

2.6.4 Recording of emerging seedlings, potting out and identification of plants

Every month, emergent seedlings were recorded. This entailed counting all new seedlings, recording the samples from which they had germinated and marking them with a pin to ensure no duplication of counting (Plate 2.1b). They were identified as being grasses, geophytes or dicots during this initial count (Chapter 5; 5.2.2). Where identity was certain or the plant family or genus was readily recognisable this was recorded at the same time.

Details of each seedling (sample code, etc.) were recorded (Appendix 2.4) and seedlings of adequate size were pricked out (transplanted) from seedling trays into a pot (with Kirstenbosch General Mix) and labelled with a singular code. These pot codes were used as identifiable codes for any new seedlings that emerged (if these were readily recognisable as a species that had previously emerged). From then on only "new", or apparently unique, species were pricked out into uniquely coded pots (Chapter 5). Plants were pricked out and grown on to enable those that were not positively identified to species level (at the seedling or post-seedling growth stage) to flower and fruit thus improving chances of species identification.

Where more than one plant of a species germinated, duplicates were pressed for identification purposes. Pressed specimens were mounted and identified using a field herbarium from the region (Pienaar, pers comm).

2.7 Data capture methods

Various types of data were collected and collated during the course of the study. In the field, data collected included phenological data (Appendix 2.2); relative percentage cover of all sites sampled; dominant above-ground species for each site sampled at the time of sampling as well as photographic records that included plant and site data and records of topographical land-marks identifying the position of sites on and around Tafelberg[10]. Where possible, coding was used to describe spatial placement of samples and also to improve data capture speed.

Written data were recorded on designed data-capture forms generated on Microsoft Excel®. All data was transferred by the author onto Excel® which was the preferred data base for the study.

2.8 Data analysis methods

The nature of the seed bank study is such that a number of variable components form the broader picture of the study area as well as influence the results. For this reason it was decided to utilise a combination of straightforward statistical analysis of means, percentages and standard deviation as well as a multivariate statistical approach to analyse data.

Variables analysed included open- versus closed-canopy variation in soil composition and seed bank germination; comparisons of soil and germination trials between the top, slopes and plains of Tafelberg; issues relating to different aspects (NW and SE); seasonal differences; soil type and soil components; number of plants germinated; the relative percentage of canopy cover per site and the types of species that were found within each site. There was also an initial investigation into whether any trends could be clearly identified on the plains regarding the distance between the sites surveyed and the distance these sites lay from the footslopes of Tafelberg.

2.8.1 Extrapolating values for unsampled sites

The top south central site (TSO) on Tafelberg was not sampled for seed bank analysis during October[11] and use was made of a forecasting tool to speculate on potential seasonal changes this site may have shown (Chapter 5). Results from the top north west (TNW) and the top south east (TSE) sites were used to predict possible trends through application of the following formulae used in Microsoft® Excel: These predictions are not presented as statistically rigorous owing to the relatively small sample size but are provided for interest value (Chapter 5).

$$y = a + bx$$

where: $a = \overline{Y} - b\overline{X}$

and: $$b = \frac{n\sum xy - (\sum x)(\sum y)}{n\sum x^2 - (\sum x)^2}$$

where: X and Y values are either averages or the summation of values from April and October samplings respectively (i.e. X values are from April), from both TNW and TSE.

10 The photographic record is not presented with this thesis and is a separate tool to aid the umbrella project.

11 The top south central site was not sampled owing to inclement weather (refer 2.2.1).

2.8.2 Coefficients of similarity: expressing plant community associations

An index of similarity (or community coefficient) was used to interpret similarities between the major habitat types identified during this study and between seasonal sampling episodes on the top and south east plains of Tafelberg (Chapter 5, Tables 5.8 and 5.9). Sørenson's similarity index (*sensu* Sørenson, 1948) was used as this expresses measured species occurrences plotted against those that are theoretically possible; and, provides a measure of the ratio of the number of common species to the average number of species in two habitats or seasons (Mueller-Dombois and Ellenberg, 1974). The index is expressed as a percentage where a value of 100% indicates complete similarity (identical plant community species composition).

The formula applied in Sørenson's similarity index (IS_S) is as follows:

$$IS_S = \frac{2c}{(A+B)} \times 100$$

where: A = total number of species in habitat A or season A
B = total number of species in habitat B or season B
c = number of species common to both habitats or seasons

2.8.3 Multivariate statistical analyses

The computer package used for multivariate analyses of soil and site data (Chapter 6; Figures 6.1 and 6.2) was Canonical Correspondence Analysis (CANOCO) (*sensu* Ter Braak, 1986). This multivariate analysis technique was developed to correlate known environmental variables with community composition (Ter Braak, 1986) and was chosen to aid in the challenge of attempting to relate species-environment relationships with community composition data (Ter Braak, 1986).

Analysis of variance (ANOVA) for identifying trends of seed density (in seeds.m^{-2}) in response to effects of site, micro-habitat and season on the top and on the south east plains of Tafelberg was undertaken with the use of a Microsoft®-Windows application (STATISTICA©, 1999). Results of multivariate ANOVA are presented in Chapter 5 (Table 5.10).

2.9 Synopsis of study methodology

The overall study design allowed adequate, replicate sampling over a diversity of habitats and terrains. Several component studies provided a breadth of investigation seldom applied in many of the seed bank investigations considered during literature review for this project.

Statistical analyses of both raw and compiled data confirmed (rather than detracted from) trends implied from field observations and scrutiny of unrefined information as well as trends, or realities, identified by many other researchers in semi-arid and arid regions. Clear-cut trends were indicated with respect to soil-related habitats (Chapter 3; Chapter 5) and to canopy-related micro-habitats (Chapter 3; Chapter 5) on- and off Tafelberg. While the phenology study (Chapter 4) continued over only one year's cycle, the results nonetheless provided a useful indicator of plant response related to habitat and selected environmental pressures. Results from germination trials (Chapter 5) appeared to substantiate findings on both habitats and degraded landscapes while offering new light on some of the initial questions posed by this study.

Given the variety of options and methods available to answer key questions and test hypotheses proposed by this study (Chapter 1; Chapter 6), it is suggested that all methods applied were well suited to the task at hand.

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CHAPTER 3: ANALYSIS OF SOILS ON- AND OFF THE MESA TAFELBERG

3.1 Overview of the role of soil in maintenance and distribution of biodiversity

The potential for restoration of heavily utilised rangelands is not solely dependent on the presence of available, soil-stored seed and fertile adult plants of desirable plant species. Restoration potential is also profoundly linked to the presence, condition and sustainability of the medium in which most plants thrive, namely soil.

Many plant species are able to thrive in a broad diversity of environmental conditions and habitats and are distributed over a wide geographic range. On the other hand, some species are confined to specific soil types such as coastal sands or Renosterveld clays. Still others are restricted to distinct niches, such as dune slacks or rocky outcrops, on particular soils. These niches may be defined by a combination of environmental and ecological determinants that may include variables such as altitude and aspect, soil depth, soil texture and soil nutrient status, average annual rainfall and mean summer temperature. Soil environments in arid and semi-arid conditions are acknowledged by researchers as being highly variable or patchy with regard to the distribution of both nutrients and textural components (Hunter *et al*, 1982; Fuls and Bosch, 1991; Fuls, 1992; Kellner and Bosch, 1992; Milton and Dean, 1999) with concomitant patchiness of faunal (e.g. Lovegrove and Siegfried, 1989), floral (e.g. Palmer *et al*, 1999) and seed distribution (e.g. Yeaton and Esler, 1990).

Whitford (1999) views soil as the most essential element of terrestrial ecosystems. In general edaphic conditions provide the fundamental plant habitat since soil is the medium from which most plants draw nutrients and moisture. Soil shelters plant roots and provides an environment for a diversity of macro- and micro-organisms on which plants depend. The soil medium also holds the future of most plant species, as a seed bank of seeds, bulbs and other propagules, for at least some period of a given year if not for many years (Simpson *et al*, 1989). In order for seeds to germinate and for seedlings to establish successfully, seed banks are dependent upon the relative permanence, stability of structure, chemical composition and depth of the soil medium.

This seed bank study examined two principal issues. The first investigated the temporal and spatial composition of existing seed banks on the plains, slopes and top of Tafelberg and the environment in which these seed banks are found. The second aimed to determine the potential of using *in situ* soil-stored seed for restoration of the apparently degraded plains through the use of dynamic management principles which allow germination and seedling establishment. Within this latter context, active reseeding on the plains, with seeds of appropriate species gathered manually from the relatively less degraded top and slopes of Tafelberg, was considered[1] as a means of improving existing soil-stored seed banks on the plains. Both issues required greater understanding of the composition and status of soils on- and off Tafelberg.

This component of the study investigated the variation in soils to provide requisite background environmental data for the seed bank study. Soil analyses were undertaken (Chapter 2) to provide clarity on the distribution of soil properties (for example, soil nutrient and texture patterns) across the landscape. This study component further aimed to focus on potential challenges and opportunities, with respect to soil condition, for restoration of the degraded plains surrounding Tafelberg.

3.2 Synopsis of the formative pedology of the study area

Soils in the Eastern Mixed Nama Karoo (Hoffman, 1996) are derived primarily from the sedimentary Beaufort Group of the Karoo Supergroup (Geological Survey, 1996; Hoffman, 1996). Elements of both the Tarkastad and Adelaide Subgroups are present in the Middelburg District (Geological Survey, 1996). The A-horizon generally comprises poorly developed soils overlying rock and silt and clay accumulation are common in depressions and pans (Rutherford and Westfall, 1994).

The top of Tafelberg comprises a rock-cap of resistant dolerite dating from the Jurassic period (Geological Survey, 1996). This remnant dolerite appears to be residual from roughly the start of the African erosion cycle (De Villiers, 1990) which commenced during the Gondwanaland dismemberment. Tafelberg is surrounded by slopes of the Burgersdorp Formation (Tarkastad Subgroup). These slopes display interdigited fine grained sandstone and red- and green-grey mudstone (Geological Survey, 1996; Holmes, pers comm). The plains are primarily mantled by alluvial and colluvial soils with several outcrops of mixed (red, purple, grey and blue-green) mudstone with subordinate sandstone most noticeably present on the south east, south west and north west plains (Geological Survey, 1996).

3.3 Variation in soil chemistry, texture and nutrient status of soils on- and off Tafelberg

The following paragraphs summarise the results of analyses from soil samples taken from 22 sites on- and off Tafelberg (Refer Table 2.1 for detail on site codes and numbering). Physical and chemical properties of various soil elements are discussed and key issues that have emerged from this component of the seed bank study are examined.

[1] To a lesser extent, the potential for seed naturally dispersed from the "conservation islands" found on the mesas by wind, water and animals was also considered.

Complete results of soil chemical and physical analyses are presented in Appendix 3.1. It is clear from the literature, from field observation and chemical analyses, that soils from Tafelberg and the surrounding plains show high levels of diversity in depth, texture, structure and origin as well as in relative nutrient content of the soils. The results of soil analyses reveal variation between both micro-habitat soil samples (e.g. between open- versus closed-canopy) as well as between soil samples extracted from broader habitats or eco-types (e.g. between plains, top and slopes). While there were indeed differences between open- and closed-canopy samples, nonetheless the general trends between plains, slopes and top were relatively congruent, following the same patterns, for both open- and closed-canopy samples.

Chemical analysis of soil samples by Elsenburg[2] indicated that many nutrient elements of the samples exceed "agriculturally satisfactory" standards[3] however these generally refer to standards set for soils used for crop production (Kruger, pers comm). Further, analyses by Elsenburg do not distinguish between "available" and "unavailable" nutrients. For example, it is possible that even though soil phosphorus levels were found to be "high" on the plains, the total available phosphorus may be a fraction of the total amount measured.

Finally, even though the soil sampling was conducted over the period of two successive seasons (April 1998 and April 1999) the patterns of nutrient distribution, soil reaction and soil texture provide a clear picture of the top, slopes and plains of Tafelberg. There were no unusual nor catastrophic environmental incidents such as a fire or abnormally high rainfall between the two sampling events that might have influenced the results to any great degree.

3.3.1 Variation in soil carbon content as an estimate of soil organic matter[4]

The key element in photosynthetic energy transformations, and essentially involved in all life processes (Brady, 1990), carbon is the largest single constituent of soil organic matter (SOM) (Sparks, 1990). Since SOM plays a vital role in soil structure and soil reaction (Sparks, 1995), through its high cation exchange capacity (CEC) and water-holding capacity, Brady (1990) considers SOM to be the single largest factor responsible for stability of soil aggregates.

Throughout the study area, variation in soil carbon (Figure 3.1) was evident. With an overall average of 34% more carbon in soils from closed-canopy than from open-canopy samples,

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2 Elsenburg Agricultural College, Western Cape.

3 Confer Appendix 3.1; Figures 3.2 and 3.3. These are included for interest value.

4 Soil organic matter is considered synonymous with humus (Sparks, 1995). Humic substances comprise 60-80% of soil organic matter (Brady, 1990). Since the C/N ratio is considered to be relatively constant (between 10:1 and 12:1, with arid soils slightly lower, e.g. 8:1), for any given soil (Brady, 1990; Sparks, 1995), it is acceptable to focus on carbon as an estimate of total soil organic matter. Nitrogen can however be a limiting factor in maintenance and availability of carbon in soils (Brady, 1990) and it will thus be necessary to further investigate the C/N ratio of soils in the Tafelberg area.

the average percentage of carbon from soils on top of Tafelberg was more than triple the average found on both plains and more than double the average from both slopes (Table 3.1). Soils from the south east plains contained the lowest percentage of carbon and hence the least organic matter (Table 3.1; Figure 3.1).

Table 3.1: Summary of variation in percentage soil carbon, as an estimate of soil organic matter (SOM), between soil samples removed from open- and closed-canopy sites, on the plains, slopes and top of Tafelberg. Data are presented as mean percentage of soil carbon ± standard deviation.

soil carbon factor ⇩	Habitat ⇨	NW plains n = 4	NW slopes n = 4	Top sites n = 6	SE slopes n = 4	SE plains n = 4	Total for study site n=22
mean % carbon: open-canopy		0.76% ± 0.34	1.14% ± 0.51	2.45% ± 0.36	0.87% ± 0.15	0.45% ± 0.24	1.25% ± 0.84
mean % carbon: closed-canopy		1.16% ± 0.43	1.78% ± 0.58	3.33% ± 0.28	1.79% ± 0.76	0.78% ± 0.27	1.91% ± 1.06
mean % carbon: open-plus closed-canopy		0.96% ± 0.42	1.46% ± 0.61	2.89% ± 0.55	1.33% ± 0.71	0.62% ± 0.29	1.58% ± 1.00
ratio of mean % carbon: open- versus closed-canopy		0.66	0.64	0.74	0.49	0.58	0.66

Soil organic matter is noted by Watkeys (1999) as being scarce throughout most of the Karoo regions. This appears to be a trend for arid soils globally and Brady (1990) suggests a range of between 0.2-1.7% SOM for mineral aridisols (dry soils) noting that aridisols are usually lowest in SOM of all soil types. Ellis (1988) notes that SOM in the A-horizon of the broad physio-graphical region (BPR) he defines as Eastern Karoo (EK)[5], is higher than in the neighbouring Central Karoo BPR. He presumes this to be due to relatively higher rainfall in the EK BPR. He documents that average SOM from 18 soils in the EK BPR was 0.54%[6] (Appendix 3.2).

Soil organic matter comprises accumulated, decomposed and partially disintegrated plant and animal residues as well as a complex of other organic compounds that are the result of microbial decay processes (Brady, 1990, Sparks, 1995). The higher level of carbon measured from closed-canopy than from open-canopy samples[7] is thus readily explained by the observed accumulation of plant and animal detritus under closed-canopy patches. Wind and water move leaf litter, seeds and other debris along the soil surface. These "organic mulches" containing seeds are trapped by fallen branches, plant clumps, emergent rocks and grass tufts and form the basis of favourable micro-habitats for germination and seedling

5 The EK BPR incorporates the Tafelberg locality.
6 There is unfortunately no distinction made between micro- or macro-habitat sampling.
7 This generalisation has a single exception, namely one site on the sparsely vegetated south eastern plains (FSE2) where the open-canopy soil sample yielded 0.02% more SOM than the closed-canopy soil sample.

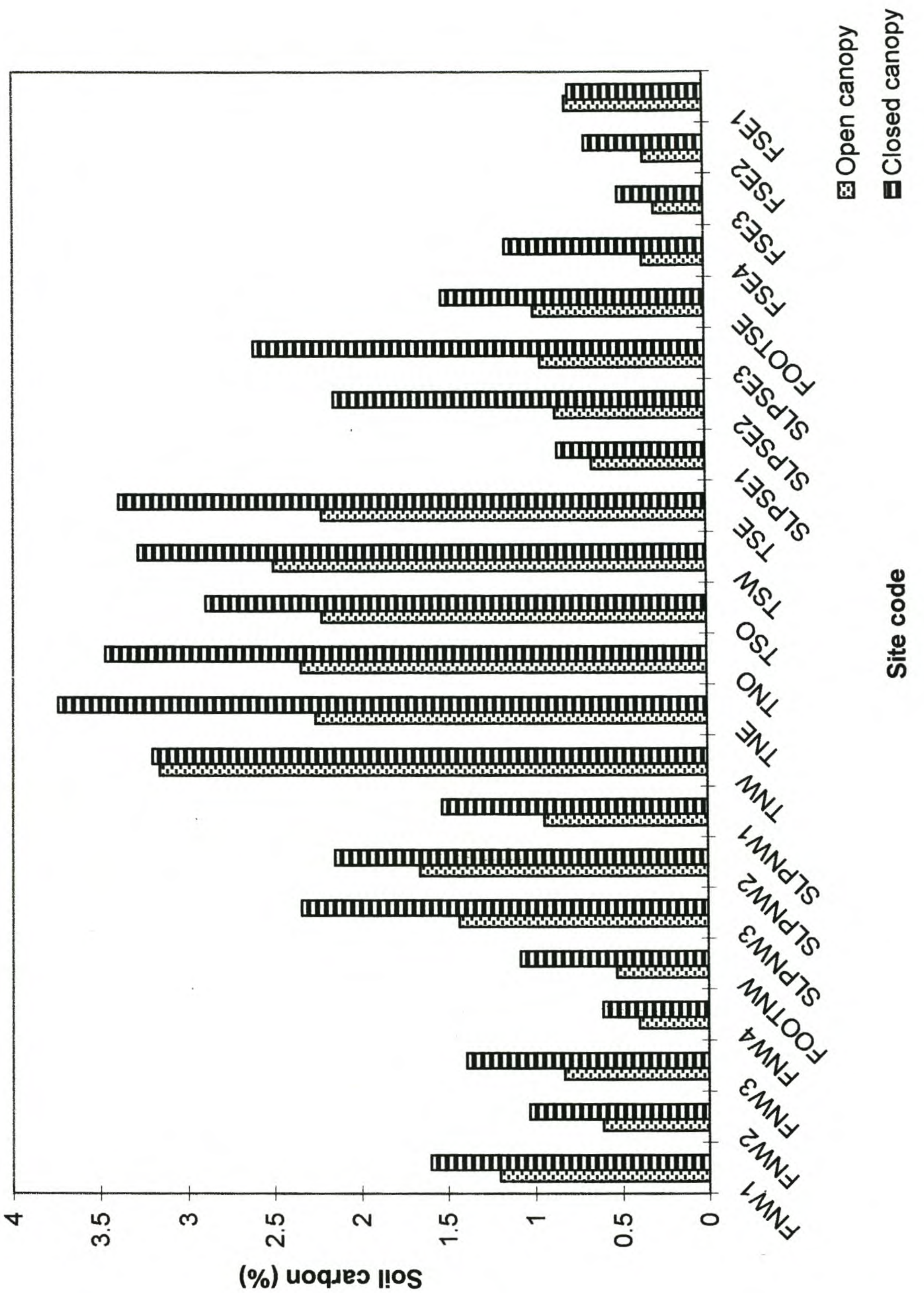

Figure 3.1: Variation in the soil carbon content of open- and closed-canopy soil samples removed from the plains, slopes and top of Tafelberg. Read site codes as F= plains, SLP = slopes and T = top sites. Refer Table 2.1 and Figure 2.1 for codes and placement of sites.

establishment (Chapter 5). Further, a higher density of emergent rocks (which trap debris); a greater diversity and relatively more dense plant canopy cover; as well as a lower intensity of grazing, on the top and slopes, ensure that there is a greater source of plant material to contribute to SOM in these sites than on the plains.

Dissimilarities in soil carbon content have significant implications for any attempts at restoration, since it is possible that plants presently growing on the top and slopes of Tafelberg may be unequivocally adapted to a relatively higher soil carbon content. Since one broad proposal is to utilise plant propagules from mesas for restoration of the heavily utilised plains, it will be crucial to determine SOM requirements for basic ecological sustainability of biological diversity in afflicted areas as well as SOM needs of species that are proposed for revegetation purposes.

Range condition and species composition are directly linked to sustainability of soil organic matter. In long term trials conducted in semi-arid rangelands in the Orange Free State (South Africa), organic carbon decreased by over 4% after two years of induced change from "good" to "poor" condition of the rangeland. After 15 years, overall loss of organic carbon, from the same trials, was in the order of 33% (Snyman, 1997).

Loss of organic matter from arid ecosystems has a number of significant implications. Activities of soil biota provide a vital contribution to the distribution of organic matter through processes of decomposition, dispersal and soil stabilisation (Steinberger, 1995). Soil biota are clustered at differing densities in these systems and are closely correlated with, and dependent upon, plant litter or debris for survival and activity (Steinberger and Whitford, 1983; Steinberger and Whitford, 1988; Steinberger, 1995; Whitford, 1999). Thus continued loss of soil organic matter impinges upon the measure, activities and survival of local micro-biota and may eventually reduce the inherent capacity of functional soils to sustain natural processes, leading to loss of soil biodiversity and potentially to dysfunctional soils.

Owing to the nature of SOM (with its inherent role in soil structure and chemical reaction) loss of SOM from soils through any means or agent, eventually leads to a reduction in soil fertility through leaching and erosion (of especially the more mobile soil nutrients and particles) (Brady, 1990; Snyman and van Rensburg, 1993; Sparks, 1995) and to a decrease in water infiltration rate and water retention ability (Snyman and van Rensburg, 1993; Snyman, 1998). This implies a decline over the longer term of nutrient and trace elements, such as copper, potassium, magnesium and manganese (Brady, 1990), with concomitant lowering of overall nutrient status of soils thus affected. It further implies surface run-off and localised droughts in those areas that are less able to utilise natural precipitation effectively (Snyman, 1998).

It is considered a matter of urgency that the status, and direction of transformation, of soil organic matter in rangeland soils be investigated at the regional and national level.

3.3.2 Variation in soil nutrient elements other than carbon

3.3.2.1 Discussion of some general trends in soil nutrient elements with respect to open- and closed-canopy samples

Distinct variations in some nutrient- and trace element ratios of open- versus closed-canopy samples were noted. For example, average zinc and boron contents of soils from open-canopy samples were consistently much lower than for closed-canopy samples, containing an average of 63% and 72% that of closed-canopy samples respectively (Table 3.2). Average soil potassium content was lower (for 90% of samples) for open-canopy samples than for closed-canopy samples (Table 3.2).

Table 3.2: Summary of ratios and overall trends of soil nutrients, texture and chemical reaction between open- versus closed-canopy samples from Tafelberg

SOIL FRACTION ⇨	pH	Na	P	K	Ca	Mg	Cu	Zn	Mn	B	Stone	Sand	Silt	Clay
lower or higher value from open-canopy	↓	↑	↓	>↓	↓	↓	↑	>>↓	↑	>↓	>>↑	↓	>↑	↑
Ratio of open:closed canopy (n=22)	0.98	1.17	0.98	0.80	0.83	0.94	1.11	0.63	1.06	0.72	1.53	0.95	1.26	1.12

There appeared to be no consistent overall differences between open- and closed-canopy samples for phosphorus, sodium, calcium, magnesium, copper or manganese soil components. There are differences however, for some of these soil constituents, once one examines the broader eco-type (e.g. plains or slopes) from which samples were removed. For example, closed-canopy samples on the south east and north west plains displayed on average 69% of the sodium levels found in open-canopy samples (Appendix 3.3). On the other hand, the reverse was true on the south east slopes where open-canopy samples displayed on average 68% of the amount of sodium found in closed-canopy samples. Similarly, all open-canopy samples taken from both plains contained a marginally higher mass of copper than closed-canopy samples but these differences were not so clear-cut for the top and the slopes (Figure 3.2). These habitat differences will require further investigation; however it is likely that open-canopy expanses on the plains accumulate salt crusts in the top soil layer, accounting for some of the elevated levels of salt-forming elements such as copper and sodium. Soils from closed-canopy sites are more likely to contain actively growing plant roots that would utilise nutrients, thereby creating a divergence in the average soil nutrient content of the two micro-habitats.

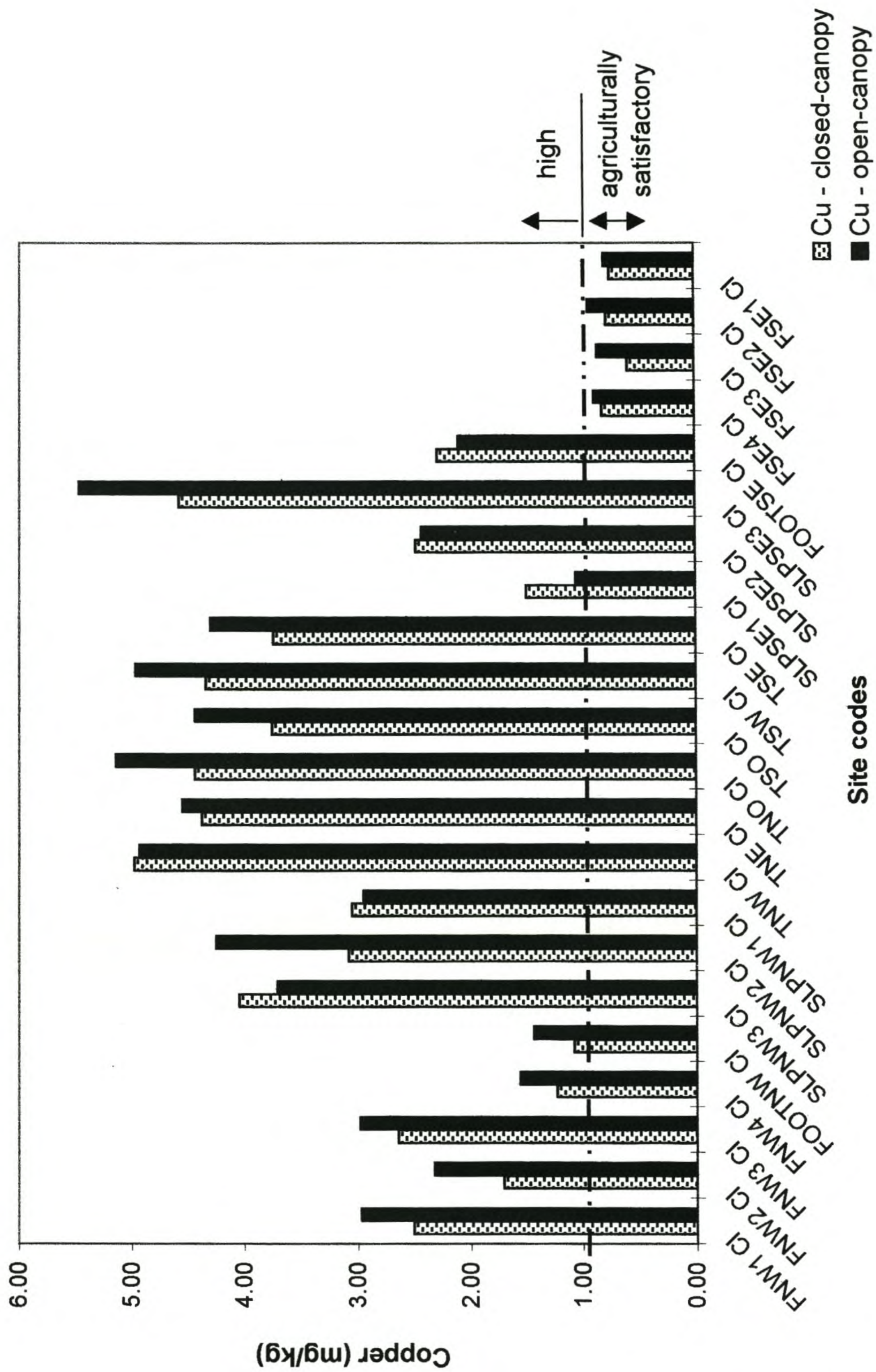

Figure 3.2: Soil copper content of open- and closed-canopy soil samples from the plains, slopes and top of Tafelberg. Refer Figure 2.1 and Table 2.1 for codes and placement of sites. F = plains, SLP = slopes and T = top sites

On the whole there were significant levels of correlation[8] between the copper (Figure 3.2), phosphorus (Figure 3.3), calcium, magnesium and manganese content from open- and closed-canopy soil samples. Lower levels of correlation between open- and closed-canopy samples were found for zinc, potassium, sodium, boron and soil pH[9]. In general, where an open-canopy sample contained a high level of a nutrient relative to another open-canopy sample, then the closed-canopy sample contained a similarly high level of that nutrient and *vice versa*.

3.3.2.2 Discussion of general trends in soil nutrient composition on- and off Tafelberg

3.3.2.2.1 The essential nutrients

a) Potassium

One of the essential plant nutrients[10], potassium performs what must be a crucial role, in semi-arid regions, with regard to the maintenance of turgidity in plant cells (Galston *et al*, 1980). One of the most mobile elements in soils, potassium levels in mineral soils are generally high but even at high levels do not appear to be toxic to plants or animals (Galston *et al*, 1980; Brady, 1990). Potassium levels in sandy soils tend to be lower than those in other soils (Brady, 1990).

Ellis (1988) considered potassium in the EK BPR to be at high levels in the A-horizons and other horizons where *in situ* shale is the parent material but in medium supply where unconsolidated material is the parent material (Appendix 3.2). This appears to be borne out by the relatively high potassium content of soils throughout the Tafelberg sites (Figure 3.4a; Appendix 3.1). Potassium levels on the south east plains were relatively lower in comparison with all other eco-types, although the average soil potassium content appears to be reasonable overall. Owing to the high mobility of available forms of the element, continued leaching of the sandy soils on the south east plains (refer 3.3.2.3) may reduce potassium levels over time. This could eventually become a limiting factor for restoration of the plains, if this is not already the case.

b) Phosphorus

Phosphorus is one of the elements considered essential for plant growth, performing a critical role in plant structure and function. Phosphorus was found to be a key determinant in plant distribution in the succulent Karoo (Esler and Cowling, 1993). Generally, soil is the primary

[8] Correlation coefficients, between open- and closed-canopy samples for these nutrient elements, were ≥+0.97 (Appendix 3.3).

[9] Correlation coefficients, between open- and closed-canopy samples for these nutrient elements and pH, lay between +0.80 and +0.93 (Appendix 3.3).

[10] Phosphorus, potassium and nitrogen are considered nutrients essential for plant growth. Brady (1990) notes that a high measure, of all three elements, is insoluble in soil solution and is thus unavailable for plant use.

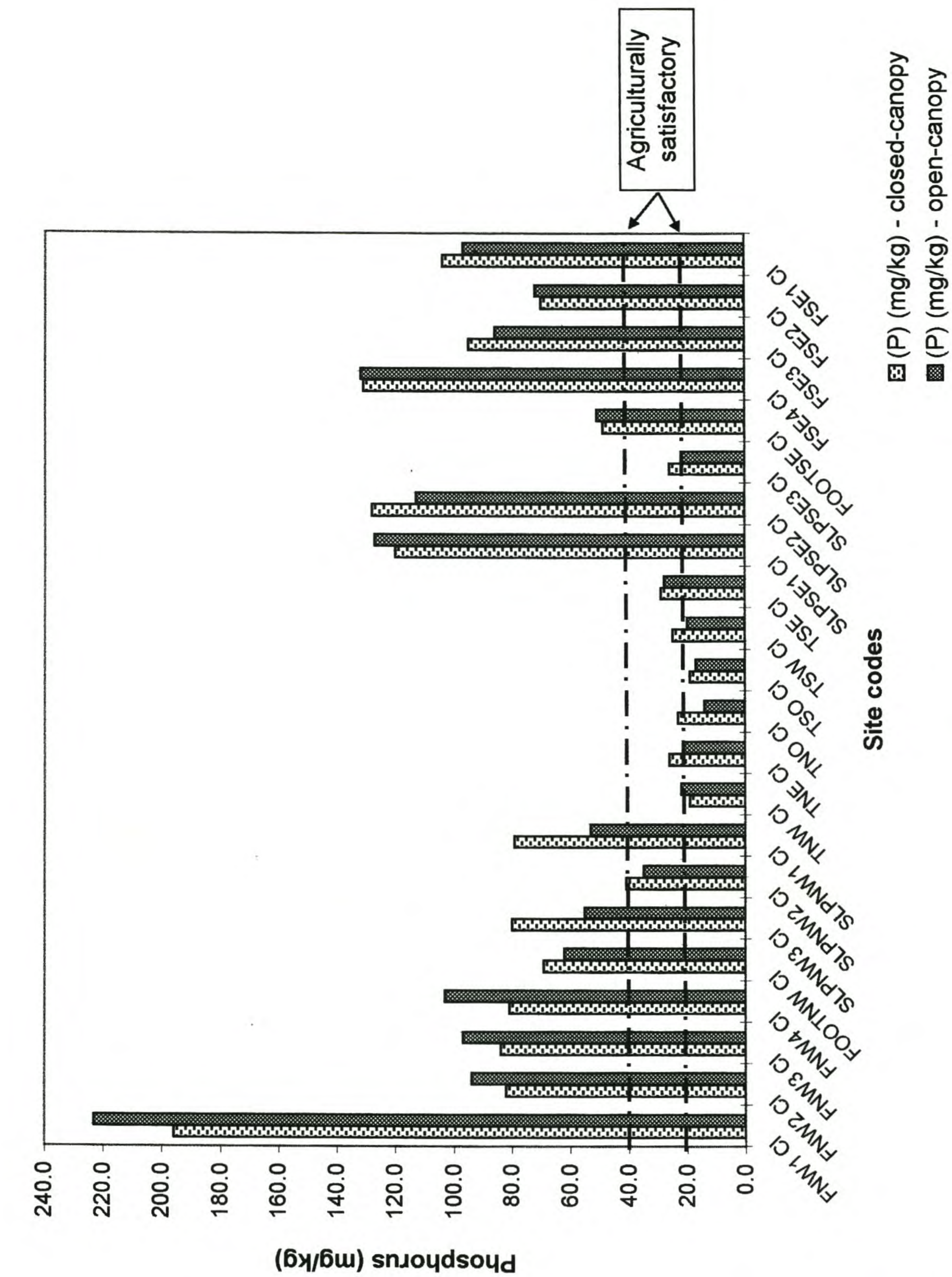

Figure 3.3: Variation in soil phosphorus content of open- and closed-canopy soil samples removed from the plains, slopes and top of Tafelberg. Refer Figure 2.1 and Table 2.1 for codes and placement of sites. F = plains, SLP = slopes and T = top sites.

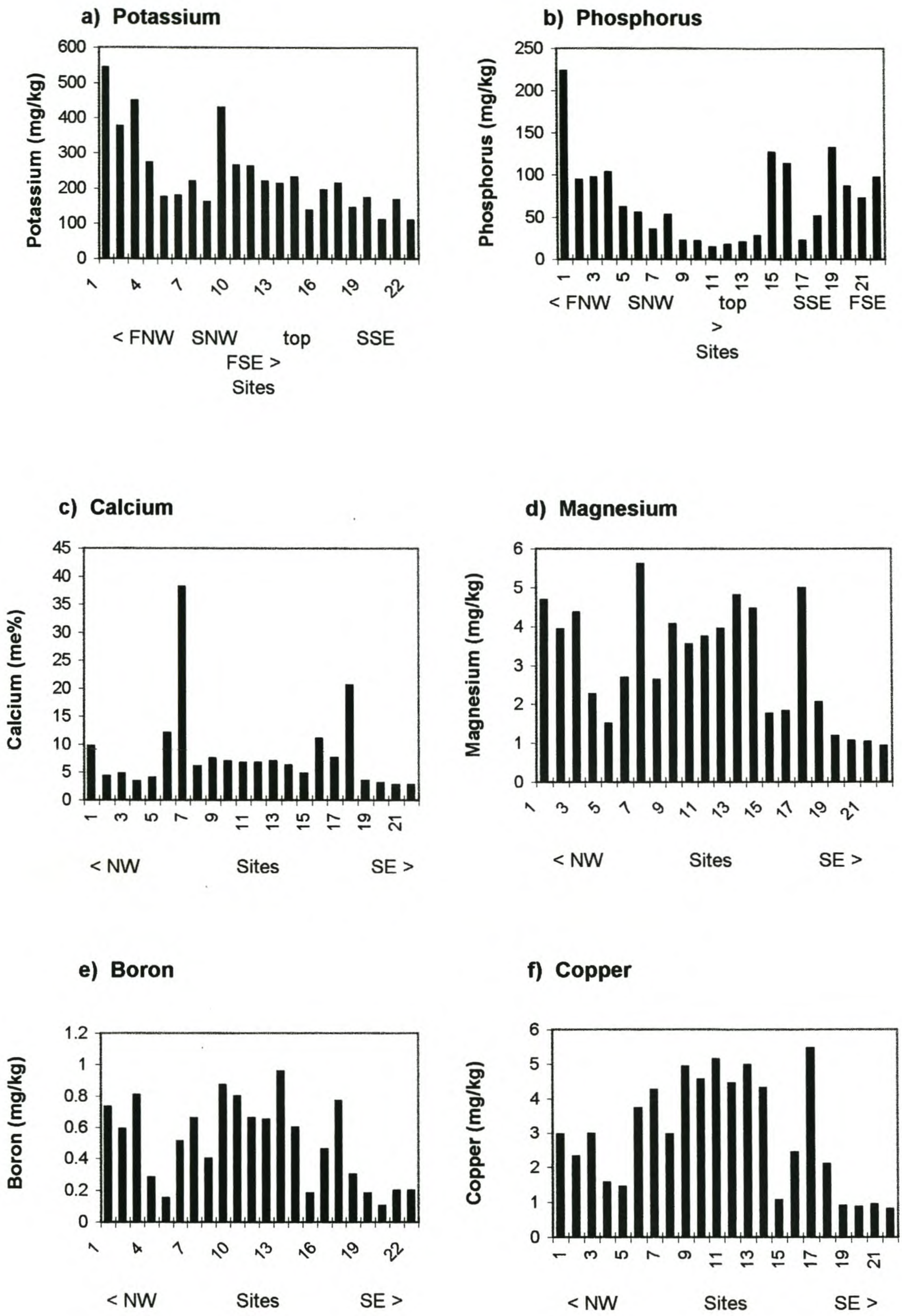

Figure 3.4: General trends of soil nutrient composition and texture across the plains, slopes and top of Tafelberg (samples from open-canopy sites from FNW1 to FSE1. Refer Table 2.1, Figure 2.1 for detail on site numbering and site placement respectively.

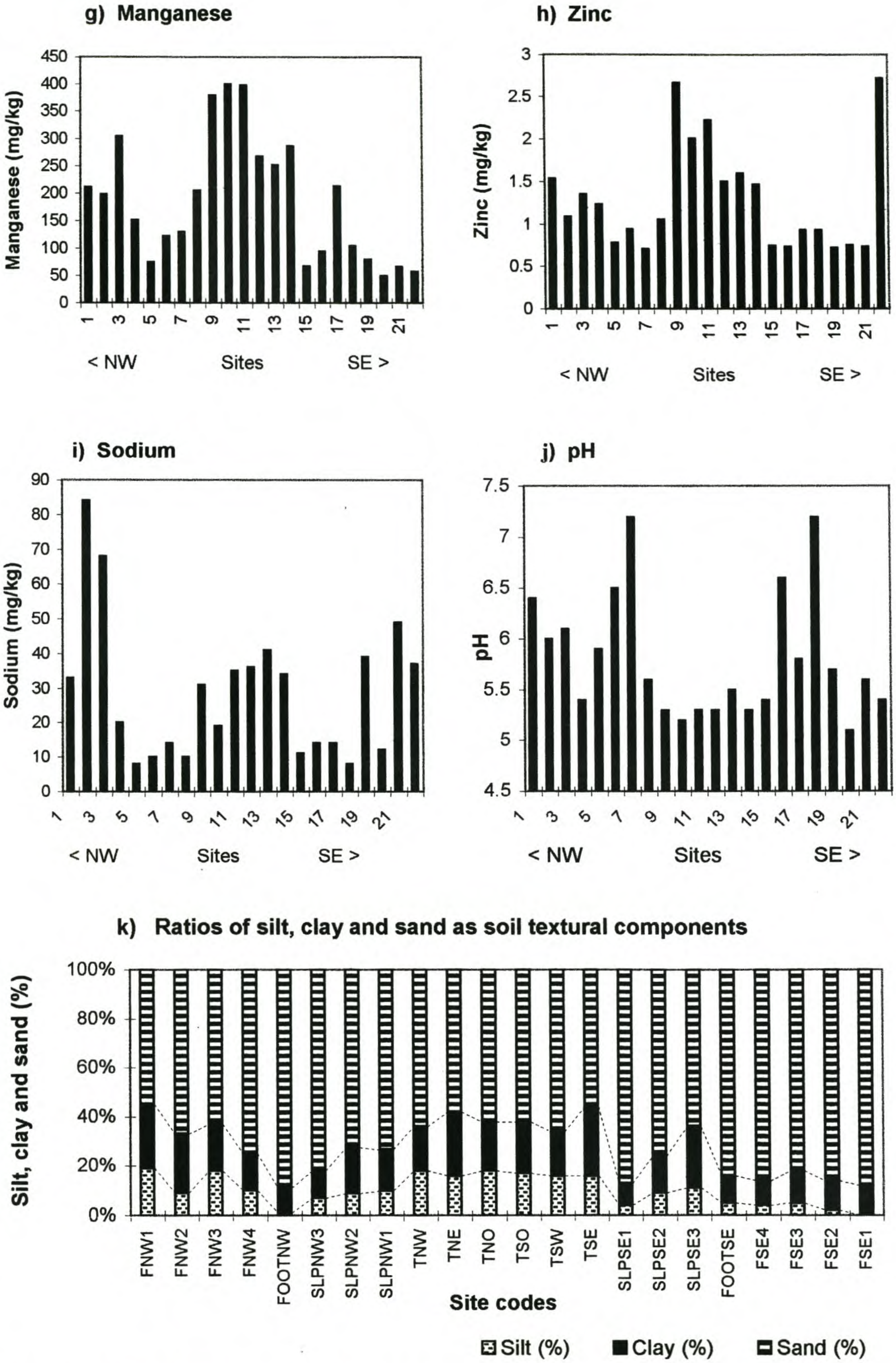

Figure 3.4: (cont) General trends of soil nutrient composition and texture across plains, slopes and top of Tafelberg (samples from open-canopy sites from FNW1 to FSE1. Refer Table 2.1, Figure 2.1 for detail on site numbering and site placement respectively.

natural source of phosphorus, however, available phosphorus in soils is low globally (Brady, 1990). This phenomenon is caused by the relative unavailability of inorganic phosphorus, as well as the readiness with which this element combines with others, forming relatively insoluble compounds which precipitate out of the soil solution (Brady, 1990).

