

Structure and Function of *Heuweltjies* across a Rainfall Gradient in the South-Western Cape

by

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Declaration

I, NozukoBooi, declare that the work contained in this thesis is my own original work, except where otherwise stated. It is being submitted for the degree of Master of Science at the University of Stellenbosch and has not been previously, partly or in its entirety, submitted to any other university for a degree.

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Abstract

Heuweltjies are below ground termitaria found along the west coast and the south-western and -eastern Cape. They traversing different climates, soil and vegetation types within the Succulent Karoo and Fynbos biomes. From a birds eye view, *heuweltjies* appear as near-circular landscape features, demonstrating clear difference in vegetation structure to their surroundings. A study of aspects of the structure and function of *heuweltjies*, mima-like mounds of south-western South Africa was undertaken. The main aim of the study was to investigate topsoil properties and processes and vegetation structure and the ecophysiology of plants growing on these mounds, and compare it to areas off these patches.

Four study sites across a rainfall gradient were chosen for soil and vegetation studies (two within the Succulent Karoo and two at the Fynbos biome). Ten sampling sites on *heuweltjies* and 10 off *heuweltjie* (interpatch) were chosen at each study site for these analyses. Soils samples from the top 10 cm were analysed for total nitrogen (N) and carbon (C) content, phosphorus (P) concentrations, particle-size distributions, pH and electrical conductivity (related to salinity). Soil biogeochemistry studies (i.e. potential N mineralization, potential soil respiration and phosphatase activity) were also done in the laboratory. In the field, the cover of soil cryptogams, selected plant growth forms and selected physical variables at each site, on and off *heuweltjies*, were estimated on 1m² grids. Two of the study sites, one in the Succulent Karoo and one in Fynbos, were chosen for field measurements of stomatal conductance, predawn and midday xylem water potentials of two growth forms (deciduous and evergreen non-succulent shrubs) at selected times in the duration of the study. Leaf samples were taken to make once-off measurements of specific leaf area, C and N isotope compositions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), and foliar N content. Furthermore, a fertilization experiment that has been running at the Tierberg Karoo Research Centre (Succulent Karoo) since 1997, where 10g m⁻² of N have been added to interpatch vegetation twice annually, was included in the stomatal conductance and xylem water potential studies. The aim of including the fertilization experiment was to ascertain whether interpatch vegetation will eventually resemble *heuweltjie* vegetation in ecophysiology following N fertilization. Soil water probes were inserted, 10 cm deep, on one on *heuweltjie* and one off *heuweltjie* site for the

long-term estimation of gravimetric water content and temperature at the Tierberg Karoo Research Centre.

Heuweltjie soils were found to be hotspots for nutrients and biogeochemical activity. They had elevated levels of total % C, % N and available P (mg kg^{-1}) compared to surrounding interpatch soils. pH and electrical conductivity ($\mu\text{S cm}^{-1}$) of these soils were also high compared to interpatch areas. *Heuweltjie* soils have higher silt content and retain more water, and for a longer period following a rainstorm. Potential soil respiration, potential N mineralization and alkaline and acid phosphatase activity were generally higher on *heuweltjies*. Cover of the selected plant growth forms differed little between *heuweltjies* and the surrounding vegetation but site differences were observed. *Heuweltjies* differed from interpatches in the cover of soil cryptogams, with higher cover of mosses and lower cover of lichens on mounds. There was higher cover of plant litter and termite frass on the *heuweltjies*. There was a decrease in soil available P and increase in non-succulent shrub cover from low to high rainfall areas. On the other hand no significant differences were found in the xylem water potential of interpatch and *heuweltjie* plants at either of the study sites. At the Tierberg Karoo Research, stomatal conductance of interpatch plants was higher and water use efficiency ($\delta^{13}\text{C}$) lower compared to that of *heuweltjie* plants suggesting some level of water stress for *heuweltjie* plants at this site. Here, *heuweltjie* plants also had higher foliar N, lower C/N ratio values, signs of high photosynthetic potential and highly decomposable litter and higher $\delta^{15}\text{N}$. At Jonaskop, stomatal conductance and water use efficiency did not differ between *heuweltjies* and interpatch plants. There were also no differences in foliar N concentrations, C/N ratios and $\delta^{15}\text{N}$ between *heuweltjie* and interpatch plants at this site. Plants growing in high N plots (the fertilizer plots) had higher xylem water potential and more variable stomatal conductance than those growing in control plots.

The results of this study have shown *heuweltjies* to be hotspots for nutrients and biogeochemical cycling, and given enough water, will be ideal patches for plant growth. In the Succulent Karoo, high salinity (and finer textured soils) on the *heuweltjies* may contribute to water stress during dry periods, and together with disturbance, provide bottom-up controls on plant physiology, and ultimately, vegetation structure. In the Fynbos, plants may be limited by nutrients on *heuweltjies*, possibly because of increased interspecific competition, while increased rainfall may also lead to more nutrients leaching

from the topsoils. The results presented are especially relevant to restoration programs, and may shed some light on restoration trajectories after overgrazing, cultivation and mining activities.

Opsomming

Heuweltjies is ondergrondse termitaria wat langs die weskus, die suid-wes en oos Kaap van Suid Afrika voorkom. Hulle kom voor onder verskillende klimaatstreke, grondtipes en planttipes wat binne die Sukkulente Karoo en Fynbos biome voorkom. Vanuit die lug uitgesien, verskyn *heuweltjies* as sirkelvormige landskapseienskappe, wat duidelike verskille in plant struktuur en die omringende omgewing demonstreer. 'n Studie van aspekte van struktuur en funksie van 'n *heuweltjies*, mima-agtige hope vansuidwestelike Suid-Afrikais onderneem. Die hoofdoel van die studie was om die eienskappe van oppervlakgrondeen -prosesse, plant struktuur, en die ekofisiologie van plante wat op *heuweltjies* groei te ondersoek, en dit te vergelyk met areas af van hierdie kolle.

Vier studieareas wat oor 'n reënvalgradient strek is gekies vir grond en plantegroei studies (twee binne die Sukkulente Karoo en twee binne die Fynbos biome). Tien monsterareas op *heuweltjies* en 10 af van *heuweltjies* (omringende areas) is gekies binne elke studiearea vir die bogenoemde analyses. Grondmonsters van die boonste 10 cm van die grond is geneem en geanaliseer vir totale stikstof (N) en koolstof (C), fosfor (P) konsentrasies, gronddeeltjiegrootte, pH, en elektriese geleidingsvermoë, (hou verband met soutgehalte). Grond biogeochemie studies (d.i. potensiële stikstof mineralisasie, potensiële grond respirasie en fosfatase aktiwiteit) is ook in die laboratorium uitgevoer. In die veld was die dekking van grond kriptogame, geselekteerde plant groeivorms en fisiese veranderlikes by elke lokaliteit, beide op en van *heuweltjies* op 1m² vierkante bereken. Twee studie lokaliteite, een in die Sukkulente Karoo en een in die Fynbos, is gekies vir veld metings van huidmondjiegeleiding, voor dagbreek en middag xileem potensiale van twee groei vorms (bladwisselende en immergroen nie-sukkulente struik) op geselekteerde tye gedurende die studie. Blaarmonsters is geneem om eenmalige metings te maak van die spesifieke blaararea, C en N isotoop komposisies ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), en blaar N inhoud. Verder is 'n bemestingeksperiment wat by die Tierberg Karoo Navorsing Sentrum (Sukkulente Karoo) loop sedert 1997, waar 10gm⁻² van N jaarliks twee keer bygevoeg word by die plante wat tussen *heuweltjies* groei ingesluit in die stomata geleiding en xileem water potensiaal studies. Die doel van die

bevrugting eksperiment was om vas te stel of die omliggende plante (af van *heuweltjies*) uiteindelik soos die van die *heuweltjiessal* lyk in terme van ekofisiologie nadat dit met stikstof bemest is. Grondwater monitoreringsapparaat was ingesit (10cm diep) op een op *heuweltjie* en een lokaliteit af van die *heuweltjie* vir die langtermyn bepaling van gravimetrieëse water inhoud (m^3m^{-3}) en temperatuur by die Tierberg Karoo Navorsing Sentrum.