Ellis (1988) notes that soil phosphorus in the Eastern Karoo BPR is generally low in both the A- and B- soil horizons where *in situ* shale is the parent rock, but is present at medium levels where unconsolidated material is the parent material.

Levels of soil phosphorus in soils on the plains surrounding Tafelberg nevertheless appear to be relatively high, peaking at 223 $mg.kg^{-1}$ on the far north west plains. These levels drop to a measured low of 14 $mg.kg^{-1}$ on top of Tafelberg (Figure 3.2; Figure 3.4b and Appendix 3.1). As mentioned above (3.3), it is not clear from the soil analyses what proportion of this element is in a form that is available to plants. This information may be required for the successful implementation of a restoration programme.

c) Calcium

An essential nutrient, the role of calcium in cell membrane permeability and plant cell wall structure (Galston *et al*, 1980) must render it a limiting nutrient of soils in arid and semi-arid zones. Certainly Esler and Cowling (1993) found calcium in soils to be a determinant of plant distribution in the succulent Karoo. The most common soil group in the Nama Karoo Biome is, however, rich in lime (Rutherford and Westfall, 1994) and soils in the broad Nama Karoo Biome are predominantly alkaline (Vorster and Roux, 1983).

This appears to be the case on and around Tafelberg, where soil calcium content is considered by Elsenburg to be high for all soil samples analysed (Table 3.1). Soil calcium was marginally lower from open-canopy samples than from closed-canopy samples. However, the profile of average calcium distribution was relatively uniform for all sites with two significant departures on the middle site on the north west slopes and the south east footslopes (Figure 3.4c and Appendix 3.1). For example, average soil calcium for all 22 sites, from both open- and closed-canopy samples, was 8.97me% ±8.8, however, if the two above-mentioned sites are excluded from the equation, average soil calcium for the remaining 20 sites was 6.58me% ±3.35.

d) Magnesium

Considered to be an essential nutrient (Brady, 1990) magnesium plays a significant role in photosynthesis (Galston *et al*, 1980) and was also considered to be a factor in the natural determination of plant distribution in the succulent Karoo (Esler and Cowling, 1993). Soils on and around Tafelberg appear to be well supplied with magnesium (Table 3.1; Figure 3.4d) although these levels were noticeably lower on the sandy south east plains.

3.3.2.2.2 The trace elements (micro-nutrients)

Trace elements or micro-nutrients (Brady, 1990) are those essential for plant growth in very small quantities relative to the essential elements[11]. With the exception of boron (Figure 3.4e), all micro-nutrients assessed from soil samples appear to be present in high average quantities in soils around and on Tafelberg (Table 3.1).

On- and off Tafelberg, boron, copper (Figure 3.4f) and manganese (Figure 3.4g) followed similar patterns of abundance to that of SOM (refer Figures 3.1, 3.2 and 3.5). An assessment of statistical correlation of these three nutrient elements (Appendix 3.4) indicated that there may be direct correlation factors linking them. It is probable that these factors may include the combined cation exchange capacity of the clay and silt fractions (refer 3.3.3) as well as that of the SOM content of the soil (refer 3.3.1). Owing to the mineral nature of these soil micro-nutrients (Brady, 1990), a primary source (of these elements[12]) is likely to be the rocks and minerals that are the parent material of the soils of Tafelberg and the surrounding plains.

To a lesser extent, but nonetheless evident, zinc (Figure 3.4h) followed similar trends (to the three above-mentioned micro-nutrients and SOM) showing relatively high concentrations of these nutrient elements on the north west plains. The levels of zinc increased gradually with increasing altitude, peaking on top of Tafelberg but tailing off noticeably on the south east plains. A conspicuous exception for the soil zinc fraction was seen on the furthest site on the south east plains (FSE1) where the zinc content of both open- and closed-canopy samples was roughly three times higher than for other samples from the south east plains.

Ellis (1988) noted that zinc was well supplied in all soil horizons of the EK BPR with shale parent material but was present at medium levels in B- and other horizons where unconsolidated material was parent material (Appendix 3.2). The higher zinc content from the site FSE1 may then possibly be explained by a shale layer that is close to the soil surface (refer 5.3.1.1) while other sites on the south east plains appear to comprise a higher proportion of alluvial soils (unconsolidated parent material) and thus have a lower zinc content.

Ellis (1988) noted manganese for the EK BPR as being at high levels in both A- and B-horizons from both *in situ* shale and unconsolidated parent material (Appendix 3.2) and very high levels

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[11] The essential elements (nutrients) are considered to be nitrogen, phosphorus, potassium, calcium, magnesium and sulphur (Brady, 1990).

[12] Rocks and minerals are likely to be the primary source of soil boron, phosphorus, zinc, potassium and calcium.

of manganese from some horizons with *in situ* shale parent material. Levels of manganese in the soils of Tafelberg are all higher than satisfactory limits described by Elsenburg for cultivated soils.

Boron is well supplied in both A- and B- horizons and horizons of the EK BPR (Ellis, 1988) where both *in situ* shale and unconsolidated material are parent material. The analysis of soils from Tafelberg indicate that boron is present at satisfactory levels for most of the sites sampled, The exceptions to this are found in the sandy sites (FNW4 and FootNW) on the north west and for all sites on the sandy south east plains.

Boron plays an essential role in plant metabolism (Kabata-Pendias and Pendias, 1984, Pais and Jones, 1997). Boron deficiency can reduce water absorption by plants and may lead to death of meristematic cells amongst other consequences (Galston *et al*, 1980; Kabata-Pendias and Pendias, 1984; Brady, 1990). According to Galston *et al* (1980) boron has a narrow range dividing toxicity and deficiency thus, in the event that leaching of this element from the sandy soils is taking place, it is possible that localised boron deficiency may occur.

Copper is integrally linked with plant physiological processes including respiration, cell wall metabolism and photosynthesis (Kabata-Pendias and Pendias, 1984; Pais and Jones, 1997). Copper is relatively mobile and soluble in soil-solution (Kabata-Pendias and Pendias, 1984) and is therefore usually readily available for plant use, especially in more acidic soils (Brady, 1990). This can lead to copper toxicity problems in soils that are very acid. Significant bio-accumulation of copper salts may occur at or near the soil surface[13] (Kabata-Pendias and Pendias, 1984).

Copper in the EK BPR is plentiful in both A- and B-horizons, in soils from both *in situ* shale and unconsolidated parent materials (Ellis, 1988) (Appendix 3.2). There is a strong positive correlation between the presence and quantity of copper with the presence of carbon in the top-soils of the Tafelberg study site[14] (Figure 3.5).

Schröder (1959) notes several consequences of copper imbalances in soils and plants grown on these soils. Copper deficiency in livestock can cause several debilitating diseases. These include significant effects on the growth and appearance of wool, hair and fur as well as afflictions such as enzoötic ataxia (swayback, lamkruis) in lambs. Although toxicity is rare, it can take place following accumulated intake. Long term or chronic copper poisoning may cause haemolysis, jaundice and death (Schröder, 1959).

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[13] It is possible that this phenomenon may be partly responsible for the slightly higher copper content of open-canopy samples relative to that of closed-canopy soil samples.

[14] A correlation coefficient of $\approx +0.93$ was obtained for closed-canopy samples of carbon and copper content. Overall, for average copper and carbon from both open- and closed-canopy samples, the correlation coefficient was $\approx +0.92$.

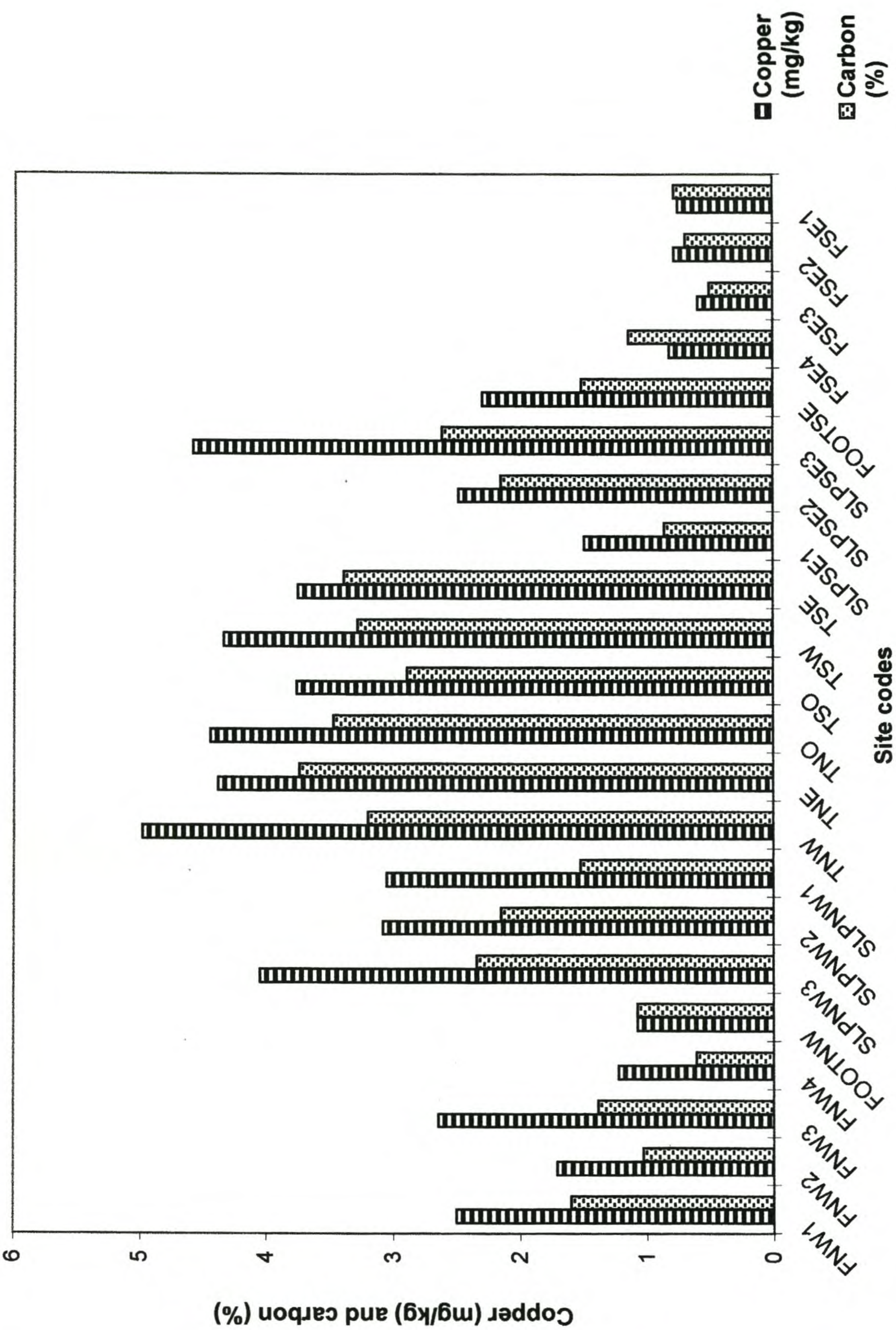

Figure 3.5 The relation between copper and carbon contents of closed-canopy soil samples from sites on the plains, slopes and top of Tafelberg. Refer Figure 2.1 and Table 2.1 for placement and codes of sites

Reduced levels of copper, through leaching and heavy grazing, may therefore prove to be a limiting factor for plant growth as well as potentially inducing a variety of deficiency diseases in livestock. It is possible that a copper deficiency may result should there be a continued decrease in canopy cover with a concomitant decrease in overall SOM on especially the sandy, south east plains. The effect of continued loss of copper may thus be a significant impact to the overall biodiversity of the area as well as to the wool-farming industry in the longer term.

3.3.2.3 Synopsis of general trends in soil nutrient composition on- and off Tafelberg

It appears that all analysed essential elements and micro-nutrients were present (at time of sampling) at levels suitable for plant growth and should not be limiting nutrient factors for plant growth and restoration in these habitats. Soils from the top, slopes and plains surrounding Tafelberg are not deficient in phosphorus, potassium, calcium or magnesium although levels of potassium, calcium and magnesium were lowest overall on the south east plains. This may be a natural consequence of the physical nature of the parent materials from which these soils are derived or there may be accelerated loss of these elements through long term reduction by slow leaching, erosion and heavy cropping by livestock from the south east plains.

Many nutrient- and trace elements are relatively mobile in soil solution and an assortment of factors may accelerate changes in nutrient levels. It appears that prospective nutrient deficiency, through natural and possibly accelerated processes of erosion and gradual leaching of sandy soils, is a possibility on the south east plains and will warrant further investigation. On the north west plains significantly higher levels of nutrient elements, particularly on higher clay fraction soils, may indicate gradual, natural (and possibly accelerated) accumulation of surface salts and salt ions (including sodium (Figure 3.4i)). This is a recognised phenomenon in arid and semi-arid areas as well as a feature of pans and poorly drained soils (Brady, 1990). This aspect requires further investigation since soil samples were removed from the top 50mm of soil only and no deeper sampling was undertaken.

High intensity cropping (which could arguably include high intensity grazing) with no addition of micro-nutrients can deplete micro-nutrient and essential element levels in soils (Brady, 1990). Long term, albeit gradual, depletion of soil nutrients can eventually reduce nutrient levels to the degree where nutrients are in short supply affecting plant growth and survival and defeating future restoration attempts. Soil nutrient status must be factored into any proposed restoration programme firstly as a means of habitat identification; secondly to determine where and how nutrients are being lost or gained at an accelerated or undesirable rate; and, finally to ensure that soil nutrient requirements are met for desirable plant species used in restoration programmes.

3.3.3 Variation in pH as a measure of soil reaction

The role played by the pH of soils in determining the availability of nutrients (Kabata-Pendias and Pendias, 1984; Brady, 1990) and the distribution of plant species (Lloyd, 1989; Cowling *et al*, 1992; Esler and Cowling, 1993) is well documented. Brady (1990) notes that a pH range of between 6 - 7 is optimal for plant growth.

Soils in semi-arid regions are described by Brady (1990) as generally having a relatively high pH (≥7) owing to both low SOM content as well as lower rainfall and consequent lack of heavy leaching of these regions. Ellis (1988) found soils from the EK BPR to be generally neutral to alkaline in reaction (i.e. ≥7).

Mean soil pH for open- and closed-canopy sites on- and off Tafelberg was 5.8 and 5.95 respectively. Measured pH was generally lower for open-canopy than for closed-canopy samples for roughly 70% of samples (Table 3.3). While overall variation in pH does not appear to be significant (2% difference) between open- and closed-canopy samples, there was a significant difference in soil pH between broad eco-types on- and off Tafelberg. The north west plains and both slopes have average pH values above 6.1 while the top and south east plains of Tafelberg have average pH values of roughly 5.4 (Table 3.3). Reasons for these lower, more acidic soil pH values are probably different given dissimilarities in soil nutrient content and soil texture.

There was a relatively high SOM content of soils on the top and slopes of Tafelberg and this would contribute to the formation of acids in the soil[15]. Conversely, a relatively higher clay soil fraction on the slopes, top and north west plains (with the exception of the sandy FNW4) was probably a contributing factor to a higher average pH value of soils from these sites.

Clay and SOM have a high cation exchange capacity and are able to adsorb base-forming cations such as Ca^{2+}, Mg^{2+}, K^{+} and Na^{+} more readily (and to a greater extent) than the relatively larger soil particles such as sand and silt (Brady, 1990). It is possible then that the relatively low average pH of soils on top of Tafelberg results from complex interplay between the presence of acids (formed from decaying organic matter) and the substantial presence of ions of base-forming mineral elements. It is also likely, given the relatively low levels of disturbance of this habitat, that the pH is at a satisfactory ecological equilibrium.

Of interest is that, despite higher average pH values for the north west plains and slopes, the north west plains site closest to Tafelberg and the north west footslope site both have relatively low average soil pH values of 5.6 and 5.75 respectively. Both sites were heavily grazed and

[15] Decomposing SOM forms organic and inorganic acids (Brady, 1990).

also had a higher average sand component relative to other sites on the north west plains and slopes. It is probable that a relatively higher rate of leaching of these sandier soils, which were also correspondingly low in SOM, will have gradually reduced levels of base-forming cations thereby inducing soil acidity (Brady, 1990). This is possibly also the case on the sandy south east plains. This is a natural phenomenon, however if the soils are becoming acidified at an accelerated rate as a result of over-utilisation and loss of nutrients, then a disequilibrium exists and will need to be remedied for effective restoration of these degraded areas.

Table 3.3 Average soil pH for the top, slopes and plains of Tafelberg. Data are presented as mean pH ± standard deviation. Refer Figure 3.4j.

habitat ⇨	NW plain	NW slope	Top sites	SE slope	SE plain	All sites
average pH closed-canopy	6.28 ± 0.41	6.43 ± 0.81	5.38 ± 0.098	6.53 ± 0.56	5.43 ± 0.096	5.95 ± 0.66
average pH open-canopy	5.98 ± 0.42	6.3 ± 0.71	5.32 ± 0.098	6.25 ± 0.81	5.45 ± 0.26	5.81 ± 0.62
average pH	6.13 ± 0.42	6.36 ± 0.70	5.35 ±0. 098	6.39 ±0.66	5.44 ±0.18	5.88 ± 0.64

Soil acidity and alkalinity are extremely complex issues affected by many determinants including temperature, season and soil moisture (Galston *et al*, 1980; Brady, 1990). Further investigation of soil reaction, more specifically the change in soil reaction over time, would be required to determine the factors, natural or induced, influencing specific pH values in the Tafelberg area. Existing levels of soil acidity are presently well within limits conducive to plant growth. What is apparent is that the change (over time) in soil pH may potentially be used as an indicator of soil degradation in combination with other factors such as reduction in canopy- or basal cover, soil organic matter and finer soil particles such as silts and clays.

3.3.4 Variation in soil texture

Soil texture refers to the particle size distribution of the inorganic component of soils and is a property of soil that is not readily prone to change. The proportion of each particle size fraction is considered to be a basic property of a given soil (Brady, 1990). Erosion and deposition can nevertheless alter soil texture over time. These essentially natural and necessary processes (Novellie, 1999) may be accelerated by natural events, such as flooding and high wind events, or by anthropogenic processes, such as over-utilisation of pastures (Snyman, 1986), that exaggerate the incidence and/or magnitude of erosion and deposition.

Soil texture variation between open- and closed-canopy samples is evident (Appendix 3.1, Table 3.2, Figure 3.4k). Average stone- and silt contents of open-canopy samples were higher (roughly 153% and 126% respectively) than for closed-canopy samples. This may be the result of a number of factors but high overall variability between sites of the silt- and stone soil fractions (Appendix 3.1) is evident. Non-significant coefficients of correlation (Appendix 3.4) between SOM, silt and stone may signify that accumulation, through deposition, of silt in pans and depressions (Rutherford and Westfall, 1994) may be a strong contributing factor to the higher silt load in these sites. A further contributing factor may be that on the plains, where sheet erosion evidently occurs, there is a degree of pedestal formation around individual plants and plant clumps as a result of the erosion of loose surrounding soils that are not held in place by plant roots. Soils from these, generally closed-canopy, pedestals appear to be deeper than the soil from surrounding open-canopy expanses. It is possible that gradual, or dramatic, removal of top soil from open-canopy patches exposes pebbles as well as the degraded shale layer that lies close to the surface on the plains.

Soil texture was also variable between the slopes, the top and both of the plains (Figures 3.4k, 3.6 and 3.7). Sand was the dominant soil component throughout the whole study site. The average percentage of sand on top of Tafelberg was approximately 63% while on the south east plains this rose to an average of almost 85% (Figure 3.6). The clay soil fraction showed a converse trend with an average of almost 21% clay in soils on the top and only 9% clay in soils on the south east plains (Figure 3.6).

The average soil texture composition of both slopes was relatively similar (Figure 3.7). Both slopes showed soils with relatively low clay and silt levels, roughly half of those found on top of Tafelberg. The average stone content of samples from all sites on Tafelberg was roughly 10% and the stony slopes accounted for most of this soil fraction (Figure 3.6; Figure 3.7). Both slopes appeared to show soil textural gradients between the top of the slopes and the footslope (Figure 3.4k) although these gradients are not clearly defined. Further sampling at closer intervals will be necessary to clarify and refine understanding of these habitats.

Conspicuous differences between soil textures on the two plains were evident. The north west plain appears to be a large pan with a relatively high clay content. The sandy south east plain is drained by several water-courses and erosion is more pronounced than on the north west plains. According to Snyman and van Rensburg (1986) even a flattish slope may experience substantial run-off and erosion, especially under conditions of low plant cover. Both wind- (Brady, 1990) and water erosion (Snyman and van Rensburg, 1987) displace finer soil particles more readily than larger particle sands and pebbles. Brady (1990) comments that sandy soil is more erodible than soil with good overall structure and that displacement of clay particles through wind erosion is inversely correlated with the degree of soil structure

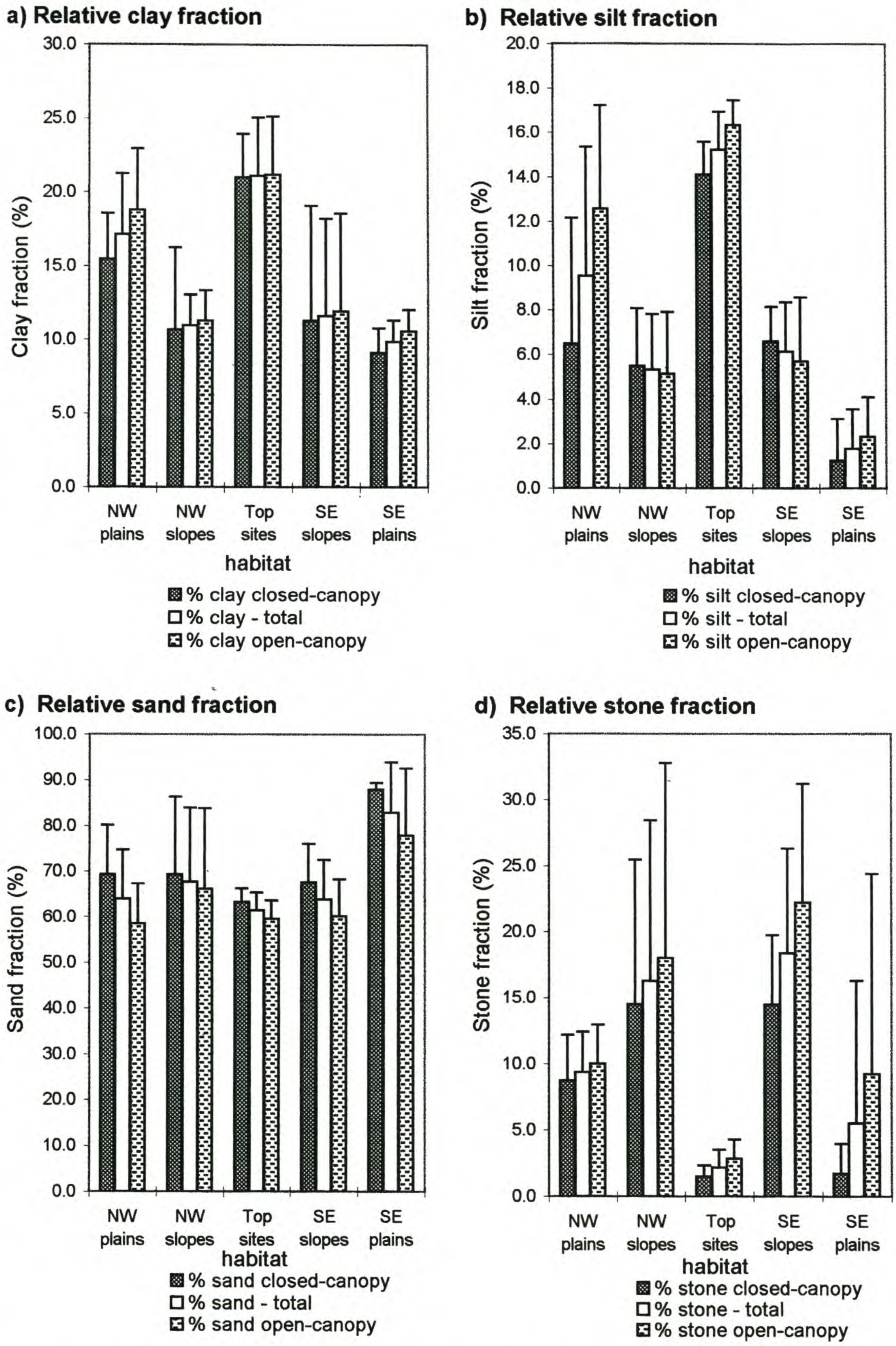

Figure 3.6 Relative fractions of averaged soil texture elements, of soils from open- and closed-canopy samples, removed from plains, slopes and top of Tafelberg

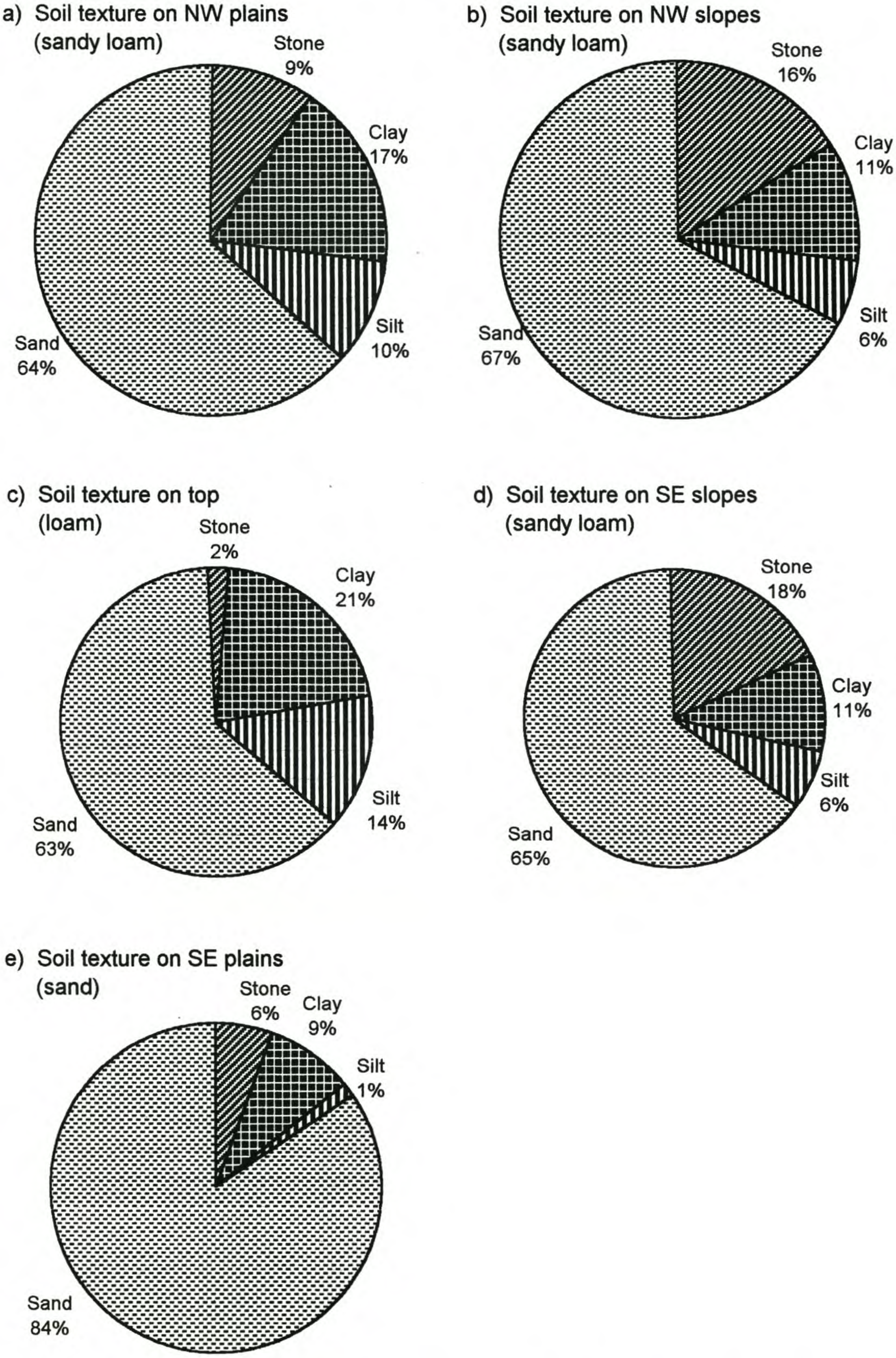

Figure 3.7: Comparison of average soil texture, of both open- and closed-canopy samples, from the plains, slopes and top of Tafelberg. Soil texture class in brackets.

and also of soil moisture[16]. Rutherford and Westfall (1994) note that silt and clay particles accumulate in pans. This is confirmed by the average clay and silt components of soils, from samples on the north west plains of Tafelberg, (17% and 10% respectively), as opposed to those from the south east plains (9% and 1% respectively) (Figure 3.6).

Available nutrient levels in soil are considered to be directly proportional to the clay content of soil (Kabata-Pendias and Pendias, 1984; Brady, 1990). Clay, along with humus, controls most physical properties in soils through an inherently high cation exchange capacity (CEC) and also contributes fundamentally to soil structure (Brady, 1990). The loss of clay particles from the soil is thus not considered desirable but clay is readily removed by both water- and wind erosion, the latter primarily in very dry conditions. Soil conservation and improvement, particularly of the silt- and clay fractions of soil, should be a primary component of any proposed restoration programme.

3.4 Summary of restoration potential and challenges to restoration presented by the soils of Tafelberg and the surrounding plains

3.4.1 An overview of the soils and degradation in the vicinity of Tafelberg

There were significant variations in soil chemical- and physical composition between the top, slopes and plains of Tafelberg. Spatial separation of micro-habitat sampling (i.e. open- versus closed-canopy) also revealed some contrasting soil characteristics. The soil nutrient and textural composition of the slopes appeared to be intermediate between the plains and top of Tafelberg but require further sampling to clarify affiliation with, and gradients between, these habitats. Particularly conspicuous differences were identified between the soil environment on the flat top of Tafelberg and that of the surrounding plains.

Given the snapshot in geological time, of soil composition in the Tafelberg locality, it is not possible to definitively conclude whether variations in soil composition have been caused, or influenced, by factors external to natural environmental- and ecological processes. While it is entirely possible that all existing patterns, of nutrient distribution and soil texture classes, are natural properties of soils in the area, it is unlikely that this is indeed the case.

The plains have been extensively used for many decades, even for centuries, as rangelands. Plant species commonly found on these plains[17] indicate that over-utilisation of natural pastures has taken place. Differences in soil composition may have been accelerated by anthropogenic

[16] Dry clay particles, in soils with poor overall structure, are highly susceptible to wind erosion (Brady, 1990).

[17] Many of these species are ephemeral, spinescent or otherwise less palatable, low in productivity or toxic. Several species found in relative abundance on the plains (e.g. *Geigeria ornativa, Chrysocoma ciliata* and *Walafrida saxatilis*) are considered to be indicators of veld degradation (Roux *et al*, 1994).

factors, such as bad veld management and over-utilisation, with concomitant loss of overall plant cover (Acocks, 1988; Vernon, 1999); soils (Roux and Opperman, 1986); soil organic matter (Du Preez and Snyman, 1993; Snyman and Oosthuizen, 1999) and other nutrients (Snyman *et al*, 1985; Snyman and van Rensburg, 1986; Brady, 1990). It is probable that these divergent soil characteristics will affect the nature and direction of future attempts to utilise propagules of desirable plant species, found in abundance on Tafelberg, for restoration of the degraded plains.

For example, a primary requirement for restoration of the plains is to increase canopy-cover[18] using a diversity of desirable plant species. Biological diversity is dependent on the maintenance of a broad diversity of habitats and vegetation components (Bosch and Kellner, 1991; Whitford, 1996; Snyman, 1998). Given the potentially plant-unfriendly soils that were categorised from open-canopy samples (on especially the south east plains[19]) it may be difficult, costly and also not time-effective (Wiegand and Milton, 1996) to attempt to increase canopy-cover by sowing seeds (from plant eco-types occurring on Tafelberg) into open-canopy expanses on the south east plains. Locally occurrent, indigenous pioneer plant species which are able to germinate, establish and, most importantly, to survive in open-canopy spaces, on sandy soils with relatively low SOM and nutrient levels, must be identified for an interim phase of restoration of the plains.

3.4.2 The challenge facing the potential for restoration of degraded rangelands

Farm managers and researchers are presented with a convoluted dilemma in an apparent spiral of declining rangeland condition. Domestic livestock must graze but pastures are arguably changing, becoming less productive than before (Acocks, 1953; Roux and Vorster, 1983; Danckwerts and King, 1984; Roux and Theron, 1987; Dean and Macdonald, 1994). Scotney and Dijkhuis (1990) note trends of dwindling SOM and soil fertility in cultivated regions of South Africa and also note the significance of this phenomenon in non-cultivated areas. Foraging livestock reduce vegetation cover through removal of palatable plant material and through trampling (Roux, 1980; Dean, 1992). Trampling, especially at high stocking rates, may impact soil quality by reducing soil permeability and water absorption (Du Toit, 1986[20]; Dean, 1992, Hiernaux *et al*, 1999). Grazing at lowered intensity, or even resting veld, does not necessarily improve veld productivity or condition (Wiegand and Milton, 1996; Jeltsch *et al*, 1999).

Researchers have indicated a direct link between reduction of vegetation cover and increased surface run-off (Snyman and Fouché, 1993; Snyman, 1998; Whitford, 1999). Snyman and van

[18] Basal cover is considered to be a more accurate indicator of veld condition in semi-arid and arid regions than canopy cover (Fourie *et al*, 1984; Snyman *et al*, 1985; Snyman and van Rensburg, 1990).

[19] For example these soils are low in SOM and fine soil particles, shallow and relatively leached of potassium in comparison with soil samples from the top and slopes.

[20] In: Snyman (1998).

Rensburg (1986) found reduction in plant cover to be the single biggest factor increasing surface run-off and sediment loss (Snyman and van Rensburg, 1997). Reduction in overall plant cover thus increases both the likelihood and occurrence of water erosion (Snyman and van Rensburg, 1986; Morgan, 1995) and wind erosion (Brady, 1990). This can lead to localised loss of top soil, especially silt and dry, loose clay particles (Brady, 1990; Snyman and van Rensburg, 1987) as well as lighter humus particles (Brady, 1990). This in turn gradually leads to an overall increase in the ratio of sand particles and renders soils more prone to erosion (Brady, 1990). Reduction of the clay fraction and soil organic matter also gradually decreases overall nutrient holding capacity of soil through diminished cation exchange capacity (Brady, 1990; du Preez and Snyman, 1993). This increases leaching of more mobile nutrient elements, especially during random high rainfall events. Snyman and van Rensburg (1986) noted a strong correlation between degraded veld and reduced water use efficiency (WUE). This effect is proposed by these researchers as the cause of localised droughts even after sufficient rainfall.

This chain of events alters the soil environment, as well as the potential for plant survival and reproduction. This may lead to a decrease in species that are sensitive to change in edaphic conditions, with a concomitant increase in those species which are tolerant of change. This change in the vegetation composition may further be accelerated by selective grazing of live-stock[21] (Kellner and Bosch, 1992; Du Toit *et al*, 1995). Continued loss of top soil through erosion will also arguably displace a percentage of seeds contained in the top soil. This may further reduce future potential plant cover and the cycle of rangeland degradation continues.

The following serves as an example of cyclical rangeland soil degradation. In sandy soils with low soil organic matter, leaching may reduce the copper content of soils (Ferreira, 1958; Kabata-Pendias and Pendias, 1984) and increase acidity of the soil[22]. Paradoxically, copper becomes more readily available in soil solution as soils become more acid (Kabata-Pendias and Pendias, 1984; Brady, 1990). The leached (more acidic) soils release more of the previously unavailable copper from the mineral soil base. This newly available copper in soil solution may be vulnerable to further leaching, leading to localised deficiency of soil copper (and other similarly leachable nutrients). In areas such as the seasonal pans on the north west plains, where an accelerated rate of fine soil particle deposition is occurring, a different outcome is likely owing to increased overall cation exchange capacity of soils and inadequate drainage (under conditions of low rainfall and evaporation). There is a tendency for salt accumulation in these finer textured soils and the probability of a build-up of toxic levels of nutrients in these areas is possible, magnified by the high cation exchange capacity of clay particles, which adsorb these ionic nutrients.

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21 Grazing may also potentially deplete future components of total SOM.
22 Through loss of base-forming cations (refer 3.3.3, above).

3.4.3 Opportunities for programmes to examine the restoration of soils in degraded rangelands in the Tafelberg vicinity and beyond

Restoration of degraded plains in the Tafelberg district will be complicated by the diverse needs and conditions of the various lowland habitats. The formulation of an integrated programme of restoration, that focuses on improving soil organic matter and on rehabilitation and conservation of soil environments, is vital. Practical, comprehensible indicators that allow land managers to identify soil degradation and accelerated change in soils must be prepared as a point of departure. Secondly, managers must have pragmatic guide-lines, that enable them to decide on economically appropriate means and technology to slow down degradation and initiate improvement in soil condition. Finally, local soil, vegetation and grazing indicators for assessing vegetation and soil change must be developed (once a monitoring and improvements programme has been instituted).

Recently a number of publications and projects have initiated integrated responses to range-land degradation by connecting agriculture with ecology; research with practice and social needs with basic ecological functioning. These endeavours have included a handbook (Milton and Dean 1996); a national research programme on the restoration of degraded rangelands described by Kellner (1999); a national consensus mapping exercise on land degradation (Hoffman *et al*, 1999) and a comprehensive study on the socio-ecology and biophysical elements of communal rangelands described by Hoffman and Todd (1999a). These and other researchers have formed formal (and informal) networks through funding from bodies such as the National Research Foundation[23] that seek to integrate disciplines, skills and research capacity in order to debate and tackle issues of ecosystem functioning and land degradation. It is vital that these networks be expanded and maintained through national and provincial policy formulation and implementation.

While debates persist as to whether, how, in what manner and how extensively rangelands are degraded (Hoffman *et al*, 1999b; Turner and Ntshona, 1999) soils of semi-arid regions continue to be redistributed and arguably thoroughly degraded, by accelerated erosion and deposition.

The Departments of Agriculture and Land Affairs must be required to examine the need for integrated policy development that addresses national needs at the local level, integrating social requirements with biophysical and ecosystem functioning. Significant delays in the formulation of the National Action Plan (NAP) for the Convention to Combat Desertification (CCD) (Oettle, pers comm.) have been potentially disastrous for the environment and the national economy when one considers the probable overall annual rate of soil loss and the loss of soil quality.

[23] The National Research Foundation (NRF) sponsors a forum (the Arid Zone Ecology Forum) which brings together researchers from many disciplines on an annual basis.

Fuggle and Rabie (1983) estimated that in 1970, the agricultural land available per capita was 0.86ha. Owing to rapid human population increase this dwindled to 0.5ha per capita by 1980 and they estimated a decrease to 0.2 hectares per capita by 2020. Soil and vegetation degradation impact on agricultural sustainability but the costs are not only due to loss of productivity. Siltation of rivers and dams, as well as eutrophication of water, by silts high in leached nutrients are economically and ecologically expensive (Braune and Looser, 1989) since the national average soil loss was estimated by Schoeman and Scotney (1987) to be 2.5 tonnes/ha per annum.

Finally, while it may prove difficult to achieve economically viable results within a realistic time frame, opportunities exist for dynamic and novel solutions to an ongoing problem. Restoration programmes and agricultural policy development require a cogent focus on appropriate and alternative land use options. These alternatives must encourage and empower land managers to set aside sufficient natural rangeland areas to explore improved veld management. It is essential that managers and landowners be encouraged to understand the systems and pressures that influence their land. There must be a broad recognition of the delicate interplay between natural environmental systems and the natural resources that these systems sustain. The impacts of human-induced degradation should be brought under control on these tracts of land in order for long-term sustainability of the medium that supports their livelihood, namely soil.