Daar is gevind dat grond op *heuweltjies* “skerpkolle” is vir voedingstowwe en biogeochemiese aktiwiteit. Hulle het ook verhoogte vlakke van totale %C, % N, en beskikbare P (mg kg^{-1}) teenoor die omliggende areas om die *heuweltjies*. pH en elektriese geleidingsvermoë ($\mu\text{S cm}^{-1}$) van hierdie gronde was ook hoër in vergelyking met die omliggende areas. *Heuweltjie* grond het ‘n hoër sout inhoud gehad en behou meer water vir ‘n langer periode na ‘n reënstorm. Potensiële grond respirasie, potensiële stikstof mineralisasie, en alkaliese en suur fosfatase aktiwiteit is oor die algemeen hoër op *heuweltjies*. Die voorkoms van die geselekteerde plant groeivorms verskil min tussen *heuweltjies* en die omliggende omgewing, maar verskille tussen studie areas is opgemerk. *Heuweltjies* het verskil van areas af van *heuweltjies* in die voorkoms van grond kriptogame, met ‘n hoër voorkoms van mosse en ‘n laer voorkoms van ligene op die *heuweltjies*. Daar was hoër voorkoms van plantafvalmateriaal en termiet uitwerpsel op die *heuweltjies*. Daar was ‘n afname in grond P (mg kg^{-1}) en ‘n toename in nie-sukkulente struik bedekking van lae tot hoë reënval areas. Daar was geen verskil in die xileem water potensiaal van plante op die *heuweltjies* of af van die *heuweltjies* by enige van die studie lokaliteite nie. By die Tierberg Karoo Navorsing Sentrum was huidmondjie geleiding van plant in die areas tussen *heuweltjies* hoër en die water gebruik doeltreffendheid ($\delta^{13}\text{C}$) laer in vergelyking met die van die *heuweltjie* plante, wat op ‘n sekere vlak waterstres dui in *heuweltjie* plante by hierdie studiearea. Hier het *heuweltjie* plante ook hoër blaar N, laer C/N waardes, tekens van hoër fotosintetiese potensiaal en hoogs afbreekbare afvalmateriaal gehad asook hoër $\delta^{15}\text{N}$. By Jonaskop het huidmondjie geleiding en water gebruik doeltreffendheid nie verskil tussen *heuweltjie* en omliggende plante nie. Daar was ook geen verskille in blaar N konsentrasies, C/N verhoudings en $\delta^{15}\text{N}$ tussen *heuweltjie* en omliggende plante by hierdie studiearea nie. Plante wat groei in hoë stikstof plote, het hoër xileem water potensiaal (minder stres) en meer veranderlike stomatal geleiding as die plante wat in die kontrole plote groei.

Die resultate van die studie het getoon dat *heuweltjies* “skerpkolle” is van voedingstowwe en biogeochemiese siklusse, en gegewe genoeg grondwater, sal ideale areas wees vir die groei van plante. In die Sukkulente Karoodra hoë soutgehalte (en fyner grond teksture) op die *heuweltjies* by tot water stres gedurende droë tye, en saam met versteurings dra dit by tot grond tot plant kontrole op plantfisiologie, en uiteindelik plant gemeenskapsstruktuur. In die Fynbos word plante op die *heuweltjies* beperk deur te min voedingstowwe, moontlik omdat daar ’n toename is in intraspesifieke kompetisie, terwyl hoër reenvalkan lei tot hoër logging van voedingstowwe vanuit die bogrond. Die resultate wat hier gerapporteer word is veral relevant vir restourasieprogramme, en mag lig werp op restourasie trajekte na oorbeweiding, aanplanting van gewasse en mynbou-aktiwiteite.

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Chapter 1: General Introduction to *heuweltjies* in the south-western Cape

The primary goal of ecology is to understand and explain the distribution of living things, (plants, animals and microorganisms) in the natural environment. Why do things occur where they do, look the way they do and why do they ‘behave’ as they do? Answers to these questions will help in dealing with global changes in the general outlook of the earth’s surface, and the consequences of those changes. As it is difficult to study ecological phenomena at a global scale, ecologists prefer to split the world into manageable masses, such as biospheres, biomes, regions, landscapes, ecosystems etc. Landscapes are land mosaics with a repeated pattern of local ecosystems or land use types (Forman, 1995). The south-western Cape of South Africa is an ecologically diverse region, containing several landscapes, which are a combination of agricultural farmlands, natural vegetation and human settlements. Heterogeneity exists at various scales, from large-scale vegetation and soil differences associated with mountains and valleys to above and belowground termitaria, which influence patterns and processes at the local scale. Top-down controls such as rainfall, both spatial and temporal patterns, drive ecological processes at regional and local scales. Fire acts as another ecological driver, in areas where fuel biomass is enough to allow fire to spread across the landscape (Cowling, 1992). Bottom-up controls such as relief and geomorphology interact, with top-down controls to bring about patterns of structural and species diversity.

In the south-western region and Northern Cape Province of South Africa, soil mounds known as *heuweltjies*, are associated with past and present activities of termites, particularly the termite *Microhodotermes viator* (Coaton and Sheasby, 1974; Moore and Picker, 1991). *Heuweltjies* give rise to geomorphological heterogeneity (Midgley and Musil, 1990; Milton et al., 1992; Ellis 2002; Herpel, 2008). Their soils are high in plant nutrients in a matrix of soils, with relatively low nutrient status and variable soil physical and hydrological properties. The vegetation contained on the mounds, is distinctly different from the surrounding plant communities (Midgley and Musil, 1990; Milton et al., 1992; Esler and Cowling, 1995). Plant regeneration is significantly different on and off the *heuweltjies*, thus influencing vegetation structure. Apart from the activities of the resident termites, *heuweltjies* are also the habitat of an array of animal biota, with whistling rats (*Parotomys brantsii*) significantly impacting vegetation through their burrowing activities, which disturb the soil surface and subsurface (Desmet and Cowling, 1999). For example, whistling rats attract predators such as puffadders

(*Bitisarietans*), which hunt the rats and use the burrows for shelter. Thus, *heuweltjies* are likely contributing to increasing the pedo- and biodiversity of the region (Francis et al., 2007; Petersen, 2008), and should be a focal point for ecological research and conservation.

Within the natural landscape there may be areas of disproportionately high biogeochemical activity (hotspots), making them more important than their size would suggest (McClain et al., 2003). There has been growing interest in attempting to understand the pattern and function in such areas, so as to understand the ecosystems processes of the landscape as a whole (Chapin et al., 2002; Burt and Pinay, 2005; Richardson et al., 2007). The results of such studies demonstrate the extent of spatial and temporal heterogeneity, created by hotspots in natural ecosystems. Hotspots also show the value of the conservation of ecosystem engineers, for example, large species such as the brown bear, for the maintenance of ecosystem processes (Holtgrieve et al., 2009), and how a lack of knowledge of the functions of such species may impede conservation (Miegroet and Johnson, 2009).

Termite mounds have been considered by some as hotspots of nutrients and biogeochemical processes (Duponnois et al., 2006; Gutierrez and Jones, 2006). In the landscape of the south-western Cape, *heuweltjies* may function as hotspots. The consequences of their existence for functioning in this landscape may be great as they cover large areas. As the environmental controls on hotspots are very different, from those of the surrounding inter-patch areas, an understanding of processes on the patches can only be acquired through extensive study (Chapin et al., 2002).

Anthropogenic stressors are reducing plant and animal and structural diversity on *heuweltjies* (Steinschen et al., 1996). Heavy grazing has been shown to result in a change in soil nutrients, and composition of the shrub community in Namaqualand, in host biome, Succulent Karoo (Allsopp, 1999). Armstrong and Siegfried (1990) have shown that sheep prefer to graze on plants growing on *heuweltjies*, and that even at intermediate levels of veld degradation, *heuweltjies* may be completely devoid of vegetation (Esler et al., 2006). Fynbos, another south-western Cape biome that hosts *heuweltjies*, is threatened by fragmentation caused by crop production, alien invasions and plant harvesting (Kemper et al., 2000; Cowling et al., 2003; Candra et al., 2009). The south-western Cape is well known for its wine industry; large tracts of natural vegetation on fine-textured soils have been

replaced by vineyards. In the last decade, increasing effort has gone into restoring degraded agricultural patches, and remnants of Fynbos on wine farms with the establishment of initiatives such as Biodiversity and Wine (Winter, 2004). Interestingly, in permanently modified areas, despite a long history of cultivation and modification, the legacies of *heuweltjies* on agricultural landscapes are still noticeable (Shange et al., 2006).

The soil properties of *heuweltjies* impact plant productivity and composition, aspects which are important both to crop production and quality (Matson, 1997), as well as applied conservation. However, conservation and restoration may be hampered because as yet, there is little knowledge about the structure and function of these mounds. Furthermore, global change poses significant threats to biodiversity in the south-western Cape; projected temperature change scenarios may exceed the thermal threshold of the most vulnerable of its endemics, while rainfall patterns may change (Chown and van Jaarsveld, 2001; Musil et al., 2005; Nielson et al., 2005; Broennimann et al., 2006) the distribution of plant and animal biota. We currently do not have a clear picture of how *heuweltjies* are structured generally across different biomes and climatic regions in order to deal with these expected changes.

The issues outlined in the preceding paragraphs, served as the main motivations for the initiation of the current study. A number of studies have looked at the physical and functional aspects of *heuweltjies*, such as soils (Ellis et al, 2002; 2004), plant regeneration (Esler and Cowling, 1995), plant competition (Riginos et al., 2005), and vegetation composition (Knight et al., 1989; Midgley and Musil, 1990). These studies, however, are constrained by scale as they have been conducted at single sites (Knight et al., 1989; Midgley and Musil, 1990). Site-specific studies of *heuweltjies*, make a limited contribution to understanding the functional significance of these hotspots, because *heuweltjies* occur over a wide range of vegetation types, and across a gradient of rainfall quantity and seasonality. There is as yet little information regarding the functional aspects of *heuweltjies*, especially those related to soil. Uncovering of knowledge on the biogeochemical cycles of *heuweltjies*, and the ecophysiological properties of plants associated with *heuweltjies* and non-*heuweltjie* areas, would add significantly to a mechanistic understanding, which would assist in their restoration and reconstitution after degradation caused by overgrazing, cultivation and mining. Specifically, the aims of this study were to address the following key questions:

- How do selected soil physical and chemical properties on and off *heuweltjies* vary along a climatic gradient?
- Do soil biogeochemical cycling rates on *heuweltjies* along a climatic gradient support the hypothesis that *heuweltjies* are biogeochemical hotspots within their host ecosystems?
- How do vegetation composition and structural characteristics of *heuweltjies* vary along a climatic gradient?
- How do selected ecophysiological parameters of plants common to *heuweltjies* and interpatch areas differ?

This thesis is structured in such a way that each data chapter represents a manuscript prepared for publication. For this reason repetition, especially regarding methods is unavoidable but is kept to its minimum. This chapter places the thesis into context by giving a short introduction to *heuweltjies*, stating the key questions and outlining the thesis structure. In chapter two, the literature review of research on *heuweltjies* thus far, is presented and this also provides further motivation for the specific objectives of this study. In chapter three, soil properties and nutrient cycling rates (biogeochemical cycles) of the important plant nutrients N, P and C are assessed. The first two of the four key questions listed above, are addressed in this chapter. Chapter four reports on the results of a survey of the growth form composition of *heuweltjies* at four sites across a rainfall gradient. Selected ecophysiological properties are determined, and compared between plants growing on the *heuweltjies* and those in the interpatches. Individuals of common species *Pteronia pallens* and *Tripteris sinuata* at the Tierberg Karoo Research Centre, in the Succulent Karoo near Prince Albert, and *Pteronia paniculata* at Jonaskop, which is situated at an ecotone between Succulent Karoo and Fynbos biomes close to the town of Villiersdorp, were chosen for this purpose. However, for the purpose of this study only the Fynbos vegetation (Breede Shale Renosterveld) was sampled at Jonaskop and this is, therefore, considered a Fynbos site. Chapter five provides a synthesis of the findings in this thesis. The implications of such findings are discussed along with suggestions for future research. All referencing follows the Journal of Arid Environments.

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Chapter 2: Literature review of *heuweltjies* in south-western Cape

2.1. *Heuweltjies* – an Introduction

Heuweltjies are belowground termitaria, slightly raised above the soil surface, which occupy a significant proportion of landscapes in the Succulent Karoo and the Fynbos. Research on *heuweltjies*, began as part of studies on the soils of the Succulent Karoo (Merryweather, 1965; Coaton and Sheasby, 1974). When these studies revealed their pedological distinctiveness, authors began speculating as to their origins. *Heuweltjie* origins have remained mysterious even with almost 100 yrs of examination (Lovegrove and Siegfried, 1989). However, there is suspicion that the southern harvester termite, *Microhodotermes viator* (native to southern Africa), is partially, if not fully, involved in their formation and maintenance (Lovegrove and Siegfried, 1986; Lovegrove and Siegfried, 1989; Milton and Dean, 1990). *Heuweltjie* researchers have also been successful in few other key areas, for example, the discovery that *heuweltjies* are hotspots for nutrients (Milton et al., 1992; Walton 2006); harbor vegetation that differs from their surroundings (Knight et al., 1989; Midgley and Musil, 1990); and support various types of animal biota (Milton et al., 1992). These lead to the conclusion that they contribute significantly to plant, animal and structural diversity of the Succulent Karoo and Fynbos biomes within the south-western Cape region. Le Maitre et al., (2007) also demonstrate the role *heuweltjies* play role in the hydrological cycle of the Succulent Karoo, at the landscape level. Even with the close examination that has been paid to certain aspects of *heuweltjies*, their structure and function characteristics have received little attention from researchers.

Heuweltjies contrast with termite hills built by other termite species in the Fynbos, which are visible aboveground. They are functionally similar to those occurring in the savanna region of southern Africa, which have been shown to provide important nutrient resources to grazers and which, like *heuweltjies*, are grazed preferentially by game and cattle (Grant and Scholes, 2006). Such structures are also found in many other regions of the world and are receiving increasing attention and recognition as hotspots of soil processes and crucial resources in often resource poor environments (Ndiaye et al., 2004; Konaté et al., 1999; Turner, 2006). However, environmental degradation has increasingly led to the destruction of termitaria in the Cape and elsewhere (Fig 2.1). Aboveground termitaria often remain in the landscape as nutrient-rich patches, which also differ from the surrounding interpatches in terms of soil microbial

and faunal composition (Cadet et al., 2004). The following sections review the literature on *heuweltjies* in terms of origins, distribution, soils and vegetation properties. They also provide further motivation for the study of structure and function on *heuweltjies*, which is the focal point of this thesis.



Fig 2.1 Photo shows the degree of disturbance and human transformation at the landscapes on which *heuweltjies* occur. Picture taken at Jonaskop, part of Riversonderend Mountain Range. *Heuweltjies* on the hill slopes are marked by circles and arrow points a degraded area that is under restoration.

2.2. Age and origin of *heuweltjies*

Heuweltjies are known to be very old structures (Whitford and Kay, 1999). Their exact age and origin, however, is still debated. Estimates for their age fall between 4,000 and 30,000 yrs old (Moore and Picker, 1991; Midgley et al., 2002) but most of the literature puts them between 20,000-30,000 yrs old (Midgley et al., 2002; Francis, 2008; Potts et al., 2009). There are at present two schools of thought, largely supported for *heuweltjie*genesis. First, the Termite-Mole-rat hypothesis suggested by Lovegrove

and Siegfried (1989), suggests that the southern harvester termite *M. viator* and mole-rat, *Cryptomys hottentotus* are involved in the formation and maintenance of *heuweltjies*, which is continuous and still go on at present. This hypothesis is popular with many, though the involvement of the mole-rat has been questioned by some (Milton and Dean, 1990; Moore and Picker, 1991). Moore and Picker (1991) support the involvement of *M. viator* in *heuweltjie* genesis. Their argument states that the mounds are formed as a result of calcretisation of the basal mound parts which causes the termite to move up in the soil profile and thus form mounds. More recently, Picker et al., (2007) studied the density of *heuweltjies* along a rainfall and vegetation productivity gradient, and found that *heuweltjie* density increased with vegetation productivity in the Karoo. Their results implied that *heuweltjies* are in equilibrium with current vegetation, and thus support the claims of Lovegrove and Siegfried (1989). The spacing between *heuweltjies* may indeed be as a result of intraspecific competition amongst *M. viator* colonies (Lovegrove and Siegfried, 1986; 1989). Currently, *M. viator* is found in many 'active' *heuweltjies*, and the distribution of the termite coincides with their distribution (Lovegrove and Siegfried, 1986). The nesting behavior of *M. viator* bears similarities to the nests discovered within the *heuweltjies* soils profile (Coaton and Sheasby, 1974).

The second school of thought is in agreement with the Termite-Climate hypothesis, suggested by Burgers (1975). Briefly, the Termite-Climate hypothesis postulates that, a termite, now extinct, built large termitaria similar to those of *Macrotermes spp.* in savanna. These termitaria have been eroded over time to become the low-lying *heuweltjies* we see today. Burgers (1975) claims that, further, this termite may have lived at the time when the Cape was grassier and food was plentiful. Midgley et al., (2002) present three lines of argument against *M. viator* as the perpetrator of *heuweltjies*. The first is that, the distribution of *heuweltjies* and that of *M. viator* are not completely congruent, for, there are areas where the termite is present, and *heuweltjies* are not. Secondly, they suggest that mounds of *M. viator* are too small to end up as *heuweltjies* of 20 m diameter or more. They also speak of the failure of the authors to identify *M. viator* as the species, which constructed the tunnels found in the basal layer of *heuweltjies*. Ellis (2002) noted that *heuweltjies* occur in the older parts of the Karoo landscape. Laurie (2002) used a central place transport model to describe the overdispersion pattern of *heuweltjies*, and implies that pattern observed, could only have come about after thousands of years of termite movement, and *heuweltjies* are therefore old and relict structures. As things stand, it seems that the issue is not whether or not a termite is involved in the formation of *heuweltjies* but which termite

species it was and how long ago. This summation, though not conclusive, has functional significance.

2.3. Spatial properties of *heuweltjies* in the south-western Cape

The distribution of *heuweltjies* falls mostly within the Succulent Karoo biome but they also occur in the wetter parts of the Cape Floristic Region (Lovegrove and Siegfried, 1986) (Fig 2.3). Their northern limit is just along the coast of Namibia up to Aus and along south-eastern coast they have been seen as far as the town of Kirkwood (Lovegrove and Siegfried, 1986). This distribution crosses gradients in rainfall, altitudes, soil and vegetation types (Lovegrove and Siegfried, 1986; Picker et al., 2007). Their density is site-dependent with the average estimated to be around 2.0 per hectare by Lovegrove and Siegfried (1989). Picker et al., (2007) found that their density depended on soil fertility in interaction with rainfall. At sites with high soil fertility they found a positive relationship between the density and rainfall (average $318.6 \pm 155.8 \text{ km}^{-2}$) whereas *heuweltjie* density at low soil fertility (average $261.0 \pm 61.1 \text{ km}^{-2}$) sites showed no such relationship (Picker et al., 2007). The size of *heuweltjies* varies greatly and also depends on the site. The mean (\pm SE) area of 50 *heuweltjies* at Tierberg Karoo Research Centre (TKRC) is $89 \pm 7 \text{ m}^2$. Whereas at Worcester, Villiersdorp and Stellenbosch means (5 *heuweltjies*) are $633 \pm 74 \text{ m}^2$, $497 \pm 72 \text{ m}^2$ and $383 \pm 21 \text{ m}^2$ respectively.

2.4. Soils of *heuweltjies*

The physical aspects of *heuweltjie* soils show a departure from those of their surroundings (interpatch soils). Ellis (2002) described a cross-section of a *heuweltjie* in Namaqualand and other areas and showed that, in these areas, *heuweltjies* contain a subsurface hardpan layer that is sometimes absent in the surrounding soils. The centre of this *heuweltjie* hardpan is calcic (cemented by calcium carbonate) and changes to become more petroduric (cemented mainly by silica) at the edges and in interpatch areas (where present) (Fig 2.2). Hardpans are a common feature of arid ecosystems such as the Succulent Karoo (Francis et al., 2007).