3.5 References

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CHAPTER 4: PLANT PHENOLOGICAL RESPONSE TO ENVIRONMENTAL GRADIENTS ON AND AROUND TAFELBERG

4.1 Introduction to a preliminary investigation of plant phenology in the Tafelberg locality

Excessive loss of rangeland vegetation, through either frequent overgrazing or by regularly grazing veld during inappropriate seasons, reduces the ability of existing plants to reproduce themselves, thereby limiting the total available amount of soil- and canopy-stored seed for future generations (Acocks, 1988; Danckwerts and Stuart-Hill, 1988; Milton, 1994). Especially in the case of highly palatable species this may eventually lead to an overall population decline[1] and even to localised loss of desirable species from readily accessible grazing areas (e.g. O'Connor, 1991).

There is significant current debate as to whether natural environmental circumstances or anthropogenic causes best explain observed changes in vegetation composition (refer Chapter 5). There is also a great deal of research that has been conducted on the change in climatic conditions over time and the effect of climate change on vegetation composition. This research includes an examination of past climates (e.g. Werger, 1983; Avery, 1988; Meadows and Sugden, 1988; Sugden and Meadows, 1989), interpretation of present climates (e.g. Tyson, 1986; Zucchini *et al*, 1992), mooted projections of future climatic outcomes and cycles (e.g. Huntley, 1990; Tyson, 1993) and the possible influences that climate change may exert on both habitat and biological communities (e.g. Graham and Grimm, 1990; Ellery *et al*, 1991; Macdonald and Midgely, 1996) (refer Chapter 5).

Rainfall over most of southern Africa is highly seasonal and within the past century, a regular series of alternating wet and dry spells has been recorded that has varied systematically for at least the past eight decades (Tyson, 1986). Tyson (1986) notes that temperature undergoes a similar oscillation, but inverse to rainfall. Several studies on palaeoenvironments of the Karoo region have identified mesic cycles operating in periods of thousands of years (e.g. Lancaster, 1989). Deacon (1983) notes glacial and inter-glacial cycles operating in periods of millions of years. Deacon further (1983) comments that we are presently in an interglacial period (warmer and generally wetter than a glacial period). Meadows and Sugden (1988) show evidence of a decreasing effective moisture gradient in the eastern Karoo over the past 3500 years. Nash *et al* (1994) suggested that Kalahari climates during the Quaternary sub-era have fluctuated around a semi-arid mean or what Avery (1990) refers to as "low-amplitude environmental change" during the Holocene epoch. Thus regular annual seasonal cycles of temperature and

[1] Reduction in overall effective reproductive output and population size may result in an increased likelihood of localised extinction (Newman and Pilson, 1997).

rainfall are also influenced by cyclical periodicity operating at the meso- (i.e. decades and centuries) and also at the macro-climatic (i.e. millennia and aeons) scale. Several authors have noted vegetation changes at various scales concomitant with these climatic fluctuations (e.g. Werger, 1983; refer Chapter 5 for more detailed discussion of vegetation change).

The Nama Karoo Biome (*sensu* Rutherford and Westfall, 1994) has a rainfall range between 50-600 mm (Desmet and Cowling, 1999) and mean annual rainfall for most of the biome ranges from about 100 to 520mm (Rutherford and Westfall, 1994). Rainfall is unpredictable[2] and strongly seasonal. Duration and timing of precipitation may be variable, highly localised or patchy (Desmet and Cowling, 1999; Cowling and Hilton-Taylor, 1999) usually taking the form of dramatic but brief thundershower events (Desmet and Cowling, 1999; personal experience). Rain occurs mostly in the latter part of summer and in autumn (Hoffman and Cowling, 1987; Hoffman, 1996; Desmet and Cowling, 1999) with weak spring peaks in the Eastern Karoo (Hoffman and Cowling, 1987).

Uncertain timing and duration of rain events impact on the natural restoration of veld since rainfall (along with other factors) appears to play a significant role in stimulating bud initiation, flowering and thus seed set of at least some shrub species[3] (Hoffman, 1989; Milton, 1992a). Further, and possibly more importantly, seedling recruitment can only succeed during those years or months when sufficient periodic rainfall allows firstly germination and then establishment of young plants (Donaldson, 1989; Esler and Philips, 1994; Milton, 1994; Milton, 1995).

Interpretation of plant phenological response to quantifiable climatic and environmental conditions such as seasonality (of e.g. rainfall) and predation (e.g. grazing) can provide researchers and managers with tools that allow them to predict the timing, or delay, in onset of vegetative growth, budding, flowering and seeding of desirable, but dwindling, plant species (e.g. Milton and Hoffman, 1994; Wiegand *et al*, 1995; Kellner and Booysen, 1999). Even though rainfall events in the Nama Karoo are relatively unpredictable with respect to timing, quantity and patchiness (Hoffman & Cowling, 1987; Cowling and Hilton-Taylor, 1999), managers may be able to predict peak germination, growth- and flowering seasons using known rainfall patterns and cues as management tools for predicting plant phenological responses. With this knowledge, optimal grazing management and opportunistic restoration may be accomplished in an event-driven region (e.g. Walker *et al*, 1986; Westoby *et al*, 1989; Walker, 1993; Snyman, 1998).

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[2] There is an overall gradient ,from east to west and south to north, of increasing variability and decreasing quantity of rainfall. The Nama Karoo in general has a more variable rainfall relative to that of the Succulent Karoo. However, the Eastern Mixed Nama Karoo is influenced by a number of weather systems, owing to its relatively central position on the sub-continent, and experiences a relatively less variable rainfall than the rest of the Nama Karoo (Desmet and Cowling, 1999).

[3] Esler (1999) notes that cues for flowering are manifold and that in some instances, vegetative flush growth in response to increased available moisture may trigger flowering time and increased flower production (e.g. Milton, 1995).

This phenology study provided a comparison, over a period of one year, of plant responses to local environmental conditions of rainfall and grazing pressure. The primary focus was on flush vegetative growth (leafing), budding, flowering and seeding responses with an attempt to identify grazing pressures among a variety of different plant growth forms (refer Appendix 2.2; Table 2.1 and Figure 2.1 for data on field survey, site descriptions and site localities respectively).

The objective of this component study was to initiate an understanding of plant phenological response to environmental gradients of rainfall, and to a lesser extent grazing pressure, through analyses of quarterly data from 30m transects on the plains and top of Tafelberg (Chapter 2). As noted above and discussed in more detail in Chapter 5, excessive loss of vegetation adversely affects total reproductive output of plants, reducing potential seed bank density and diversity. With improved understanding of plant phenological response, it may be possible to identify and interpret some of the pressures on seed banks in the Tafelberg locality. The overall aim of this component study is thus to inform the interpretation of the seed bank study through providing guidelines that may enable restoration of degraded rangelands and allow sustainable management of rangelands currently considered to be in good condition.

4.1.1 Overview of rainfall gradients for the study area

Tafelberg is situated in the Eastern Mixed Nama Karoo (Hoffman, 1996), a summer rainfall region which receives average annual rainfall of between 300 and 500mm (Hoffman, 1996). Assessment of rainfall data from Station # 0120338 on the farm Tafelberg Hall for the period 1898 to 1999 (W. Asher, pers comm) showed that March experiences highest average monthly rainfall and the most reliable rainfall (relative to other months, refer Table 4.1) for this station.

Mean annual rainfall from 1898-1999 was 341mm ± 115mm and the coefficient of variation in rainfall for this period is 33.71. Between 1989-1999 mean annual rainfall was 355mm ± 123mm; with a coefficient of variation of 34.71. Over the past four years (Figure 4.1) rainfall patterns have been consistent with long-term trends with a mean annual rainfall of 358mm (± 75mm).

Seasonal rainfall for Tafelberg Hall is presented in Figure 4.1a and quarterly rainfall (related to the three month period prior to each transect assessment) is supplied in Figure 4.1b. Between May and September the Tafelberg area appears least likely to experience reliable rainfall nor any large amount (e.g. >25mm) of precipitation (Table 4.1, Appendix 4.1). From October to April, roughly 83% of mean annual rainfall is experienced. Highest average quarterly rainfall (relating to the period preceding each quarterly assessment) and the highest number of rainfall events occur between January to March (Figure 4.1b; Table 4.1).

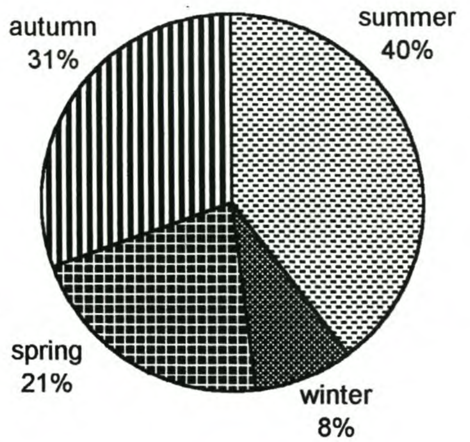

Figure 4.1a: Ratio of seasonal rainfall for the farm Tafelberg Hall. Data from 1898-1999 supplied by W. Asher
Autumn = Mar-May; Summer = Dec-Feb
Spring = Sep-Nov; Winter = Jun-Aug

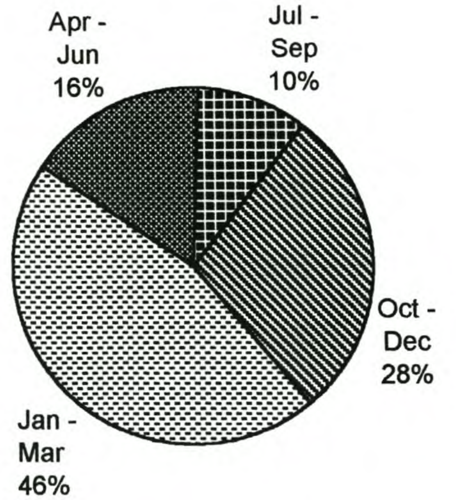

Figure 4.1b: Ratio of quarterly rainfall as related to plant phenological study. Data for Tafelberg Hall from 1898 to 1999 supplied by W. Asher

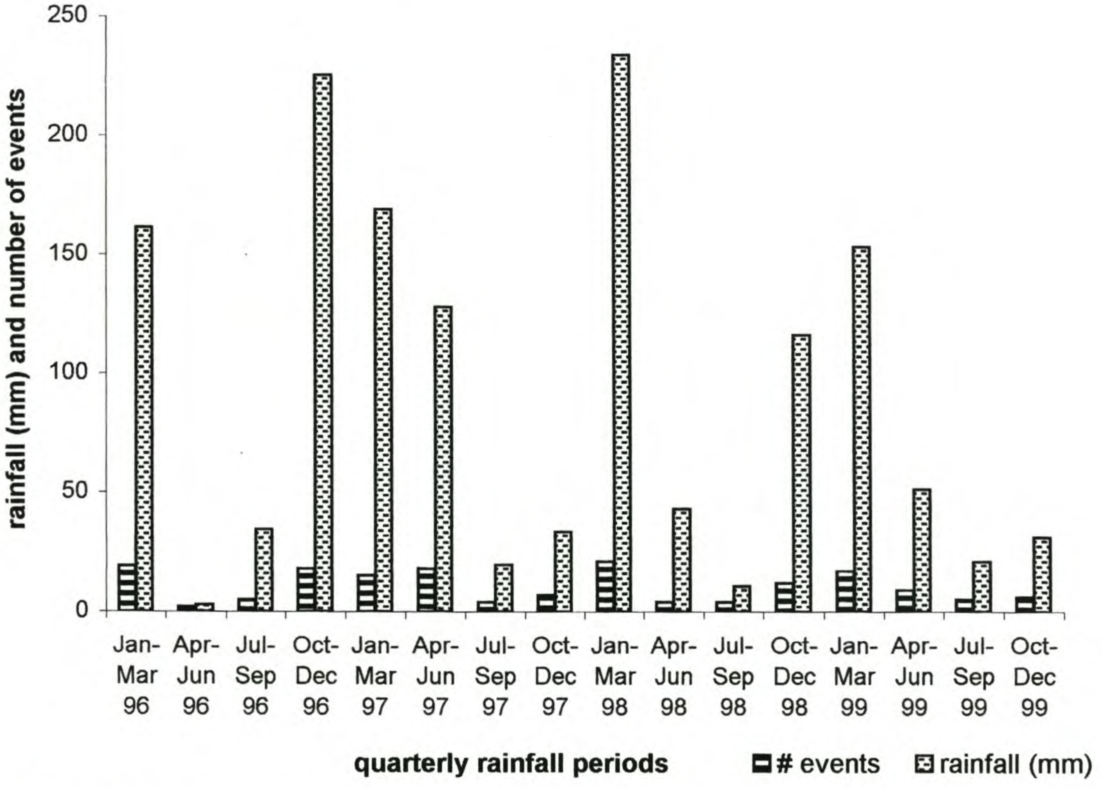

Figure 4.1c: Quarterly rainfall for Tafelberg Hall from 1996 - 1999. The number of events is calculated as the number of discrete rain events recorded irrespective of the number of days (or hours) of that event within the quarterly period given. Rainfall data supplied by W. Asher

Table 4.1: Summary of averaged monthly rainfall for Tafelberg Hall from 1898-1999. The number of rain events is calculated as the number of discrete rain events recorded in that month, irrespective of the number of days (or hours) of that event. Data are presented as means ± standard deviation for both monthly rainfall and rain events. Rainfall data supplied by W. Asher.

Month	mean monthly rainfall (mm)	average # of rain events per month	Coefficient of variation	# "no-rainfall" months from 1898 - 1999	# years with <15mm rainfall in that month	# years with >25mm rainfall in that month
January	46.2 ± 39	4.9 ± 2.8	84.4	6	19	62
February	51.1 ± 37.6	6.3 ± 3.6	73.7	3	21	69
March	59.5 ± 39.7	6.6 ± 3.0	66.6	1	12	79
April	29.0 ± 23.2	4.2 ± 2.6	79.8	6	35	50
May	16.6 ± 18.7	2.5 ± 2.2	112.4	20	63	30
June	8.9 ± 10.9	1.6 ± 1.4	122.6	25	75	9
July	9.0 ± 13.6	1.4 ± 1.6	151.3	34	85	10
August	10.7 ± 17.8	1.7 ± 1.7	165.8	29	75	13
September	14.5 ± 18.2	1.97 ± 1.89	125.5	29	67	25
October	24.8 ± 23.1	3.2 ± 2.4	93.1	8	40	40
November	34.2 ± 31.4	4.1 ± 2.8	91.9	9	36	53
December	39.2 ± 37.7	4.4 ± 3.3	96.2	11	35	53

4.2 Plant phenological response in the Tafelberg study area

Changes in plant growth, flowering and seeding were noted over the one-year study. Flushes of vegetative growth, budding and flowering periods were evident, apparently as a consequence of rainfall during the preceding several months (Figure 4.2), on the plains and top of Tafelberg, despite firstly observable differences in above-ground vegetation composition and secondly different environmental pressures acting on these two broad habitats[4]. For example, total precipitation on top of Tafelberg exceeds that on the plains since the mesa receives regular mists that do not deliver moisture to the plains (personal observation; W. Asher, pers comm). Further, grazing pressures on top of Tafelberg are lower than on the plains and the differential grazing pressures may play a role in determining plant species composition on the top and plains.

Despite dissimilarities in species composition and total canopy cover, the two major growth forms on both the top and plains are small shrubs[5] (5 to 50 cm) and grasses. These comprise an

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[4] Vegetation on top of Tafelberg is dominated by perennial, or persistent (refer Table 5.1), grasses and shrubs while the plains have a relatively low abundance of persistent grass and shrub species (personal observation; refer also 5.3.1.6).

[5] This category does not include succulent shrubs for this component study.

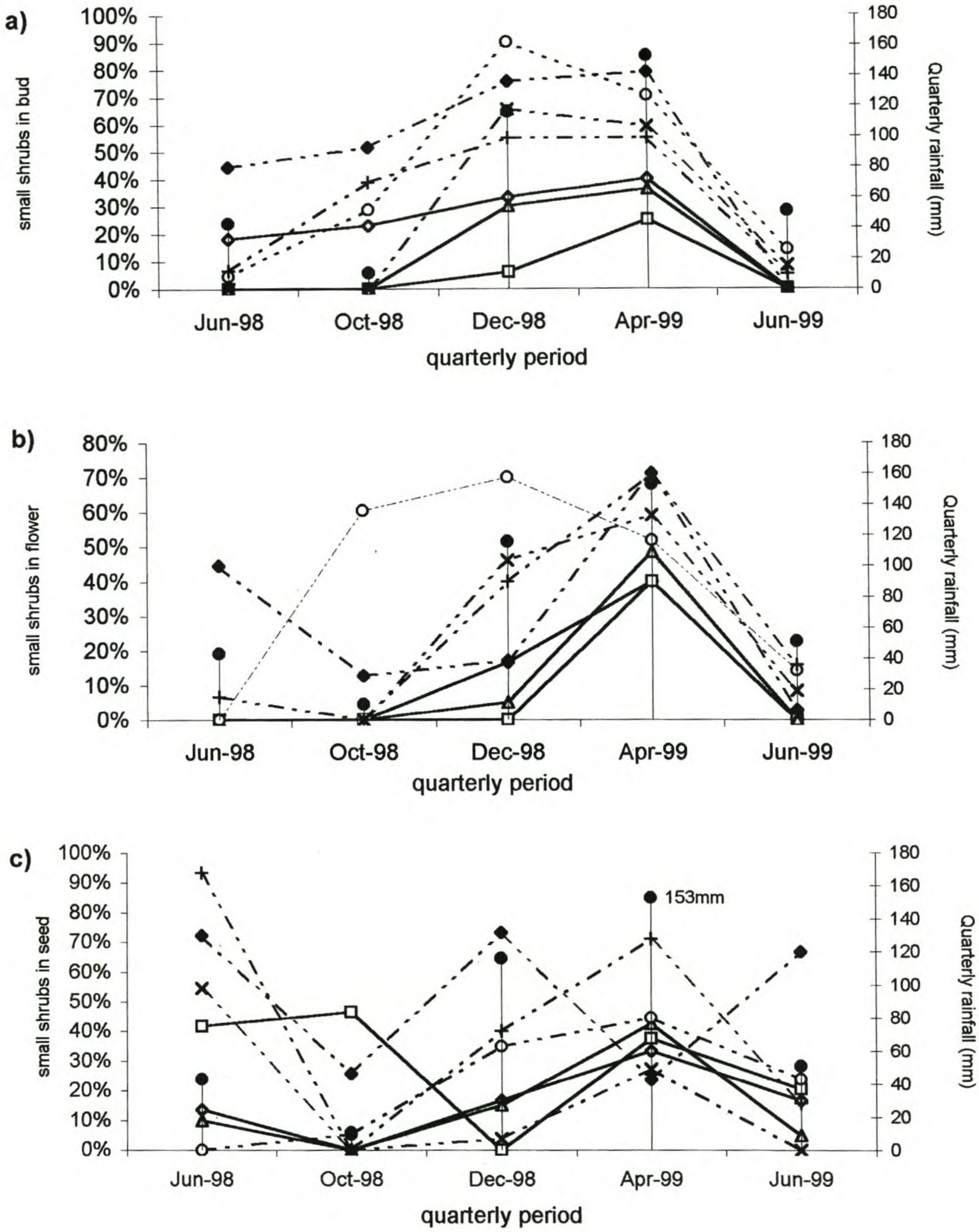

Figure 4.2: Percentage of small shrubs in a) bud, b) flower and c) seed on top (solid lines) and plains (stippled lines) of Tafelberg. Percentage budding, flowering and seeding is the proportion of the total number of small shrubs counted on each 30m transect at quarterly intervals in bud, flower or seed between June 1998 and June 1999. Refer Table 2.1 and Figure 2.1 for detail on site codes and localities. NW, SW, NE and SE are the four compass half points; F = sites on plains; T = top sites. Rainfall figures are for a preceding three month period.

KEY:

—◇— TNW —□— TSE —△— TSO
– ✕ – FNW – ◆ – FNE – ○ – FSW
– + – FSE ● Total rainfall for preceding 3 month period

average of 40% ± 16% and 37% ± 18% respectively of all plants found on the seven transects assessed. The phenology study focused primarily on small shrubs to examine major trends, owing firstly to the complexity of identifying and separating grass species into numbers of plants (due to relatively high levels of clumping) and secondly to high levels of grazing on the plains[6].

4.2.1 Description of vegetation on the plains

Each of the four plains' transects assessed differ from each other with respect to canopy cover, plant species diversity and composition (Figure 4.3) indicative of "patchiness" and habitat diversity on the plains. Nonetheless, dominant growth forms on the plains (Figure 4.3:a-d) are similar overall[7], being composed of a variety of less palatable or low production shrubby species that include spinescent plants[8], ephemeral herbs[9], toxic plants[10], other common but relatively unpalatable species such as *Pentzia incana*, the dominant karoo bush for the region, as well as annual grass species (predominantly *Aristida* spp.) and a variety of succulent shrubs[11] (refer Chapter 5 for further details on above-ground vegetation in the study locale).

Canopy height on the plains is roughly 30 - 50cm and plant canopy cover is highly variable alternating from relatively unvegetated areas (particularly on the north- and south-west plains) with less than 1 plant per $10m^2$, to other areas which are covered relatively densely but with primarily unpalatable or low-production species (e.g. *Aristida* "lawns"). Occasional emergent shrubs include *Rhus* and *Lycium* spp..

4.2.2 Description of vegetation on the top of Tafelberg

Vegetation on top of Tafelberg (Figure 4.3:e-g) is characterised by grassy *Themeda* and *Ehrharta* shrublands[12] with a diversity of palatable, high-production, perennial grass and shrub species interspersed with bush clumps[13]. The highly palatable species *Limeum africanum*, *Felicia muricata*, *Eriocephalus africanus*, *Osteospermum* spp. and *Walafrida geniculata* (an indicator of good veld condition (Le Roux *et al*, 1994)) are common on top of Tafelberg.

Canopy cover is generally much more dense on top of Tafelberg than on the plains although emergent rock is common. In some seed bank plots (refer Figure 2.1) on the north west, rock

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6 In many instances, as a direct result of grazing, there were generally very few grass plants or clumps with identifiable flowers or seed heads as these had been eaten by stock.

7 The north west plains site (FNW4) was in many respects an anomaly resembling more a clay tennis court than any of the other sites. In general, growth forms on the plains were similar.

8 Including *Zygophyllum incrustatum*, *Lycium* spp. and *Barleria rigida*.

9 Including *Hypertelis salsoloides* and *Ifloga glomerata*.

10 Including *Geigeria ornativa*, *Gnidia polycephala* and the karoo pioneer *Chrysocoma ciliata*.

11 These include *Drosanthemum duplessiae* and the spiny *Eberlanzia ferox*.

12 Substantial tracts of *Themeda triandra*, *Digitaria eriantha*, *Ehrharta calycina* and other palatable grasses are common on top of Tafelberg.

13 *Diospyros* spp., *Rhus* spp., *Buddleja glomerata* and *Tarchonanthus camphoratus* are predominant bush clump plant species.

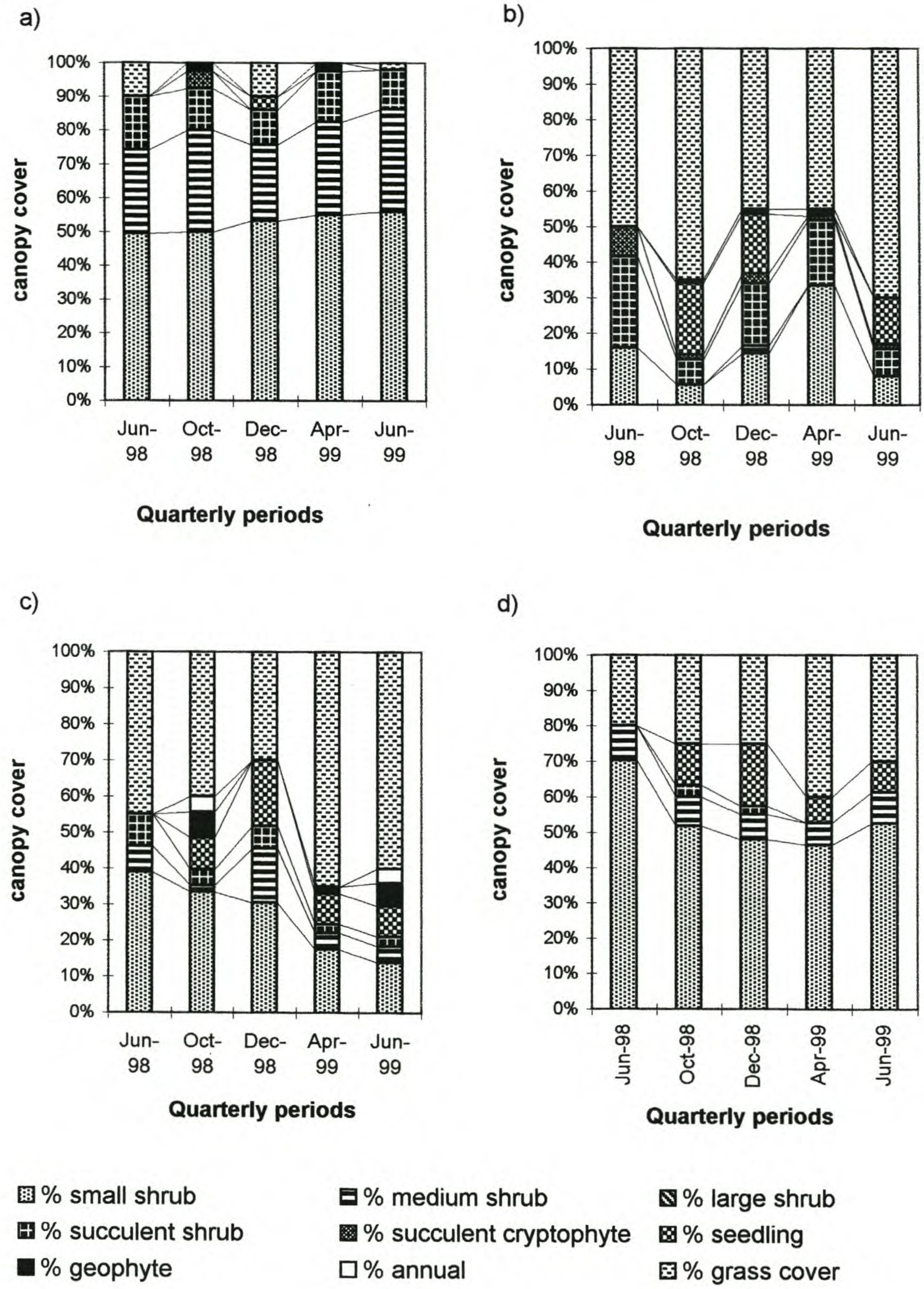

Figure 4.3: Proportional composition of canopy cover on 7 transects assessed on the plains (a = FNW4; b = FSE4; c = FSW4; d = FNE4) and top (e = TNW; f = TSE; g = TSO) of Tafelberg (See Figure 2.1 and Table 2.1 for site codes and site localities). Proportions presented as the relative percentage of total canopy cover of each category along the transect.

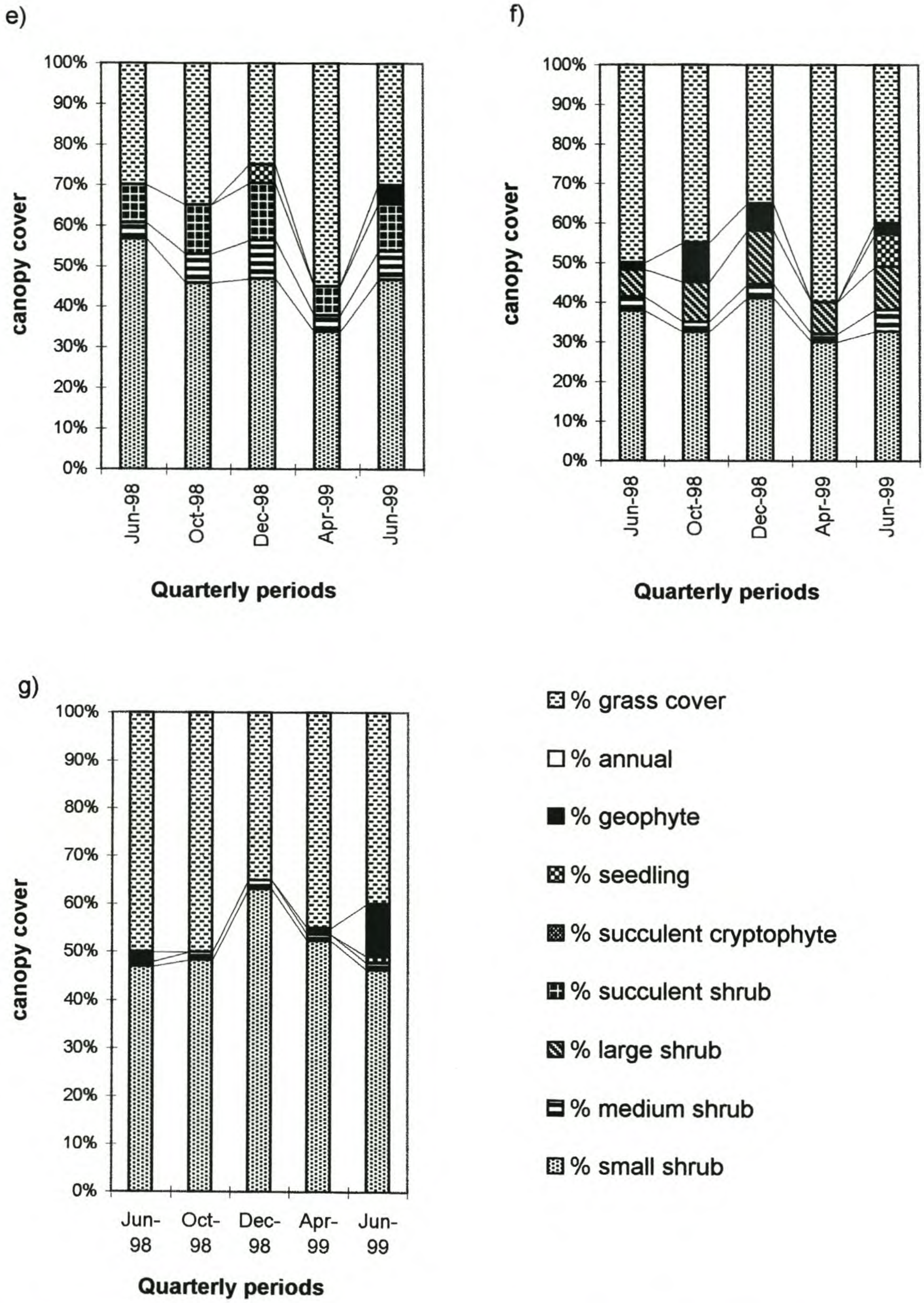

Figure 4.3: (continued) Proportional composition of canopy cover on 7 transects assessed on the plains (a = FNW4; b = FSE4; c = FSW4; d = FNE4) and top (e = TNW; f = TSE; g = TSO) of Tafelberg (See Figure 2.1 and Table 2.1 for site codes and localities). Proportions presented as the relative percentage of total canopy cover of each category along the transect.

occupied as much as 55% of a single 25m^2 plot. Wind-shear is high near this top north west transect and appears to reduce flowering and fruiting on this part of the Tafelberg plateau. Many grasses and small shrubs appeared to be "wind-pruned" forming a relative lawn in places. It is probable that some of the data for this transect, attributed to grazing pressure, was caused by wind-shear although *Pelea capreolus* (Grey Rhebok) and *Pronolagus rupestris* (Smith's Red Rock-Rabbit) were regularly noted on this part of Tafelberg (personal observation).

While all three transects on top of Tafelberg differ from each other in plant species composition, diversity and canopy cover (Figure 4.3:e-g), all contain a relatively similar mixture of palatable shrub and grass species with very few annual grasses or shrubs noted. Species composition of all three top transects is very different from that on the plains.

4.2.3 Spatial and seasonal comparisons between the top and plains of Tafelberg

Esler (1999) noted that flowering in the Nama Karoo is generally staggered, with mass flowering being an unusual event taking place primarily during high rainfall years. This view concurs with Hoffman (1989) who noted opportunistic plant response to rainfall events and apparently pulse-activity responses (Noy-Meir, 1973) to rainfall events[14] in Karoo shrubland. Species-specific timing of flowering, seed-set and seed dispersal (e.g. Hoffman, 1989; Johnson, 1992; Esler, 1999) is likely to play a role in staggered phenological response. Genetic heterogeneity further ensures that individuals of a given species will flower earlier, and others later, than the average peak flowering season (or the opportunistic response) of that species.

The patchy nature of resources (e.g. Dean and Milton, 1999; Palmer *et al*, 1999) and rainfall (e.g. Noy-Meir, 1973; Desmet and Cowling, 1999) in semi-arid areas are likely to contribute to variable flush growth and to patchy (or localised) budding, flowering and seeding in these semi-arid areas. The following paragraphs describe the assessment of plant phenological response on the top and plains of Tafelberg.

4.2.3.1 Plant phenology of four transects on the plains over a one year period

Small shrubs on the plains responded to early spring rainfall and probably to increasing temperatures[15] with an onset of flush vegetative growth ("leafing") starting between June

[14] Soil moisture appeared to be strongly correlated with flush growth (Hoffman, 1989).

[15] Midgely and Van der Heyden (1999) note that water availability and temperature are two main selective pressures (along with nutrient availability and herbivory) moulding both form and function of Karoo plants. No accurate temperature data for Tafelberg currently exists and no correlations between temperature and moisture can be given for this site. Differential temperature gradients between the top and plains are noticeable with a conspicuous decrease in temperature as altitude increases (personal experience). This is probably enhanced by higher relative ambient moisture on top of Tafelberg from frequent mists and dews. The relatively tardy flush growth response on top (Figures 4.4; and 4.2.4) when compared with the plains is possibly related to the temperature differential.

and October 1998 (Figure 4.4) which appeared to continue until at least April 1999. Flower buds were found during all seasons on the two transects (NE and SE) on the easterly plains (Figures 4.2 and 4.4), but for all plains' transects budding peaks were noted between December and April. This was followed by a peak in flowering between December and April and a consequent seeding cycle that began before April 1999 and continued into June although limited seeding continued throughout the assessment period (Figures 4.2 and 4.4).

Transects on the north- and south east plains were situated in camps that were not as heavily grazed as those containing the north- and south west transects (Figure 4.5a). Sheep were removed from the south east camp during April 1999 and replaced with a small herd of Nguni cattle (*circa* 30 head) by the owner, R. Gilfillan, in an attempt to reduce grazing pressure on this camp. The north- and south west transects were in camps that were regularly grazed and the south west camp appeared to contain sheep during every quarter under assessment[16] (personal observation).

Even though winters in the study area are cold, with regular frosts and low rainfall, winter dormancy or deciduousness appeared to be the exception rather than the rule with nearly 100% of all species retaining all or most of their leaves during both June 1998 and June 1999. The primary exceptions were the two transects in those camps (on the north- and south west plains) with highest observed grazing pressures (Figure 4.5a). Roughly 64% of small shrubs and 80% of succulent shrubs[17] were fully deciduous during the June 1998 assessment of the south west transect. The north west transect showed 50% of small shrubs to be semi-deciduous with no loss of leaves in any other plant form category. No other transect on the plains exhibited more than 7% deciduousness during the same two assessments.

Drought and over-grazing appear to affect vegetation in various comparable ways (e.g. Novellie and Bezuidenhout, 1994; Milton and Hoffman, 1994; O'Connor and Roux, 1995). It is speculated, but not confirmed by this study, that deciduousness of plants (found along heavily grazed transects in the north- and south west camps) may be a phenological response, contributed to by grazing pressure and selected for by long term, high intensity grazing pressure over a period of two centuries (refer Chapter 7, 7.3(e)).

Average percentage grass cover varied from quarter to quarter (Figure 4.5b) rising to a peak in April 1999 for all transects except the south east plains[18] and the north west plains where grass cover was zero during the April assessment. It is likely that grass cover increased in

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[16] To date of writing no figures have been obtained for stocking rates of these camps. This data will be needed for future work on the seed bank study. (Refer 5.2, below)

[17] This did not include *Eberlanzia ferox*. During site visits no deciduousness in this species was observed.

[18] Grass cover continued to increase on these plains presumably owing to reduced grazing pressures.

Rainfall for previous 3 month period	43mm	10.5mm	116mm	153mm	51mm
Response | **Date assessed >**	***Jun-98***	***Oct-98***	***Dec-98***	***Apr-99***	***Jun-99***
a) flush growth (leafing)					
Top north west		38%	100%	100%	
Top south east			100%	100%	
Top south central			100%	100%	
north west plains		100%	100%	100%	
north east plains		100%	100%	100%	
south west plains		100%	100%	100%	
south east plains		100%	100%	100%	
b) budding					
Top north west	18%	23%	33%	40%	
Top south east			6%	25%	
Top south central			30%	36%	
north west plains			65%	59%	8%
north east plains	44%	52%	76%	79%	
south west plains			25%	75%	
south east plains	7%	39%	55%	55%	5%
c) flowering					
Top north west			17%	40%	
Top south east				40%	
Top south central			5%	48%	
north west plains			47%	59%	8%
north east plains	44%	0.13	17%	71%	3%
south west plains			25%	75%	
south east plains	7%		40%	71%	16%
d) seeding					
Top north west	14%		17%	34%	17%
Top south east	41%	47%		38%	21%
Top south central	10%		15%	42%	5%
north west plains	55%		4%	27%	
north east plains	73%	26%	73%	24%	67%
south west plains	100%	80%	25%	75%	50%
south east plains	93%		40%	71%	16%

Figure 4.4: Phenological response of small shrubs on the top and plains of Tafelberg. Given as a percentage of the total number of small shrubs counted along a 30m transect in a) flush growth; b) bud; c) flower and d) seed. Shading indicates that more than 50% of small shrubs on transect exhibited the specified response. See Figure 2.1 and Table 2.1 for detail on site localities.

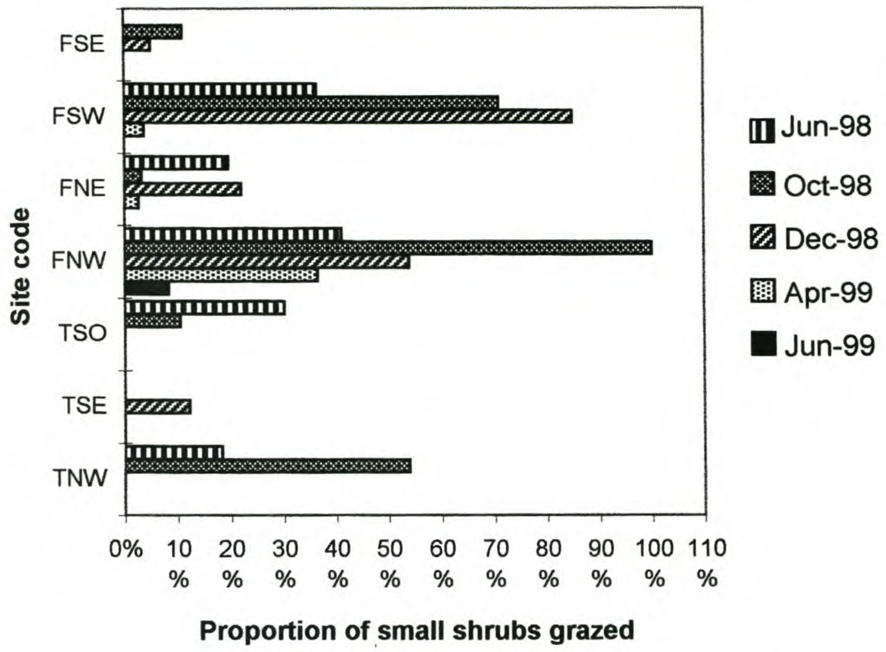

Figure 4.5a: Estimated grazing pressure on small shrubs. Given as the proportion of total number of small shrubs counted along a 30m transect, that showed evidence of having been grazed. No weighting was given for either the extent or the severity of grazing. Refer Table 2.1 and Figure 2.1 for detail on site codes and localities. F = plains; T = top of Tafelberg.

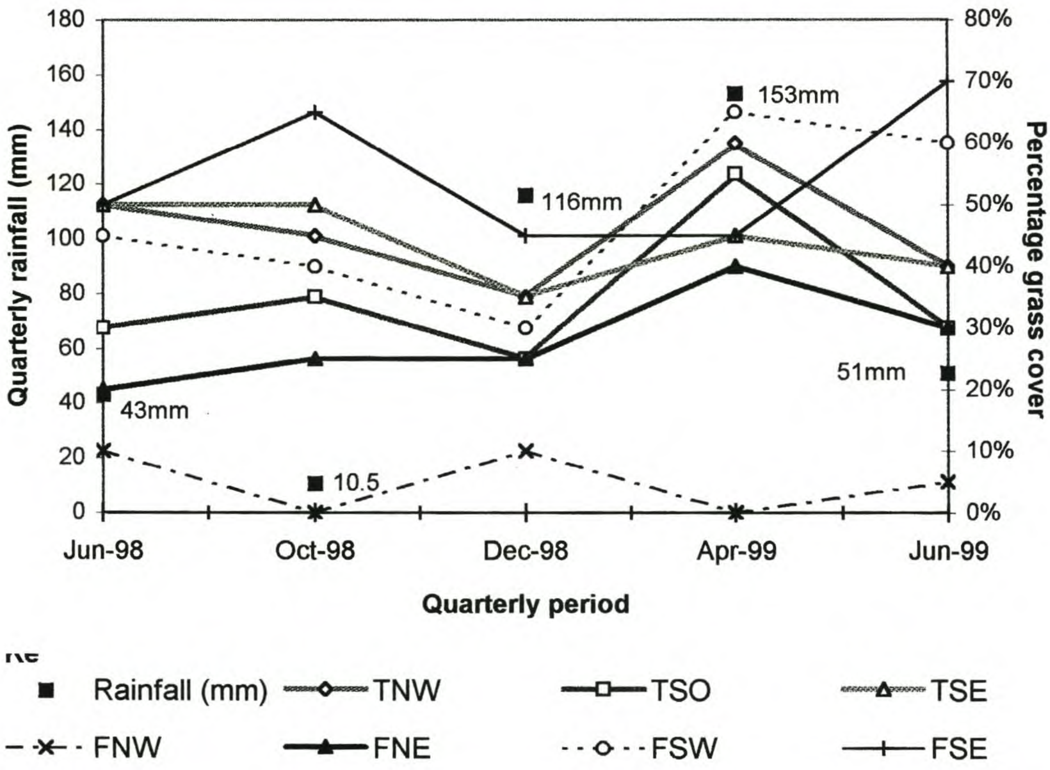

Figure 4.5b: Percentage grass cover along seven 30m transects on top (T) and plains (F) of Tafelberg. Grass cover estimated as a percentage of total canopy cover. Rainfall figures given are for the previous quarter. (e.g. 116 mm fell between Oct - Dec 1998) (W. Asher pers comm).

response to mid- and late summer rainfall (e.g. O'Connor and Roux, 1995) and favourable temperatures (e.g. Midgely and Van der Heyden, 1999).

A higher number of seedlings were counted during the October and December 1998 assessments than for any other quarter. During October and December, an average of 10% ± 8.27% and 14% ± 6.7% respectively of the total number of plants counted along all four plains' transects were seedlings. Seedlings were found mostly on the plains where, owing to lower overall canopy cover (relative to the top of Tafelberg), a higher number (relative to the top of Tafelberg) of vacant, available sites and "safe" sites (e.g. Fowler, 1988; Wiegand *et al*, 1995) for germination may be found. This pattern was consistent with findings in the germination trial study (Chapter 5) where high numbers of ephemeral species germinated from plains' samples.

Seeding peaks on the plains occurred during June and December with some seeding in April (Figures 4.2 and 4.4). These peaks are not completely clear from this short duration preliminary assessment, varying between transects and from species to species (4.3, below).

4.2.3.2 Phenology of three transects on top of Tafelberg over a one year period

Overall, plant phenological response on top of Tafelberg appeared similar for all three transects assessed despite variation in plant form and species composition between them (Figure 4.3b). Average grazing pressure is lower on top relative to the plains (Figure 4.5a; and 1.5.4, above) and average grass cover is roughly 42% (±10%) on top of Tafelberg, comprising predominantly persistent grass species.

The budding peak for small shrubs on top of Tafelberg appeared to be between December and April with flowering peaking around April[19] (Figures 4.2 and 4.4). This is speculated to be influenced by lower temperatures (relative to the plains) experienced on top of Tafelberg[20].

Between 10% and 26% of small shrubs in two transects (top south central and top south east respectively) on top of Tafelberg were semi-deciduous during June 1999. Deciduousness on top appeared to be low relative to the plains. Environmental conditions on the top are generally milder, or more temperate, owing to higher ambient moisture from dews and mists and lower summer temperatures than on the plains (personal observation). Further, scattered bush-clumps provide a milder micro-climate than the sparsely vegetated and wind-swept plains and this may ameliorate both summer and winter temperature extremes particularly at, or near, ground level.

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19 Both the budding and flowering peaks on top of Tafelberg lag slightly behind those of the plains.

20 This moot point could be clarified through assessment of phenological response on transects along an altitudinal gradient up the slopes of Tafelberg, not undertaken during this preliminary investigation.

Seeding of small shrubs on the top appears to peak around April, however, as with the plains there appears to be more than one peak, especially on the top south central transect, where peak seeding occurred during October 1998. Few seedlings (<5% of the total number of plants counted along the transect) were noted on top of Tafelberg during the year of assessment presumably owing to dense canopy-cover (relative to the plains, limited interplant spaces and low levels of disturbance through grazing.

4.3 Discussion

Despite the patchy nature of rainfall, resources and habitat in the locality of Tafelberg (personal observation) and the apparently close-to-average mean annual rainfall during the year of assessment, there emerged some strong peaks in flush growth and reproductive response for plants both on top and on the plains of Tafelberg. While both plant growth-form and species composition differ significantly between the top versus the plains, primary differences in plant phenological response between the two broad habitats appeared to be firstly a delay in the onset of flush growth in plants on the top of Tafelberg relative to those on the plains (Figure 4.4)[21]. Secondly there appeared to be higher, more intense, peaks of budding, flowering and seeding among plants on the plains relative to those on top of Tafelberg (Figures 4.2 and 4.4).

Vegetation on the plains is mainly of low palatability relative to the top of Tafelberg, typically dominated by ephemeral and spinescent plant species and characterised by relatively large interplant spacing. Even though significant differences exist in dominant growth forms, species composition and canopy densities between the top and plains of Tafelberg, there nonetheless appears to be a remarkable level of synchronicity in response to seasonal influences which are presumably an interplay between temperatures and rainfall.

Differences in peak seeding times for both the top and the plains appear to be slightly more haphazard than the differences for flush growth, budding and flowering but fairly clear peaks in seeding across the top and plains appear especially during April 1999 (Figure 4.2). This aspect of the phenology study in particular requires longer term data collection (i.e. over a period of several years) to identify conspicuous seasonal trends for seeding and seed dispersal. Inter-specific variability with regard to factors that include differential timing and duration of seed set (e.g. O'Connor and Pickett, 1992); varying dispersal strategies (e.g. O'Connor, 1991; Esler, 1993; Van Rooyen, 1999) diverse seed and capsule types (e.g. Van Rooyen, 1999) and potential differences between the growth seasons of arid zone C_3 and C_4 plants (e.g. Kemp, 1983) may need to be assessed on a species-by-species basis for those species deemed to be important contributors to the stability and economic value of rangelands.

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[21] Presumably this lag time is due to cooler temperatures on the top relative to the plains.

Grazing can play a role in determining phenological response of plant communities by defining or shaping vegetation characteristics, especially in heavily utilised areas. Increased grazing pressure can result in an increase in ephemeral plant species (Hoffman and Cowling, 1990). Annual species have a large seed bank that is constantly and abundantly replenished (Van Rooyen, 1999). Depending upon a variety of factors including dormancy regimes, a proportion of these seeds germinate readily in response to environmental factors that include disturbance; increasing moisture gradients in both soil and atmosphere as well as changes in temperature. The general strategy of ephemeral plants is to grow as fast as possible, flower as profusely as possible and to set large amounts of seed as soon as possible within the constraints of a harsh environment. Thus ephemeral plants, which are ideally suited to the rigours of a semi-arid or arid environment may flower and set seed more abundantly (Van Rooyen, 1999) than their longer-lived neighbours (Esler, 1993).

Plant species that are unpalatable owing to spinescence or toxicity or that are able to tolerate heavy grazing (5.1.2.3, below), become more abundant at the expense of palatable species over time (O'Connor, 1991). On the relatively[22] heavily grazed plains surrounding Tafelberg, ephemeral and spinescent plant species are abundant and there is a paucity of palatable species. Those plants that can ensure their input into future generations through either increased flowering and seed set, or through defence mechanisms or traits are bound to be selected for by high grazing and other environmental pressures. While it is not possible to substantiate this with data from the preliminary phenological investigation, it is speculated that a complex interplay of environmental factors increase the inherited flowering response of plant species under a high selection pressure over time. The capacity of plants to survive and thrive on the plains under a complex interplay of event-driven natural environmental pressures and some extreme external pressures from grazing and human-induced droughts (e.g. Snyman and Oosthuizen, 1999) must provide a strong selection force on evolution of increased reproductive output.

At most times of the year there is some activity with respect to reproductive output or seed production by small shrubs (Figure 4.2; Figure 4.4). Low-intensity grazing may improve this through firstly stimulation of vegetative growth (e.g. McNaughton, 1983) and secondly through improved seed dispersal by for example ingestion and deposition in faeces (Milton *et al*, 1990; Milton, 1992b). By way of example, even though the top of Tafelberg (an area of roughly 40ha) hosts a permanent herd of at least twenty Rhebuck as well as a number of Steenbuck, Red Rock Rabbits and Duiker and is regularly visited by Kudu and Chacma baboons (personal observation) the vegetation on the top of Tafelberg is composed of a multitude of highly palatable shrub and grass species present in significant quantities.

[22] The plains are grazed far more intensively than the top (and upper slopes) of Tafelberg.

On the other hand, high intensity or long duration grazing may continually reduce desirable plant species through continued loss of vegetative material and thereby lowered survival and production potential or through continued loss of flowers, fruits and seed prior to successful seed-set and dispersal. The plains around Tafelberg have been more or less continuously grazed for at least the past century. For the purposes of this debate an occasional six week, or even twelve month, rest period would arguably play a relatively insignificant role in the much longer time period spanning the decades and centuries of effectively continuously grazing veld. Acocks (1988) provides anecdotal evidence of the conversion of the Colesburg District (Eastern Cape) from sweet grassveld into "the sea of *Aristida* and *Eragrostis* which appears after a good rainy season today".

Each phase of a plant's response to the environment, whether this be dormancy or vegetative flush growth, budding or seeding, plays a significant role in determining the next generation of plant recruits, through affecting the actual and potential seed available for future generations in both the canopy and the soils of a natural pasture. It does not take much effort to calculate the effect of losing even one percent of a following year's potential reproductive output over the long term. After a period of 100 years at the seemingly minuscule rate of loss of 1% of potential reproductive output per year, whether through loss of leaf, bud, flower, seed or a combination of these, one is left with roughly 37% of the initial total population. This does not take into account those years when rainfall is low and seedling recruitment, plant survival and reproductive output are all severely challenged nor does this take into account the increased pressure on preferentially grazed species which may be continually selected for by hungry grazers.

The continual (albeit gradual) loss of reproductive potential and loss of desirable, selected-for plant species from plant communities (through an array of inappropriate management strategies) will inevitably lead to the decline of seed of these species from canopy- and soil-stored seed banks. These seed banks (examined in detail in Chapter 5) determine the future vegetation composition and thus the economic and ecological value of rangelands for future generations. Wiegand and Milton (1996) are dubious as to whether restoration of severely degraded rangelands will be possible, or economically viable within a human lifetime. It appears that soil-stored seed banks are already in crisis on the plains (Chapter 5) and given the above-ground vegetation composition, dominated by spinescent and less palatable plant species, canopy-stored seed banks may not be depended upon to quickly restore the degraded plains.

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CHAPTER 5: ANALYSIS OF RESTORATION POTENTIAL OF SOIL-STORED SEED BANKS IN THE TAFELBERG VICINITY

5.1 Introduction

5.1.1 A brief review of seed bank theory and research

Soil-stored seed banks represent the capacity of plants to regenerate and reproduce. Bigwood and Inouye (1988) noted that seed banks may be defined as "the collection of viable, dormant seeds in the soil of a defined area". Leck *et al* (1989) advanced this definition, reasoning that a seed bank is made up of seeds and fruits in, or even on top of, the soil. For the purposes of this thesis, this definition will be extended further to include propagules such as bulbs, corms and other organs of vegetative reproduction similar to that described by Harper (1977) as a "bud bank".

Seed banks have long been investigated by researchers and Darwin[1] is noted by Bigwood and Inouye (1988) as the likely first proponent of seed bank theory. Seed banks have since been investigated in almost all habitats, from deserts (e.g. Westoby *et al*, 1982; Abramsky, 1983; Reichman, 1984) to forests (e.g. Brown and Oosterhuis, 1981) and from wetlands (e.g. van der Valk and Davis, 1978) and mediterranean climates (e.g. Pierce, 1987; Ne'eman and Izhaki, 1996) to grasslands (e.g. Rice, 1985).

While much data have been assimilated from all over the planet, for diverse habitats and systems, there remain gaps in information on seed banks. These gaps are owed in part to the nature of the medium in which they are stored[2] as well as to other factors such as diverse seed sizes and shapes (e.g. Thompson *et al*, 1993; Ter Heerdt *et al*, 1996) as well as dormancy regimes and mechanisms (e.g. Thompson and Grime, 1979; Freas and Kemp, 1983). Not surprisingly gaps in information, regarding for example reproduction biology and community dynamics of individual species (Van Rooyen, 1999), and an as yet incomplete understanding of systems and processes guiding habitats in which they grow (Whitford, 1999), further confound complete understanding of seed bank ecology.

Seed banks and seed bank ecology in southern African arid and semi-arid areas have been studied by a number of researchers (e.g. Van Rooyen and Grobbelaar, 1982; Dean *et al*, 1991; Esler, 1993; De Villiers *et al*, 1994a; Günster, 1994; Milton, 1995a). According to Esler (1999) only three in-depth seed bank studies have been conducted in the Karoo region. Van Rooyen and Grobbelaar (1982) investigated seed populations in the Namaqualand Broken Veld (*sensu*

[1] Darwin (1859) described seeds in mud on a lake bed in "The Origin of the Species".

[2] For example, soil particles are often larger than some seeds, bound together in structural arrangements that contain seed and it is challenging to determine spatial distribution of seeds with exact precision. One cannot examine the total seed bank of an area without either disturbing or removing the soil medium in some manner.

Acocks, 1953; vegetation type 33) and De Villiers (1993) studied Namaqualand pioneer plants[3]. Esler (1993) investigated seed banks in the Succulent Karoo Biome (*sensu* Rutherford and Westfall, 1986), concentrating primarily on Mesembryanthema and other perennial species that are dominant vegetation components of that region. Other studies have focused on plant community-, or individual species', responses to environmental cues such as rainfall (e.g. Milton, 1992), drought (e.g. Milton *et al*, 1995), grazing (e.g. O'Connor and Pickett, 1992) and seed production (e.g. Milton and Dean, 1990; Milton, 1995b) and the influence these various factors have on, for example, seed bank composition and/or distribution as well as on vegetation change.

5.1.2 Vegetation change: its relevance to seed bank research and interpretation

Scheepers and Kellner (1995: cited in Snyman, 1998) estimated that roughly two thirds of South African rangelands are in a moderate to serious stage of degradation and evidence for accelerated vegetation change in the Karoo, over the past several hundred years, does appear to be convincing. Debate continues nonetheless as to whether human induced changes, through inappropriate management practice, or natural fluctuations in climate and climate change at local, regional or global scales are the main influencing factors on the apparent change in vegetation composition.

Many studies (e.g. Avery, 1988; Palmer *et al*, 1990; Bousman and Scott, 1994) have documented, hypothesized and debated apparent changes in Karoo vegetation in response to pressures and processes including climate change (e.g. Meadows and Sugden, 1988; Avery, 1990; Avery, 1991) and rangeland utilisation (e.g. Shaw, 1875 (cited in: Vernon, 1999); Acocks, 1953; Roux and Theron, 1987; Hoffman and Cowling, 1990; Dean and Macdonald, 1994; O'Connor and Roux, 1995).

5.1.2.1 Palaeontological evidence for vegetation change

Meadows and Sugden (1988) recorded evidence for a significantly wetter environment in the vicinity of Compassberg[4] around 3590 years before present (BP) and stated their impression of a steadily decreasing effective moisture gradient in the area since that period. Interestingly, the activities of both Khoi herders and Trekboer farmers appeared to disturb vegetation sufficiently[5] to be identifiable in these palaeoecological studies (Meadows and Sugden, 1988). Scott (1990) observed a reduction in the grassy component (from analysis of polleniferous sediment) around 300 years BP in upland Karoo areas and related an increase in the shrubby component, within the past 150 years, to modern stock farming practises.

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[3] Both of these studies focused primarily on annual species, dominant in this region.

[4] Compassberg, the highest peak in the Sneeuberg range (2502m), lies 60 kilometres wsw of Tafelberg (1653m).

[5] These authors note however, that in neither the case of the Khoi herders nor in the case of the Trekboers were geomorphological or hydrological thresholds exceeded.

Bousman and Scott (1994) studied pollen samples from hyrax dung middens at the Blydefontein Basin and concluded that while overstocking with domestic stock may have influenced, or contributed to, a change in overall species composition, the shift between grasslands and shrub vegetation is climatically (more specifically rainfall) related and could not have been initiated by livestock. Further, various studies on climate change in the Quaternary sub-era have recorded large scale temporal and spatial shifts in vegetational components (of biogeographical regions) owing to regional- and global-scale shifts in climate (e.g. van Zinderen Bakker, 1983; Hilton-Taylor, 1987; Scott, 1995). These can be so significant as to shift the boundary of the Nama-Karoo Biome, for example, to the south of the Swartberg Mountains (Avery, 1982).

It is likely that these historical changes in the above-ground vegetation will have been associated with concomitant fluctuations in the density and location of the seed bank composition although the extent of this cannot be, or has not been, determined.

5.1.2.2 Challenging orthodoxy: searching for patterns of vegetation change in semi-arid systems.

Roux (1966) placed grazing in the context of seasonal rainfall, noting the effects of both natural climatic and land use regimes. A widely held international perception of desertification being the singular result of land use management was challenged by various researchers (e.g. Danckwerts and King, 1984; Danckwerts and Stuart-Hill, 1988; Forse, 1989). Locally, the recognition of semi-arid and arid ecosystems as being highly sensitive to fluctuating environmental pressures (and especially effective rainfall) began to gather momentum (e.g. Ellery *et al*, 1991; Fuls and Bosch, 1991). The application of succession theory[6] for land management and description of vegetation change in semi-arid South African rangelands[7] was strongly challenged by Mentis *et al* (1989). These authors welcomed new approaches and paradigms that called for the application of non-equilibrium models to describe and explain the event-driven nature of process and change operating in arid and semi-arid grassland systems (e.g. Walker *et al*, 1986; Westoby *et al*, 1989). Such paradigms propose that episodic events (including disturbances through, for example, fire, grazing, floods and droughts) effect vegetation change in a manner that is effectively multi-dimensional and multi-directional in both space and time. Mentis *et al* (1989) further promoted a dynamic, integrated and multi-disciplinary approach to rangeland science in South Africa, recommending opportunistic management to best accomplish sustainable agriculture in arid and semi-arid regions.

[6] Orthodox succession theory proposed a typically linear state of transition from pioneer (bad veld) to climax (good veld) vegetation (e.g. Weaver and Clements, 1929 - cited in Milton and Hoffman, 1994). Offshoots of these theories have been used in the past two decades (e.g. Tainton, 1981; Bosch, 1988; Bosch, 1989) to describe rangeland condition and vegetation change in South African rangelands.

[7] That suggested, for example, the eastward expansion of Karoo shrubs into grasslands could be ascribed simply to grazing management (e.g. Acocks, 1953; Bosch, 1988))

Hoffman and Cowling (1994) substantially criticised the notion of an expanding Karoo[8], by means of purely anthropogenic pressures, through evaluation of anecdotal records, historical trends and current evidence. These authors proposed that broad climatic conditions (particularly rainfall cycles) affect vegetation composition through fluctuation (as opposed to linear, or uni-directional change) of proportional shrub and grass cover in response to seasonal, and longer-term, cyclical rainfall.

Milton and Hoffman (1994) advanced this perception through a balanced appraisal of South African arid and semi-arid rangeland ecology. These authors explored the event-driven, or non-equilibrium, nature of these systems and compiled the first state-and-transition[9] models designed specifically for rangeland management and rehabilitation of Karoo areas. While the importance of appropriate and sustainable land management strategies was clearly recognised, the need for a more lucid understanding of the natural environment and ecosystem functioning was highlighted by these proponents of non-equilibrium theory.

There appears then to be a growing, and hopefully commonly held, understanding that a diverse number of variables including natural climatic cycles such as rainfall (Hoffman *et al*, 1990), natural processes such as erosion (Snyman and van Rensburg, 1986) and external factors such as grazing during inappropriate periods (Danckwerts and Stuart-Hill, 1988) can and do influence overall vegetation composition and species diversity of semi-arid and arid rangelands in this country (Westoby *et al*, 1989) and elsewhere (Pickup *et al*, 1998).

5.1.2.3 Vegetation change: the impact on seed banks or *vice versa*?

How do these theories and factors influence seed banks and seed bank research? Seed banks logically play an important role in the maintenance of ecological and genetic diversity. For this reason enhanced knowledge of seed bank dynamics provides invaluable insight into the impacts of natural or anthropological disturbance on ecosystems.

For example, Danckwerts and Stuart-Hill (1988) recorded significant mortality of certain drought-sensitive grass species (Decreasers[10]), with an increase in abundance of other grass species (Increaser I) in response to drought. This was especially prevalent when coupled with injudicious grazing practices that allowed livestock to select for palatable species that were also drought sensitive. Esler and Phillips (1994) experimentally investigated the association between drought

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[8] Several researchers raised concerns regarding this assumption (e.g. Acocks, 1953; Roux and Vorster, 1983; Roux and Theron, 1987; Bosch, 1988; Bosch, 1989).

[9] Westoby *et al* (1989) proposed the concept of state-and-transition models for non-equilibrium systems such as semi-arid and arid ecosystems.

[10] Decreaser/Increaser ecological categories defined by Foran *et al* (1978). Decreasers (e.g. *Themeda triandra*) decrease in abundance under conditions of both over- and under-utilisation. Increaser I species (e.g. *Cymbopogon plurinodis*) increase with under-utilisation. Increaser II species (e.g. *Digitaria eriantha*) increase with overgrazing.

and successful seedling establishment. Results from these trials indicated a strong selection pressure in favour of more drought-tolerant species. Milton (1994) proposed that an increase in abundance of unpalatable plants in grazed rangelands could in part be attributed to the impact of grazing on recruitment of desirable, palatable species. Milton (1995a) then recorded the consequential role of rainfall in seedling survival and establishment, as well as the role played by domestic stock in selective grazing of preferred species, leading to a dominance of less palatable or unpalatable plants. Further, the total successful reproductive output of plants has been shown to be reduced by factors including over-utilisation (Milton and Dean, 1988; Milton and Dean, 1990; O'Connor and Pickett, 1992; Turner, 1999), parasitization (Milton, 1995b), seed predation and granivory (Kerley, 1991; Kerley, 1992) and drought (Westoby *et al*, 1982; Milton, 1992; Milton, 1994). These factors clearly influence the total yield of viable seeds for future regeneration.

Researchers have directly linked vegetation composition and recruitment with the availability of viable seed (Acocks, 1953; Parker *et al*, 1989). Others have noted that some shrubs, grasses and long-lived perennials in arid and semi-arid rangelands have weakly persistent seed banks (e.g. Kemp, 1989; Esler, 1993) while many annual or ephemeral species have relatively large, persistent seed banks (Venable and Lawlor, 1980; Van Rooyen, 1999). This latter aspect appears to be linked to an ephemeral species' life history and may be viewed as a "back-up" survival mechanism especially in unpredictable environments where suitable germination episodes may not occur with any regularity. In general, long-lived species[11] are assumed to have relatively short-lived seed banks while short-lived species have persistent seed banks.

Weakly persistent seed banks may be due in part to factors such as reproductive strategies that entail limited annual replenishment of soil-stored seed (Esler, 1993) and also to factors that include predation (Inouye *et al*, 1980). Seed persistence on the other hand is influenced by factors such as seed structure and size (Thompson *et al*, 1993), by anti-predation mechanisms (Hendry *et al*, 1994), by dormancy mechanisms (Freas and Kemp, 1983) or by combinations of these and other traits. Overall seed bank density and persistence is determined by the balance of "gains"[12] and "losses"[13] to the seed bank. Gains and losses to the seed bank and thus the seed bank size and composition can be influenced by existing and historical management strategies as well as by diverse natural environmental factors.

Seeds, of species not possessing traits ensuring their presence in ensuing generations, are thus arguably selected against just as certainly as palatable, or drought-intolerant, seedlings

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[11] These have "above-ground longevity" and thus a longer term potential reproductive output as a survival mechanism.

[12] Gains may be estimated as the number of seeding events and the quantity of viable seeds produced.

[13] Losses may be estimated as the loss of seed through factors that include natural seed decay (in the absence of germination cues), predation, parasitisation and germination (which may or may not be successful).

and adult plants are selected against by over-grazing and lengthy drought periods respectively, or even by a combination of the two. Thus a level of pre- and post-germination selection is in operation, affecting overall species composition and also regeneration potential of rangelands.

Seed banks (especially those of longer-lived species with short-lived seed banks) in semi-arid and arid rangelands may therefore be under threat from the same, or similar, changes as the visible, or above-ground, vegetation component. Vegetation change is logically dependent upon firstly the existing state and latent potential of a system; secondly on a broad spectrum of variable environmental pressures (both natural and anthropogenic) operating on that system; and, finally on the variable response, or responses, of the system to these diverse pressures. The long-held legend that natural pastures are self-sustaining and self-restoring may be grinding to a halt in the light of current approaches to integrated agro-ecology (Giliomee, 1992).

5.1.3 Seed bank ecology and distribution in the Nama Karoo Biome

The flora of the Nama Karoo Biome is inadequately described and no reliable estimates of the floral diversity currently exist (Cowling and Hilton-Taylor, 1999). Even less is known of the ecology or distribution of seed banks in the Nama Karoo Biome (Esler, 1999). This study set out to initiate an inquiry into the state of existing seed banks in the locality of Tafelberg in the eastern Nama Karoo Biome. The aim was to assess relative differences and similarities between areas that have been heavily grazed for decades (in this case primarily the plains) and other less heavily utilised areas (mainly the relatively less accessible mesa, Tafelberg).

The premise for this study was that a source of dormant, soil-stored seed of desirable plant species may exist in degraded areas, that, given an opportunity to germinate and to establish, may improve above-ground biodiversity and productivity of apparently degraded rangelands. A further premise was that less heavily utilised sites may provide source populations of seed, from desirable plant species, that could be used to restore degraded areas.

5.2 An overview of seedling emergence data

A diversity of species was recorded from both April and October 1998 samplings (Chapter 2). By completion of this thesis, not all plants had flowered and not all species could be assessed equally[14]. This work is ongoing, with species recorded as they flower, however for the purposes

[14] This was principally the case for grasses that germinated but had not flowered (mainly from the October sampling, although 8 plants from the April sampling had still not flowered by time of writing). The majority of dicot species were relatively simple to separate into species-specific categories or codes on the basis of leaf morphology and growth form, but many grass species exhibited similar leaf morphology and growth forms and were complex to identify accurately. The intended differentiation of data into categories that included palatability status was not achieved within the two year time-frame but is continuing in future research.

of this thesis, species-specific data is superseded by an estimation of general trends (5.2.2, below). These trends include comparisons between dicots versus grasses and other monocots; and, ephemerals versus longer-lived (or persistent) species (Table 5.1). Where species-specific data is available, this is provided.

5.2.1 Germination rates

Seeds germinated relatively rapidly once irrigation commenced. The trend for samples overall and individually, spanning temporal and spatial parameters, was that 93% to 100% of total germination[15] occurred within the first five months after which germination tailed off significantly (Figure 5.1). Monitoring continued for eight months but samples were monitored informally for a further year (April sampling) and six months (October sampling) to record further germination. Occasional germinations occurred during this time but less than 50 seedlings (roughly 1% of the total number of seedlings from the trials) from all 468 soil samples were observed.

5.2.2 Differentiation of emerging plant species

As seedlings emerged they were catalogued into elementary groups namely dicotyledonous plants or "dicots", "grasses" and "other monocots" (e.g. members of the Cyperaceae, Iridaceae, etc.). As plants matured and became identifiable these were potted into uniquely coded pots for identification purposes (Plate 5.1). Owing to variable leaf (and overall) morphology of many plant species, many species (especially grasses and members of the Asteraceae) were potted out into more than one uniquely coded pot, resulting in one or more duplicates of a single species[16].

Once it became apparent that not all species would be identifiable by the conclusion of this thesis, other means of differentiating patterns of emergence and spatial distribution into broad but descriptive categories were sought. These categories are outlined in Table 5.1.

At the time of writing, at least 29 plant families and 75 genera were represented in a total[17] of 4164 seedlings germinated during germination trials (Appendix 5.1). Some 116 species were recorded, sixty of these from the April 1998 sampling and 97 from October 1998. While 55 species have been confirmed common to both sampling times (Appendix 5.2), 11 species were unique to the April sampling and 49 unique to the October sampling.

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[15] "Total germination" is regarded here as being the grand total of seedlings germinating from all samples over the two eight month periods during which trials were conducted.

[16] These data can only be analysed for species-specific trends once plants flower and identifications completed.

[17] The total does not include species deemed to be wind-blown or soil-stored weeds. Kirstenbosch general mix does contain weed seed (personal experience) and numerous wind-blown seeds were observed on trays. Weeds are omitted from data presented here. Refer Appendix 2.4 for details of germination trial data recording.

Table 5.1 Preliminary descriptive categorisation of plant form- and functional guilds, of plants germinated during seed bank germination trials, pending final identification of plant species. Persistent species may or may not have nutritional value but perform a role in ground-holding during times when ephemeral species are absent.

number	Category	Description
1	ephemeral dicots	Any dicotyledonous plant that matured, flowered, set seed and died within a six month period. Also referred to in many texts as "annuals".
2	ephemeral grasses	Any grass plant that matured, flowered and died within a six month period. Also referred to in many texts as "annuals".
3	ephemeral monocots	Any monocotyledonous plant other than a grass that matured, flowered, died or became dormant within a six month period.
4	ephemeral weedy dicots	Any cosmopolitan weed species that matured, flowered and died within a six month period and which may have been a contaminant via wind-blown or otherwise distributed seed.
5	ephemeral cryptophytes	This category was discarded and lumped into category 1
6	persistent cryptophytes	Any cryptophyte that did not complete its reproductive cycle and die "naturally" within the year of assessment.
7	persistent dicots	Any dicotyledonous species that did not complete its reproductive cycle and die "naturally" within the year of assessment.
8	persistent grasses	Any grass that did not complete its reproductive cycle and die "naturally" within the year of assessment.
9	persistent monocots	Any monocotyledonous plant other than a grass that did not complete its reproductive cycle and die "naturally" within the year of assessment.
10	persistent succulents	Any succulent species that did not complete its reproductive cycle and die "naturally" within the year of assessment.
11	persistent weedy dicots	Any cosmopolitan weed species that did not complete its reproductive cycle and die "naturally" within the year of assessment and which may have been a contaminant in the sample from wind-blown or otherwise distributed seed. These were counted but not included in given totals.
12	not sure	Any plant species that has not flowered and which is not readily identifiable on the basis of leaf morphology.

A total of 234 plant "types" were potted into coded pots during germination trials. Of these coded plants, 20 are as yet unidentified to family level, 106 to genus level and 139 to species level. Since many of these plants appear to be duplicates of previously recorded species (based on leaf morphology and growth form as these plants have not yet flowered) it is likely that the final number of species will be only modestly higher than presented in this thesis. Final results will nonetheless reveal a greater clarity with regard to spatial and temporal distribution of all species recorded and in particular will elucidate the distribution of members of the family Poaceae.

5.3 Comparative results of germination trials

There were notable spatial and temporal differences recorded between results of germination trials from April and October samplings[18]. Synopses of relevant differences are presented in Tables 5.2 - 5.4 and a more comprehensive synopsis is presented in Appendix 5.3.

[18] A clearer distinction of species-specific spatial variation of seed banks between the seventeen sites will unfortunately only be possible once all plants have flowered and have been identified.

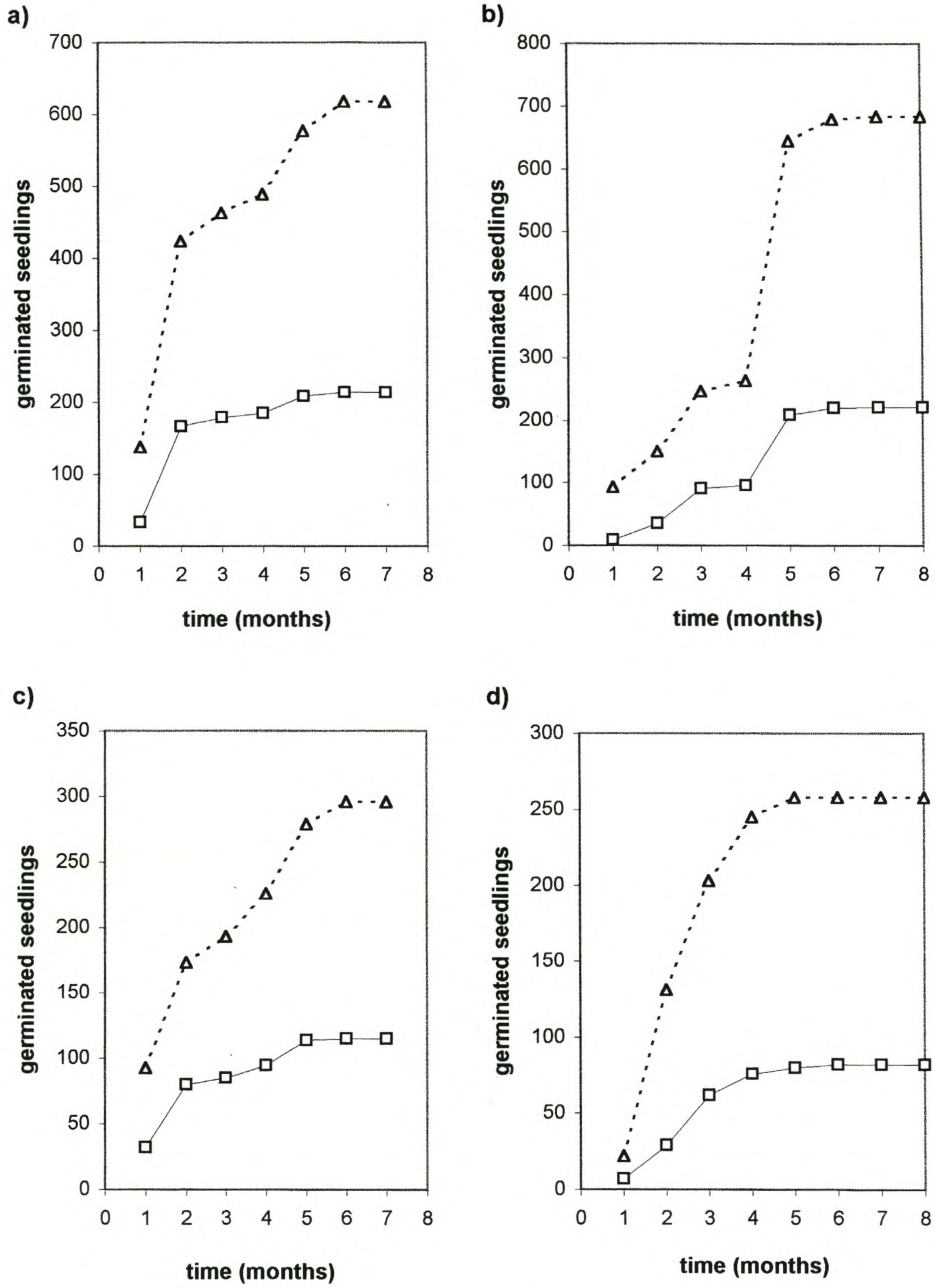


Figure 5.1a Seasonal comparison of cumulative germination from an April (a) and October (b) sampling on the south east plains, as well as April (c) and October (d) sampling from sites on top of Tafelberg. Stippled lines represent samples removed from closed-canopy micro-habitats and solid lines represent samples removed from open-canopy micro-habitats

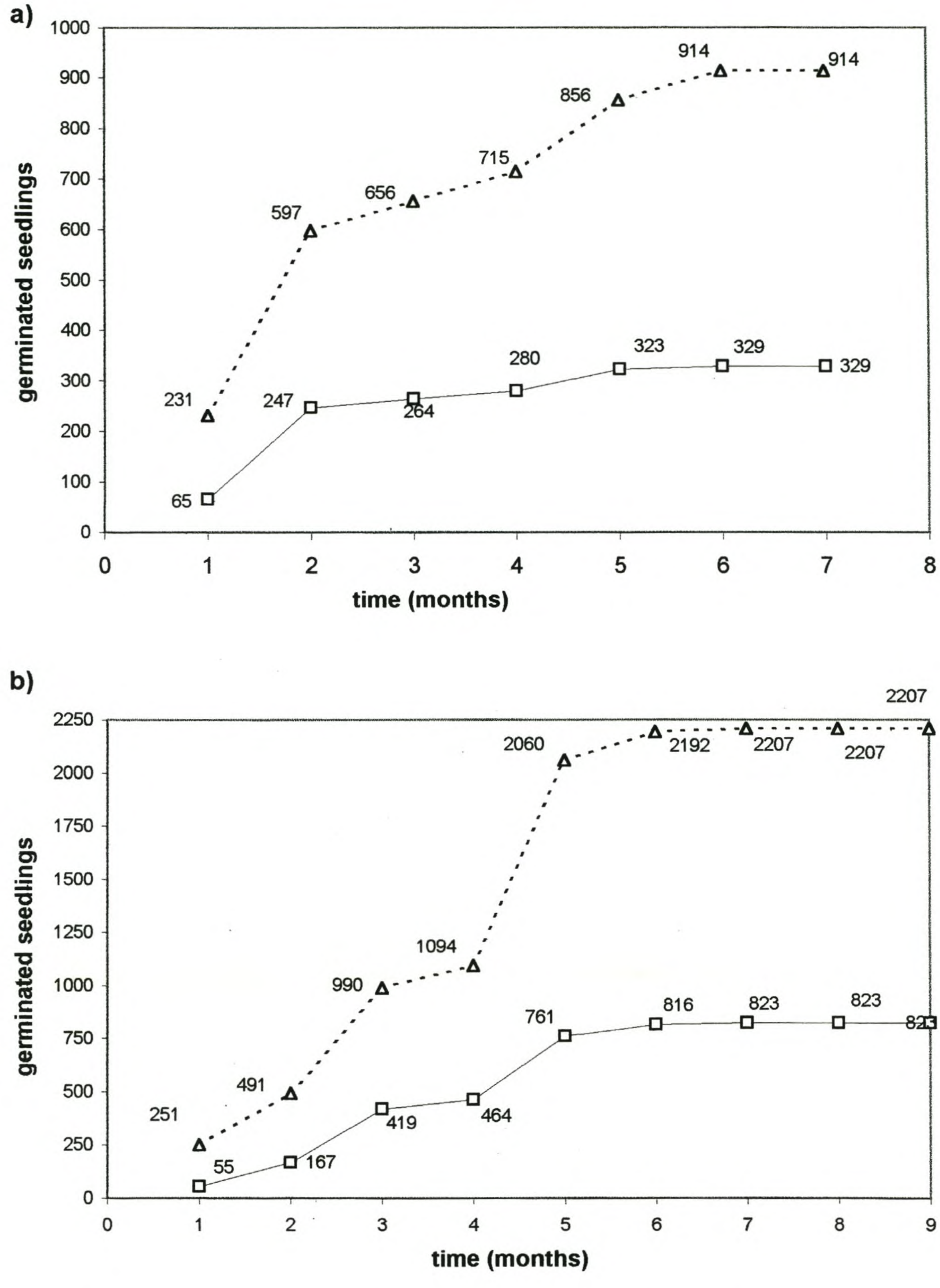
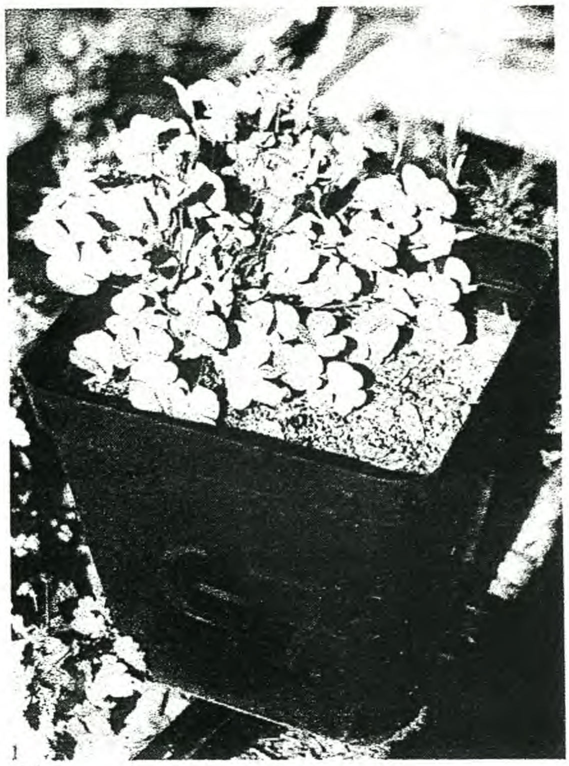


Figure 5.1b: Cumulative germination from germination trials for all April (a) and October (b) samples from on and off Tafelberg. Stippled lines represent samples removed from closed-canopy micro-habitats and solid lines represent samples removed from open-canopy micro-habitats. (Note that these totals include weed species).

a)



b)

c)

d)

Plate 5.1 Photographs of some plant species germinated from samples on- and off Tafelberg. Note pot coding in red on black pots. Photograph a = *Crassula* cf. *montana;* Photograph b = *Oxalis* cf. *commutata*; Photograph c = *Hermannia cf. cernua;* Photograph d =. *Buddleja glomerata*

5.3.1 Spatial distribution of seed across the landscape at the vegetation unit and micro-habitat scale

5.3.1.1 Depth trials to assess relative spatial distribution of seed banks in the soil

The vertical spatial distribution of seed within the soil profile is a component of seed bank studies not always examined by researchers even though these data can aid comprehension of seedling recruitment and above-ground vegetation patterns following disturbance. Seeds in arid areas are generally found near the soil surface (Reichman, 1984; Kemp, 1989). Gradients of seed distribution in soil were documented in seed bank studies conducted in Namaqualand[19] (Van Rooyen and Grobbelaar, 1982; De Villiers *et al.*, 1994a; De Villiers *et al*, 1994b). Vertical distribution patterns in these studies showed a steep decline in the number of seeds with increasing depth. These Namaqualand findings were primarily of seeds of annual plant species and correlate with findings by Freas and Kemp (1983) in the Chihuahua Desert (North America) that many arid annual species are unable to germinate from much below 10mm. Barnard (1987) found in glass house trials, with a selection of different Karoo grasses and shrubs, that optimal depth for successful germination of seeds appeared to be between 2 to 20mm.