In Namaqualand, Ellis (2002) attributed the calcic/petrocalcic hardpan layer at the center of the *heuweltjie* to termite activity; he found termite activity to be highest at the centre. In contrast, the petroduric hardpan at the edges and interpatches, he argued, was due to the cementation of silica (Ellis,

2002). At higher rainfall sites (150-450 mm yr⁻¹), he found that hardpans in the interpatches disappear while the calcic layer at the centre of the *heuweltjie* remained. At sites with even higher rainfall (> 450 mm yr⁻¹) hardpans disappear altogether. Other studies support these observations (Midgley et al., 2002; Francis, 2008; Petersen, 2008; Potts et al., 2009). Francis (2008) who gives an even more detailed description of a *heuweltjie* soil profile in Namaqualand found that the hardpan layer at the centre of *heuweltjies* had a strong sepiolitic¹ element, which is associated with presence of calcite in the soil profile. The work of Francis (2008) in Namaqualand mostly supports that of Ellis (2002). Francis (2008) suggested that the foraging of termites enriched the *heuweltjie* centre with Ca and Mg and lead to the formation of calcite and clay at the centre leaving silica to precipitate at the edges. The precipitation of calcite created suitable conditions for the formation of sepiolite. Water enriched in Mg-Si moved downslope and caused the precipitation of a sepiolitic zone on the outer side of the calcrete (Francis, 2008). *Heuweltjie* soils are lighter in colour and have water absorbent surface horizons and neocutanic B1 subsurface horizons, in comparison to red, water-repellent surface horizons and red apedal B and neocutanic subsurface horizons of the profiles between *heuweltjies* (Prinsloo, 2005). In other areas, such as Worcester, the soil colour of *heuweltjies* is darker due to the higher cover of termite frass.

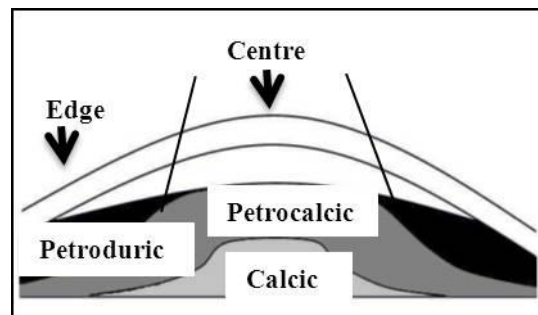


Fig 2.2. Schematic of the horizons/hardpans of *heuweltjies* in Namaqualand (Source: Ellis, 2002)

Particle size distribution analyses showed an accumulation of fine particles, clay and silt, on *heuweltjies* (Midgley and Musil 1990; Milton et al., 1992). The clay content was up to 40% higher and the soil layer was two times thicker on the *heuweltjies* in Worcester than between the *heuweltjies* (Midgley and Bösenberg, 1990). The increase in the clay content on many, but not all, of the

¹ Sepiolitic horizons, as described by Francis (2008), refer to horizons that have a enough sepiolite to be detected by X-ray diffraction, to turn methyl orange to purple-pink and clings strongly to the wetted tongue.

heuweltjies is maybe due to the mound building activity of termites, mixing soils and bringing the finer textured subsoils to the surface.

The soil water content of *heuweltjies* is higher after good rains (Midgley and Bösenberg, 1990; Herpel, 2008) probably because these retain more water as a result of a finer texture (Midgley and Bösenberg, 1990). Similarly, Milton et al., (1992) found that *heuweltjies* had higher soil water content at TKRC (near Prince Albert) and Dean (1992) noted that infiltration rates of water in *heuweltjie* soils were much higher than the surrounding soils in the same site. Infiltration rates are improved through preferential flow channels and as well as microtopographic heterogeneity on the soil surface, which can act as traps for material transported in overland flow from the surrounding landscape (Le Maitre et al., 2007). Also, the free carbonates create better physical conditions.

Termites attract other animals to *heuweltjies* including aardvark and rodents, both of which create holes and tunnels, further improving water infiltration and soil aeration (Milton and Dean, 1990; Dean, 1992). However, in Namaqualand *heuweltjies* are drier than the interpatches (Francis et al., 2007). This contradiction raises the question of whether climate has an impact on soil properties of *heuweltjies*. All these results are from the Succulent Karoo, and there are virtually no data available for the Fynbos (including Renosterveld).

Virtually all studies on chemical properties of *heuweltjies* soil (mainly carried out in the Succulent Karoo) show that these patches have higher nutrient content than their surrounding soils (Midgley and Musil, 1990; Milton et al., 1992; Esler and Cowling, 1993; Herpel, 2008). N was found to be higher on *heuweltjies* in all these studies; P and K were found to be higher only in certain sites but no clear trends have been established. Micronutrients were higher in the *heuweltjie* soils than the interpatch soils in Worcester (Midgley and Musil, 1990) and at the TKRC (Milton et al., 1992; Esler and Cowling, 1993).

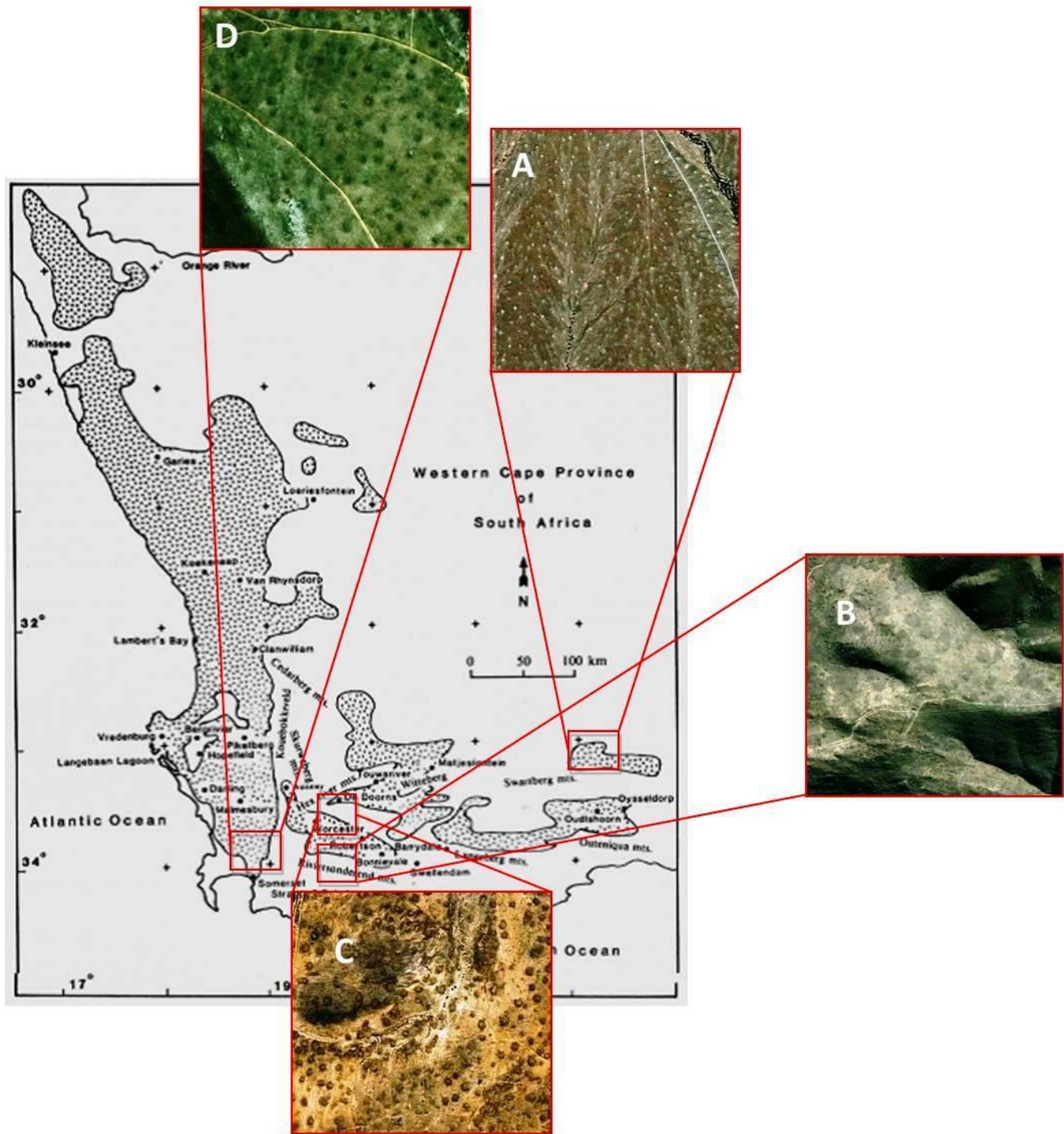


Fig 2.3. Distribution of *heuweltjies* (dotted areas on the map) in the western and south-western Cape (Source: Lovegrove and Siegfried, 1986), aerial images of *heuweltjies* at four sites in the south-western Cape are also shown (Source: GoogleEarth, November 2009). Pictures are not to scale. A = Tierberg Karoo Research Centre, B = Worcester Veld Reserve, C = Jonaskop, D = Wiesenhof Game Reserve. Direction of increasing rainfall (with changing seasonality) is from A to D.