In order to ensure firstly that a proposed sampling depth of 5cm would be adequate and secondly that vertical distribution of seeds in the Nama Karoo Biome would be comparable with findings from arid and semi-arid systems elsewhere, eighteen "depth" samples[20] were taken from three sites on the south east (SE) plains in October 1998.

Owing to shallow average soil depth on the plains, three of the eighteen 0-5cm depth samples did not attain a 5cm depth; six of the 5-10cm samples did not attain the 10cm depth and only seven samples were deeper than 10cm. Of these seven, only two attained a depth of 15cm before encountering compacted, decomposed shales (Chapter 2). No seedlings germinated from 10-15cm soil samples. Eight seedlings emerged from the 5-10cm depth trial and only five of the fourteen 5-10cm samples yielded any seedlings at all. A total of 330 seedlings germinated from the samples removed from 0-5cm (Table 5.2).

In summary, significantly few samples deeper than 5cm yielded any seedlings during germination trials (Table 5.2) and no species germinating from below 5cm were novel when compared with those germinating from the top 5cm layer of soil. Patterns of emergence, in time as well as in "types" of species (predominantly ephemeral plant species), were in accord with those from standard germination trials. It appears then that soils deeper than 5cm do not contain significant seed banks where soils of this depth do occur on the south east plains.

[19] Only in old cultivated lands were seeds found by these researchers at significant densities at a depth of between 20-25mm, otherwise seeds were found predominantly on, or very near, the soil surface.

[20] One open- and one closed-canopy sample was taken from each of three plots on each of three sites investigated. Each sample comprised 3 sub-samples (0-5cm; 5-10cm and 10-15cm) thus a total of 54 samples were attempted. In practice only 39 samples in total were removed, owing to relatively shallow soils (Table 5.2).

Table 5.2 Results of germination trials from samples removed at three depths (0-5cm; 5-10cm and 10-15cm), for open-canopy (O/C) and closed-canopy (Cl/C) micro-habitats, taken from three sites (FSE1, FSE2 and FSE4) on the south east plains of Tafelberg.

results ⇩	Site code⇨	FSE 1			FSE 2			FSE 4			Mean (all sites)		
Sampling depth (cm)		0-5	5-10	10-15	0-5	5-10	10-15	0-5	5-10	10-15	0-5	5-10	10-15
Max. soil depth (cm)		8			13			15			10.5		
Mean soil depth (cm) open-canopy ±SD		3.7 ±0.6			7.7 ±0.6			13 ±3.5			8.1 ±4.4		
Mean soil depth (cm) closed-canopy ±SD		6.3 ±1.5			11.3 ±1.5			14 ±1.7			10.6 ±3.6		
Possible # samples		6	6	6	6	6	6	6	6	6	18	18	18
Actual # samples taken		6	2	0	6	6	2	6	6	5	18	14	7
Total # seedlings		125	2	n/a	83	3	0	122	3	0	330	8	0
# seedlings (O/C)		43	0	n/a	25	0	0	31	0	0	99	0	0
# seedlings (Cl/C)		82	2	n/a	58	3	0	91	3	0	231	8	0
# grasses (O/C)		6	0	n/a	6	0	0	8	0	0	20	0	0
# grasses (Cl/C)		12	0	n/a	14	2	0	39	0	0	65	2	0
# dicots (O/C)		37	0	n/a	19	0	0	22	0	0	78	0	0
# dicots (Cl/C)		66	2	n/a	43	1	0	51	3	0	160	6	0
# other monocot (O/C)		0	0	n/a	0	0	0	1	0	0	1	0	0
# other monocot (Cl/C)		4	0	n/a	1	0	0	1	0	0	6	0	0

The selected sampling depth of 5cm, for seed bank trials, was considered adequate to capture trends of soil-stored seeds on and off Tafelberg and also (given findings here and in semi-arid systems elsewhere) to be adequate for seed bank sampling elsewhere in the Nama Karoo Biome.

5.3.1.2 Spatial variation between closed-canopy versus open-canopy samples

The primary difference between closed- and open-canopy sampling was the contrast in the number of seedlings germinating from the two micro-habitats (Refer 5.4.1.1, below). All sites sampled[21] consistently showed a significantly higher number of plants and broader species diversity germinating from closed-canopy samples than from open-canopy samples. For all plots (both April and October collections (preliminary data)) samples from open-canopy sites yielded an average of 51 ±25 seedlings and 15 ±4 species per site while samples from closed-canopy sites yielded an average of 140 ±66 seedlings and 21 ±4 species per site. Germination trials conducted on the April 1998 sampling yielded 1219[22] seedlings of which 25.7% of plants germinated from open-canopy and 74.3% from closed-canopy samples. The October sampling produced 2948[23] seedlings of which 27.0% germinated from open-canopy and 73.0% from closed-canopy samples. For both trials there was thus roughly a 3-fold difference between open- and closed-canopy samples. Establishment of exact ratios of species

[21] Six sites during April 1998 and sixteen sites during October 1998

[22] The total number of seedlings germinated from 180 samples comprising 15 open- and 15 closed-canopy samples (30 in total) from three sites on the south east plains and three sites on the top of Tafelberg (refer Chapter 2).

germinated from open- and closed-canopy sites is complicated at this stage by incomplete species identification. However, open-canopy samples from April sampling yielded roughly 70% of the average number of species of closed-canopy samples while for the October collection, open-canopy samples yielded roughly 77% of the average number of species of closed-canopy samples. For the present level of species identification there is no obvious, nor any statistically significant, correlation between any of the three broad groups (grasses; other monocots; dicots) nor any of the twelve categories listed in Table 5.1, with regard to spatial distribution of these groups or categories between open-canopy versus closed-canopy samples.

Esler (1993) noted the role played by micro-topography in determining spatial distribution of seeds. Significant micro-habitat variation between open- and closed-canopy seed banks was found at Tierberg in the Succulent Karoo, where closed-canopy sites contained on average 3.5 times the number of seeds contained by neighbouring open-canopy sites (Esler, 1993). There is then a degree of correlation between this phenomenon at the locality at Tafelberg and that at Tierberg.

Given the increased levels of run-off and thus erosion in areas with low basal cover (Snyman and Van Rensburg, 1986; Whitford, 1999), it is probable that closed-canopy sites capture, and hold on to, seeds that are more commonly swept away (by wind, water or other agents of dispersal) from open-canopy sites. For example, Roux (1960, cited by Esler, 1999) found seeds of *Tetrachne dregei*[24] to be highly vulnerable to displacement by sheet erosion and Whitford (1999) noted that organic debris is displaced by sheet erosion. Organic debris and silt-laden water flow would arguably contain seeds that could be displaced by erosion during flood events, eventually being deposited in a water course or pan[25]. The assumption for this germination trial study is that a proportion of seeds may thus be lost through erosive processes (similar to those influencing soil loss) from especially open-canopy (low basal cover) micro-habitats. Increased run off and erosion owing to reduced overall basal- and canopy cover (Snyman and van Rensburg, 1986) will therefore also continually reduce the potential available seed banks in open-canopy spaces. Given findings, by researchers in arid and semi-arid areas, that seeds below a certain depth in these areas do not germinate and are effectively "lost" from the seed bank (e.g. Kemp, 1989) it is likely that a percentage of seeds, in the postulated seed-bearing sediments, may then be lost completely to the system, for example, through deposition in deep mud.

[23] The total number germinated from 288 samples removed from 2 sites on the top, 4 sites on each slope and 4 sites on each plain, each site contributing 9 open- and 9 closed-canopy samples (Chapter 2).

[24] *Tetrachne dregei* is a Nama Karoo and Grassland Biome grass species found in a diversity of habitats from riverbanks to mountain slopes (Gibbs Russell *et al*, 1990)

[25] Soil and organic matter loss from interplant (open-canopy) spaces, through wind- and water erosion, is discussed in more detail in Chapter 3.

Open-canopy sites are essentially hostile to seeds not only because of "insecurity of tenure" (owing to wind- and water erosion) but also because of higher temperatures and rates of evaporation than closed-canopy sites (e.g. Roux and Theron, 1987). Open-canopy micro-habitats contain "nano-habitats"[26] consisting of small soil disturbances such as natural roughness or depressions in the soil surface (e.g. Reichman, 1984), animal diggings (e.g. Reichman, 1984; Dean and Milton, 1991a) or holes from fossorial insects (e.g. Dean, 1992). These nano-habitats can provide improved water infiltration (Dean, 1992), act as "traps" for organic matter (Steinberger and Whitford, 1983a; Dean and Milton, 1991a) and may become germination sites for seeds in otherwise hostile open-canopy sites (Dean and Milton, 1991a; Dean and Milton, 1991b).

5.3.1.3 Spatial variation between sites on top of Tafelberg

Of 56 species germinated from samples taken from sites on top of Tafelberg (Appendix 5.2), 8 germinated from all three sites while 11 species were common to two of the three sites. The grasses *Themeda triandra*[27] and *Digitaria eriantha* are well represented in germination trials from all sites on top of Tafelberg as are dicotyledonous species such as *Sutera halimifolia*, *Lightfootia nodosa* and various other persistent dicotyledonous and grass species that appear to be absent, or present in much lower measure, in seed banks from sites examined on the plains.

Some plant species germinated only from samples removed from one site on top. For example, *Buddleja glomerata* and *Silene burchelli* var. *burchelli* germinated from samples from the top north west (NW) site while *Wahlenbergia cernua* germinated only from samples taken from the top south east site (Appendix 5.2). Overall trends show that persistent species predominate on all three sites on top of Tafelberg. A low percentage (roughly 6%) of all seedlings germinating from samples taken from the top sites were ephemeral species and samples from sites on top of Tafelberg contain a roughly equivalent mix of persistent- grass and dicotyledonous species.

5.3.1.4 Spatial variation between sites on the slopes of Tafelberg

The north west and south east slopes are rocky, with gradients of approximately 2.1:1 (1:0.48) and 2.6:1 (1:0.38) respectively. Although both slopes are grazed by livestock, there appears to

[26] While it is recognised that scale is relative and that scrapes or other disturbances are recognised as micro-habitats in their own right, the term "nano-habitat" is applied here to distinguish between the use of the preferred term "micro-habitat" for open- and closed-canopy sites and smaller components of open- and closed-canopy micro-habitats.

[27] *Themeda triandra* appears to be absent from the plains surrounding Tafelberg with the exception of a few isolated remnant populations. The plateau and upper slopes of Tafelberg host significant populations of this and other palatable grass species.

be significantly lower grazing pressure higher up the slope than near the footslopes and lower slopes (personal observation; W. Asher, pers comm; R. Gilfillan, pers comm). The footslopes are relatively highly utilised by domestic stock.

Samples from the top, middle and lower north west slope sites (SNW) yielded mainly persistent grass and dicotyledonous species. An average of roughly 6% of seedlings from these sites were ephemerals while 75% of all seedlings from samples removed from the north west footslope site were ephemerals. The ratio of ephemerals to persistent plants increased (Table 5.3; Figure 5.2) with a decrease in altitude. This may be directly correlated to a combination of increased accessibility to livestock and an increase in harsh environmental conditions (of heat and drought).

Sites on the south east slopes (SSE) showed similar gradients of increasing abundance of ephemeral plant species with decreasing altitude (Table 5.3; Figure 5.2). The SE footslope yielded a low germination overall. This site was riddled with active termite nests, vegetation was relatively sparse and the overall percentage of the site without cover of plants or rocks (45%) was the highest of all sites on the SE slopes and plains. It is possible that termites may have played a role in the denudation of both above-ground vegetation[28] and removal of leaf litter and plant detritus (personal observation; Dean and Milton, 1999).

Table 5.3 Comparison of the total numbers of all seedlings and those of ephemeral plants germinating from samples removed during October 1998 from the north west (SNW) and south east (SSE) slopes.

⇩ SITE	total # seedlings		% ephemeral species	
	open-canopy	closed-canopy	open canopy	closed canopy
SNW1 (top)	79	91	2.5	1.1
SNW2 (middle)	60	74	13.3	2.7
SNW3 (lower)	22	98	18.2	9.2
NW Footslope	95	232	77.9	73.7
SSE1 (top)	28	63	3.6	19.0
SSE2 (middle)	20	128	0	59.4
SSE3 (lower)	19	150	10.5	70.7
SE Footslope	14	56	28.6	35.7

Of 57 species (preliminary data) recorded germinating from all eight sites on the NW and SE slopes of Tafelberg, a total of 19 are common to both slopes (Appendix 5.2). Seven species were identified as germinating solely from the NW slopes and a further 9 species germinated only from samples removed from the SE slopes. The large shrub *Rhus burchelli* and at least one *Pentzia* species were present in samples from both slopes however, although at least two

[28] Termites (species unknown but probably *Microhodotermes viator*) were observed harvesting green and dead vegetation from bushes, including *Drosanthemum* spp., as well as dead plant debris from the ground on the south east plains and footslope sites.

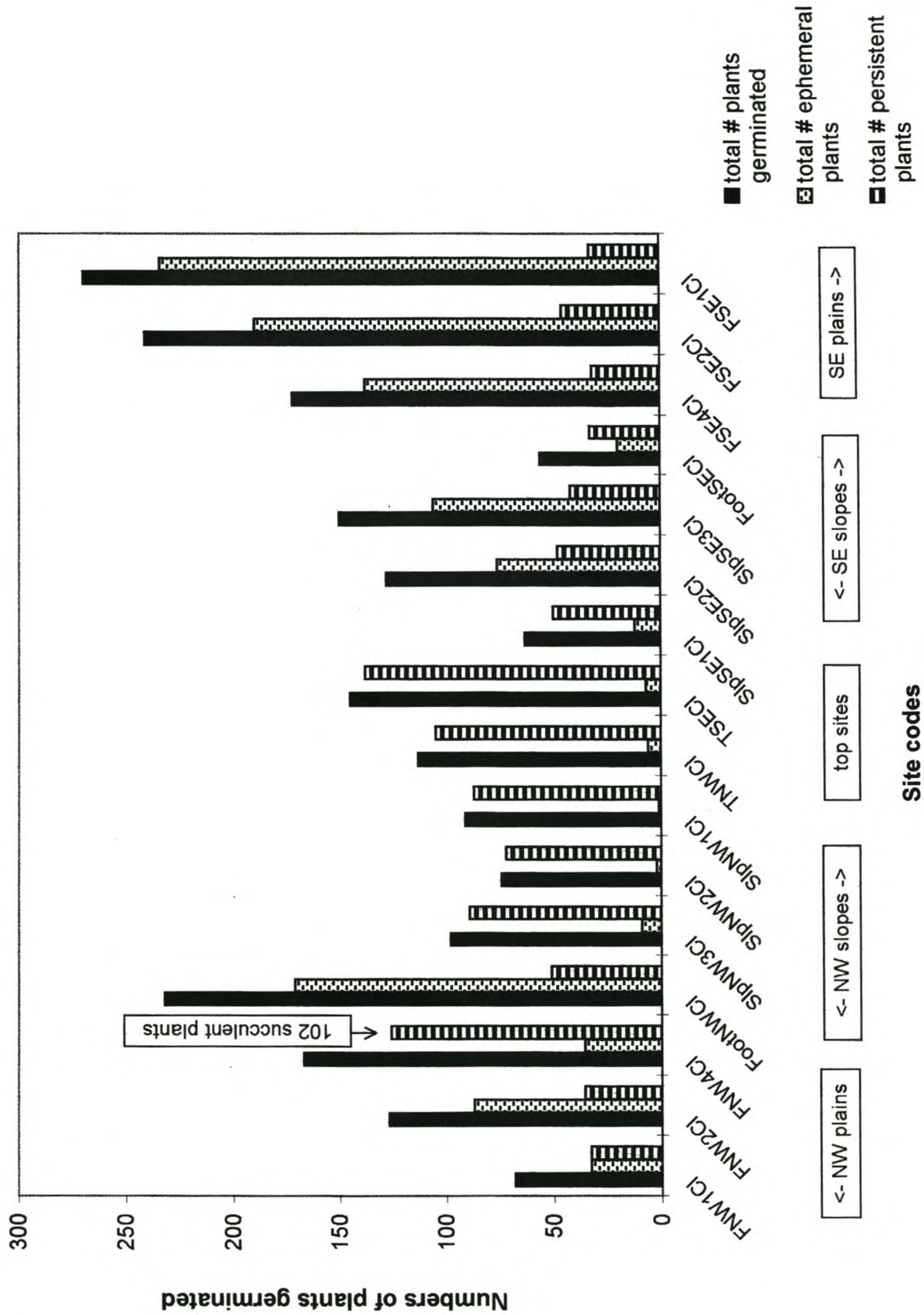


Figure 5.2: Ephemeral (species that germinate, reproduce and die within a one year cycle) versus persistent (perennial) plant species that germinated from samples taken from closed-canopy sites on- and off Tafelberg during the October 1998 sampling.

species of *Eriocephalus* are abundant on both slopes, these (two species) only germinated from samples removed from the NW slopes and not from the SE slopes. *Sutera halimifolia*, *Walafrida geniculata* and *Jamesbrittania tysonii* were well represented in samples from both slopes. *Buddleja glomerata* germinated from samples removed from the SE slopes. Seedlings of grass species such as *Themeda triandra*, *Digitaria eriantha*, *Eragrostis obtusa* and *Tragus berteronianus* were well represented in samples from both slopes while *Aristida* spp. were notably absent from samples removed from the slopes. *Themeda triandra* did not germinate from samples removed from either of the footslope sites.

It is significant to note that, owing to steep gradients of both slopes, all sites sampled (with the exception of footslope sites and to a lesser extent the lowest slope' sites i.e. SNW3 and SSE3) showed a conspicuous level of geological instability. This instability was evidenced by a high proportion of loose soil and surface rock. As a result, there appeared to be an environmental disturbance factor in these sites with active wind- and water erosion reducing plant "footholds".

5.3.1.5 Spatial variation between sites on the plains of Tafelberg

Samples from the SE plains demonstrated trends similar to those recorded from the slopes (Figure 5.2). The further from the base of Tafelberg samples were removed, the higher the number of plants germinated with a concomitant increase in germination of ephemerals[29]. The number of persistent species' seedlings for all sites investigated on the SE plains was roughly equivalent with an average of 37 ±7.8 seedlings per site.

In contrast with the SE plains the mean number of plants germinating from NW plains' samples decreased with increasing distance from Tafelberg[30] (Figure 5.2) and samples from the furthest site (FNW1) showed both lowest germination (for all sites on the NW) and the lowest number of ephemeral plant seedlings. While germination from the site closest to Tafelberg on the north west (FNW4) was highest for all plains sites, total germination for this site was skewed by germination of a high number (102) of succulents (family Mesembryanthemaceae (mesems))[31] (Plate 5.2; Figure 5.2). If the high number of mesems germinating from this site is corrected for, then the average germination of persistent species for the NW plains is very similar to that of the SE plains with an average of approximately 36 ±3.5 seedlings per site.

[29] The overall ratio of ephemeral to persistent plant species on the SE plains was 4.4:1. In other words, an average of 22.7% of seedlings were persistent species.

[30] The NW plains are heavily grazed (personal observation) and it is possible that differences between NW and SE plains may be strongly correlated to grazing pressures but this is not clear with existing data.

[31] A single soil-sample yielded 80 of these 102 mesems (thought to be Phyllobolus sp.).

Plate 5.2 Photograph of a single sample of seed bank soil from the site on the north west plains closest to Tafelberg (FNW4) during seedling emergence trials. Note the high number of mesems germinating from the sample (Figure 5.2). In total 79 mesem seedlings germinated from this single sample (one sub-plot) while 83 germinated from the three component sub-plot samples (plot 3) and 102 germinated from the 18 samples removed from the whole FNW4 site. Note that this sample is mislabeled – no seed bank soil samples were removed from FNW3 during the course of this study and FNW3 was used erroneously in place of the code FNW4.

Species composition of seedlings germinated from NW and SE plains' samples appears to be quite different[32]. The number of ephemeral dicots from samples on the SE plains is roughly five-fold higher than from the NW plains. Of 53 species germinated from SE plains' samples[33], and 44 species from the NW plains, twenty-four were common to both plains. Sixteen of these 24 species are relatively widely distributed between the plains, slopes and/or the top of Tafelberg (Appendix 5.2).

5.3.1.6 Synopsis of spatial variation between sites on- and off Tafelberg

Overall, preliminary results of spatial variation in seed banks on- and off Tafelberg revealed a heterogeneous landscape with reasonably high species turnover between all sites on the top, slopes and plains. In total, 11 species were common to the plains and the slopes and the top of Tafelberg[34] while 52 species were restricted to samples either from the top, or from one of the slopes or from one of the plains sites (Appendix 5.2). The remaining species show some continuity of distribution between the broader habitats of plains, slopes and top.

Table 5.4 Summary of the average number of seedlings per site from different plant categories (Table 5.1) for broad habitat types of top, plains and slopes. For the purposes of simplicity, the category of "persistent shrubs" here combines "persistent cryptophytes" (category 6); "persistent dicots" (category 7) and "persistent succulents" (category 10) into one category. All other categories are consistent with Table 5.1. Data are presented as means ± standard deviations.

Descriptive category (refer Table 5.1)	NW plains # seedlings/site (n=3)	NW slopes # seedlings/site (n=4)	Top sites # seedlings/site (n=3)	SE slopes # seedlings/site (n=4)	SE plains # seedlings/site (n=3)
persistent grasses	11.2 ± 10.7	31.3 ± 24.2	36.7 ± 25.7	14.8 ± 6.6	7.8 ± 7.8
persistent shrubs	22.3 ± 6.6	25.9 ± 14.4	33.9 ± 18.3	15.5 ± 11.4	18.5 ± 18.6
ephemeral grasses	22.0 ± 27.1	16 ± 29.4	2.3 ± 2.5	2.0 ± 1.77	19.3 ± 22.9
ephemeral dicots	15.8 ± 9.9	14.5 ± 24.2	1.4 ± 1.3	15.5 ± 11.4	87.6 ± 52.8
ephemeral monocots	0.33 ± 0.8	3.38 ± 8.8	1.1 ± 2.1	0.5 ± 0.9	8.3 ± 6.7
mean # persistent spp.	33.5	57.2	70.6	30.3	26.3
mean # ephemeral spp.	38.1	33.9	4.8	18.0	115.2

The main trends indicate significant differences between the numbers of ephemerals (annuals, short-lived and insubstantial) and the number of persistent plants (perennial, with some grazing, and/or ground-holding potential) found on- and off Tafelberg (Figure 5.2). While the actual numbers of plants germinated may appear to be highest from the plains, these are predominantly tiny (≤ 5cm in height), ephemerals, many of which complete their life cycle and die within three

[32] It remains unclear whether species turnover is higher between sites at equivalent distances from Tafelberg on different plains, or between different sites on the same plain.

[33] The total number of species includes April and October samplings. October sampling revealed a higher species diversity on the NW- (average of 22.5 (±2.4) species) versus the SE plains (average of 18.3 (± 3.7) species) per site. April sampling investigated only the SE plains and revealed an average of 16.5 (± 4.6) species per site.

[34] One such example is the Increaser II species *Digitaria eriantha* (5.1.2.3, above)

months. Persistent- grasses and dicots germinated in roughly equivalent proportions from samples taken on the top and slopes of Tafelberg (Table 5.4) but on the plains, the average number of persistent dicot seedlings exceeded the number of persistent grass seedlings in the ratio of 2.4:1 (SE plains) and 2:1 (NW plains). While these rudimentary figures may change once identifications are complete, the ratios are unlikely to change significantly. It appears then that seed banks, on especially the SE plains, are dominated by seeds of ephemeral species.

Of the ten most common species germinated from all sites on- and off Tafelberg, seven are ephemeral plants (Table 5.5) while, of the remaining three, two (*Sutera halimifolia* and *Themeda triandra*) are found predominantly on the top and slopes of Tafelberg.

Table 5.5 List of the ten most common seedlings germinated from both the April and October germination trials. Data are preliminary and may change once identification is completed.

Genus, species or description	number of seedlings germinated	Plant category (refer Table 5.1)	Broad habitat or locality F = plains, S = slopes NW = north west; SE = south east
cf. *Aizoaceae* sp. 1	818	ephemeral dicot	FNW / SNW / FSE
cf. *Poa pratensis*	200	ephemeral grass	SNW† / SSE / Top†
Ifloga glomerata	182	ephemeral dicot	FNW / FSE / SNW / Top†
Aristida sp. 1	164	ephemeral grass	FNW / FSE
Sutera halimifolia	142	persistent dicot	FSE* / SNW / SSE / Top
Pentzia sp. 4	120	persistent dicot	FNW / FSE / SNW / SSE / Top†
Themeda triandra	119	persistent grass	SNW† / SSE† / Top
Tragus berteronianus	112	ephemeral grass	FNW / FSE / SNW / SSE / Top
Poaceae sp.	104	ephemeral grass	FNW† / FSE / SNW
Bulbostylis humilis	104	ephemeral monocot	FSE / SNW / Top†

Note: † denotes that five or less seedlings of this species germinated from samples removed from this locality
* denotes that only one seedling of this species germinated from samples removed from this locality

It is clear that, at least spatially, seed banks exhibit significant differences between the top, slopes and plains of Tafelberg. A number of researchers have noted the patchy distribution of resources in arid and semi-arid rangelands (e.g. Hunter *et al*, 1982; Steinberger and Whitford, 1983b; Levin *et al*, 1984; Milton, 1990; Novellie, 1990; Steinberger, 1995; Vernon, 1999; Watkeys, 1999) and the patchy distribution of seeds in these environments (e.g. Yeaton and Esler, 1990; Esler, 1993; Van Rooyen, 1999). The completed species-specific identification of all species germinated in these trials will no doubt elucidate further intra-site[35] and inter-site[36]

[35] By intra-site is meant at sub-plot and plot scale within the same site.

[36] For example, between two sites within the same broad habitat, e.g. the SE plains.

differences with regard to patchy distribution of seeds across the Tafelberg landscape. However, even with preliminary data, it appears that patchiness of seed distribution alone cannot account for the relative paucity of persistent plant species from the plains nor can patchiness account for a high average density of ephemeral plant species on the SE plains.

Shrubby species and other longer-lived perennials in the southern Karoo (Esler, 1993) and generally in deserts (Kemp, 1989) form a longer-lived above-ground component, commonly having a transient seed bank, generally relying on limited annual replenishment of seeds (Kemp, 1989; Esler, 1993). This is also commonly found to be the case in grasslands (Roberts, 1981, Rice, 1989). In contrast, ephemeral species in semi-arid regions tend to have a large and often persistent seed bank (Venable and Lawlor, 1980; Freas and Kemp, 1983; van Rooyen, 1999) as do seed banks of ephemerals in grasslands (Rice, 1989). For these reasons, and in accordance with the results of the germination trials and the above-ground study (Pienaar, pers comm), findings at Tafelberg indicate that existing seed banks on the plains are depleted, to a significant measure, of seeds of persistent plant species other than those presently found above ground. While some desirable, persistent species may indeed be represented in dormant remnant seed banks on the plains this appears to be the exception rather than the rule.

5.3.2 Seasonal (temporal) variation in seed distribution across the Tafelberg landscape

5.3.2.1 Sites on top of Tafelberg (April and October collections)

There was initial concern that reduction in sampling intensity (but sampling a broader area) might reduce the validity of results from October[37]. The primary difference between April and October samplings, for sites on top of Tafelberg, was a roughly two-fold increase in the average number of plants germinated per sample (i.e. per sub-plot) in October compared with April sampling (Appendix 5.3a). There was also an overall, roughly equivalent increase in the number of both grass and shrub seedlings in October compared with April. This was possibly due to seeds that were distributed during autumn and winter (April to October 1998) germinating from these samples (Chapter 4). Estimated percentage grass cover, for the top north west and top south east sites, increased marginally from April to October with grasses forming the dominant canopy component in both seasons (Chapter 4). Based on preliminary data, 38 species germinated from April sampling and 33 species from October sampling with 15 of these common to both seasons' sampling[38].

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[37] Sites were sampled at different intensities (Chapter 2). During April, 30 samples/site were removed and in October 18 samples/site were removed. Comparative data for the two seasons relied on the mean number of seedlings (all categories) recorded from each season (Appendix 5.3). Main spatial trends appeared to be unaffected by a reduction in sampling intensity.

[38] The October sampling included only 2 sites on top of Tafelberg while April sampling investigated 3 sites with a higher number of replicates.

5.3.2.2 South east plains (April and October collections)

As for the top of Tafelberg, the main seasonal difference between April and October samplings for the SE plains was a roughly two-fold overall increase in the average number of seedlings germinating from samples (Appendix 5.3b). The average number of grasses per sub-plot rose in October by roughly 800% for closed-canopy samples[39]. These were predominantly ephemeral grasses and the total number of persistent shrubs and grasses did not change significantly between the April and October trials. Dicots (both ephemeral and persistent) were the dominant seedlings germinating from FSE germination trials. These constituted an average of 84% of the April- and 64% of the October germination trial seedlings with ephemeral species constituting 75% and 65% of these totals in April and October respectively. The mean estimated percentage canopy cover for the SE plains increased slightly from April to October with grasses (primarily *Aristida* spp.) forming the dominant canopy cover component in both seasons. Based again on preliminary data, a total of 35 species germinated from April samples while 42 germinated from October samples. Of these, at least 24 species were common to both seasons' samples.

5.4 Discussion of the state of seed banks in the Tafelberg locality

5.4.1 Implications of the seed bank study

Comparative data from an above-ground vegetation study at Tafelberg (E. Pienaar, pers comm) can not yet be drawn into this thesis, however preliminary data from germination trials correspond well with personal field observations. With few exceptions[40] germination trials appear to depict the above-ground picture adequately. It was hypothesized that remnant, genetically diverse seed banks would afford the luxury of restoration through appropriate, passive land management practises without active intervention. This does not appear to be the case and the principal issue arising from seed bank study is that there does not appear to be a significant seed bank of persistent nor relatively desirable plant species remaining on the plains of Tafelberg. Further, researchers have shown that there is often variable correlation (in some instances even a lack of correspondence) between species present in a seed bank and existing vegetation in a number of habitats (Brown and Oosterhuis, 1981; Bigwood and Inouye, 1988) especially those that are undisturbed (Warr *et al*, 1993). Warr *et al* (1993) furthermore noted that above-ground species composition and the composition of soil-stored seed banks, in regularly disturbed habitats, are often similar.

[39] The equivalent proportion for open-canopy micro-habitat samples was of the order of a 15-fold increase in the number of grasses germinating from the October sampling compared with the April sampling. The number of grasses germinated from open-canopy samples taken on the SE plains was very low when compared with closed-canopy samples (roughly 30% of the total, refer 5.3.1.2) but the trends were the same.

[40] Most noticeably that of the relatively common *Indigofera sessilifolia* which is present on the SE plains but yet has not been recorded in the germination trials.

While this study has not conclusively proved that this is indeed the case, nor can it prove prior existence of higher proportions of persistent or palatable plants on the plains, existing trends are clear. Through personal observation and data collected in the vicinity (Pienaar, pers comm) it appears that few sizeable communities, or even individual plants, of highly desirable rangeland plant species exist, or remain, on the plains and lower slopes surrounding Tafelberg.

5.4.1.1 Comparisons and analyses of germination trial data

Table 5.6 Comparison of estimated seed bank densities on and off Tafelberg, Eastern Nama Karoo, and data adapted from studies by other researchers in southern Africa and elsewhere. Data presented as estimated mean of seeds/m^2 ± SD where available.

STUDY AREA Habitat	**open-canopy**	**closed-canopy**	**other micro-habitat**	**Author/s**
Tafelberg, SA (Apr 1998)				F.E. Jones (this study)
SE Plains	467 ±191	1371 ±495		
top = plateau sites	267 ±83	693 ±64		
Tafelberg, SA (Oct 1998)				F.E. Jones (this study)
NW Plains	670 ±206	1337 ±553		
SE Plains	819 ±210	2530 ±559		
NW slopes	861 ±382	1572 ±790		
SE slopes	314 ±94	1214 ±675		
top = plateau sites	450 ±134	1433 ±251		
Goegap Nature Reserve, SA				Van Rooyen & Grobbelaar (1982)
old fields			41000	
plateau			23000	
ridge			5000	
valley			13750	
hillside			9750	
Tierberg Karoo Research Centre, SA				Esler (1993)
summer	71 ± 74	147 ±126		
winter	18 ± 28	61 ± 59		
Mojave Desert, USA				Nelson & Chew (1977)
plains (autumn '72)	269	3578		
plains (autumn '73)	6151	37259		
Wyoming, USA				Mull & McMahon (1996)
shrub-steppe plains	263±449	1128±1289		
Sonora Desert, USA				Reichman (1984)
plains - rodent diggings			15000	
natural depressions			63800	
plains	5600	13400		
North-western Cape SA				Dean *et al* (1991)
dune soils			*circa* 300 - 4000	
gravel plains			*circa* 100 - 1500	

Studies in other regions of southern Africa and elsewhere showed divergent estimations of seed numbers (Table 5.6). Not all researchers noted micro-habitat divisions and many did not sample in a variety of broad habitats. Nonetheless, estimates of seed densities (Table 5.6) showed high variability of seed numbers in a variety of habitats, micro-habitats and over seasons. Seed bank densities in the Mojave Desert were strongly influenced by good rainfall between the summer of 1972 and the following year (Nelson and Chew, 1977) and appeared to be seasonally influenced in the succulent Karoo (Esler, 1993). Similar seasonality appears at Tafelberg where, following winter seeding (Chapter 4), seed densities (October) were roughly two-fold greater than that found during sampling in the previous autumn (April) for both the SE plains and the top of Tafelberg. Inter-seasonal differences at Tafelberg were not limited to seed abundance but included a turnover in species diversity (5.3.2, above, Appendix 5.2; Tables 5.7 and 5.8) at both the intra-site and inter-site levels. Again, although species numbers on the SE plains are almost as high as those from the top of Tafelberg, the vast majority of these plains' species are ephemerals while most of those from the top sites are persistent (perennial) species.

It is thus clear from all studies which analysed habitat, micro-habitat and seasonal contrasts that seed bank densities show trends similar to those indicated by this seed bank study. All studies that investigated open- versus closed-canopy trends showed that closed-canopy micro-habitats invariably contain higher seed densities than open-canopy micro-habitats. High variability, with regard to seed densities, appears to be inherent between broad habitats and even between two years sampled during the same season within the same habitat.

Species-specific seasonal variation at the Tafelberg study site showed similar trends with notable intra-site and inter-site variation recorded. By way of example, a total of 56 species (preliminary data) germinated from the top of Tafelberg while 53 species germinated from the SE plains over both seasons' sampling (5.3.2, above). In total, 25 of these species were common to both the SE plains and the top of Tafelberg (Table 5.7). On examination of one or other of the seasons, the number of species identified (per habitat) drops as does the number of species in common. During October sampling for instance, 42 species were recorded from the SE plains and 33 from the top of Tafelberg[41]. Of these, 13 were common to both habitats. By comparison (from the results of October-sampling germination trials) the top of Tafelberg shared 13, 19 and 21 species in common with the NW plains, the SE slopes and the NW slopes respectively.

Table 5.7 Numbers of species common to the top and south east plains of Tafelberg in April, October or during both seasons (preliminary data). Some species were common to both habitats but germinated from samples removed during different seasons (e.g. germinated from April's top samples and from October's SE plains samples).

Habitat ↓ / **Sampling season →**	**April only**	**October only**	**April and October**	**Different seasons**	**total number spp. in habitat / common**
South east plains	11	18	24		53
Top of Tafelberg	23	18	15		56
common to both habitats	8	7	6	4	25

[41] A higher number of species is expected from the top of Tafelberg once plant identifications are completed. However, most of these yet unidentified species are perennial grasses (as well as some shrubs) not germinated from samples taken from the SE plains. It is expected that the species composition "gap" between these two habitats will widen once these data have been collated and interpreted in future research.

When compiled as an index of plant community similarity, the total results (including both seasons' sampling for the top and SE plains) are revealing. While comparison between the SE and NW plains showed highest similarity indices, the SE plains appeared to show higher indices of similarity with the top habitat (Table 5.8) than do any of the other sites.

Table 5.8 Index of similarity (*sensu* Sørenson, 1974) for five habitats on and off Tafelberg. Indices are expressed as percentages and measure the ratio of common to average number of species between any two habitats (Chapter 2) (preliminary data).

Habitat	**NW plains**	**NW slopes**	**Top sites**	**SE slopes**	**SE plains**
NW plains	**100**	46.2	26.8	37.5	57.1
NW slopes	*46.2*	**100**	45.2	50.0	37.5
Top sites	*26.8*	*45.2*	**100**	40.0	50.5
SE slopes	*37.5*	*50.0*	*40.0*	**100**	43.9
SE plains	*57.1*	*37.5*	*50.5*	*43.9*	**100**

When seasonal differences were isolated, however, contrasts in community structure between the top of Tafelberg and the SE plains were highlighted since Sørenson's similarity index dropped to 32% and 29% for the April and October samplings respectively (Table 5.9). It is believed that replicated sampling (across two seasons) for the top and the SE plains (but not the other three habitats) increased the probability of detecting common species between these two habitats. A number of the species in common between the top and the SE plains were ephemerals (e.g. *Ifloga glomerata, Bulbostylis humilis* and *Oropetium capense*). These germinated predominantly from samples from the plains but were rare (i.e. only one or two seedlings germinated) in samples from the top (Appendix 5.2). On the other hand the converse was found where perennial species, prevalent in samples from the top of Tafelberg, germinated in isolated samples from the SE plains in very low numbers and/or during only one season. These included *Sutera halimifolia*, *Digitaria eriantha* and *Pelargonium* cf. *multicaule*. Other species common to both habitats included ubiquitous species such as *Chrysocoma ciliata*, *Tragus berteronianus*, and *Pentzia incana* which were widespread on the slopes, plains and on the top of Tafelberg (Appendix 5.2).

Table 5.9 Index of similarity (*sensu* Sørenson, 1974) for two habitats, namely the SE plains and the top of Tafelberg, related to seasonal variation. Indices are expressed as percentages and measure the ratio of common to average number of species between the two habitats over two seasons (Chapter 2) (preliminary data).

Season / habitat	**April / SE plains**	**April / Top**	**October / SE plains**	**October / Top**
April / SE plains	100	31.5	62.3	21.7
April / Top	31.5	100	18.9	42.3
October / SE plains	62.3	18.9	100	29.2
October / Top	21.7	42.3	29.2	100

In general, the closest similarities in plant community composition (between habitats) appear to be between the NW and SE plains. The Sørenson index of similarity for these two habitats for the October sampling alone is 55.4% (Table 5.8). The lowest indices of similarity between habitats are evident between different seasons for the top and SE plains habitats (Table 5.9).

Of significant interest is that the seasonal contrast between the April and October sampling on the SE plains shows an index of similarity of 62% (Table 5.9) while that on top of Tafelberg is 42%[42]. This appears to indicate a trend that diversity on top of Tafelberg is higher than that found on the SE plains[43].

Seasonal contrast and variation are evident with respect to seed bank potential at Tafelberg. Micro-habitat differences between open- and closed-canopy sites are evidently the most significant in determining seed densities (Table 5.10) however multivariate analysis of variance of seed densities in response to site, micro-habitat and seasonality indicated profoundly significant effects for all three variables (Table 5.10). Further, although no significant three-way interaction was noted between the three, strongly significant two-way interactions were evident between season-x-micro-habitat; site-x-micro-habitat; and, to a marginally lesser extent, season-x-site.

Table 5.10 Results of a multivariate analysis of variance of seed densities (seeds.m^{-2}) in response to site (i.e. FSE1; FSE2; FSE4; TSE; TNW; and TSO) and micro-habitat (i.e. open- versus closed-canopy) measured during April and October (season). Degrees of freedom = df; F = F ratio; p-level = level of significance; * = significant.

EFFECT	df Effect	F	p-level
Season	1	42.4588	0.000000*
Site	5	8.1089	0.000000*
Micro-habitat	1	118.3763	0.000000*
Season-x-site	5	2.5194	0.029883*
Season-x-micro-habitat	1	13.2834	0.000320*
Site-x-micro-habitat	5	4.0803	0.001369*
Season-x-site-x-micro-habitat	5	1.0492	0.389045

5.4.2 Interpretation of germination trial data: a perspective

Seeds of many grasses and shrubs in arid and semi-arid environments germinate readily in response to rainfall and long term dormancy amongst perennial plant species appears to be the exception rather than the rule (Roberts, 1981; Rice, 1989; Esler, 1993). Evidence for changing

42 Only two sites were sampled during October in this habitat. It is likely this percentage may have been slightly lower had the top south central (TSO) site been sampled in October. Seven species were "unique" to this site (i.e. germinated only from samples from the TSO site and from no other site on top of Tafelberg). Fifteen species were "unique" to the Top south east site and a further 15 were "unique" to the top north west site.

43 These trends will be investigated further in future research.

composition of vegetation in the Nama Karoo is strong and a variety of environmental factors appear to be dynamically at play in this (or these) transformation/s. According to palaeo-ecological evidence (e.g. Meadows and Sugden, 1988; Cockroft *et al*, 1988; Sugden and Meadows, 1989; Scott, 1990; Avery, 1991; Bousman and Scott, 1994) a metaphorical pendulum of macro-climatic oscillations between wetter and drier cycles has been operating for millennia, even for aeons. During wetter cycles, grasses become relatively more abundant, dominating pollen samples from palynological studies (Scott, 1990). In drier cycles, such as over the past few millennia (Cockroft *et al*, 1988), and particularly over the past 300 years, shrubby vegetation becomes more abundant (Scott, 1990). This fluctuating cycle of alternating predominance between shrubs and grasses in response to macro-climatic conditions is clearly a natural phenomenon. The response of especially grasses to rainfall quantity, timing and seasonality is obvious even during shorter cyclical periods (Hoffman *et al*, 1990; Milton *et al*, 1995) (Chapter 4). This natural environmental certainty (or uncertainty depending on how these alternating cycles are viewed) could be used opportunistically to good effect to manage rangelands in event-driven climates (Mentis *et al*, 1989; Westoby *et al*, 1989; Milton and Hoffman, 1994).

The crucial obstacle facing rangeland researchers and managers today lies with the existing state of an apparently degraded resource that may have gradually lost the ability to bounce from karroid scrub to grassland and back again (a "buffer capacity") depending upon the over-riding climatic conditions. This buffering capacity naturally includes firstly the associated species-specific micro-flora and -fauna (e.g. Allsopp, 1999; Whitford, 1999) and secondly the species-specific agents of pollination and dispersal (e.g. Esler, 1999). Associated organisms are depleted as plant populations dwindle placing further stress on reduced plant populations, potentially leading to localised extinctions (Bond and Richardson, 1990).

Persistent grass and dicot species are indeed present above ground on the plains, but these are predominantly "less-palatable" species[44] relative to those found in abundance on the top and slopes of Tafelberg. Soil-stored seed banks appear to be derived from existing above-ground species. In the event that a higher diversity and abundance of palatable and otherwise desirable species ever occurred in this area then remnant seed banks of these species appear to be at least depleted and quite possibly exhausted. Owing to the presence of small, isolated remnant populations or individuals of, for example, *Themeda triandra*[45], *Sutera halimifolia*, *Sutherlandia frutescens* and *Walafrida geniculata* on the plains however, it is likely that a higher proportion of highly palatable species did exist on the plains in historical

[44] The dominant persistent dicot species observed on both plains are *Pentzia incana*, *Eberlanzia ferox*, *Chrysocoma ciliata*, *Drosanthemum duplessiae*, *Zygophyllum incrustatum*, *Lycium* spp. and *Eriocephalus ericoides* while the dominant persistent grass is *Eragrostis obtusa*. (personal observation). These observations are similar to those recorded from the germination trials.

[45] A small population of *T. triandra* on the plains is being monitored at the time of writing (Hendricks, pers comm).

times. This phenomenon has been documented in rangeland systems elsewhere (e.g. Westoby *et al*, 1989; O'Connor, 1991) and Hoffman (1989) found over-grazed areas in the Eastern Karoo to be lower in species diversity than neighbouring, better regulated tracts.

Given the history of ranching in the Tafelberg locality (refer 1.5.2) it is likely that vegetation change and habitat transformation over the past two centuries has taken place at an accelerated rate, leading to a depleted natural resource and also logically to less biologically diverse habitats.

Under "utopian" conditions, at the start of a new cycle of increasingly wetter climatic conditions, small isolated populations of highly palatable grasses would occupy favourable remnant habitats on the plains. These would be source populations for replenishing and revegetating the plains, taking advantage of their relative success during wetter conditions. Under present day conditions many, if not most, of these remnant populations no longer exist owing to continued heavy grazing and habitat transformation[46]. This loss of buffer capacity is by no means limited to grasses but is believed to extend to the dicotyledonous fraction of the vegetation component.

The reduction of species diversity and basal cover may in itself lead to habitat degradation that in turn leads to loss of biological diversity (Bosch and Kellner, 1991). Presently, we are left with these remnant habitats primarily in the form of tracts of land that are relatively inaccessible to livestock, on mesas or in road reserves, for example. These refugia undoubtedly play a crucial role in retaining some of the species that are able to thrive under diverse and often adverse habitat conditions. However, these often isolated and spatially separated refugia may not be suitable for the survival and spread of some habitat-specific species, or clones of species, that are intrinsically adapted to "life on the plains" and all that this entails.

The future desired state of the plains surrounding Tafelberg and indeed those in the broader Nama Karoo Biome will need to be determined through discussion and workshopping of options. It is likely, given the depauperate state of existing seed banks as well as the present (and recent past) level of utilisation of the area that active intervention will be required to improve the overall above-ground species composition of the plains.

In summary, this assessment of seed banks on- and off Tafelberg appears to indicate strongly that the low-lying rangelands are degraded. The seed banks on the plains show no great promise of restoration potential nor of latent, currently unrepresented, biological diversity. Since low seed densities are so clearly associated with open-canopy micro-habitats (5.4.1.1, above) reseeding of selected "refuge"[47] habitats with appropriate nurse- and pioneer

[46] For example: wetland degradation through cultivation of lucerne and other fodder crops; water course diversion; excessive utilisation of both seasonal and permanent wetland and riparian areas by livestock, etc.

[47] These are small habitats that could be set aside on the plains, to act as refugia for desired plant species and clones, in order to maintain species diversity through a reserve or conservancy network approach.

plants will need to be undertaken, coupled with management regimes that capitalise on opportunistic management (e.g. through choosing appropriate seasons for revegetation attempts) of these rangelands. It is critical to set about increasing both vegetation cover as well as the numbers of desirable plant species on the plains.

Some level of grazing is considered desirable for at least certain Karoo species (Milton and Dean, 1990) to stimulate shoot growth (McNaughton, 1983) and preferably with rest periods between grazing episodes (Van der Heyden *et al*; 1999). However, the realities of historically inadequate and inaccurate stocking rate estimates have today arguably led to a break-point in long term sustainability of these semi-arid systems. It is up to researchers and land managers as to how constructively and creatively these challenges are faced.

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CHAPTER 6: INTEGRATING SOIL ANALYSIS, PLANT PHENOLOGY AND SEED BANK DATA: TOWARDS THE ECOLOGICAL RESTORATION OF DEGRADED RANGELANDS

6.1 Approaching an integrated seed bank study in the Tafelberg locality

At the outset of this thesis, several key questions were raised with regard to the state of soil-stored seed banks in the Tafelberg locality (1.4.1). These questions raised issues *apropos*:

- the methods to apply in order to obtain adequate information on soil-stored seed banks within the constraints of a two-year study;
- the identification of the various macro- and micro-habitats, on and off Tafelberg, in which soil-stored seed banks are found;
- the influence that these diverse habitats exert on seed bank composition and distribution;
- the environmental pressures, hazards and variables that influence the persistence and composition of seed banks.
- the natural distribution and habitat preference of plant species on the top and plains of Tafelberg and whether many plant species would have ranges that spanned both the plains habitats and the mesa habitats; and,
- the composition of soil-stored seed banks and whether these conformed to that of existing, above-ground vegetation, i.e. whether dormant seed banks of palatable and productive plant species persist in soils, particularly those of the plains.

Chapter 2 presents an account of methods applied for all components of this seed bank study. A discussion regarding methodological approach is advanced in Chapter 7, presenting both alternative approaches to this study and identifying potential studies leading out of this work.

6.2 A review of findings from the integrated seed bank study at Tafelberg

Three component studies were undertaken in order to provide firstly baseline data focusing on the soils of Tafelberg and surrounding plains (Chapter 3); on selected environmental conditions and associated plant phenological response (Chapter 4); and on the spatial and temporal distribution and composition of soil-stored seed banks on and off Tafelberg (Chapter 5). A literature survey was also undertaken in order to provide a structural basis for the overall study.

The underpinning postulation for the umbrella study (refer Chapter 1; 1.2.1) is that conservation islands, in the form of isolated and less accessible mountains (refer Chapter 1, 1.5.4.), harbour plant species once abundant on now degraded and over-utilised plains. This seed bank study hypothesised firstly that seed banks are degraded to a degree that corresponds significantly with observable habitat degradation. Nevertheless, it was proposed that dormant seed banks of palatable plant species remain on the degraded plains and that while the plains may presently appear to be species-depauperate[1] relative to montane refugia, that this is an aspect relating primarily to above-ground vegetation composition. Further contentions were firstly that appropriate future management of these plains will facilitate restoration of former plant species diversity and composition and secondly that the relatively less degraded hills may passively[2] or actively[3] be used as future sources of seed for restoration of degraded plains. What these hypotheses somewhat naively did not take into account, was the existing condition of the plains' habitats and micro-habitats and the centuries of rangeland utilisation that have led to the present day circumstance of a generally degraded landscape.

6.2.1 A brief review of habitat and micro-habitat differentiation on- and off Tafelberg

Five macro-habitats were identified in broad terms as the south east (SE) plains and SE slopes, the north west (NW) plains and NW slopes and the top of Tafelberg. These habitats were identified in the field and substantiated by findings from two baseline studies (soil analyses (Chapter 3) and germination trials (Chapter 5)). Two primary micro-habitats, namely those under the canopy of plants (closed-canopy) and inter-plant spaces (open-canopy) were distinguished. A variety of factors was found to contribute to spatial heterogeneity of all macro- and micro-habitats. These included obvious factors of soil type (Chapter 3) and altitude[4].

Soil habitat appeared to play a significant role in contributing to habitat differentiation and thus to plant species composition or in this case (with species-specific data yet incomplete) plant category composition (Figures 6.1 and 6.2). In these figures, plant category composition[5] of emergent seedlings was related to key soil characteristics of soil texture (Figure 6.1) and soil nutrient composition (Figure 6.2). The results were processed with the aid of a multivariate direct gradient analysis technique "Canonical Correspondence Analysis"[6] (CCA) (*Sensu* Ter Braak, 1986) (Chapter 2). The resultant CCA ordination diagrams provided an indication of major trends identified during soil analyses (Chapter 3) and seedling emergence trials (Chapter 5) but further interpreted plant category composition with respect to soil environment, or basic habitat, variables.

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1 Primarily of palatable and persistent grass and shrub species.

2 "Passive" in this instance relates to the natural spread of wind-, water- and animal-dispersed seed into degraded areas.

3 "Active" in this context implies harvesting seed from source populations followed by active reseeding of degraded areas.

4 Altitudinal gradients are assumed to influence factors including temperature, precipitation and grazing intensity.

5 Refer Chapter 5, Table 5.1 for further detail on plant categories as applied for this study.

6 Using the Windows- and DOS based programme application "CANOCO".

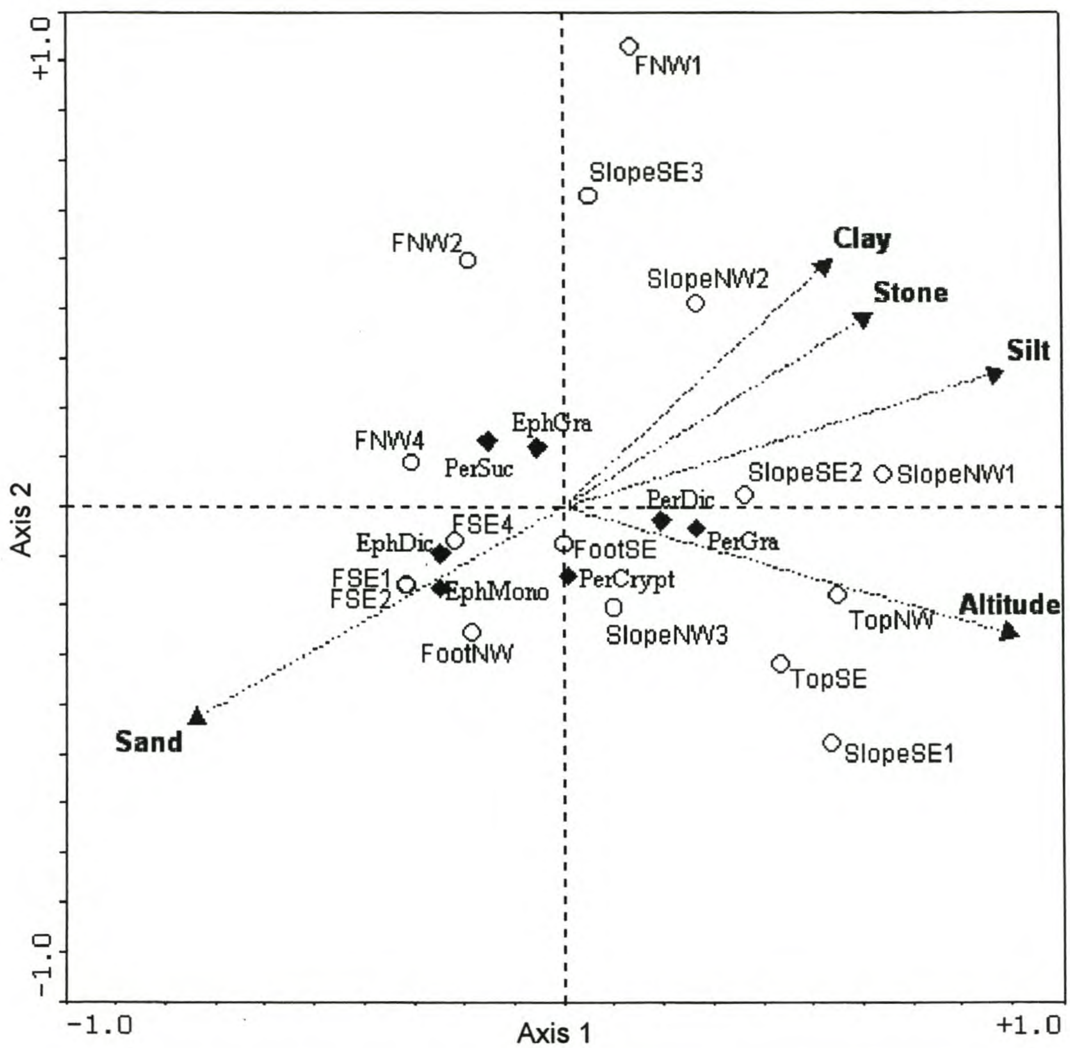

Figure 6.1: The distribution of plant categories (refer Table 5.1) of emergent seedlings from samples removed from closed-canopy micro-habitats at sixteen sites on the top, slopes and plains of Tafelberg. A canonical correspondence analysis (CCA) diagram with sites (O), plant categories (◆) and environmental (soil texture and altitude) variables (arrows).

Plant categories are: PerSuc = perennial succulent, PerGra = perennial Grass, PerCrypt = perennial cryptophyte, PerDic = perennial dicot, EphGra = ephemeral grass, EphDic = ephemeral dicot, EphMono = ephemeral monocot.

Sites on plains are prefaced with "F". FSE1 and FNW1 are furthest from Tafelberg on south east and north west plains respectively. Lowest sites on slopes (above footslope sites) are SNW3 and SSE3. (Figure 2.1 and Table 2.1 contain detail on site location and coding). Clay, stone, silt and sand values were attained through relative percentage composition of soil textural components in each site.

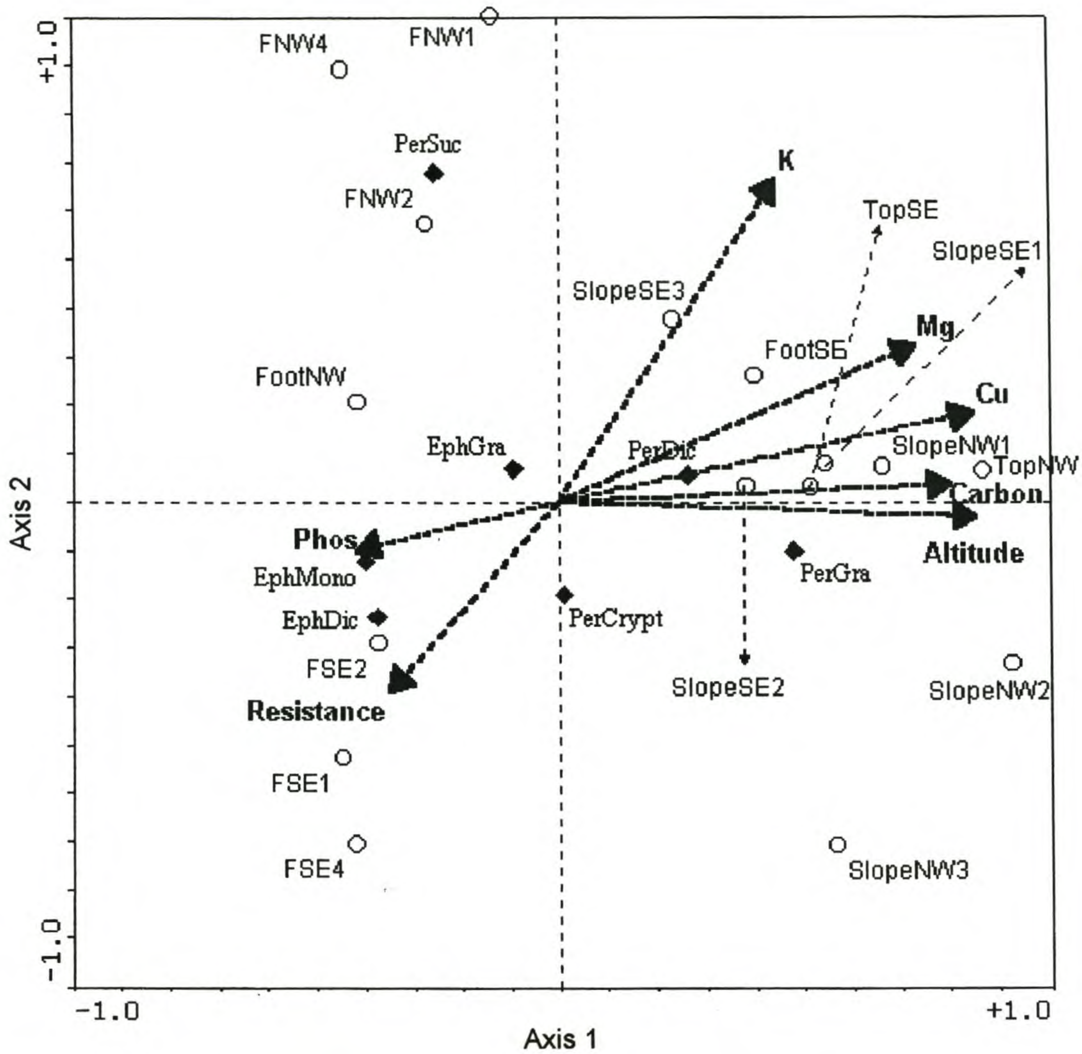

Figure 6.2: The distribution of plant categories (refer Table 5.1) of emergent seedlings from samples removed from closed-canopy micro-habitats at sixteen sites on the top, slopes and plains of Tafelberg. A canonical correspondence analysis (CCA) diagram with sites (O), environmental (soil nutrient) variables (arrows) and plant categories (◆).

Plant categories are: PerSuc = perennial succulent, PerGra = perennial Grass, PerDic = perennial dicot, PerCrypt = perennial cryptophyte, EphGra = ephemeral grass, EphDic = ephemeral dicot, EphMono = ephemeral monocot.

Sites on plains are prefaced with "F". FSE1 and FNW1 are furthest from Tafelberg on south east and north west plains respectively. Lowest site on the slopes (above the footslope sites) are SlopeNW3 and SlopeSE3. (Figure 2.1 and Table 2.1 contain further detail on site location and coding). Soil nutrient values used were untransformed soil analysis measures as presented in Appendix 3.1.

While the presence of ephemeral- and perennial species was not strongly correlated with soil texture, there was nevertheless some clustering of broad habitats (i.e. slopes, plains and top sites) along soil textural gradients (Figure 6.1). Seedlings of ephemeral dicots and monocots germinated mainly from sandy habitats[7] while perennial- grasses and dicots germinated primarily from samples removed from higher altitude habitats with a higher fine-texture fraction (primarily silt but also clay). Seedlings of perennial succulents and ephemeral grasses germinated mainly from low altitude sites apparently largely independent of soil texture.

Several trends emerged from CCA ordination of soil nutrient variables (Figure 6.2). Ephemeral dicots and monocots appear to be the primary plant categories that thrive and produce seed effectively in nutrient depauperate[8] soil environments. It must however be recognised that sites on the plains are relatively more disturbed than those on the upper slopes and top of Tafelberg. It is possible that a combination of disturbance factors (climate, grazing, trampling and reduced canopy cover) on the plains may in fact facilitate the success of ephemerals (Dean and Milton, 1991; Van Rooyen, 1999) as much as (or possibly more than) the natural soil habitat (e.g. texture or nutrient levels). On the other hand, disturbance in the form of grazing lowers the production (both vegetative and reproductive) of persistent, palatable species (e.g. Turner, 1999) and may reduce the number of safe-sites in which seedlings of these species can germinate (and establish) without being eaten (Oesterheld and Sala, 1990; Milton, 1994).

Reduced levels of soil nutrients[9] through habitat degradation may be a limiting factor for fast and successful establishment[10] of persistent and palatable grass- and shrub species during times of adequate rainfall and low-intensity (or absence of) grazing. While this cannot be proven within the limitations of this study, there remains an over-riding perception of strong selection pressures against persistent, palatable grasses and shrubs through a combination of factors including habitat degradation, over-grazing and climatic extremes on the plains.

Seedlings of perennial grasses (and to a lesser extent perennial dicots) germinated almost exclusively in association with higher altitude sites. Associations between higher altitude sites and higher nutrient levels of carbon, copper and magnesium are debated in Chapter 3. There is a strong correlation between higher soil organic matter (found in higher altitude sites) and these nutrient elements for several reasons that include the relatively high cation exchange capacity of humic matter and clay which are relatively more abundant on top of the mountain (Figure 6.1).

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[7] Sandy soils are more prone to degradation relative to those with a higher clay content (Brady, 1990). Refer Chapter 3 for further detail on this point.

[8] The plains are depauperate in the leachable nutrient- and trace-elements potassium, carbon, copper and magnesium relative to the top of Tafelberg.

[9] These nutrients are vital for establishment and growth (Chapter 3; 3.3).

[10] At least to the point of reproductive maturity.

A further trend drawn from Figure 6.2 is the relative association of particularly the plains' sites along soil nutrient and soil reaction gradients. Not dealt with in detail in Chapter 3, resistance is a measure of dissolved ions (in this case those of electrolytic soil nutrients) in soil solution (Brady, 1990). The higher the resistance, the lower the relative abundance of these ionic solutes in the soil. Resistance of soils on the SE plains was lowest overall of all habitats. This is directly correlated with low levels of potassium (which is the most readily leached nutrient) in the sandy soils found on the SE plains and (Chapter 3, 3.3.2.2.1(a), Appendix 3.1).

In conclusion, the habitats and related soil environmental properties appeared to play a role (not unlinked to grazing intensity) in determining the relative abundance of seedlings germinating within broad plant categories defined by this study. Further, the first hypothesis proposed for this study namely "The composition of seed banks is strongly correlated to the degree of habitat degradation at both the landscape and micro-habitat scale" aptly describes findings from both the soil analysis and germination trial studies.

What has not been satisfactorily proven is whether degraded habitats have influenced vegetation composition i.e. has vegetation composition been influenced by climate; by grazing; by habitat degradation; or, by a combination of all three? What of the environmental hazards, pressures and variables that influence persistence and composition of seed banks? What may be deduced regarding the condition and distribution of seed banks in the vicinity of Tafelberg? Finally, if the above-ground vegetation appears to have changed, what effect has this had on seed banks and the natural distribution of species in this locality?

6.2.2 The influence of environmental stress on seed bank composition and distribution

6.2.2.1 Soil habitat pressures and hazards

In Chapter 3, through interpretation of soil analyses from on- and off Tafelberg, there is an attempt to show probable degradation of the NW and SE plains' habitats. The sandy SE plains are naturally prone to erosion owing to the erosive nature of sandy soils. Coupled with long-term, high-level use and concomitant loss of overall basal cover (through grazing) these soils are arguably degrading at a rate faster than would be predicted for a natural habitat under medium or low-intensity grazing. Soil nutrient levels (of especially the leachable nutrients) are generally low in comparison with those from the slopes and top of the mountain and are also low relative to those on the NW plains. It is mooted that, although leaching and erosion are natural aspects of these sandy soils, a higher rate of nutrient loss is taking place and may eventually (coupled with loss of above-ground biomass through grazing and high disturbance) lead to a consequential depletion of available nutrient resources in this habitat.

The NW plains are low-lying relative to the SE plains, forming part of an apparently extensive seasonal wetland or a system of ephemeral pans and have a much higher overall clay fraction than the SE plains. While deposition of silt and clay appears to be the more common feature of these plains, a relatively high water table further renders these plains prone to salt accumulation which is enhanced by the high relative cation exchange capacity of clay particles. It is mooted that rates of deposition (of silts and nutrient salts) in pans (such as these plains) are accelerated through (amongst other) higher rates of erosion elsewhere.

The relatively high water table on these plains contributes to salt crust formation through accumulation and evaporation and thus to a potentially toxic build-up of salts on or near the soil surface (e.g. Brady, 1990). Van Rooyen (1999) and Palmer *et al* (1999) cite several studies which confirm that high salt levels inhibit germination of a diversity of plant species. Thus, while contrasting processes and pressures operate on these two very different habitats, the long term outcome could be similar in that habitat degradation is taking place at a higher rate than may naturally occur, with attendant negative impacts on the biological diversity and productivity of the two distinct systems. It is important to bear in mind that this phenomenon has been taking place over an extended period.

Significant soil environment impacts, that may influence seed bank composition, distribution and survival were identified. These included:

- soil habitat degradation through diminished plant cover and increased surface run-off;
- habitat degradation through soil loss and altered soil texture;
- habitat degradation through trampling and compaction thereby reducing soil permeability;
- loss of seed during soil loss events (erosion);
- toxicity build-up through salt accumulation (deposition);
- apparent loss of soil organic matter through extensive grazing; and,
- accelerated alteration of soil nutrient composition through a variety of factors including leaching, salt accumulation and soil erosion.

6.2.2.2 Plant phenological responses to environmental pressures

The study on plant phenological response to rainfall and grazing (Chapter 4) showed that while peaks of budding and flowering are apparent on the top and plains of Tafelberg[11] the seeding response follows a rather more protracted period. The reproductive response is believed to be species-specific, guild-specific and also to be influenced by environmental differences (such

[11] These peaks apparently follow periods of rainfall and probably higher temperatures.

as habitat and micro-climate) as well as intra-specific heterogeneity. Differential fruiting- and seed ripening periods further complicate the seeding response. Overall there appears to be some activity relating to plant fecundity at all times during the year, whether this is purely survival and some seed distribution during the dry winter months, or vegetative growth and active reproduction during higher rainfall months.

The implications of this (admittedly limited) study (refer Chapter 7; 7.1 (i) and (j)) are that grazing, at all times of the year, can impact on plant growth and on reproductive activity through factors that include:

- altered above-ground vegetation composition through preferential grazing of palatable species by domestic livestock leading to a predominance of less palatable or non-palatable species;
- loss of vegetative growth and thus reproductive potential for all plants grazed;
- loss of seed or reduced reproductive output for all plants grazed; and,
- further adverse change in the above-ground vegetation composition leading to reduced seed bank densities of desirable plant species.

6.2.2.3 Limitations placed on seed banks by environmental pressures: results from germination trial research

Results from germination trials on the SE and NW plains indicate high levels of disturbance on the plains and footslopes relative to the upper slopes and top of Tafelberg. This is deduced from the composition of plant species germinating during seedling emergence trials (Chapter 5). Generally, ephemeral species thrive under high-disturbance and high-stress regimes owing to the capacity of this plant guild to thrive under adverse conditions. Such conditions may include limited available time for growth and reproduction owing to pressures of regular, high intensity grazing and also the limited and irregular precipitation windows common in the Nama Karoo.

The proliferation of ephemeral species in response to environmental disturbance has been identified in many regions and vegetation types including Renosterveld (e.g. Rebelo, 1995), Namaqualand (e.g. Van Rooyen, 1999) and elsewhere in arid regions (e.g. Fox, 1989). The naturally harsh environmental conditions of semi-arid and arid regions appear to lend themselves to the success of ephemeral species (Fox, 1989). The climatic constraints of the study region (coupled with injudicious management) may have expedited the situation at Tafelberg, leading to a plains' flora dominated by low-palatability species that include tiny ephemerals, spinescent species and toxic plants (Chapter 5). Most of the palatable species observed on all the plains during field trips were sheltered from grazers by spinescent or otherwise less palatable nurse plant species. Most of the species germinated from plains' samples during seedling emergence trials were ephemeral dicots and grasses as well as a mix of spinescent and other less palatable species. Remarkably few seedlings from the plains' samples were of highly palatable or even persistent species. It is likely that seed densities of desirable species on the plains are low, to extremely low.

Clear indications that seed bank densities are related to micro-habitats and affected by season were provided in Chapter 5 (refer 5.4.1.1). Reduced overall plant cover through grazing arguably reduces total seed abundance and may in turn lead to a further reduction in total canopy cover. This in turn reduces the number of seed-trapping micro-habitats and also reduces seedling safe sites. In other words, loss of canopy cover through:

- excessive grazing and thereby lost vegetative and reproductive output; and,
- reduced successful plant establishment owing to erosion, lowered reproductive output and degraded habitats

directly and adversely affects seed densities, especially of palatable and otherwise desirable plant species.

6.3 Comparisons with other studies in semi-arid regions

Owing to the short period of time spanning the collection and interpretation of data, only trends and probabilities can be inferred and these are essentially limited to the study locale. When coupled with research from localities in other semi-arid and arid regions however, data collected and analysed from Tafelberg take on a more widespread significance, providing a picture of heavily utilised rangeland plains.

There are, for example, similarities to rangeland studies in Namaqualand (Steinschen *et al*, 1996). These authors described a vegetation relatively denuded of palatable herbaceous plants and dominated by unpalatable species and annual grasses (in this case *Stipa capensis*). This parallels the Tafelberg scenario where *S. capensis* is substituted by an abundance of the annual grasses *Aristida congesta* and *A. adscensionis* (refer Chapter 5, 5.3.2.2). The seeds of all three of these low-production grass species can damage wool quality and are known to cause skin injuries and pelt damage to sheep (Steinschen *et al*, 1996; Gibbs Russell *et al*, 1995).

Depth trials conducted at Tafelberg indicated a paucity of seeds below a 5cm depth. This concurs with numerous studies on the vertical distribution of seed banks in semi-arid and arid regions globally (refer Chapter 5, 5.3.1.1). There are also marked parallels to studies in the Succulent Karoo described by Esler (1993). This author noted micro-habitat differences in seed abundance and -distribution, finding much higher numbers of seeds in closed-canopy than in open-canopy sites (refer Chapter 5, 5.3.1.2). She further described seed bank persistence of perennial species, noting seasonal variability in seed abundance and transience of seeds of especially perennial or shrubby species. Both of these trends appear to be very similar to those found at Tafelberg.

A range of other broad comparisons between this study and research elsewhere may be drawn. These include firstly observed gradients of grazing intensity such as those researched around water-holes in the Kalahari by Van Rooyen *et al* (1994). A variety of grazing gradients, from high to low intensity use were observed spatially at Tafelberg from close to watering points to the far edge of stock camps and also from the heavily grazed plains up the slopes of Tafelberg although none of these were quantified empirically. Secondly, numerous authors have described overall vegetation change in response to excessive rangeland utilisation. These include the prevalence of spinescent, toxic or otherwise unpalatable species in above ground plant communities (e.g. O'Connor, 1991). Such plant community descriptions closely mirror the scene at Tafelberg (refer Chapter 4, 4.2.1) where centuries of use by horses, ostriches, sheep and cattle breeds have left expanses of bare, shallow soils covered in places only marginally with perennial plants that are dominantly survivor species (those which are tactically or systemically unpalatable to livestock). Following rains, an abundance of ephemeral plant species germinates. Many of these are tiny (<5cm), live for less than three months, seed prolifically and die. Annual pioneer grasses that are indicators of disturbance also prevail (personal observation). These include *Aristida* spp. and *Tragus berteronianus*, species considered by Gibbs Russell *et al* (1995) to be probable indicators of poor veld management. Finally, in studies on defoliation in Sahel grasslands, Turner (1999) noted that species composition was strongly correlated with both recent rainfall distribution and long term grazing history of rangelands and less associated with current (or very recent) grazing use. Further, this author notes that grazing history can affect physical and chemical properties of soils and argues that both climatic variability and long term grazing history are the two most important factors affecting the condition, productivity and plant species composition of semi-arid rangelands.

It is probable that much damage was done to the plains surrounding Tafelberg through extensive ostrich farming[12] during the "ostrich feather boom" of the late nineteenth century[13] and intensive sheep farming between the early 1900's and the late 1960's. This intensive stock farming did not necessarily abate with the initiation of the Stock Reduction Scheme in 1969 (Dean and Macdonald, 1994; Hoffman *et al*, 1999) and the combination of intensive grazing and severe drought periods must have caused significant damage to the habitat, vegetation composition and seed banks.

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12 The impacts of unsustainable ostrich farming were noted by Gatimu (1996)
13 Described by Eve Palmer in "The Plains of Camdeboo"

Given the dynamic, non-equilibrium nature of semi-arid rangelands, during drought periods even low-intensity grazing (i.e. relative to stocking rates as prescribed by Department of Agriculture) may be excessive. While recommended stocking rates were believed by officials and managers to be appropriate and optimal, during high rainfall months or years, researchers (e.g. Danckwerts, 1982; Danckwerts and King, 1984) argued that recommended stocking rates exceeded ecologically sustainable stocking rates and would lead to veld degradation especially if the veld was in poor condition at the outset. It is likely that long term use of rangelands over the centuries would inevitably, albeit gradually, have degraded rangelands and these authors' findings should ring a warning bell for those whose lands may be threatened by degradation or for those who are attempting to rectify previously degraded rangelands without consideration of both climatic- and grazing pressures.

6.4 Discussion of integrated pressures on seed banks on- and off Tafelberg

The changes in vegetation, at Tafelberg and elsewhere, through the combined pressures of climate, intensive (and/or) long term grazing are debated in Chapters 3 and 4 of this thesis. Soil loss and soil deposition further deplete and transform habitats (Chapter 3) and changes in soil nutrient status are probable owing to the continued removal of plant material without significant returns to ensure sustainability of the soil environment. Coupled with soil and plant cover loss is the loss of seeds (especially small seeded species, but also wind- and water-dispersed larger seeds) that are washed away by sheet erosion or swept far away from their basic habitat by winds to be buried in silts or deposited in unfavourable habitats. Erosion is keenly exacerbated by a reduction in plant cover (Snyman and van Rensburg, 1986; Brady, 1990) and those plant species that are able to firstly flower and then to set seed in the face of grazing pressures and irregular rainfall may lose a consequential percentage of seed through soil loss.

The first hypothesis posed namely "The composition of seed banks is strongly correlated to the degree of habitat degradation at both the landscape and micro-habitat scale" (Chapter 1, 1.4.2) is clearly valid. Soil loss contributes to a changing basic growth medium, especially in interplant spaces, through reducing already-shallow soils to a bare minimum of substrate covering decomposing shales and hardpan. Few seedlings are able to readily penetrate such dense soils in the search for ground moisture and few can survive the intensity of summer sun in the baked interplant spaces. Interplant spaces thus become the literal breeding ground for short-lived, small-rooted species that can opportunistically take advantage of high upper soil-moisture gradients following rain events or -periods. As grazing continues unabated interplant spaces increase in size and plant islands reduce in volume leading to further acceleration in soil and seed loss. Reduced basal (or canopy) cover (through grazing and/or drought) reduces not only plant islands (that hold soils in place) but will also diminish the ability of natural veld to trap seeds. Seeds, which require a deeper soil medium for survival, that land in these relatively impenetrable interplant spaces may germinate but will arguably not survive without the means to "follow" the downwards soil moisture cline between rainfall events and will undoubtedly perish. A "Catch 22" situation thus arises, or has already arisen, in that the reduction of overall plant cover is likely to reduce not only the output of existing cohorts but also adversely impacts on maintenance and survival of future generations in the form of seed banks.

With regard to the second hypothesis proposed by this study, namely "There is greater floral diversity stored below ground in degraded areas than currently represented above ground" both the above-ground vegetation (personal observation; E. Pienaar, pers comm) and seed banks (Chapter 5) on the plains of Tafelberg appear to be depauperate in perennial and palatable species. Both the above-ground plant communities and seed banks show strong trends of long term abuse through injudicious grazing practises. There appear to be no pleasantly surprising findings with regard to dormant seeds of palatable species on the plains that are awaiting a less stressful environment to germinate and establish.

The third hypothesis proposed in Chapter 1 stated that "...soil-stored genetic material may be used to re-establish the presence of broader floral biodiversity". While ephemeral species are abundant and contribute in part to a soil-holding function, rangelands on the plains appear to have insignificant seed banks of desirable species for rangeland use. A comparison between seed banks on the top and plains of Tafelberg showed a contrasting abundance of plant categories (Figures 6.1 and 6.2; Chapter 5, Table 5.4). If perennial grasses did once occur abundantly on the plains of Tafelberg these species appear to be long gone. Judging by preliminary data, from species-specific assessment of seedling emergence trials, even the so-called "Increaser II" species *Digitaria eriantha* is largely absent from seed banks on the plains.

Finally, with respect to the fourth hypothesis (Chapter 1) namely "Hills are relatively less degraded than plains, acting as refugia for populations of species that may be used as a source of material for restoration of degraded plains (e.g. for reseeding of the plains)" the closest source populations for seeds of palatable and desirable species[14] are mainly presently located on, or in, areas that are relatively inaccessible to livestock. These include the upper slopes and tops of mesas (such as Tafelberg) and fenced off areas such as road reserves (e.g. Milton and Dean, 1988; Palmer *et al*, 1999). The basic soil, aspect and gradient habitats on the slopes and plains of Tafelberg are divergent from those found on either of the plains for differing reasons. There are a number of generalist plant species that

[14] In other words, seeds of any palatable species that once occurred on the plains but that have now been excluded, or forced into localised extinction, through unsustainable land management practises.

are able to thrive under a diversity of habitat conditions (refer Chapter 5; 5.3.1.6 and 5.4.1) and these may be able to spread, through various means of seed dispersal, onto the plains of Tafelberg. The time such a process as this would require is however not expected to be economically viable nor practicable within the limits of the human lifetime. Further, it may also be possible that ecologically sustainable stocking rates are not economically viable (Kellner and Bosch, 1992).

6.5 Conclusion and preliminary recommendations for further action

It appears then from both the observed rangeland condition and from results of germination trials (Chapter 5) to be convincing that the plains surrounding Tafelberg may rightfully be described as degraded. It is contended that this has been brought about through a long history of excessive land use by land managers who did not take the sensitivity of the total environment into account. In other words, when low moisture availability for plant use was a threat to plant survival and to reproductive capacity, land managers inadvertently (or in some cases knowingly) continued to stock livestock at rates that exceeded ecological (if not also the human-estimated) carrying-capacity of veld.

While contemporary land managers may be prepared to down-size herds in order to improve veld condition, this may not be a solution since immediate improvement in veld condition is unlikely (Wiegand and Milton, 1996). The inertia of recovery from long term over-utilisation is estimated to exceed that of the average farmer's active lifetime (Wiegand and Milton, 1996; Jeltsch *et al*, 1999). This may lead to a loss of enthusiasm and optimism on the part of land managers and could compromise long term restoration and conservation objectives. It is thus vital that achievable and proactive restoration strategies be sought that capacitate manager-and-researcher teams to accomplish observable short term goals. These short term goals must be structured within the framework of a long term strategy for restoration and improvement of the productive capacity and biological diversity of semi-arid rangelands.

There are significant differences between habitats on the top, slopes and plains of Tafelberg and a need exists to experiment with which desirable species presently found on the top and slopes of the mesa will establish, survive and promote the establishment of other plants on the plains. There is a need to create safe-sites for germination and micro-habitats for seedling survival. Experimentation with restoration methods that builds on existing and local affordable technologies for restoration must be encouraged and funded at the highest level. Such research can be applied world-wide and, as South Africa is already at the forefront of restoration ecology and restoration technology research, could provide valuable insight into a far-reaching global dilemma. Where possible, research must be conducted on active farms in order to improve the researcher-manager relationship and to further active involvement with land managers.

Managers who see results are more likely to experiment further and derive their own successful technologies, thereby encouraging other managers to attempt similar strategies.

Rangelands have been treated as resilient systems that "renew" without intervention and little attempt has been made to ensure that nutrient and organic matter levels are kept at acceptable levels. Rangelands could be viewed as croplands and efforts could ensure that nutrients and organic matter are replaced at a rate at least equivalent to their overall loss by grazing. This could be achieved through ingenuous methods of grazing management that ensure that nutrient cycles are viewed as part of an integrated management objective to actively improve biological diversity, thereby optimising grazing potential. Conserving and managing mesas as reservoirs of floral and faunal genetic material and biological diversity will be an excellent start to approaching the potential restoration of degraded rangeland plains but it may not be enough. Active intervention and innovative strategies will be required that include the identification of suitable expanses of rangeland plains as conservation habitat to be managed for conservation of floral and faunal diversity in diverse and functional plains habitats. These conservancies may become key components of the rangeland landscape, providing sources of seed at the local level for rangeland managers to reseed selected habitats on their own farms.

Economic schemes that may include tax incentives could be devised for managers who actively seek to improve biological diversity through conservancies and localised community-based action. National, regional and district level strategic and integrated environmental management frame-works need to be formulated through consultative and inclusive workshopping on soil loss, rangeland degradation and alternative land use and management themes.

Degraded systems are prone to further degradation, being more sensitive to the vagaries of natural stresses such as droughts (e.g. Snyman and van Rensburg, 1986; Hoffman and Todd, 1999). On the other hand the sustainable management of terrestrial ecosystems, through the maintenance and improvement of vegetation composition and total environmental functioning, allows that ecosystem to recover, or to bounce back, more readily after disturbance. Rangeland condition should be viewed by landowners and managers as an integral part of a long term investment for a sustainable and productive future.

Finally, assessment of seed bank state, distribution and condition is a constructive and pliable tool for assessment of rangeland condition and restoration potential especially in combination with habitat appraisal. It is considered imperative that techniques be developed that allow *in-situ* seed bank assessment by land managers for establishing the state and condition of areas considered to be degraded and of refuges that might be preserved as potential seed production localities for future restoration programmes.