The pH of the first 10 cm of *heuweltjie* soils was higher than the pH interpatch of soils at Namaqualand and Worcester (Midgley and Musil, 1990; Ellis, 2002). At TKRC, no differences were found between the pH of *heuweltjies* and that of interpatch soils (Milton et al., 1992). There is an accumulation of free salts on *heuweltjies* in almost all sites where they have been analyzed, with exception of Na, which was only high on *heuweltjies* at the TKRC (Midgley and Musil 1990; Milton et al., 2002; Agenbag et al., 2008; Herpel, 2008). Herpel (2008) also showed the general trend of high nutrients and salts on *heuweltjies* but noted that slope has large influence on these results. Table 2.1 summaries the soil the properties of *heuweltjies* as known thus far for the areas where most *heuweltjie* work has been done.

2.5. Properties and dynamics of *heuweltjie* vegetation

As with the soils, most of the literature on this subject represents research in the Succulent Karoo. Esler and Cowling (1995), who worked at the TKRC (Mucina and Rutherford, 2006) describe *heuweltjie* vegetation as that dominated by short-lived annuals with a high degree of dormancy to compensate for high levels of disturbance in these patches. On mounds, deciduous and succulent plants were found to be common by Knight et al., (1989) in the Clanwilliam area. Midgley and Musil (1990) also found similar patterns of distribution of deciduous species in Worcester but could not provide enough evidence to support the same pattern for succulent species. The *heuweltjies* found in the wetter Fynbos biome are more common in the lower lying, more fertile Renosterveld (Picker et al., 2007). The plant community structure of these *heuweltjies* differs substantially from those in the Succulent Karoo biome, tending toward woody species with bird-dispersed seeds (Walton, 2006). Ellis (2004) is the only study that reported on the pattern of vegetation cover on *heuweltjies* for different areas. This pattern appeared to be related to rainfall. In areas with high rainfall (e.g. Stellenbosch) *heuweltjies* were completely covered by vegetation whereas in dry areas *heuweltjies* were either bare or partially covered. However, these patterns could not to be explained entirely by rainfall. Ellis (2004) had turned to soil features for further explanation, and yet patterns remained indefinable.

Table 2.1 A summary of the properties of *heuweltjie* soils as described in the literature, only shown for selected sites all of which are in the Succulent Karoo. The data are as reported in the literature (including the units). At the Worcester Veld Reserve pH was measured in CaCl₂, at Namaqualand and the Tierberg Karoo Reserve Centre in water and at Jonaskop it was not specified. At all sites exchangeable cations were measured except at Worcester Veld Reserve. ¹Ellis, 2002; ² Ellis, 2004; ³Midgley and Musil, 1990; ⁴Milton et al., 1992; ⁵Agenbag et al., 2008 ;⁶Herpel, 2008 ;⁷Petersen, 2008; ⁸Midgley and Bösenberg, 1990.

| Soil properties | Namaqualand | | Worcester Veld Reserve | | Tierberg Karoo Research Centre | | Jonaskop | |
|---------------------------|---------------------------------|---------------------------|---------------------------------|---------------------------|---------------------------------|---------------------------|---------------------------------|---------------------------|
| | <i>Heuweltjies</i> ² | Interpatches ² | <i>Heuweltjies</i> ³ | Interpatches ³ | <i>Heuweltjies</i> ⁴ | Interpatches ⁴ | <i>Heuweltjies</i> ⁵ | Interpatches ⁵ |
| <i>Physical/Hydrology</i> | | | | | | | | |
| Clay/Silt (%) | 27-44.2 | 19.1-33.0 | 46 | 25 | 35-47 | 7-27 | - | - |
| Water | 13mm ⁶ | 9mm ⁶ | 9-11.5% ⁸ | 4-5% ⁸ | - | - | - | - |
| Hardpans ¹ | Yes | Yes and No | - | - | - | - | - | - |
| <i>Chemical</i> | | | | | | | | |
| pH | 8.5 | 7.5 | 7.1 | 4.4 | 8.3 | 6.1-8.5 | 6.3 | 4.2 |
| EC | μS cm ⁻¹ | μS cm ⁻¹ | | | μS cm ⁻¹ | μS cm ⁻¹ | | |
| | 114-172 | 34-64 | - | - | 2700-7300 | 400-3200 | - | - |
| <i>Nutrients</i> | mg kg ⁻¹ | mg kg ⁻¹ | mmol kg ⁻¹ | mmol kg ⁻¹ | mg kg ⁻¹ | mg kg ⁻¹ | mg kg ⁻¹ | mg kg ⁻¹ |
| N | 0.059-0.068 (%) | 0.026-0.056(%) | 84.62 | 61.97 | 1518-3831 | 462-742 | 3446.9 | 1390.5 |
| P | 50 | 2 | 2.43 | 0.54 | 65.5-117.0 | 24.4-69.8 | 45.7 | 36.3 |
| Ca | 70-300 | 30-50 | 146.6 | 11.17 | 848-7517 | 1361-2954 | 3206.3 | 651.7 |
| K | 3-7 | 1-1.5 | 7.98 | 2.32 | 509-1640 | 237-382 | 165.0 | 87.7 |
| Na | 9300 ⁶ | 11590 ⁶ | 6.6 | 6.3 | 458-2303 | 89-239 | 22.0 | 53.3 |
| Mg | 10600 ⁷ | 2200-3200 ⁷ | 45.7 | 8.9 | 711-2059 | 210-884 | 854.0 | 620.7 |

Typical *heuweltjie* taxa in the Succulent Karoo include *Eurphobia mauritanica* (Midgley and Musil, 1990), *Psilocaulon utile* and *Malephora lutea* (Milton et al., 1992). In contrast, the interpatch vegetation is dominated by long-lived, less succulent taxa such as *Pteronia spp.*, *Galenia africana* and *Ruschia spp.* (Midgley and Musil, 1990). In the Fynbos, *heuweltjies* are dominated by *Olea europaea* subsp. *africana*, *Maytenus acutifolia*, *Rhus* and *Salvia* species. These species often occur as bush clumps (Walton, 2006). The interpatches, however, are most commonly associated with dominance by *Dicerotheramnus rhinocerotis* (formerly *Elytropappus rhinocerotis*). In some areas, these structural differences are clear from simple observation (Fig 2.4).

Studies on plant reproductive ecology show that species growing on the *heuweltjies* produced more seeds even in areas where plant cover on the *heuweltjie* was lower than interpatches (Milton and Dean, 1990). Also, there is more variance in the size of seeds of *heuweltjie* species, thus the probability of finding a large seeded species is higher (Esler and Cowling, 1995). Seeds of interpatch vegetation are, however, more likely to germinate and once established seedlings compete strongly with adults on the *heuweltjies*. In the interpatches adults either have a neutral effect or act as nurse plants in low rainfall areas (Riginos et al, 2005). Under higher rainfall, both nursing and competitive effects were observed with no differences between mound and off mound sites. The higher degree of disturbance and competition on the *heuweltjies* may explain the need for plants to retain a soil seed bank (Esler and Cowling, 1995).

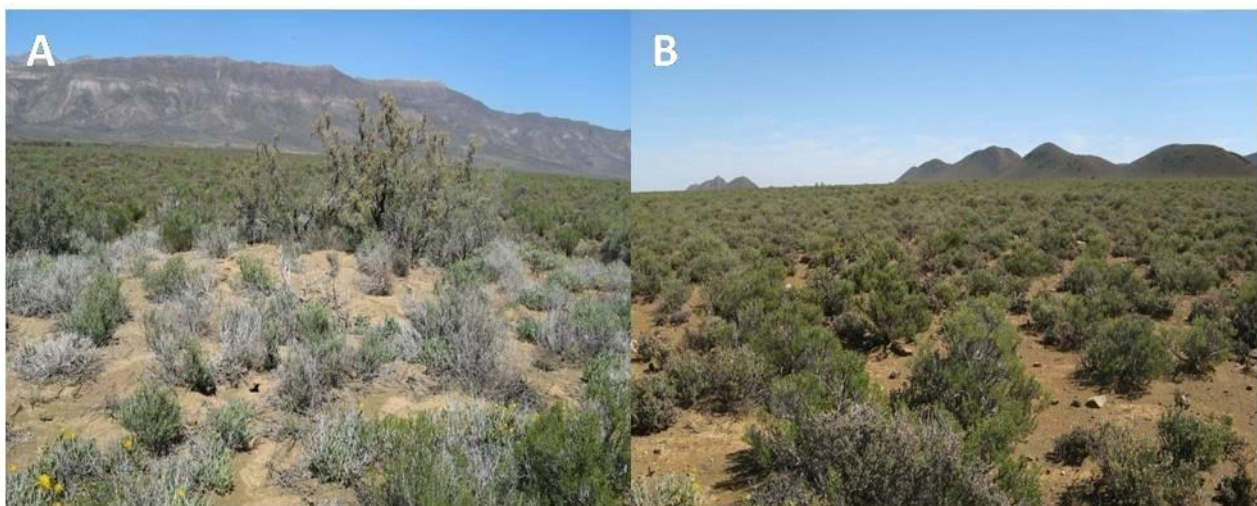


Fig 2.4. The photograph shows the differences in vegetation structure between the interpatches and *heuweltjies* at the Tierberg Karoo Research Centre, near Prince Albert. *Malephora lutea* is common on the *heuweltjies* (A) and *Pteronia pallens* dominates interpatch vegetation (B). The weak structure of *heuweltjie* soils is evident. There is also evidence of disturbance (holes) made by whistling rats (*Parotomys brandtsii*) on the *heuweltjie*.