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CHAPTER 7 RECOMMENDATIONS FOR FUTURE RESEARCH ON SEED BANKS IN THE NAMA KAROO

7.1 Alternative approaches to this study

There are a number of alternative methods and techniques that might have been applied to gain information on the state and composition of seed banks in the study area (Chapters 2 and 5). In truth, I believe the most appropriate methods were those that were applied to this study, primarily owing to the time and financial constraints of a two year Master's degree as well as to my background training and experience in the field of horticulture.

While it was initially hoped to be able to extend this study to investigate several flat-topped mesas this was not possible. With extra time and finance (and thus extra personnel), much more comprehensive sampling might have been achieved, in a greater diversity of habitats and over a much greater study area.

With the benefit of hindsight, several variations and improvements on some methodological components applied for this thesis would have been appropriate. These are discussed briefly in recognition of certain limitations of this study and as recommendations for future research.

7.1.1 Potential pre-treatments for stimulation of germination

a) Frosts are regular in the Middelburg district with roughly 180 frost-free days per year (Du Toit, 1996). An investigation of the significance of cold-stratification on seed bank soils is recommended. For example, replicate seed bank soil samples or seeds gathered from the area could be treated with a variety of temperatures (e.g. 4°C, 2°C, 0°C) for various time periods (e.g. one day, three days, one or more week weeks). Alternating temperature treatments in order to approximate average winter day- and night temperatures may also prove beneficial. These treatments may encourage those species, with temperature dependent dormancy mechanisms, to germinate.

b) Fires are an infrequent occurrence in the study region (Roux and Vorster, 1983; W. Asher, pers comm) owing in part to low vegetation density and sparse canopy. Fires do however occur and the top of Tafelberg is set alight every few years by lightning strikes (W. Asher, pers comm; R. Gilfillan, pers comm). It is possible that, with a denser grass canopy and higher average biomass, the plains may have burned more frequently in the past. Pierce *et al* (1995) found seeds of a number of Karoo succulent species (Mesembryanthemaceae) to be stimulated to germinate with smoke extract (De Lange and Boucher, 1990). An assessment of the capacity of different concentrations of smoke extract (e.g. Brown and Van Staden, 1997) to stimulate germination of seeds in the Nama Karoo is recommended.

While debate remains as to whether all species which germinate in response to smoke extract are dependent upon this germination cue (Pierce *et al*, 1995) the use of smoke extract on seeds of Karoo species may nevertheless provide a higher, more species-diverse germination response than achieved during the course of this study.

c) Climatic variables are diverse and almost no environmental factor operates in isolation. It is therefore recommended that combinations of a) and b) be attempted. For example, cold stratification followed by treatment with smoke extract. These treatments are advocated in order to improve germination rates and diversity of seedling emergence trials and are not suggested as restoration methods. Depending upon research outcomes from the proposed trials reseeding efforts (through, for example, broadcast seeding during rainy periods) may benefit from pre-sowing seed treatments that remove dormancy inhibitors and improve *in situ* germination. This could reduce seed loss through granivory and seed predation (e.g. Abramsky, 1983; Kerley, 1991) by improving germination response in favourable environments.

7.1.2 Potential *in situ* studies

a) A component study that was desired but which was not undertaken, owing to limited time and resources, was an investigation into *in situ* watering trials in 5x5m plots adjacent to existing seed plots. Numerous variations of this potential study are possible and include setting up exclusion plots with no additional treatments or watering; watering replicate plots with smoke extract, or setting up a smoke tent (De Lange and Boucher, 1990) in order to assess field germination potential and identify preferred germination sites.

7.1.3 Limitations of finite time horizons

a) The time taken for persistent, or perennial, plant species to flower is species dependent and although many plant species were readily identifiable to at least family level within a few months of germination, this was not possible in a number of other instances. As noted in Chapter 5 a number of plants, especially grasses, did not flower within the period of a year[1]. It is recommended that germination trials be conducted over a flexible time period not less than two years from the time of sowing of seed bank soils to allow identification data to be completed. While this work is ongoing in continuing research, the limitations placed on desired outcomes and conclusions of this thesis (owing to the lack of clear species-specific data) were considerable. Many perennial plants that germinated in these trials initiated budding during mid to late summer (personal observation).

[1] Some plants had yet to flower some 20 months after trials commenced and could not be identified to genus and species level (refer Chapter 5, section 5.2.2). The plants that had not flowered were mainly grasses from the October sampling.

7.1.4 Facilities, location and equipment

a) Ideal germination conditions for the study were possibly within a drier, brighter and probably warmer climate than that provided at Kirstenbosch. However this limitation was overridden by factors that included the availability of suitable premises; ease of access; low cost; and, the fact that all trials were conducted in the same place so that a level of continuity was in place for each set of trials.

b) Due to funding constraints, no rainfall nor temperature gauges were installed at the study locale. Knowledge of differential temperature and moisture gradients between the top; NW and SE slopes; and plains would have provided greater understanding of local habitat determinants and climatic extremes. A record of daily maximum and minimum temperatures and total monthly or weekly rainfall (for the top and plains of Tafelberg) would have been convenient to aid interpretation of plant phenological response data.

7.1.5 Inclusion of other component and base-line studies

a) An initial aspiration for this study was to include an interpretation of some data from the above-ground vegetation assessment (Pienaar, pers comm). This data was not readily available by the time of completing this thesis. While personal observation and relatively detailed field notes taken during sampling expeditions aided interpretation of germination trials, data from the vegetation assessment would have provided a valuable context for this study. It is recommended that seed bank assessments be closely correlated with above-ground vegetation data in order to improve interpretation of results. Both of these projects are continuing in future research and the results will be published.

b) Sampling plots were located along a SE to NW grid, with random placement (at roughly 300m site-to-site intervals). The seed bank study could have been improved by also conducting a survey of those areas on the plains' landscape that are less utilised by domestic stock (owing to gradients including distance from water-point, etc.). These areas could have been analysed for soil- and seed bank composition and distribution and compared with high use areas (such as those surrounding watering points) as a separate study. A variety of gradients (e.g. Van Rooyen *et al*, 1994) such as species composition and seed distribution could have been investigated under these conditions.

c) No species-specific germination trials were undertaken during the course of this study. Such trials might have established seed dormancy patterns between ephemeral and persistent plant species. As a result, there remained a lack of clarity as to which seeds in the soil-stored seed banks were germinating, those from the previous season or those from some seasons prior to investigation. This aspect requires further investigation.

7.1.6 Alternative- and improved variables and habitat classification

a) As time elapsed and more information was uncovered, it was realised that the variable assessed as "canopy cover" could have been an assessment of "basal cover". Research by various investigators have identified close relationships between degradation, surface run-off and plant basal cover (e.g. Snyman and Van Rensburg, 1986). While canopy cover provided a reasonable estimation of overall plant cover between sites, basal cover can provide a more accurate estimate of potential soil loss and might have been a more appropriate measure to apply for some components of this study.

b) The plant phenological study provided an abridged estimate of plant response to rainfall and proved valuable for that reason. Apart from obvious limitations of assessing a single year's data (which should ideally have been extended for several years) several component studies could have provided a more distinctive assessment of local vegetation growth and reproductive activity. These could have included a species-specific assessment of plant phenological response for a variety of species occurring on- and off Tafelberg. It might have been valuable to gain *in situ* data for a variety (e.g. 30 plants of 10 selected species) of identified palatable and desirable species as well as for plants considered to be "problem" species. These latter would include those that are unpalatable; increasing as a result of over utilisation; and, those that are harmful to livestock and/or to desirable plant species through, for example, their toxicity and competitive ability respectively.

c) Numerous perennial plant species (especially grasses) that germinated during seedling emergence trials did not flower during the first year after germination[2] (personal observation). It is likely that even long inter-grazing periods (e.g. six months to a year) as practised by many land managers are insufficient to enable seedlings to reach reproductive maturity under a high-intensity grazing regime. Under such conditions it is possible that individual, non-reproductive seedlings may be trampled, eaten entirely or at least grazed to the point where productivity is lowered and both vegetative (e.g. Van der Heyden *et al*, 1999) and reproductive output (e.g. Milton, 1994a) is severely reduced. Milton (1994b) noted similar consequences during research on reseeding trials in the southern Karoo and implications for veld restoration are significant. A second plant phenology component study could thus have included an empirically designed and instrumented species-specific germination-to-flowering time gradient for the same palatable and problem species assessed above.

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[2] With hindsight, a separate experiment might have been undertaken with sufficient replicates to research this aspect. This was not done and, owing to limited space and time, replicates were discarded once identified and not brought to reproductive maturity. Records were not kept as to the time interval between germination and flowering although for some species this can be inferred by comparing updated versions of plant identification data.

7.1.7 Soil nutrient and other soil-related issues and studies

a) Carbon content of soils provides a relatively good estimate of soil organic matter since the carbon:nitrogen ratio is considered to be relatively constant (between 10:1 and 12:1, with arid soils slightly lower, e.g. 8:1), for any given soil (Brady, 1990; Sparks, 1995). It is thus acceptable to focus on carbon as an estimate of total soil organic matter (Chapter 3, 3.3.1). Nitrogen can however be a limiting factor in maintenance and availability of carbon in soils. It would have been preferable to get an idea of the nitrogen content of soils even if skewed by potentially high levels of urea and other less assimilable forms of carbon in areas where high intensity grazing, with concomitant urine and stool residues, was practised. It is recommended that detailed tests of soil nitrogen content be undertaken and that these be compared with and correlated to the soil carbon component.

b) Soil sampling for chemical and texture analysis was done at ten sites[3] established during April 1998 and other sites were only established during June 1998. The remainder of soil sampling was completed during April 1999 in order to sample during the same season as the previous year. It would have been appropriate to have waited for final placement of all study sites before sampling in order to reduce the risk of inter-annual variations. It may also have been useful to have sampled the entire study area during different seasons (e.g. winter and summer) as well as with a year's interlude between samplings in order that inter-annual variation might be evaluated.

c) Soil moisture and soil structure were not analysed for this study. It is recommended that these be examined in future studies in order to identify relationships between, for example, soil structure and carbon content. Seasonal comparisons of soil moisture would allow insight into relationships between soil moisture and rainfall. Soil structure could be examined in a diversity of habitats and micro-habitats and associated with plant types and species present.

d) Iron performs various important functions related to respiration and photosynthesis (Galston *et al*, 1980; Kabata-Pendias and Pendias, 1984; Pais and Jones, 1997) and is an extremely important component element in an event-driven and often moisture-limited environment where fast response to rainfall is a necessity. This trace element was not investigated in soil analyses for this study and should be investigated in future research.

e) Soil quality is not only a function of the structural and chemical properties of the soil medium but is also dependent upon a diversity of interactions between plants and micro-organisms including mycorrhizal associations (e.g. Allsopp, 1999; Whitford, 1999). These were not investigated in the field nor during seedling emergence trials. In-depth or even strategic research into the role and function of plant-associated micro-flora and -fauna may enhance understanding of seed dormancy mechanisms, seedling emergence strategies and root associated symbioses that could aid restoration attempts in future research trials.

7.2 Some comments regarding the constraints of field sampling and data capture

7.2.1 Field sampling

a) The Tafelberg area is heterogeneous with regard to the degree of rockiness, stoniness, soil depth and percentage vegetation cover. As a result the judgement of open- versus closed-canopy sampling was taken to be a relative estimate within each site rather than attempting to establish exact replications of open- and closed-canopy above-ground vegetation. For example on top of Tafelberg it was a challenge to locate suitable open-canopy samples, while in many places on the plains it was a challenge to locate suitable closed-canopy samples. In other instances the sampling hole contained rocks or else the stone and pebble content was very high.

b) During high wind events, common in the Middelburg district, it was difficult to remove soil from holes since wind gusts blew soil as it was scooped from the hole. This was overcome with makeshift screens in the field but the use of a lightweight, durable and portable screen that can be readily erected up-wind of the sampling hole is recommended.

c) Termitaria, in certain of the sites, most notably in the site on the footslopes on the south-east, made sampling holes difficult to excavate since these termitaria resemble "glued" soils. Further, there were some interesting moments when some surprisingly large soldier termites tried their best to harvest my fingers.

d) Dry soils were difficult to excavate, especially on the plains, as these were extremely hard and compacted or else crumbled into dust. On the other hand, wet soils were exceptionally heavy and a challenge to carry down a mountain with no paths. These wet soils took a relatively long time to dry and had these been seed bank soil the moisture might have influenced the outcome of germination trials (should any seed germinate prematurely in the high moisture soil). No seed bank soils for this study were very moist at the time of sampling, but several soil analysis samples (from April 1998 sampling) were very wet indeed and took a few days longer to air-dry than those that had been collected prior to rainfall. Several seedlings were noted in these samples.

[3] The sites first established were four sites on the south east plains and six sites on top of Tafelberg (Chapter 2).

7.2.2 Germination trials

a) The challenge to keep track of the high number of species as well as the high number of germinated seedlings was managed by using dressmakers' pins, which have a plastic bead on the pinhead (e.g. Plate 5.2). These did not damage seedlings and were reusable.

b) Many seedlings were not easily identifiable or recognisable until after the seedling phase and this was especially the case with grasses. Only a few species were simple to recognise when newly emergent. These were recorded and removed. Those with no clear identifying features were left in the seedling tray until some clear feature emerged or until they were becoming too big to risk transplanting at a later stage.

c) Having worked for several years in plant nurseries, including Kirstenbosch, I have been witness to many failed labelling exercises. These failures were caused mainly by human error, where an individual pulled a label out of a pot or tray without replacing it or else misplacing it into another, similar, pot or tray. For this study, labels for seed trays were inserted into the soil at an acute angle (e.g. Plate 5.2) with only the sample code visible. Coded pots were marked with nail varnish (e.g. Plate 5.1). The acetone lightly dissolves the outer layer of the plastic pot and the coding is not easily removed thus reducing the likelihood of inadvertently misplacing a label.

d) Seedlings were pressed to aid identification of other, newly germinated, plants. The dried, pressed specimens did not however aid identification of live, newly emergent species and the most crucial aid to identification and recognition of newly emergent species proved to be the plants that were grown on in coded pots. Photographing plants as young seedlings proved to hold the same challenges noted above. The sheer volume of diverse species reduced the time available for keeping accurate and consistent photographic records of young plants. The volume of germination that did occur was not expected.

e) Some plants that were pricked out died before positive identification could be made. This was an infrequent occurrence and 4 plants were lost in total. Of these, 3 were identified to family level, one to genus level and one to species level with a degree of uncertainty[4].

f) Some plant species were represented by only one specimen. In three instances this single specimen was lost prior to potting up through factors that included caterpillar- and guinea fowl damage, damping off and unexplained mortality. Again, identification of these species was given to the nearest certainty.

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4 Identifications were speculative, based on data from the above-ground assessment (Pienaar, pers comm).

7.3 Recommendations for other potential studies and areas of consideration

a) Establish reseeding trials with desirable, palatable grass species including *Themeda triandra*, *Digitaria eriantha*, *Ehrharta calycina* and *Stipagrostis* spp. on the plains utilising seed from closest sources (both on- and off mesas) in exclosures.

Hypothesis: It is possible to use reseeding methods to restore valuable grazing grass species to the plains under conditions of reduced grazing pressure.

b) Allocate some areas that are less utilised and seed with a plantation of *Acacia karroo*. Allow livestock to graze, or trim, these into an umbrella shape from small (0.5m). Utilise trimmed branches as mulching and as seedling protectors in the vicinity. Adult trees could be used as fuelwood (diversification of land use) and trees can be used as shade and browsing. These may contribute towards raised nitrogen levels in the soils as well as raising soil organic matter content. Further, plant "hedges" of *Acacia karroo* as buffers for allocated conservation areas instead of using fencing. These will serve as windbreaks as well as source material for thorny branches to aid in improving safe germination sites.

Hypothesis: The use of *Acacia karroo* in controlled plantations as soil conditioners will improve soil composition through addition of soil organic matter and raised nitrogen levels as well as provide safe germination sites for other small shrubs and grasses.

c) Investigate the phenology of desirable fleshy-fruited plant species. Since fleshy fruits offer a small amount of liquid it may be an advantage for fleshy-fruited species to fruit during dry times of the year. These fruits will be spread by birds, bats and other animals.

Hypothesis: Planting desirable, fleshy-fruited plant species near homesteads or in enclosures will increase the chance of these plants spreading into neighbouring rangelands.

d) An investigation into the horticultural potential of desirable Karoo plant species. Many of these[5] are currently used in the horticultural industry and a number of others[6] show great horticultural potential.

Hypothesis: Horticulturally attractive, indigenous Karoo plant species could be utilised by farmers in enclosures and near homesteads in garden landscaping. These could be used as parent-stock plants for seed for restoration purposes while at the same time providing an educational purpose in cultivation, seed-harvesting techniques, etc.

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[5] For example *Eriocephalus africanus*, *Chrysanthemoides monilifera*, *Gazania krebsiana*, *Sutherlandia frutescens*, *Schotia afra*, *Rhigozum obovatum* and *Osteospermum sinuatum*..

[6] For example *Sutera halimifolia*, *Felicia muricata*, *Garuleum bipinnatum* and *Hermannia filifolia*..

e) It appeared that some small shrubs lost their leaves in winter in areas with high intensity grazing pressure while others of the same species growing under relatively reduced- or under no grazing pressure did not. While it is recognised that deciduousness and dormancy are strongly linked with life history and physiological characteristics, this phenomenon was nonetheless remarkable and even though this could be a highly contentious area of research the issue is raised here.

Hypothesis: Deciduousness is a phenological response affected (and selected for) by a diversity of environmental pressures that include high intensity grazing.

f) Funding is available from all tiers of government for "damage control" of environmental impacts resulting from agricultural land use. These impacts include soil- and soil nutrient loss through erosion, siltation of dams and watercourses and reduced productivity. An environmental economics assessment of overall costs to the environment (and resulting damage control of inappropriate and negatively impacting land-use) could be contrasted with an assessment of the costs of formulating, instituting and regulating a programme of pro-active, sustainable land management. Land managers can be shown the longer-term benefits of managing ecosystems less intensively but sustainably as a future investment. Further, decision-makers can be shown the longer term benefits of providing suitable economic- and other incentives to land managers for sustainable land management.

Hypothesis: The overall cost[7] of the loss of productivity and the impacts of unsustainable agriculture are higher and the benefits less in the longer term[8] than the costs of managing land sustainably (within the limits of the landscape and the ecosystem).

g) Farmers and extension workers should be encouraged and enabled to maintain rainfall, wind and temperature records. These provide invaluable data for determining local cycles.

Hypothesis: The keeping and analysis of local climatic records will improve land managers' and local agricultural authorities' understanding of localised weather patterns. This will enable them to adopt an opportunistic and dynamic approach to land management in Karoo areas.

7.3.1 Final comments on observed dynamics and issues raised by this study

There appears to be a relatively constant time-lag between rainfall and seed-set. A potential mechanism to improve the seed banks of the region could be instituted through, for example, a reduction or cessation in grazing of selected camps for measured periods following favourable

7 This is the cost as measured by the discipline of environmental economics.
8 By "longer term" is meant twenty five years or more.

climatic and environmental conditions, which would allow optimal flowering, fruiting, seed-set, germination and establishment of desirable plant species.

This withdrawal or reduction of grazers for the purposes of improving seed banks would need to be undertaken in one of two ways. The first would be total withdrawal to improve SOM, reduce grazing pressure, increase the number of seedlings and increase ground cover (no matter what the species composition). The second would be to drop grazing levels by reducing stocking rates dramatically. While these methods will undoubtedly impact on present-day earnings of land managers, the long-term benefits of improved veld condition may well outweigh these losses. For this reason, land managers require incentives and support to initiate and persevere with veld improvement initiatives.

It is vital that the concept of "stocking rate" be revised in a forum that includes economists, agriculturists, ecologists and other specialists. The recommended regional stocking rate for one farm may be appropriate however the same stocking rate may be far too high for neighbouring farms owing to a number of factors including historical degradation, differential land-form and geology (much shallower soils, etc.) and the breed of livestock that is farmed.

There is enormous potential for economic incentives such as tax rebates or subsidies to be directed toward land-owners who protect more than a given percentage of their land[9]. One of the primary issues facing long-term sustainability of rangelands and the biodiversity they contain, is the lack of conservation status and the present- and preceding paradigm that conservation and conservation of resources is not widely considered to be a "land use". The current trend is toward a realisation that sustainable management of resources is the only means to ensure long-term returns. This requires regulation and enabling mechanisms such as providing appropriate and meaningful incentives for conservation on privately-owned land, in this case on rangelands.

[9] For example, farmers who only graze three of five camps at recommended stocking rates and the remainder at stocking rates devised specifically to manage for improved biological diversity and ecosystem functioning should be provided with sound reason for so doing.

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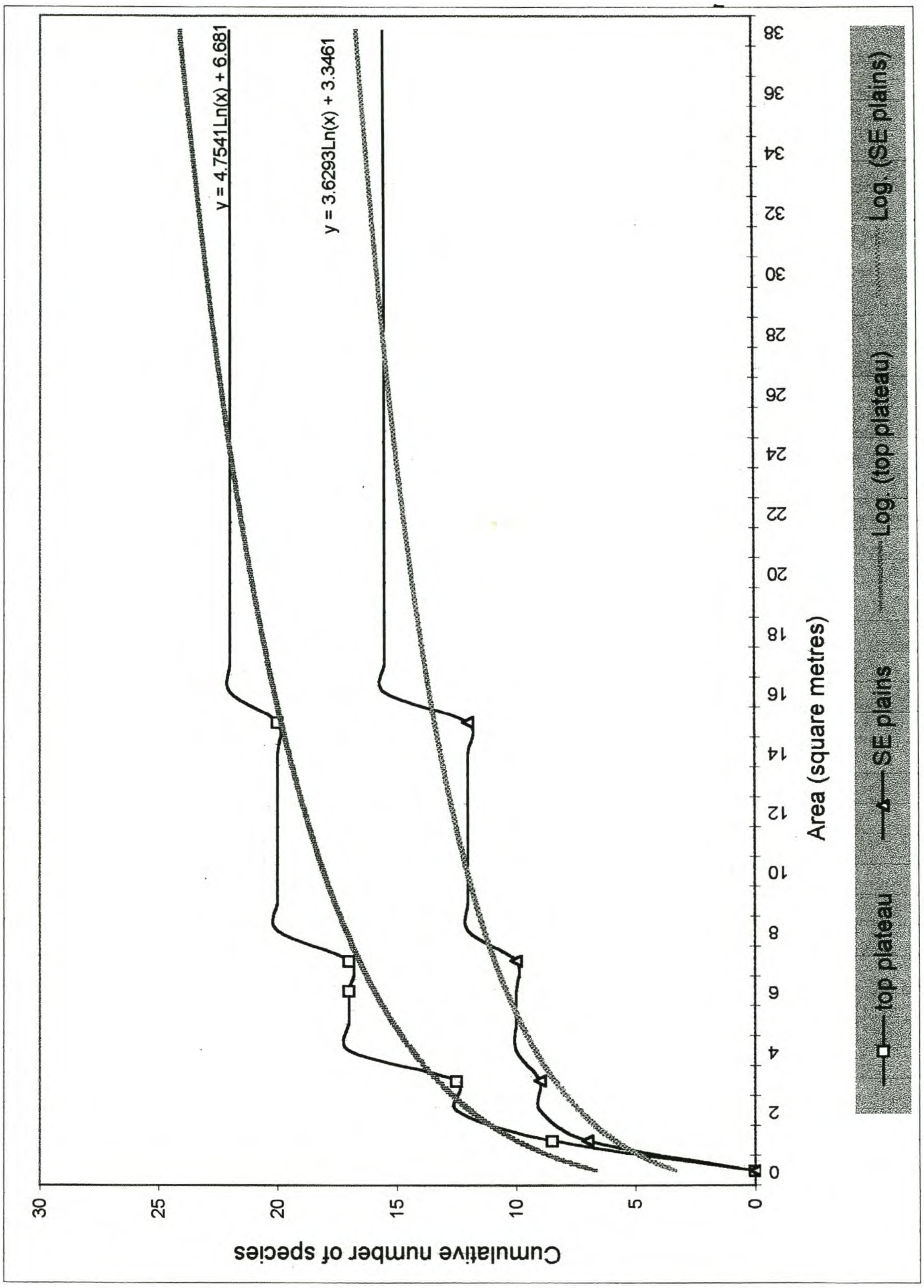

Appendix 2.1: Species area curves conducted on the top plateau and on south east plains of Tafelberg to determine optimum plot size for the above-ground vegetation assessment of the umbrella project. Trendlines derived by displayed formulae. Data provided per kind favour E. Pienaar (pers comm).

Appendix 2.2 Sample phenology survey data sheet from June 1998, top south east site

SPECIES - OR DESCRIPTION	code	# plants	non-dec	semi-dec	full-dec	leaf	bud	flower <50%	flower >50%	seeding <50%	seeding >50%	grazed (Y/N)	nurse / patient
Haemanthus sp.	geophyte	1	1	0	0	1	0	0	0	0	0	0	0
Oxalis sp.1	geophyte	1	1	0	0	1	0	0	0	0	0	0	0
Athanasia sp.1	medshrub	1	1	0	0	0	0	0	0	1	0	0	0
Helichrysum sp.1	smshrub	5	1	0	0	0	0	0	0	0	0	0	0
Dimorphotheca p.	smshrub	15	1	0	0	0	0	0	0	0	0	0	0
Osteospermum sp.	smshrub	6	1	0	0	0	0	0	0	0	0	0	0
Eriocephalus eric.	smshrub	16	1	0	0	0	0	0	0	1	0	0	0
Helichrysum sp.2	smshrub	1	1	0	0	0	0	0	0	0	0	0	0
Walafrida sp.1	smshrub	3	1	0	0	0	0	0	0	0	1	0	0
Gazania sp.	smshrub	1	1	0	0	0	0	0	0	0	0	0	0
Lightfootia sp.1	smshrub	1	1	0	0	0	0	0	0	0	1	0	0
TOTALS		51	all			2				17	4		

TOP SE JUNE 1998

plant size/type	# smshrub	#med-shrub	#lgshrub	# suc-shrub	#suc-crypt	# seedling	#geo-phyte	# annual
Totals number	48	1	0	0	0	0	2	0
non-deciduous	48	1	0	0	0	0	2	0
semi-decidous	0	0	0	0	0	0	0	0
fully deciduous	0	0	0	0	0	0	0	0
leafing	0	0	0	0	0	0	2	0
budding	0	0	0	0	0	0	0	0
flowering < 50%	0	0	0	0	0	0	0	0
flowering > 50%	0	0	0	0	0	0	0	0
seeding < 50%	16	1	0	0	0	0	0	0
seeding > 50%	4	0	0	0	0	0	0	0
grazed	0	0	0	0	0	0	0	0
nurse	0	0	0	0	0	0	0	0
patient	0	0	0	0	0	0	0	0

51

Note:

Grass 45 - 50%

Rock 15 - 20%

Appendix 2.3 Composition of "Kirstenbosch General Mix" soil medium utilised for germination trials. This medium is used to grow plants from all over southern Africa but is not suited for all plant types. Soil media for plant species having specific requirements, such as high alkalinity or acidity or a very high clay content, will require specialist advice.

Constituent	Volume / quantity	Notes
loam	$^{1}/_{11}$ m^3	Must be from a recognised source, should ideally be weed free and may need sterilisation before mixing.
sand	$^{2}/_{11}$ m^3	Must be from a recognised source and known to be non-caustic. Builder's sand often contains a high level of sodium and other alkaline-forming elements that can severely burn plant roots
compost	$^{8}/_{11}$ m^3	Must be well-rotted for two years. Kirstenbosch' source contains horse manure which is high in potassium. Should this not be the case then an alternative source of potassium should be added (see 3:2:1 SR, below)
bonemeal	$^{1}/_{2}$ kg/m^3	Supplies a good source of phosphorus to medium
Ammonium nitrate	$^{1}/_{2}$ kg/m^3	Provides an extra source of readily available nitrogen to the medium. Should a more alkaline soil be desired then lime ammonium nitrate (LAN) may be considered, preferably with specialist advice
3:2:1 SR (slow release)	1 kg/m^3	Should an alternative source of potassium be required then 3:1:5 SR may be used with an extra ¼kg bonemeal (which supplies the phosphorus "lacking" from 3:1:5 SR)

Data supplied per kind favour Fiona Powrie, ex-manager of the Kirstenbosch nursery which produces plants for Kirstenbosch gardens and Kirstenbosch annual plant sale

Appendix 2.4 Sample data form for germination trial study from open canopy samples on the north west plains, middle site (FNW2), October 1998 sampling.

TFL / FLTNW2 / P3 / Open /.2/4

DATE	date sown	total # germ	mono/ dicot	# dead	spp./germ comments	general comment	# rem-oved	Pot#	DATE removed	
30/01	15/12	1	g		grass	broad leaf	1	GID	30/05	
1/03	"	1	d		mesem		2	E4	30/05	
1/03	"	1	g		grass		1	E2	30/05	
15/03	"	1	d		mesem		2	E3	30/05	
15/03	"	2	d		Pentzia		1	E5	30/05	
15/03	"	1	d		dicot	long leaf				

TFL / FLTNW2 / P3 / Open / 5/2

DATE	date sown	total # germ	mono/ dicot	# dead	spp./germ comments	general comment	# rem-oved	Pot#	DATE removed	
15/01	15/12	1	d		pot 9?		4	8	8/03	=pot H
15/01	"	1	d		Medicago		1	weed	8/03	=pot 9
30/01	"	1	g		grass		1	30	8/03	
15/02	"	3	g		grasses		1	F2	30/05	
15/03	"	1	g		grass					

TFL / FLTNW2 / P3 / Open / 4/3

DATE	date sown	total # germ	mono/ dicot	# dead	spp./germ comments	general comment	# rem-oved	Pot#	DATE removed	
15/01	15/12	2	g		grasses		3	42	8/03	**=pot 91**
15/01	"	2	g		Tragus		3	92	8/03	
15/02	"	1	g		grass		1	A3	30/05	
15/02	"	1	g		Tragus		1	F2	30/05	
1/03	"	1	d		Trichodiadema		1	U	30/05	
15/03	"	1	g		grass	broad leaf	1	E1	30/05	
15/03	"	1	g		grass	thin leaf				
30/04	"	1	g		grass					

Appendix 3.1: Results of nutrient and textural analyses of open-canopy (O-C) and closed-canopy (Cl-C) soil samples from the plains, slopes and top of Tafelberg. Soil analysis undertaken by Elsenburg (Department of Agriculture). F = plains; SLP = slopes; T = top of Tafelberg. NW, SE, NE, SW are the four compass half points. See Chapter 2, Figure 2.1 and Table 2.1 for detail on the location of sites and site coding.

<- furthest SE plains <- SE slopes -> <- top sites -> <- NW slopes -> NW plains furthest->

	SOIL REACTION			CARBON & SODIUM		ESSENTIAL NUTRIENTS				MICRONUTRIENTS				SOIL TEXTURE				
SITE CODE	pH (KCl)	Resistance (ohms)	Acidity (H+Al) (me%)	Carbon (C) (%)	Na (mg/kg)	P (mg/kg)	K (mg/kg)	Ca (me%)	Mg (me%)	Cu (mg/kg)	Zn (mg/kg)	Mn (mg/kg)	B (mg/kg)	soil texture	Stone (%)	Sand (%)	Silt (%)	Clay (%)
FNW1 O-C	6.4 h	640 h	n/avail	1.20	33	223 h	543 h	9.68 h	4.68 h	2.97 h	1.53 h	211.50 h	0.73 s	sandy loam	10	55	19	26
FNW1 Cl-C	6.8 h	820 h	n/avail	1.60	27	196 h	509 h	12.87 h	4.85 h	2.50 h	1.80 h	192.60 h	0.66 s	sandy loam	12	66	16	18
FNW2 O-C	6 h	900 h	n/avail	0.61	84	94 h	376 h	4.30 h	3.93 h	2.32 h	1.09 h	198.70 h	0.59 s	sandy loam	13	67	9	24
FNW2 Cl-C	6.2 h	900 h	n/avail	1.03	67	82 h	394 h	3.95 h	3.24 h	1.71 h	1.15 h	149.10 h	0.66 s	sandy loam	10	79	4	17
FNW3 O-C	6.1 h	700 h	n/avail	0.83	68	97 h	449 h	4.80 h	4.36 h	2.98 h	1.35 h	304.40 h	0.81 s	sandy loam	11	63	18	19
FNW3 Cl-C	6.3 h	1340 h	n/avail	1.39	32	84 h	432 h	4.86 h	4.22 h	2.64 h	1.44 h	282.80 h	0.96 s	sandy loam	9	71	8	21
FNW4 O-C	5.4 s	1260 h	0.43	0.40	20	103 h	272 h	3.37 h	2.25 h	1.56 h	1.23 h	151.20 h	0.28 l	sandy loam	6	75	10	15
FNW4 Cl-C	5.8 h	1500 h	n/avail	0.61	12	81 h	309 h	3.02 h	2.00 h	1.23 h	1.48 h	141.50 h	0.41 l	sandy loam	4	87	1	12
FootNW O-C	5.9 h	1800 h	n/avail	0.53	8	62 h	175 h	4.00 h	1.50 h	1.44 h	0.78 s	73.82 h	0.15 l	sandy loam	2	89	1	10
FootNW Cl-C	5.6 h	1500 h	n/avail	1.08	10	69 h	194 h	3.89 h	1.35 h	1.08 h	1.07 h	63.62 h	0.25 l	sandy loam	3	91	2	7
SLPNW3 O-C	6.5 h	940 h	n/avail	1.43	10	55 h	179 h	11.98 h	2.68 h	3.71 h	0.94 s	121.90 h	0.51 s	sandy loam	10	82	7	11
SLPNW3 Cl-C	6.9 h	890 h	n/avail	2.34	11	80 h	225 h	18.32 h	2.91 h	4.05 h	2.72 h	133.00 h	0.93 s	sandy loam	8	86	7	7
SLPNW2 O-C	7.2 h	730 h	n/avail	1.66	14	35 s	220 h	38.16 h	5.61 h	4.25 h	0.70 s	129.90 h	0.66 s	sandy loam	25	74	9	19
SLPNW2 Cl-C	7.3 h	740 h	n/avail	2.15	15	41 h	274 h	45.83 h	7.05 h	3.08 h	1.71 h	40.87 h	0.98 s	sandy loam	20	70	7	23
SLPNW1 O-C	5.6 h	1520 h	n/avail	0.94	10	53 h	162 h	6.07 h	2.63 h	2.95 h	1.05 h	204.40 h	0.40 l	sandy loam	35	74	10	17
SLPNW1 Cl-C	5.9 h	1640 h	n/avail	1.53	14	79 h	282 h	7.07 h	3.05 h	3.05 h	2.39 h	198.20 h	0.69 s	sandy loam	27	74	11	15
TNW O-C	5.3 s	2100 h	0.73	3.16	31	22 l	429 h	7.52 h	4.06 h	4.93 h	2.67 h	378.60 h	0.87 s	loam	2	64	18	18
TNW Cl-C	5.4 s	1770 h	0.9	3.20	28	19 l	459 h	8.65 h	4.29 h	4.98 h	3.21 h	385.60 h	0.99 s	loam	2	60	16	24
TNE O-C	5.2 s	2000 h	0.94	2.26	19	21 l	265 h	6.97 h	3.54 h	4.55 h	2.01 h	400.60 h	0.80 s	loam	4	58	16	26
TNE Cl-C	5.5 **s**	1760 h	n/avail	3.74	30	26 s	509 h	9.74 h	4.47 h	4.38 h	3.85 h	410.10 h	1.25 h	loam	1	64	14	22
TNO O-C	5.3 s	2850 h	0.96	2.34	35	14 l	262 h	6.69 h	3.74 h	5.14 h	2.22 h	397.90 h	0.66 s	loam	1	62	18	20
TNO Cl-C	5.3 s	2370 h	1.04	3.47	26	23 s	357 h	8.19 h	3.84 h	4.44 h	3.94 h	385.10 h	0.82 s	loam	1	68	16	16
TSO O-C	5.3 s	2050 h	0.87	2.22	36	17 l	220 h	6.67 h	3.94 h	4.44 h	1.50 h	267.30 h	0.65 s	loam	5	62	17	21
TSO Cl-C	5.5 **s**	2080 h	n/avail	2.89	29	19 l	233 h	7.45 h	4.16 h	3.76 h	2.40 h	255.80 h	0.96 s	loam	1	66	14	20
TSW O-C	5.5 **s**	1950 h	0.9	2.50	41	20 l	213 h	6.97 h	4.80 h	4.97 h	1.60 h	252.20 h	0.96 s	loam	2	66	16	18
TSW Cl-C	5.3 s	1870 h	0.99	3.28	33	25 s	345 h	7.66 h	4.81 h	4.34 h	2.77 h	242.70 h	0.84 s	loam	3	64	14	22
TSE O-C	5.3 s	1700 h	0.88	2.22	34	28 s	231 h	6.21 h	4.46 h	4.30 h	1.46 h	286.80 h	0.60 s	loam	3	56	16	28
TSE Cl-C	5.3 s	1680 h	0.93	3.39	35	29 s	322 h	6.85 h	4.91 h	3.75 h	2.55 h	270.70 h	0.78 s	loam	1	64	12	24
SLPSE1 O-C	5.4 s	2140 h	0.43	0.66	11	127 h	138 h	4.77 h	1.76 h	1.06 h	0.74 s	66.71 h	0.18 l	sandy loam	30	87	4	9
SLPSE1 Cl-C	6 h	1400 h	n/avail	0.86	21	120 h	212 h	6.09 h	2.21 h	1.50 h	1.27 h	84.46 h	0.47 s	sandy loam	20	85	8	7
SLPSE2 O-C	6.6 h	1140 h	n/avail	0.87	14	113 h	195 h	10.97 h	1.82 h	2.43 h	0.73 s	93.88 h	0.46 s	sandy loam	30	76	9	15
SLPSE2 Cl-C	6.5 h	1340 h	n/avail	2.15	23	128 h	250 h	9.68 h	2.14 h	2.48 h	1.38 h	97.00 h	0.72 s	sandy loam	18	78	9	13
SLPSE3 O-C	5.8 h	840 h	n/avail	0.95	14	22 l	214 h	7.59 h	4.99 h	5.47 h	0.93 s	212.80 h	0.77 s	sandy loam	14	64	11	25
SLPSE3 Cl-C	6.3 h	760 h	n/avail	2.61	18	26 s	358 h	10.87 h	5.35 h	4.58 h	1.80 h	187.00 h	1.29 h	sandy loam	10	66	9	25
FootSE O-C	7.2 h	1300 h	n/avail	0.99	8	51 h	146 h	20.56 h	2.05 h	2.10 h	0.93 s	104.50 h	0.30 l	sandy loam	15	84	5	11
FootSE Cl-C	7.3 h	1260 h	n/avail	1.52	7	49 h	199 h	26.86 h	2.51 h	2.29 h	1.40 h	115.10 h	0.52 s	sandy loam	10	88	5	7
FSE4 O-C	5.7 h	3000 h	n/avail	0.36	39	132 h	174 h	3.44 h	1.18 h	0.89 s	0.72 s	78.90 h	0.18 l	sand	1	86	4	10
FSE4 Cl-C	5.5 **s**	2870 h	n/avail	1.15	34	131 h	185 h	3.88 h	1.34 h	0.82 s	1.09 h	80.93 h	0.35 l	sand	0	86	4	10
FSE3 O-C	5.1 s	3300 h	0.44	0.29	12	86 h	110 h	3.14 h	1.05 h	0.86 s	0.75 s	48.53 h	0.10 l	sandy loam	32	82	5	13
FSE3 Cl-C	5.3 s	3250 h	0.39	0.50	13	95 h	153 h	3.10 h	0.86 h	0.59 s	1.15 h	41.85 h	0.21 l	sandy loam	5	92	1	7
FSE2 O-C	5.6 h	4210 h	n/avail	0.35	49	72 h	168 h	2.76 h	1.03 h	0.94 **s**	0.73 s	65.77 h	0.20 l	sand	2	86	2	12
FSE2 Cl-C	5.4 s	3560 h	0.34	0.69	30	70 h	170 h	2.90 **h**	0.96 h	0.78 s	1.16 h	58.83 h	0.32 l	sand	1	90	0	10
FSE1 O-C	5.4 s	1300 h	0.27	0.80	37	97 h	109 h	2.79 **h**	0.92 h	0.80 s	2.72 h	57.30 h	0.20 l	sandy loam	2	88	0	12
FSE1 Cl-C	5.5 **s**	1280 h	n/avail	0.78	20	104 h	167 h	3.55 h	1.09 h	0.75 s	2.98 h	55.75 h	0.32 l	sand	1	90	0	10

Key:
h = "high" nutrient element content
s = "satisfactory" nutrient element content
l = "low" nutrient element content

Appendix 3.2 Summary statistics of soil nutrient status for a) carbon; b) phosphorus; c) copper; d) potassium and e) boron, manganese and zinc for the Eastern Karoo BPR (Adapted from Ellis, 1988).

a)

NUTRIENT ELEMENT	NUMBER SAMPLES	AVERAGE	MEDIAN (mg/kg)	LOWER QUARTILE	UPPER QUARTILE	SPREAD
Carbon	18	0.54	0.45	0.30	0.80	0.90

b)

NUTRIENT ELEMENT	SOIL TYPE VARIABLE	NUMBER SAMPLES	MEDIAN (mg/kg)	LOWER QUARTILE	UPPER QUARTILE	SPREAD	CLASS
Phosphorus	All A-horizon soil	17	8.0	5.0	16.0	29.0	low
Phosphorus	Shale as parent material	14	4.0	3.0	8.0	17.0	low
Phosphorus	Unconsolidated PM	8	11.0	5.0	15.0	29.0	med

c)

NUTRIENT ELEMENT	SOIL TYPE VARIABLE	NUMBER SAMPLES	MEDIAN (mg/kg)	LOWER QUARTILE	UPPER QUARTILE	SPREAD	CLASS
Copper	All A-horizon soil	18	2.5	1.5	3.6	6.5	high
Copper	Shale as parent material	17	2.4	1.8	3.1	4.9	high
Copper	Unconsolidated PM	9	4.1	1.6	6.3	6.1	high

d)

NUTRIENT ELEMENT	SOIL TYPE VARIABLE	NUMBER SAMPLES	MEDIAN (mg/kg)	LOWER QUARTILE	UPPER QUARTILE	SPREAD	CLASS
Potassium	All A-horizon soil	18	156.0	78.0	196.0	313	high
Potassium	Shale as parent material	17	117.0	78.0	156.0	235	high
Potassium	Unconsolidated PM	9	78.0	78.0	156.0	391	med

e)

NUTRIENT ELEMENT	SOIL TYPE VARIABLE	NUMBER SAMPLES	MEDIAN (mg/kg)	LOWER QUARTILE	UPPER QUARTILE	SPREAD	CLASS
Boron	All A-horizon soil	18	0.9	0.8	1.1	1.8	high
Boron	Shale as parent material	17	0.9	0.6	1.0	1.0	high
Boron	Unconsolidated PM	9	1.0	0.8	1.1	1.3	high
Manganese	All A-horizon soil	18	103	92	155	235	high
Manganese	Shale as parent material	17	123	93	177	326	high
Manganese	Unconsolidated PM	9	93	84	95	118	high
Zinc	All A-horizon soil	18	1.0	0.5	2.0	11.0	high
Zinc	Shale as parent material	17	0.7	0.4	1.6	3.9	high
Zinc	Unconsolidated PM	9	0.5	0.3	0.5	1.5	med

Appendix 3.3: Summary of average ratios of selected soil nutrients, soil textures and soil chemical reactions between open-canopy versus closed-canopy samples from the plains, slopes and top of Tafelberg. Ratios close to unity indicate similar empirical values; ratio >1 indicates lower empirical values in the open- versus the closed-canopy sample; ratio <1 indicates higher empirical value in the open- versus the closed-canopy sample. Refer Appendix 3.1 for complete empirical results of soil analyses.

HABITAT ⇩ / SOIL QUALITY⇨	pH	Na	P	K	Ca	Mg	Cu	Zn	Mn	B	Stone	Clay	Silt	Sand
NW plains - open:clsd	0.95	1.49	1.17	1.00	0.90	1.06	1.22	0.89	1.13	0.90	1.14	1.24	1.93	0.86
NW slopes - open:clsd	0.98	0.84	0.76	0.75	0.80	0.86	1.10	0.44	1.22	0.60	1.24	1.10	1.00	0.99
top sites - open:clsd	0.99	1.08	0.87	0.73	0.85	0.93	1.10	0.61	1.02	0.80	1.89	1.02	1.17	0.95
SE slopes - open:clsd	0.96	0.68	0.97	0.68	0.82	0.87	1.02	0.57	0.99	0.57	1.53	1.15	0.94	0.98
SE plains - open:clsd	1.00	1.41	0.97	0.83	0.90	0.98	1.19	0.77	1.06	0.57	5.21	1.27	2.13	0.96
both slopes - open:clsd	0.97	0.75	0.88	0.72	0.81	0.87	1.06	0.49	1.10	0.59	1.39	1.13	0.97	0.99
both plains - open:clsd	0.98	1.46	1.07	0.95	0.90	1.05	1.21	0.83	1.11	0.79	1.83	1.25	1.96	0.91

Appendix 3.4: Correlation matrices of nutrient and physical soil analyses from Tafelberg indicating the degree of correlation between empirical values of: (a) open-canopy samples and (b) closed-canopy samples. Matrix (c) shows the correlation between log(10) of empirical values for closed-canopy samples Bold font values indicate correlation coefficient -0.8< or >0.8 and indicate probable inverse- or direct relationships respectively. Refer Appendix 3.1.

a)

variable	Resistance	Na	P	K	Ca	Mg	Cu	Zn	Mn	B	Stone	Clay	Silt	Sand	Carbon
pH (KCl)	-0.555	-0.161	0.202	0.093	**0.766**	0.169	-0.016	-0.437	-0.315	0.044	0.291	-0.122	-0.154	0.165	-0.185
Resistance	1	0.031	-0.154	-0.387	-0.400	-0.498	-0.275	-0.030	-0.099	-0.394	-0.193	-0.338	-0.240	0.296	-0.041
Sodium	1	1	0.135	0.511	-0.325	0.238	-0.002	0.250	0.286	0.301	-0.408	0.326	0.271	-0.326	0.018
Phosphorus	1	1	1	0.297	-0.186	-0.312	-0.631	-0.237	-0.460	-0.357	0.203	-0.193	-0.210	0.207	-0.598
Potassium	1	1	1	1	-0.016	0.601	0.347	0.342	0.581	0.639	-0.250	0.589	0.711	-0.696	0.298
Calcium	1	1	1	1	1	0.415	0.300	-0.220	-0.062	0.223	0.298	0.063	0.038	-0.022	0.217
Magnesium	1	1	1	1	1	1	**0.844**	0.230	0.682	**0.898**	-0.111	**0.796**	**0.788**	**-0.828**	0.631
Copper	1	1	1	1	1	1	1	0.385	**0.800**	**0.888**	-0.206	0.688	**0.780**	**-0.774**	**0.838**
Zinc	1	1	1	1	1	1	1	1	0.630	0.439	-0.525	0.331	0.464	-0.434	0.639
Manganese	1	1	1	1	1	1	1	1	1	**0.818**	-0.370	0.722	**0.891**	**-0.863**	**0.789**
Boron	1	1	1	1	1	1	1	1	1	1	-0.240	0.747	**0.867**	**-0.856**	**0.757**
Stone	1	1	1	1	1	1	1	1	1	1	1	-0.160	-0.211	0.216	-0.357
Clay	1	1	1	1	1	1	1	1	1	1	1	1	**0.769**	**-0.935**	0.500
Silt	1	1	1	1	1	1	1	1	1	1	1	1	1	**-0.944**	0.724
Sand	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-0.651
Carbon	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

b)

variable	Resistance	Na	P	K	Ca	Mg	Cu	Zn	Mn	B	Stone	Clay	Silt	Sand	Carbon
pH (KCl)	-0.684	-0.264	0.272	0.050	**0.752**	0.306	0.041	-0.317	-0.318	0.211	0.618	-0.068	-0.050	0.065	-0.139
Resistance	1	0.059	-0.081	-0.373	-0.454	-0.501	-0.304	-0.044	-0.024	-0.434	-0.478	-0.270	-0.192	0.257	-0.133
Sodium	1	1	-0.012	0.422	-0.332	0.180	0.068	0.029	0.306	0.165	-0.221	0.403	0.194	-0.337	0.152
Phosphorus	1	1	1	-0.121	-0.177	-0.419	-0.620	-0.501	-0.508	-0.520	0.324	-0.487	-0.279	0.430	-0.638
Potassium	1	1	1	1	0.011	0.660	0.599	0.430	**0.765**	0.662	-0.011	0.732	0.684	**-0.777**	0.525
Calcium	1	1	1	1	1	0.557	0.283	0.027	-0.149	0.349	0.409	0.180	0.126	-0.170	0.218
Magnesium	1	1	1	1	1	1	**0.766**	0.388	0.522	**0.830**	0.191	**0.867**	0.695	**-0.864**	0.691
Copper	1	1	1	1	1	1	1	0.716	**0.781**	**0.896**	-0.016	0.722	**0.838**	**-0.849**	**0.926**
Zinc	1	1	1	1	1	1	1	1	**0.752**	0.542	-0.302	0.431	0.640	-0.576	**0.766**
Manganese	1	1	1	1	1	1	1	1	1	0.679	-0.291	0.661	**0.804**	**-0.796**	**0.785**
Boron	1	1	1	1	1	1	1	1	1	1	0.097	**0.796**	0.702	**-0.825**	**0.795**
Stone	1	1	1	1	1	1	1	1	1	1	1	-0.045	0.060	-0.003	-0.216
Clay	1	1	1	1	1	1	1	1	1	1	1	1	0.664	**-0.928**	0.699
Silt	1	1	1	1	1	1	1	1	1	1	1	1	1	**-0.895**	**0.828**
Sand	1	1	1	1	1	1	1	1	1	1	1	1	1	1	**-0.830**
Carbon	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

c)

variable	Resistance	Na	P	K	Ca	Mg	Cu	Zn	Mn	B	Stone	Clay	Silt	Sand	Carbon
pH (KCl)	**-0.774**	-0.381	0.319	0.090	0.715	0.319	0.200	-0.255	-0.207	0.280	0.528	-0.087	0.242	0.091	0.027
Resistance	1	0.154	-0.121	-0.380	-0.581	-0.537	-0.379	-0.034	-0.024	-0.457	-0.573	-0.222	-0.285	0.186	-0.201
Sodium	1	1	-0.127	0.455	-0.310	0.257	0.146	0.131	0.400	0.293	-0.322	0.569	0.052	-0.470	0.238
Phosphorus	1	1	1	-0.338	-0.277	-0.542	-0.660	-0.612	-0.564	-0.570	0.057	-0.573	-0.298	0.649	-0.710
Potassium	1	1	1	1	0.252	**0.791**	0.703	0.448	**0.794**	0.741	0.222	**0.783**	0.567	**-0.808**	0.581
Calcium	1	1	1	1	1	0.653	0.642	0.302	0.120	0.610	0.367	0.240	0.485	-0.387	0.594
Magnesium	1	1	1	1	1	1	**0.900**	0.502	0.663	**0.912**	0.308	**0.801**	0.702	**-0.870**	**0.795**
Copper	1	1	1	1	1	1	1	0.672	**0.774**	**0.938**	0.287	0.679	0.697	**-0.840**	**0.922**
Zinc	1	1	1	1	1	1	1	1	0.652	0.592	-0.015	0.482	0.197	-0.630	0.710
Manganese	1	1	1	1	1	1	1	1	1	0.719	-0.006	0.643	0.565	**-0.777**	0.711
Boron	1	1	1	1	1	1	1	1	1	1	0.252	**0.764**	0.610	**-0.830**	**0.847**
Stone	1	1	1	1	1	1	1	1	1	1	1	0.049	0.178	-0.081	-0.001
Clay	1	1	1	1	1	1	1	1	1	1	1	1	0.391	**-0.914**	0.663
Silt	1	1	1	1	1	1	1	1	1	1	1	1	1	-0.592	0.621
Sand	1	1	1	1	1	1	1	1	1	1	1	1	1	1	**-0.835**
Carbon	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Appendix 4.1a: Rainfall summary data for Station # 0120338 - Tafelberg Hall. Monthly rainfall and rain-day average data are presented as means ± standard deviation (baseline data supplied by W. Asher).

Rainfall data ⇨ / month ⇩	average rainfall (mm) ± SD	average # of rain-days ± SD	% of annual rainfall	# "no-rainfall" months over 1 century	# years with <50mm rainfall	# years with <25mm rainfall	# years with <15mm rainfall	# years with >50mm rainfall	# years with >25mm rainfall	# years with >15mm rainfall	Coefficient of variation
January	46 ± 39	5 ± 3	14%	6	67	39	19	34	62	83	84.43
February	51 ± 38	6 ± 4	15%	3	57	32	21	44	69	80	73.66
March	60 ± 40	7 ± 3	17%	1	43	21	12	57	79	89	66.59
April	29 ± 23	4 ± 3	8%	6	78	51	35	23	50	67	79.81
May	17 ± 19	3 ± 2	5%	20	93	71	63	8	30	39	112.38
June	9 ± 11	2 ± 1	3%	25	100	92	75	1	9	27	122.57
July	9 ± 14	1 ± 2	3%	34	98	91	85	3	10	17	151.34
August	11 ± 18	2 ± 2	3%	29	97	88	75	4	13	26	165.78
September	15 ± 18	2 ± 2	4%	29	97	76	67	4	25	34	125.5
October	25 ± 23	3 ± 2	7%	8	88	61	40	13	40	62	93.14
November	34 ± 31	4 ± 3	10%	9	73	47	36	27	53	65	91.88
December	39 ± 38	4 ± 3	11%	11	67	48	35	33	53	65	96.18

Appendix 4.1b: Average quarterly rainfall for Station # 0120338 - Farm Tafelberg Hall (1898-1999). Mean rainfall data are presented as means ±SD

Period ⇩ / Rainfall data ⇨	average quarterly rainfall (mm) ± SD	percentage of annual rainfall	average # of rain-days ± SD	percentage of rain-days
January - March	156 ±78.8	46%	18 ±6.5	41%
April - June	55 ±33.3	16%	8 ±4.2	20%
July - August	34 ±26.4	10%	5 ±3.0	12%
October - December	97 ±60.8	28%	11 ±5.6	27%

Appendix 5.1: Preliminary list of families, with the number of genera and species identified to date of writing. Monocotylodenous families are denoted by (M). The "other species" are those, as yet unidentified to distinct species level, that are possibly duplicates but which may be separate species. It also includes those plants that have not been identified categorically to family level but which are believed to belong to that family (marked with an asterisk). (Work in progress)
(With thanks to E. Pienaar for some assistance with preliminary identification)

FAMILY	number genera	# definite species	# other species still unidentified	Total possible
MONOCOTYLEDONAE (5 families)				
Asparagaceae (M)	1	1		1
Commelinaceae	1	1		1
Cyperaceae (M)	2	2		2
Iridaceae (M)	2	2	1 *	3
Poaceae	14	17	16	33
Subtotal	**20**	**23**	**17**	**40**
DICOTYLEDONAE (24 families)				
Aizoaceae	3	3	3 *	6
Anacardiaceae	1	1		1
cf. Apiaceae	1		1 *	1
Asteraceae	12	16	9	25
Boraginaceae	1		1	1
Brassicaceae	1	1		1
Campanulaceae	2	2		2
Caryophyllaceae	3	3		3
Chenopodiaceae	1	1		1
Crassulaceae	1	8	1 *	9
Euphorbiaceae	1	1		1
Fabaceae	6	7		7
Geraniaceae	2	2		2
Lamiaceae	1	1		1
Loganiaceae	1	1		1
Menispermaceae	1	1		1
Mesembryanthemaceae	6	7		7
Oxalidaceae	1	1		1
Scrophulariaceae	4	3	1	4
Selaginaceae	1	2		2
Solanaceae	2	2	1 *	3
Sterculiaceae	1	1		1
Thymelaeaceae	1		1 *	1
Verbenaceae	1	1		1
Sub totals	**55**	**65**	**18**	**83**
Monocot unkown family		1		
Dicot unknown family		6		
Totals	**75**	**88**	**35 ***	**123**

Appendix 5.2: Preliminary data of species identified to date of writing. Where data are known as to presence or absence in the April or the October sampling, as well as the broad locality from which samples were removed, this is given in columns 4-7. Monocotyledonous families denoted by (M). Work in progress.

Code	FAMILY	Genus / species or description	Season	plains	slope	top
C1	Aizoaceae	Galenia cf. sarcophylla	October	NW		
6	Aizoaceae	Hypertelis cf. salsoloides	Apr/Oct	NW/SE	SE	
47	Aizoaceae	cf. Adenogramma sp. 1	Apr/Oct	SE		
4	cf. Aizoaceae	cf. Aizoaceae sp. 1	Apr/Oct	NW/SE	NW	
95	cf. Aizoaceae	cf. Aizoaceae sp. 2	October	NW		
G	cf. Aizoaceae	cf. Aizoaceae sp. 3	October		NW	
52	Anacardiaceae	Rhus burchelli Sond. ex Engl.	Apr/Oct	NW	NW/SE	N
I3	Asparagaceae (M)	Asparagus sp. 1	October		SE	
28	Asteraceae	Arctotis microcephala (DC.) P.Beauv.	Apr/Oct	NW		N/O/S
A9	Asteraceae	Berkheya cf. heterophylla subsp heterophylla	October	NW		
5	Asteraceae	Chrysocoma ciliata L.	Apr/Oct	NW/SE		S
34	Asteraceae	Cineraria aspera Thunb.	Apr/Oct	SE		N
14	Asteraceae	Eriocephalus cf. ericoides (L.f.) Druce	Apr/Oct	SE	NW	O/S
H4	Asteraceae	Eriocephalus sp. 1	October		NW	
40	Asteraceae	Felicia zeyheri (Less.) Nees subsp. linifolia (Harv.) Grau	April			N/O/S
41	Asteraceae	Helichrysum cf. rosum (P.J.Bergius) Less. var. rosum	April			S
D6	Asteraceae	Ifloga glomerata (Harv.) Schltr.	Apr/Oct	NW/SE	NW	N
48	Asteraceae	Lasiopogon cf. glomerulatus (Harv.) Hilliard	Apr/Oct	NW/SE	NW/SE	
51	Asteraceae	Pentzia cf. incana (Thunb.) Kuntze	Apr/Oct	NW/SE		S
36	Asteraceae	Pentzia punctata Harv.	April			N S
1	Asteraceae	Pentzia sp. 1*	Apr/Oct	SE		
96	Asteraceae	Pentzia sp. 2*	Apr/Oct	NW	NW	
B4	Asteraceae	Pentzia sp. 3* (fine leaf)	October	NW		
E3	Asteraceae	Pentzia sp. 4*	Apr/Oct	NW/SE	NW/SE	S
F1	Asteraceae	Pentzia sp. 5*	Apr/Oct	NW/SE		
59	Asteraceae	Senecio cf. elegans	April	SE		
15	Asteraceae	Ursinia cf. nana	Apr/Oct	SE		S
26	Asteraceae	Asteraceae sp. 1 ("Star flower" Helichrysum)	Apr/Oct			N/O
C	Asteraceae	cf. Gnaphalium sp. 1	October	NW/SE	NW/SE	S
18	cf. Asteraceae	cf. Asteraceae sp. 1	April			S
P	cf. Asteraceae	cf. Asteraceae sp. 2	October	NW/SE	NW/SE	S
G1	cf. Asteraceae	cf. Asteraceae sp. 3	October		NW/SE	S
F5	cf. Asteraceae	cf. Asteraceae sp. 4	October	NW		
L7	cf. Boraginaceae	cf. Laputa sp. 1	October	NW		
3	Brassicaceae	Lepidium africanum (Burm.f.) DC. subsp. africanum	Apr/Oct	NW/SE	NW/SE	N
33	Campanulaceae	Lightfootia nodosa Buek.	Apr/Oct			N/O/S
64	Campanulaceae	Wahlenbergia cernua (Thunb.) A.DC.	Apr/Oct			S
M1	Caryophyllaceae	Dianthus basuticus subsp. basuticus var. basuticus	October			N
50	Caryophyllaceae	Herniaria erckertii Herm. subsp. pulvinata	Apr/Oct	NW/SE	NW/SE	
13	Caryophyllaceae	Silene burchelli Otth ex DC. var. burchelli	April			N
O	Chenopodiaceae	Salsola sp. 1	October		NW/SE	N
89	Commelinaceae (M)	Commelina africana L. var. africana	April			S

Key:
Plains: NW = north west plains sites / SE = south east plains sites
Slopes: NW = north west slope sites / SE = south east slope sites
Top: N = top north west site / O = top south central site / S = top south east site
Note: Species marked with an * are presumed duplicates until identification is completed

continued overleaf........

Appendix 5.2: (cont.) Species identified to date of writing (preliminary data). Where data are known as to presence or absence in April or October sampling, as well as the broad locality from which samples were removed, this is given in columns 4-7. Monocotyledonous families denoted by (M). Work in progress.

Code	FAMILY	Genus / species or description	Season	plains	slope	top
I4	Crassulaceae	Crassula cf. cotyledonis very round leaf	October	SE	SE	
44	Crassulaceae	Crassula cf. lanceolata	Apr/Oct	NW/SE	SE	
39	Crassulaceae	Crassula cf. montana subsp. 1	Apr/Oct	SE		N/O/S
81	Crassulaceae	Crassula cf. montana subsp. 2*	Apr/Oct	SE		
87	Crassulaceae	Crassula cf. montana subsp. 3*	April			S
C5	Crassulaceae	Crassula cf. muscosa	October	NW		
62	Crassulaceae	Crassula cf. tetragona subsp. acutifolia	Apr/Oct	SE		O/S
86	Crassulaceae	Crassula sp. 1	October	SE		O
L8	Crassulaceae	Crassula sp. 2	October			N
L9	Crassulaceae	Crassula sp. 3	October	SE		
K8	cf. Crassulaceae	cf. Crassulaceae sp. 1	October			S
7	Cyperaceae (M)	Bulbostylis humilis (Kunth) C.B.Clarke	Apr/Oct	SE	NW	O
19	Cyperaceae (M)	Cyperus usitatus Burch. var. usitatus	Apr/Oct	SE		O
67	Dicot sp. 1	little herb, quite tough roundish leaf	Apr/Oct		NW	O
85	Dicot sp. 2	herb, dark green leaf	Apr/Oct		NW	N/O
K	Dicot sp. 3	creeping ground cover type succulent	Apr/Oct	NW	SE	
Z	Dicot sp. 4	very smooth leaf - heavily eaten	October	NW	NW	N
H6	Dicot sp. 5	herb, long thin leaves	October		SE	
J6	Dicot sp. 6	little herb, leaf about 10mm X 3mm	October		SE	
D9	Euphorbiaceae	Euphorbia sp. 1	October		NW	
76	Fabaceae	cf. Lotononis sp. 1	April	SE		
43	Fabaceae	cf. Wiborgia sp. 1	Apr/Oct		SE	O
J2	Fabaceae	cf. Melolobium burchelli	October		SE	
60	Fabaceae	Lessertia cf. pauciflora Harv.	Apr/Oct	SE		
30	Fabaceae	Medicago cf. laciniata (L.) Mill.	Apr/Oct	NW/SE		
46	Fabaceae	Sutherlandia frutescens (L.) R.Br.	Apr/Oct	SE	SE	
J1	Fabaceae	Fabaceae sp. 1	October		SE	
49	Geraniaceae	Monsonia brevirostrata	April	SE		
27	Geraniaceae	Pelargonium cf. multicaule Jacq. subsp. multicaule	Apr/Oct	SE		N/O/S
H8	Iridaceae (M)	cf. Freesia andersoniae L.Bolus	October		SE	
C2	cf. Iridaceae (M)	cf. Iridaceae sp. 1	Apr/Oct	NW/SE		
F9	cf. Iridaceae (M)	cf. Iridaceae sp. 2	Apr/Oct	SE	SE	S
90	Lamiaceae	Salvia verbenaca L.	October	NW		
J4	Loganiaceae	Buddleja glomerata H.L.Wendl.	October		SE	N
I8	Menispermaceae	Cissampelos capensis L.f.	October		SE	
E	Mesembryanthemaceae	Drosanthemum duplessiae L. Bolus	October	NW/SE	NW	
71	Mesembryanthemaceae	Eberlanzia ferox	Apr/Oct	SE		
A3	Mesembryanthemaceae	Trichodiadema rogersiae	October	NW/SE	NW/SE	
69	Mesembryanthemaceae	cf. Mestoklema tuberosum (L.) N.E.Br. ex Glen	Apr/Oct	NW/SE		O
X	Mesembryanthemaceae	cf. Phyllobolus sp. 1	October	NW		
Y	Mesembryanthemaceae	cf. Phyllobolus sp. 2*	October	NW	SE	
E4	Mesembryanthemaceae	cf. Ruschia sp. 1	October	NW		
J5	Monocot sp. 1 (M)	Monocot sp. 1	October		SE	
F8	Oxalidaceae	Oxalis cf. commutata Sonder	October	SE	NW/SE	

Key:

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Top: N = top north west site / O = top south central site / S = top south east site
Note: Species marked with an * are presumed duplicates until identification is completed

continued overleaf....

Appendix 5.2: (cont.) Species identified to date of writing (preliminary data). Where data are known as to presence or absence in April or October sampling, as well as the broad locality from which samples were removed, this is given in columns 4-7. Monocotyledonous families denoted by (M). Work in progress.

Code	FAMILY	Genus / species or description	Season	plains	slope	top
L4	Poaceae (M)	Aristida sp. 1	Apr/Oct	NW/SE		
L5	Poaceae (M)	Aristida sp. 2	Apr/Oct	NW/SE		
72	Poaceae (M)	Chloris virgata Sw.	Apr/Oct	SE		N
56	Poaceae (M)	Cymbopogon plurinodis (Stapf) Stapf ex Burtt Davy	Apr/Oct		SE	N
20	Poaceae (M)	Digitaria eriantha Steud.	Apr/Oct	SE	NW/SE	N/O/S
T	Poaceae (M)	Enneapogon desvauxii Beauv.	October	NW/SE		
29	Poaceae (M)	Eragrostis curvula (Schrad.) Nees	Apr/Oct	NW		N S
8	Poaceae (M)	Eragrostis obtusa Munro ex Ficalho & Hiern	Apr/Oct	NW/SE	NW/SE	N
C8	Poaceae (M)	Eustachys paspaloides (Vahl) Lanza & Mattei	October		NW	N
11	Poaceae (M)	Fingerhuthia africana Lehm.	Apr/Oct	SE	SE	O/S
70	Poaceae (M)	Oropetium capense Stapf	Apr/Oct	SE		N
10	Poaceae (M)	Themeda triandra Forssk.	Apr/Oct		NW/SE	N/O/S
42	Poaceae (M)	Tragus berteronianus Schult.	Apr/Oct	NW/SE	NW/SE	N S
82	Poaceae (M)	Tragus koeleroides Asch.	Apr/Oct		NW	
73	Poaceae (M)	cf. Cenchrus ciliarus L.	Apr/Oct	SE		
H9	Poaceae (M)	cf. Poa pratensis L.	October		NW/SE	S
B9	Poaceae (M)	cf. Sporobolus africanus (poir.) Robyns & Tournay	October		NW	
various	Poaceae (M)	48 grasses that have not yet flowered - ± 16 difft. spp.*	Apr & Oct			
V	Scrophulariaceae	Jamesbrittania tysonii	Apr/Oct		NW/SE	N S
C3	Scrophulariaceae	Nemesia cf. cynanchifolia	October		NW	
38	Scrophulariaceae	Sutera halimifolia (Benth.) Kuntze	Apr/Oct	SE	NW/SE	N/O/S
A2	Scrophulariaceae	cf. Diascia sp. 1	October	NW/SE	NW	
A6	Selaginaceae	Walafrida geniculata (L.f.) Rolfe	October	NW	NW/SE	
17	Selaginaceae	Walafrida saxatilis (E.Mey.) Rolfe	April			O/S
53	Solanaceae	Solanum tomentosum L.	October	NW		
77	Solanaceae	Solanum sp. 1	Apr/Oct			N/O
F	cf. Solanaceae	cf. Lycium sp. 1	October	NW		
55	Sterculiaceae	Hermannia cf. cernua subsp. erodiodes	October	SE		O
I1	cf. Thymelaeaceae	cf. Gnidia sp. 1	October		SE	
J9	Verbenaceae	Lantana rugosa Thunb.	October		NW	

Key:

Total number of spp. 115

Plains: NW = north west plains sites / SE = south east plains sites
Slopes: NW = north west slope sites / SE = south east slope sites
Top: N = top north west site / O = top south central site / S = top south east site
Note: Species marked with an asterisk (*) are thought to be duplicates however these are treated as discrete species until identification is completed

Preliminary differentiation of temporal and spatial germination results

Number of species germinating exclusively from the April sampling........... 11
Number of species germinating exclusively from the October sampling...... 49
Number of species common to both April and October sampling.............. 55
Number of species germinating from sites on the NW plains...................... 44
Number of species germinating from sites on NW slopes.......................... 37
Number of species germinating from sites on top of Tafelberg.................. 56
Number of species germinating from sites on SE slopes........................... 39
Number of species germinating from sites on the SE plains...................... 53
Number of species germinating from both NW and SE plains................... 24
Number of species germinating from both NW and SE slopes.................. 19
Number of species germinating from sites on the plains, slopes and top.... 15
Number of species germinating exclusively from sites on the top............... 15
number of species germinating exclusively from sites on the plains............ 28
number of species germinating exclusively from sites on the slopes........... 16

Appendix 5.3a Seasonal comparison of germination trends from April and October sampling at closed-canopy micro-habitats from three sites (top north west = TNW; top south central = TSO; top south east = TSE) on Tafelberg. Total numbers of seedlings (categories A to D) were averaged at sub-plot (1X1m: categories H to K) and plot (5X5m: categories L to O) level to standardise results from different sampling intensities (5.3.1.2; Chapter 2). Standard deviation is provided in brackets where relevant. Average number of seeds m^{-2} (category P) was derived through multiplying category H by a constant of 100 (each sample measured 10X10cm, see Chapter 2). Estimated canopy cover for each season supplied for comparison (categories Q to T).

cate-gory	Site codes: top of Tafelberg.	TSE - Apr (n=15)	TSE - Oct (n=9)	TSO - Apr (n=15)	TSO - Oct (n=9)	TNW - Apr (n=15)	TNW - Oct (n=9)
A	total # seedlings germinated / site	114 ± 7.8	145 ± 22.7	103 ± 8.6	126 *	95 ± 15.0	113 ± 6.4
B	total # grasses germinated / site	57 ± 11.0	73 ± 10.4	47 ± 7.6	80 *	69 ± 10.8	65 ± 5.0
C	total # dicots germinated / site	57 ± 5.3	72 ± 14.0	50 ± 6.7	67 *	26 ± 6.1	48 ± 2.6
D	total # monocots germinated / site	0 ± 0.0	0 ± 0.0	6 ± 1.7	n/a *	0 ± 0.0	0 ± 0.0
E	% composition of grasses / site	50.00%	50.34%	45.63%	49% *	72.63%	57.52%
F	% composition of dicots / site	50.00%	49.66%	48.54%	50% *	27.37%	42.48%
G	% composition of monocots / site	0.00%	0.00%	5.83%	n/a	0.00%	0.00%
H	Ave # seedlings / sub-plot	7.6 ± 5.6	16.1 ± 12.2	6.9 ± 3.4	14.1 *	6.3 ± 4.5	12.6 ± 7.0
I	Ave # grasses germinated / sub-plot	3.8 ± 4.6	8.1 ± 5.9	3.1 ± 2.6	8.9 *	4.6 ± 2.9	7.2 ± 5.4
J	Ave # dicots germinated / sub-plot	3.8 ± 3.5	8.0 ± 7.5	3.3 ± 2.9	7.4 *	1.7 ± 2.1	5.2 ± 2.9
K	Ave # geophtyes germinated / sub-plot	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.6	n/a *	0.0 ± 0.0	0.1 ± 0.3
L	Ave # seedlings germinated / plot	38.0 ± 7.8	48.3 ± 22.7	34.3 ± 8.6	48.3 *	31.7 ± 15.0	37.7 ± 6.4
M	Ave # grasses germinated / plot	19.0 ± 11.0	24.3 ± 10.4	15.7 ± 7.6	19.5 *	23.0 ± 10.8	21.7 ± 5.0
N	Ave # dicots germinated / plot	19.0 ± 5.3	24.0 ± 14.0	16.7 ± 6.7	22.2 *	8.7 ± 6.1	16.0 ± 2.6
O	Ave # geophtyes germinated / plot	0.0 ± 0.0	0.0 ± 0.0	2.0 ± 1.7	n/a*	0.0 ± 0.0	0.0 ± 0.0
P	average # seeds m^{-2}	760	1611	687	1405.3 *	633	1256
Q	Average % grass cover / site	39%	57%	45%	62% *	30%	43%
R	Average % shrub cover / site	16%	15%	12%	8% *	9%	5%
S	Average % open ground / site	13%	5%	9%	4% *	7%	3%
T	Average % rock cover / site	31%	23%	35%	25% *	55%	49%

* Note: Values for October samples from TSO (no samples removed) were derived by means of a forecasting tool that extrapolated potential October trends for TSO using average and total values obtained from TNW and TSE (Chapter 2).

Appendix 5.3b: Seasonal comparison of germination trends from April and October sampling (closed-canopy micro-habitats) at three sites (FSE1 = furthest, FSE4 = closest to Tafelberg) on the south east plains of Tafelberg. Total numbers of seedlings (categories A to D) were averaged at sub-plot (1X1m: categories H to K) and plot (5X5m: categories L to O) level to standardise results from different sampling intensities (5.3.1.2; Chapter 2). Standard deviation in brackets where relevant. Average number of seeds m^{-2} (category P) derived through multiplying category H by a constant of 100 (each sample measured 10X10cm, see Chapter 2). Estimated canopy cover for all three sites for each season supplied for comparison (categories Q to T).

cate-gory	Site codes: SE Plains	FSE1 - Apr (n=15)	FSE1 - Oct (n=9)	FSE2 - Apr (n=15)	FSE2 - Oct (n=9)	FSE4 - Apr (n=15)	FSE4 - Oct (n=9)
A	total # seedlings germinated / site	128 ± 15.3	270 ± 21.5	277 ± 19.1	241 ± 51.7	213 ± 45.1	172 ± 27.3
B	total # grasses germinated / site	12 ± 4.6	69 ± 7.2	9 ± 2.6	69 ± 2.6	33 ± 5.6	79 ± 17.2
C	total # dicots germinated / site	106 ± 19.1	192 ± 26.3	254 ± 20.2	162 ± 44.2	165 ± 40.7	92 ± 11.7
D	total # monocots germinated / site	10 ± 3.5	9 ± 2.0	14 ± 3.1	10 ± 5.8	15 ± 1.0	1 ± 0.6
E	% composition of grasses / site	9.38%	25.56%	3.25%	28.63%	15.49%	45.93%
F	% composition of dicots / site	82.81%	71.11%	91.70%	67.22%	77.46%	53.49%
G	% composition of monocots / site	7.81%	3.33%	5.05%	4.15%	7.04%	0.58%
H	Ave # seedlings germinated / sub-plot	8.5 ± 7.9	30.0 ± 14.3	18.4 ± 11.9	26.8 ± 21.5	14.2 ± 13.7	19.1 ± 12.1
I	Ave # grasses germinated / sub-plot	0.8 ± 1.3	7.7 ± 6.5	0.6 ± 1.4	7.7 ± 4.7	2.1 ± 2.2	8.8 ± 9.2
J	Ave # dicots germinated / sub-plot	7.1 ± 8.2	21.3 ± 14.1	16.9 ± 12.3	18.0 ± 18.8	11.0 ± 13.4	10.2 ± 8.4
K	Ave # geophtyes germinated / sub-plot	0.7 ± 1.0	1.0 ± 1.1	0.9 ± 1.2	1.1 ± 3.3	1.1 ± 1.1	0.1 ± 0.3
L	Ave # seedlings germinated / plot	42.7 ± 15.3	90.0 ± 21.5	92.3 ± 19.1	80.3 ± 51.7	71.0 ± 45.1	57.3 ± 27.3
M	Ave # grasses germinated / plot	4.0 ± 4.6	23.0 ± 7.2	3.0 ± 2.6	23.0 ± 2.6	11.0 ± 5.6	26.3 ± 17.2
N	Ave # dicots germinated / plot	35.3 ± 19.1	64.0 ± 26.3	84.7 ± 20.2	54.0 ± 44.2	55.0 ± 40.7	30.7 ± 11.7
O	Ave # geophtyes germinated / plot	3.3 ± 3.5	3.0 ± 2.0	4.7 ± 3.1	3.3 ± 5.8	5.0 ± 1.0	0.3 ± 0.6
P	average # seeds m^{-2}	853	3000	1840	2678	1420	1911
Q	Average % grass cover / site	32%	27%	31%	43%	41%	56%
R	Average % shrub cover / site	28%	33%	31%	25%	31%	27%
S	Average % open ground / site	38%	38%	30%	25%	27%	17%
T	Average % rock cover / site	2%	2%	8%	7%	2%	0%

EPILOGUE

As a songwriter, musician and dreamer the language of science was an enormous challenge to control and I hope to have achieved this competently. The language of lyric is dependent on word sound, timbre and subtle intent while scientific endeavour relies on veracity, precedent and brevity (not necessarily in that order!). I laboured long and hard to wield science creatively, understanding it is quite necessary to say things such as: "In the absence of adequate rainfall (Reference A, 1989) seedlings of drought-prone species (Reference B, 1976) are more sensitive to soil disturbance (e.g. Reference C, 1995) owing to reduction in soil moisture through diminished soil cover and consequent evapo-transpiration (Reference D, 1985) and are not likely to survive (Reference E, 1993)." The minstrel in me wants to state something to the effect of "Plants take strain when there's been no rain, leave them be and in the end you'll gain" or else simply compose some song lyrics.

Storm clouds gather in the dark'ning sky, they're only teasing and they scud on by
Windmills beckon on the sun-drenched plains, plants are thirsty and the ground needs rain
In the Karoo

Cicada steadfastly drones all day, Jackal sniffs the air then away she fades
Larks skim the air, they rise then fall, Kudu seek the shade and korhaans call
In the Karoo

Dust devil dances with leaves on the ground, dust devil dances and storm clouds gather round
dust devil dances with the tapestry of browns
(there is a kind of instrumental break here that completes the meter)

Lightning parts the sky - hail streams down, rain floods the plain - water moves the ground
Sheets of brown clay surge - meanders flow, more harm is done then - than good you know
In the Karoo.

What this thesis does however encapsulate is my ripening understanding (garnered from a wealth of appreciated sources) of systems under a diversity of pressures. I believe that fluctuations in climate and a dynamic environment do indeed push and pull vegetation of the semi-arid Nama Karoo Biome through divergent stages, at one time more grassy and at another more shrubby. Residual populations of once abundant species naturally persist in favourable or protected remnant niches during wetter or drier climatic cycles, spreading slowly from these source populations as conditions favour their expansion. It appears that this has occurred many times in the past, in all biogeographical areas and under diverse conditions. There have been many natural extinctions and significant speciation owing to these kinds of biogeographical, topographical and climatic fluxes. This marvellous natural phenomenon leads to the evolution of species, to habitat diversification and also to a sort of natural buffering system that ensures the sustainability of broad biological diversity through species diversity, genetic elasticity and adaptation to name but a few.

My concern is, given the extraordinary pressures placed on these sensitive semi-arid and arid systems by often careless human land use over the past two centuries in particular, that this is the one historical period when many of the remnant habitat pockets are being or have been depleted, habitats physically altered, degraded and even possibly extinguished by continuous or excessive grazing and other inappropriate management practises. A select example of this, near at hand, is the wholesale depletion of especially West Coast Renosterveld through the planting of wheat, vineyards and orchards to the point where less than three percent of the total remains with only a minuscule proportion of this now under formal conservation.

To my mind, continued injudicious grazing methods practised previously and unfortunately presently by a number of land managers is effectively a method of cultivating and cropping land yet without adequately replacing nutrients or soil organic matter. This practice disturbs and compacts soils, stultifies plant reproduction and other floral and faunal dynamics forcing remnant plant and animal populations into refuges such as koppies, road reserves and some occasional lands that are relatively less grazed either through admirable management practise or simply through passive low usage by "weekend farmers" for example.

It is my view that most of these systems will not be able to "bounce back" naturally after this recent and present "total onslaught". I am further convinced that active intervention will be required to reseed, revegetate and restore the diversity of vegetation components and habitats on which these systems rely for resilience to change. I believe a comprehensive awareness-raising and educational initiative for all parties - from decision makers to land managers - is the first step toward slowing down and eventually reversing degradation in terrestrial and riparian ecosystems in these regions. It will be vital to establish and develop concepts such as identifying the future "desired state" of semi-arid rangelands at a strategic, as well as at a local, level through consultation, integrated research, policy formulation and enactment. The need for a strategic "State of the Environment Report" (SoER) on semi-arid areas exists since, while these are covered in the recent national SoER, the systems themselves are unique, highly sensitive and require specific attention at the highest level.

A number of potentials exist for the institution of innovative projects and programmes that look creatively at benefits, incentives and aid for land managers who actively conserve and restore private land and government-owned property. It may be necessary to encourage diversified land use, setting aside, for example, defined conservancies that take on a subsidised or even a privately sponsored "conservation" land use. It may also be necessary to focus separately on appropriate and sustainable land use alternatives for areas that are remarkably pristine as well as those that are badly degraded. It is time for decision-makers to be presented with factual persuasion regarding the intrinsic and extrinsic values of semi-arid regions and the biological diversity (in the broadest possible sense including land form and function) that these areas house. The Departments of Agriculture, Land Affairs, Environment, Tourism, Finance, Education, Trade and Industry, Labour, Welfare, Mineral Affairs, Water Affairs, Forestry, Public Works and must all be brought into the equation since all have a significant role and stake in the maintenance, use and produce of these semi-arid regions. Several of these departments bear the brunt of cleaning up and estimating the damages to communities, agricultural lands and water supplies caused by degraded catchments. Some departments hold the key to improving diversified land use or suggesting viable alternative methods of resource allocation while still others are obliged by international convention to respond to the various crises that arise from land degradation and loss of biological diversity.

Fact-finding surveys that examine the long term costs of clearing dams and repairing damages caused by excessive siltation could for example weigh up these costs against reducing silt load movement at the source and along the route of river catchments. Integrated Catchment Management need not only be seen as a mechanism for improved bureaucratic co-operation but also as a means to reduce costs to agencies downstream of the most degraded zones. This requires wisdom, integrated planning, departmental co-operation, judicious reallocation of resources and finally (and probably most importantly) a clear, dynamic and iterative strategy with willing "buy-in" from land-owners and local authorities.

This thesis represents my first attempt at significant ecological research and I hope it provides scientifically-based clarity on the issues that it set out to tackle. I wish only that it could have resolved all the problems too, but that will take a multitude of disciplines and departments to unravel and negotiate in order to identify achievable goals and prioritise the greatest needs for this predominantly semi-arid country. Forward with the National Action Programme for the Convention to Combat Desertification and may all agendas from all sides seek the ultimate - the optimal solution for combating both land degradation and loss of biological diversity through improved land use and management and a sustainable agriculture for all forever.