2.6. Hypotheses on ecosystem function of *heuweltjies*

Ecosystem structure is the species composition and ecosystem function is the flow of energy and matter through ecological systems. Three basic cycles are needed for ecosystems to continue functioning i.e. biogeochemistry (cycling of nutrients by decomposition), life cycles and food webs (Boero and Bonsdorff, 2007). By its very definition an ecosystem needs to exchange matter and energy amongst its components and environment in order to exist. Soil processes such as decomposition and nutrient cycling transfer materials and energy to and from the soil and as a consequence CO₂ is released to the atmosphere and, nutrients from dead organic matter are freed to the soil in forms that are useful to plants and microorganism (Chapin et al., 2002). However, spatial and temporal distribution of such processes is not even in many ecosystems. There are areas, hotspots, and periods, hot moments, of especially high process rates. Interest in these hotspots and hot moments is fast gaining momentum in the ecological literature today, especially after an extensive review by McClain et al., (2003) (also see Bundt et al., 2001). These authors considered the research on the identification of these hotspots as an urgent global issue that may aid the understanding of life–sustaining biogeochemical cycles. There are many examples of these hotspots in the literature. Brown bears feeding on salmon increase soil ammonium concentration and nitrous oxide emissions in riparian areas (Holtgrieve et al., 2009). Carcasses of moose killed by wolves increased soil nutrient concentrations, and caused a shift in microbial composition and biomass (Bump et al., 2009). Their existence also shows the role that animals play in regulating ecosystem processes. Groffman et al., (2008) argue for the incorporation of these hotspots and hot moments into existing N cycling models in order to better account for and understand this important ecosystem process. Similarly, as *heuweltjies* have increased contents of plant nutrients and properties such as increased clay content this may potentially increase biogeochemical reactions, thus placing them in McClain et al.,'s (2003) category of hotspots.

It is not known whether rates of soil processes are higher in soils of *heuweltjies* than the surrounding soils, however, microbial processes have been seen to be accelerated on termite affected soils in other biomes (Lopez-Hernandez, 2001). N cycling rates (N mineralization) as well as N stocks are reported to be higher in soils derived from termitaria. Similarly, soil C mineralization also seems to be elevated on termitaria (Jones, 1990), especially as soil water content is usually higher on *heuweltjies* compared to surrounding soil, thus creating both hotspots, which are more prone to form patches with more pronounced and perhaps longer lasting hot moments in the landscape. Grant and Scholes (2006) found that in a South African savanna, termite mounds were hotspots of nutrients, both in soils and vegetation and therefore affected the foraging and

movement and conservation of large mammals. N, P and Na, all nutrients sought after by the large herbivores of semiarid savannas, seem to be elevated in vegetation and soils of termitaria (Mills et al., 2009).

Even though hotspots are patches in a much larger matrix, they may significantly affect the entire landscape. The termite mounds of the Miombo woodlands have significantly taller trees with greater woody basal cover and are favoured by mega-herbivores (Loveridge and Moe, 2004). Years of pastoral activities in traditional human settlements in Kenya caused a sharp increase in soil nutrients compared to nearby soils (outside fences) which lead to changed plant species composition, richness and succession (Muchiru et al., 2009). *Heuweltjies* affect succession in the Succulent Karoo by giving a competitive advantage to unpalatable shrub species and allowing them to invade and dominate in the matrix (Yeaton and Esler, 1990). Trees growing on termite mounds in Zimbabwe had higher concentrations of nutrients and were fed on more by elephants than the trees of the surrounding woodlands (Holdo and McDowell, 2004). The deposition of guano by bats in temperate forests increased N mineralization by 380% which influences growth of herbaceous species and the development of tree seedlings, and thus affects competition between the herbs and trees (Johnson et al., 2010).

Hotspots are also an important source of greenhouse gas emissions and need to be incorporated in the models of global climate change. On a microscale soils with high organic matter emit more CH₄ (Wachinger et al., 2000). Much of the efflux in nitrogenous gases happens in small patches and at brief periods (Groffman et al., 2009). These hotspots are created by the interaction between organic matter and physical factors (rooting patterns, soil structure, topography, hydrologic flow paths and geology) which control oxygen diffusion. The hot moments can be brought about by dry-rewetting and freezing-thawing events. Conservationists may also need to consider that hotspots are more sensitive to alien plant invasions because of the high nutrient content and high disturbance. For example, *heuweltjies* are already invaded by the salt bush *Atriplex lindleyi* in some parts of the Succulent Karoo (Milton et al., 1992; Milton and Dean, 2010), and by alien annual grasses in the Namaqualand Succulent Karoo (Steinschen et al., 1996) and in the Renosterveld (Muhl, 2008). It is not known whether *heuweltjies* are patches where greenhouse emissions are elevated.

In an age where changes in the global biogeochemical cycles and reductions in biodiversity are occurring at an alarming rate, studies aimed at the mechanistic understanding of hotspots are needed

(Eviner and Chapin, 1997; Chapin et al., 2000). This study aims to examine these processes on *heuweltjies* in close detail including those related to decomposition (soil respiration) and cycling of important nutrients (N mineralization and phosphatase activity). Factors of the physical environment, the quantity and quality of the substrate and the microbial community all control decomposition. Any changes in these may have significant impact on these processes (Swift et al., 1979). As *heuweltjies* are known to differ for most of these controlling factors it is reasonable to expect that they should differ in soil processes rates and may be hotspots of these important biogeochemical cycles.

Soil nutrient stocks and process rates, on the other hand, may influence vegetation structure and plant ecophysiology (especially relating to water relations) on *heuweltjies*. The higher soil N and P of *heuweltjie* soils, for example, may affect aspects of plant growth such as productivity, which will be reflected in high stomatal conductance, high specific leaf area, high foliar N content and low C/N ratio of leaves. These observations were made for other mound plants (Hill et al., 2005). Some of the aforementioned plant traits are recognised as key predictors of other ecosystem properties and processes at local and global scales (Díaz et al., 2004). I studied these aspects by carrying out basic field and laboratory experiments and measurements. My results are especially relevant to those interested in landscape ecology, patch dynamics and in restoration ecology of the Fynbos and Succulent Karoo biomes, both hotspots for biodiversity.

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Chapter 3: Physicochemical and biogeochemical properties of soils from *heuweltjie* patches and interpatch areas across a rainfall gradient

3.1. Abstract

Heuweltjies, putatively formed by the southern harvester termite *Microhodotermes viator*, are found in areas below the Great Escarpment in the Western and Northern Cape areas of South Africa. They affect vegetation composition, animal and plant life and the hydrology of the landscape. A study was carried out to discover if *heuweltjies* are also nutrient and biogeochemical hotspots of C, N and P. Soil samples were taken on ten *heuweltjies* and interpatch areas at four sites across a rainfall gradient in the south-western Cape (including Fynbos and Succulent Karoo sites). Soils were analysed for soil properties (particle size distribution, pH, electrical conductivity, total C and N and available P) and soil processes (potential soil respiration, anaerobic N mineralization and, acid and alkaline phosphatase activities) in the laboratory. *Heuweltjies* soils had higher silt content, pH, electrical conductivity, total C and total N than the interpatch areas. There was also higher efflux of CO₂, higher N mineralization and phosphatase activity on *heuweltjies* soils. Results varied with vegetation type, with Succulent Karoo sites having higher nutrient content and N mineralization than Fynbos sites. No clear trends were observed for nutrients across the rainfall gradient on *heuweltjie* soils whereas pH and electrical conductivity declined sharply with increasing rainfall. The identification of *heuweltjies* as biogeochemical hotspots has implications for climate change, management of invasive species and restoration.

Keywords: *heuweltjies*, soil properties, phosphatases, soil respiration, nitrogen mineralization, termitaria

3.2. Introduction

Soils are dynamic combination of solids, liquid, and air. The physical and chemical properties of soils are determining factors in numerous observable ecological properties of ecosystems, at various scales. In the Mediterranean-climate region of South Africa, soil properties are implicated in the differences in floristic patterns (Fynbos versus Renosterveld) within larger landscapes, while a similar pattern is also visible within the Karoo (upland and riparian areas) (Cowling et al., 2003; Milton et al., 2003). In many ecosystems, physicochemical properties such as pH, texture and nutrients are drivers of other ecosystem properties and processes namely biogeochemical cycling

and plant species distribution. pH, for example, influences the availability of plant nutrients like P and consequently affects plant species distributions. pH also affects soil biological activity, reducing it at high acidity (Romanyá et al., 2005; Wang et al., 2006). Texture is one of the more stable physical properties of an ecosystem affecting soil water dynamics and soil water availability in turn affects vegetation structure (Dodd and Lauenroth, 1997). In a shortgrass steppe landscape the mineralization of N and C were significantly negatively correlated with the sand content (Hook and Burke, 2000) and a similar trend was found for forest ecosystems (Silver et al., 2000).

Virgin soils are replete with the activity of plant and animal life (Chapin et al., 2002). The interactions of the plants, the animals (above and below the surface) and the microorganisms with their environments drive the cycle of nutrients. For a patch of soil, the rate of nutrient cycling is determined, largely, by availability of resources to microorganisms (Gutiérrez and Jones, 2006). The distribution of soil resources are not uniform, neither are the nutrient cycling rates within ecosystems. McClain et al., (2003) noted areas (and moments) of especially high rates of biogeochemical cycling, termed ‘hotspots’ and ‘hot moments’. In terrestrial systems they may represent areas altered by the presence of an animal or a plant, such as the soils directly below shrubs in arid ecosystems (Reynolds et al., 1999).

Soil invertebrates, such as ants and termites are constantly moving plant material and soils causing significant changes in their properties (Whitford, 1996; Jones, 1990). Termites are known to contribute to decomposition rates in the Okavango Delta by collecting and consuming litter and thus speeding up decay rates (Schuurman, 2005). They also breakdown N and C compounds with the aid of symbiotic bacteria in their gut systems (French et al., 1976; Potrikus and Breznak, 1980; Kato et al., 1998). However, outside of these direct impacts, termites may also affect decomposition indirectly by changing physical, chemical and biochemical characteristics of the soils that influence nutrient mineralization (Lopez-Hernandez, 2001). Since over 90% of plant nutrients become available via recycling (Chapin et al., 2002), this constitutes a significant portion of soil nutrient stocks. Termites are at times referred to as ecosystem engineers because they bring about such significant changes that have repercussions that carry out into the whole ecosystem (Jones et al., 1994; Dangerfield et al., 1998). In an African savanna ecosystems termite mounds were found to be nutrient hotspots that help to sustain large herbivores (Grant and Scholes, 2006).

Heuweltjies, mounds occupied by the termite *Microhodotermes viator*, differ in their soil properties

from the surrounding soils. These termitaria have finer textured soils with higher water holding capacity and higher soil water content during the wet season (Midgley and Musil, 1990). Mounds also have higher percentage of macro and micronutrients, higher pH and higher electrical conductivity (Midgley and Musil, 1990; Milton et al., 1992; Esler and Cowling, 1993; Herpel, 2008). *Heuweltjies* seem to have been around for a very long time and affect large areas spanning across a wide range of climatic zones (Picker et al., 2007). Therefore, their impact on the ecosystem processes is potentially large and ongoing. The existence of these mounds may have important implications for the nutrient cycling in their host ecosystems, Succulent Karoo and Fynbos, and yet this issue has received little attention. This information is of great significance for restoration of ecosystem function in these biomes.

Biogeochemical cycles are important ecosystem processes that regulate the movement of nutrients. Soil microorganisms are the key role-players within these processes. The range of protocols available for analyzing soil biogeochemical properties has made the quantifying of these cycles relatively simple both in the laboratory and in the field. Mineralization is that part of the biogeochemical cycle where organic precursors are converted to biologically available (inorganic) stocks of nutrients (Anderson and Ingram, 1993). In arid ecosystems, where soils usually have an equate supply of nutrients and cycling is limited by water, mineralization is the critical step in the cycling process (Whitford, 1996). While the determination of actual mineralization rates is often logistically challenging, potential mineralization rates of soils can be quantified relatively easily under controlled condition in the laboratory.

Soil respiration is the rate of CO₂ emissions released from the soil as a result of metabolic functions of soil animals, microorganisms and plant roots (Singh and Gupta, 1977; Raich and Tofekcioglu, 2000; Lou and Zhou, 2006). The majority of the CO₂ is respired during the decomposition of litter and organic material in the soil (Lou and Zhou, 2006). At the same time, other nutrients are being released or immobilized depending on the competitive ability of soil organism and plant roots (Singh and Gupta, 1977). The rate of CO₂ release is affected by a number of factors including soil temperature, water, root biomass, C/N ratio of the substrate, soil pH, nutrient content, texture, soil structure, salt accumulation, depth and aeration (Keith et al., 1997; Raich, and Tufekcioglu, 2000; Wang et al., 2003; Conant et al., 2004; Wang et al., 2006; Han et al., 2007). The main drivers of soil respiration are water and temperature. Respiration increases significantly between 10 - 40°C and declines sharply above and below these temperatures (Singh and Gupta, 1977). Recent studies show that soil respiration is related to current photosynthesis for plant roots (Hogberg et al., 2001; Tang et

al., 2005). Therefore, soil respiration functions as a tool to directly evaluate how much C is available to both soil microbes and plants (Raich, and Tufekcioglu, 2000) and how quickly it cycles through the ecosystem. Higher rates of soil respiration on some termitaria, compared to nearby soils (Yamada et al., 2005), show that termite-affected soils have the potential for higher rates of C mineralization (Tripathi and Sharma, 2006). Potential soil respiration excludes the contribution of root respiration to total soil respiration.

Nitrogen mineralization is linked to the soil respiration activities in the soil. For example, when litter is being decomposed, N compounds are released together with those of carbon (Coleman et al., 2004). When the N liberated is incorporated into microbial biomass and is used for growth, it is said to be immobilized as it is not available for plant uptake. Reactions that immobilize and liberate N happen simultaneously and when the net outcome of these reactions results in 'free' N in the soil solution; this N is said to be mineralized (Chapin et al., 2002). During the mineralization of N, NH_4^+ that is released from the decomposition of proteins, chitins and nucleic acids, is readily absorbed by the plant from the soil solution (Bardgett, 2005). According to classic literature the amount of N mineralized depends on the C/N ratio (Jones and Parsons, 1970; Janssen, 1996; Kara, 2000), specifically on whether the microbes are C or N limited. When the C/N ratio is high, microbial biomass increases because of increased energy supply and the demand for N also increases which leads to immobilization. At low C/N ratios of the substrate C becomes limiting to microbial growth, biomass decreases and N becomes available (Lambers et al., 1998). Therefore, the ratio of C/N in the soil can be a controlling factor on whether net mineralization or net immobilization occurs. Termites affect the C/N ratio of soil by the consumption or the release of C and N (Zaady et al, 2003) and thus indirectly affect N mineralization rates of these soils.

Phosphorus occurs in many organic and inorganic forms in soil. Labile organic P, phosphate, is the type of P that is available for uptake by plants and microbes and occurs at very low concentrations in soil (Bardgett, 2005). This makes it limiting in many ecosystems. This has necessitated the evolution of highly specialized plant morphological and biochemical features such as cluster roots (Hagström et al., 2001) to facilitate uptake in systems with very low P e.g. Mediterranean ecosystems (Sardans et al., 2006). Plant and microbes manufacture and release enzymes termed phosphatases in response to a shortage of P. These enzymes cleave bonds and free the phosphates in the P-containing compounds in the soil. The enzymes are energy expensive and are therefore not released at leisure (Olander and Vitousek, 2000). Researchers have used the relative amounts of these enzymes in the soil as an indirect measurement of P bioavailability in the soil (Bremner and

Tabatabai, 1969). Even though the phosphatase activity is decoupled from respiration and N mineralization, much of the same soil factors affect it. Therefore, changes in chemical properties and nutrient stocks associated with *heuweltjies* may modify phosphatase activities, which may be useful as an indicator of P mineralization on and off *heuweltjie* patches.

Other soil variables that are also modified by termites can eventually lead to changes in the mineralization rates of C, N, and P. For example, an increased input of N in the soil (e.g. by fertilization) can lead to enhanced rates of N mineralization (Carroll et al., 2003). Increased C content of soils will affect soil processes, for example C and N mineralization (Chapin et al., 2002). Respiration, as previously mentioned, is affected mostly by soil temperature (Conant et al., 2004) and soil water (Conant et al., 2000), both of which may be modified as you move from *heuweltjies* into interpatch areas. Modification of pH has a significant impact on the phosphatase activity and thus the mineralization of P (Dick et al., 2000). *Heuweltjies* differ from their surrounding soils in all these properties; therefore, the ramifications for nutrient mineralization may be significant.

The current study was conducted to assess the potential impact of termite affected *heuweltjie* soils on the mineralization rates of the major plant nutrients C, N and P in the Succulent Karoo and Fynbos. In so doing I wanted to know 1) what potential impact the properties of *heuweltjie* soils have on the N mineralization, soil respiration and activity of alkaline and acid phosphatases. 2) Whether the direction of change in process rates (i.e. moving from the *heuweltjie* to the interpatch area) is the same regardless of vegetation type (Succulent Karoo vs. Fynbos). This would establish whether or not these mounds are biogeochemical hotspots in these ecosystems and thereby establishing the role of termites as ecosystem engineers in both the physical and chemical realms.

3.3. Methods

3.3.1. Study sites

All sampling was conducted at four sites across the south-western Cape, South Africa. Two sites were selected in the Succulent Karoo, the Tierberg Karoo Research Centre (TKRC) (33°10' 25.2 " S, 22°16' 10.3"E) and Worcester Veld Reserve (WVR) (33° 37' 16.56" S, 19° 28' 15.24" E), one at an ecotone between Fynbos and Succulent Karoo, Jonaskop (JON) (33° 55' 4.38" S, 19° 29' 24.54" E) and one in the Fynbos, Wiesenhof Game Reserve (WGR)(33° 50' 31.26" S, 18° 53' 8.82" E) (Fig. 3.1). Sites are tens to hundreds of kilometers away from each other and therefore show distinct

differences in climate and soils (Table 3.2). Rainfall increases from the east to west, with the Fynbos site (WGR) having the highest annual rainfall (Fig. 3.1). *Heuweltjies* are present at all sites. Differences are evident in vegetation structure between the Fynbos and Succulent Karoo sites.

TKRC has average annual rainfall of 169 mm with peaks in autumn and spring (Milton et al., 1992) with average minimum and maximum temperatures between 4.0-18.3 °C for winter and 16.0 - 32.4 °C for summer. The vegetation type, Prince Albert Succulent Karoo (Mucina & Rutherford 2006), is dominated by low succulent and non-succulent shrubs (mostly Asteraceae). The site forms part of a 12,000 ha farm, 100 ha of which was enclosed in 1987 where livestock were excluded (TKRC). Soils are derived from Ecca shales and Dwyka tillites with a sandy loam texture (Milton et al., 1992). Nitrogen is relatively low and P and potassium high in surface soils (Milton et al., 1992). *Heuweltjies* cover 3.2 % of the TKRC land area and are more or less spread evenly throughout the site. Vegetation cover is highly varied with some *heuweltjies* having low cover because of grazing by rodents and other herbivores. Typical *heuweltjie* taxa include *Psilocaulon utile* and *Malephora lutea* and *Pteronia spp.*, *Galenia africana* and *Ruschia spp.* are common in the interpatch areas. Milton et al., (1992) gives a more detailed description of the site.

At the WVR rain falls mostly in winter (June-August) with mean rainfall of 270 mm per year (data from the South African Weather Services). Average minimum and maximum temperatures for winter are between 7.8 - 18.4 °C and for summer between 16.0 - 30.4 °C. *Heuweltjies* are found on north and south facing slopes and appear to be larger than those of the drier TKRC site. Vegetation at the site is Robertson Succulent Karoo (Mucina and Rutherford, 2006). Asteraceous shrubs (*Pteronia spp.*) dominate plains. Stem succulents such as *Eurphobia mauritanica* and *Typha paniculatum* are common on the *heuweltjies*. Soils at the site are shallow, and derived from the Malmesbury shales of the Worcester-Robertson valley (Midgley and Musil, 1990; Rahlao et al., 2008).

JON forms part of the Riviersonderend Mountain range that is in the Cape Fold Belt. It is a catchment area under the protection of CapeNature. Its vegetation varies from Sandstone Fynbos on the mountain peak (above 800 m), through ecotonal Fynbos/Succulent Karoo at 600 - 800m. Robertson Succulent Karoo and Breede Shale Renosterveld vegetation types (Mucina and Rutherford 2006) alternate at the lowest point (below 600 m) (Agenbag et al., 2008); the Robertson Succulent is found on north-facing slope whereas Breede Shale Renosterveld is found on south-facing slopes. Average annual rainfall varies as you go downslope from 719.6 - 315 mm per year

and average minimum and maximum temperature are 7.6-17.8°C for winter and 15.1 - 28.1°C for summer for the nearest town (Villiersdorp). Soils are derived from Table Mountain sandstone at high elevation and Bokkeveld shales at the lowest point. For the purpose of this study, only the soils and vegetation of the Breede Shale Renosterveld were sampled at this site. As Renosterveld vegetation forms part of the Fynbos biome, this site will be considered as a Fynbos site during analyses of data and when discussing the results. This vegetation is dominated *Pteronia paniculata* and *Dicrothamnus rhinocerotis* in the interpatches and *Pteronia incana* on the *heuweltjies*. Agenbag et al., (2008) provides more detailed information with regard to this site.

WGR, near Stellenbosch, supports Cape Winelands Shale Fynbos vegetation. Average annual rainfall is near 700 mm per year with minimum and maximum temperatures averaging between 10.4 - 18.0 °C in winter and 17.0 - 27.7 °C in summer (Jacobsen et al., 2007). The soils are sandy, shallow and very stony underlying Malmesbury shales (Mucina and Rutherford, 2006). It functions as a game reserve and tourist attraction; game includes eland (*Taurotragus oryx*), wildebeest (*Connochaetes taurinus*), zebra (*Equus zebra*) and other species which roam freely. *Dicrothamnus* spp. and *Cliffortia* spp. are common both on and off *heuweltjies*.

Ten *heuweltjies* were chosen randomly at each site for soil investigations. The *heuweltjies* sampled were on the south facing slope at all sites except WGR where they are found only on the north facing slope.



Fig 3.1. GoogleEarth map showing the location of the study sites in the south-western Cape. Tierberg Karoo Research Centre (TKRC) and Worcester Veld Reserve (WVR) are in the Succulent Karoo sites. Jonaskop (JON) and Wiesenhof Game Reserve (WGR) are Fynbos sites.

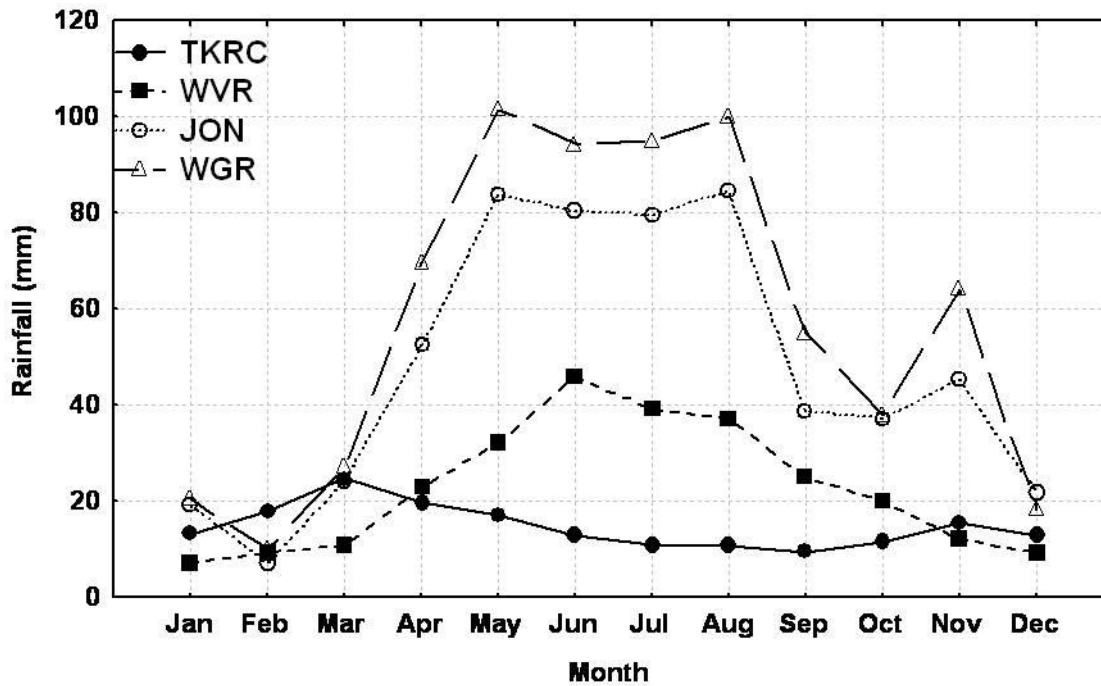


Fig. 3.2. Monthly averages of rainfall for each study sites. Tierberg Karoo Research Centre (TKRC) (represented by 113 yrs of rainfall data from Prince Albert 28 km west of TKRC) and Worcester Veld Reserve (WVR) (125 yrs) are in the Succulent Karoo. Wiesenhof Game Reserve (WGR) (8 yrs) and Jonaskop (JON) (9 yrs) Fynbos are sites. TKRC data are from S.Milton, WVR and JON data from the South African Weather Bureau and WGR data from Infruitec.

3.3.2. Sampling and Analyses

3.3.2.1. Soil Properties

Bulked soil samples (four samples from the centre towards the edges) were taken from the top 10 cm of the *heuweltjie* and interpatch (matrix) soils with steel tubes of five centimeter inner diameter. Samples were put into polyethylene bags and transported to the laboratory within hours of sampling. On arrival, they were bench dried for one to two days, put through a 2mm mesh sieve and stored at room temperatures awaiting analyses (Robertson et al., 1999). A sub-sample was taken and analysed for total C, total N and available P (Table 3.1). The Bray 2 method was used for all the soils in order to standardize even though this method is not necessarily ideal for soil with pH above 7.5. The rapid method by Kettler et al., (2001) was used to test for differences in particle size distributions. This method was followed as it is, except that clay and silt were sieved into 350 ml beakers and rinsed with 250 ml deionised water.

Soil water probes (Em50 data logging system, Decagon) were installed on *heuweltjie* and interpatch soils at one site, the TKRC to monitor water and temperature changes in the two areas over the

longer term. Probes were installed at a depth of 10 cm, the depth at which most biological activity occurs. As a result of the malfunctioning of probes, only 3 months worth of data were recorded, from May to June 2008.

3.3.2.2. *Soil respiration*

Bulk soil samples were taken from five *heuweltjies*, on and off, at each site and transported to the laboratory in sealed plastic bags. They were put through a 2 mm sieve and left to bench dry for two days. A 10g subsample was taken from each soil sample and analysed for water holding capacity. For this, the subsamples were poured into a funnel lined with filter paper and the soil was wetted through with deionised water. The funnels were transferred into paper cups and left to drip-dry in icebox overnight. Water was poured into the bottom of the ice box to create a humid environment. The next morning one gram of each sample was transferred onto aluminium trays and placed in an oven at 105 °C for 12 hours. The weight of the dry soil was used to obtain 100% water holding capacity (Robertson et al., 1999). The results are shown in Appendix A.

I used a method modified from Robertson et al., (1999) where soil was incubated for seven days and soil respiration measurements were carried out on day one and day seven. Before starting the potential soil respiration trials, three grams of each soil sample, at 65% water holding capacity, were transferred into pre-weighed glass vials. The vials were sealed with parafilm and incubated in an oven at 30°C awaiting CO₂ trails. The accumulation of CO₂ over two hours was measured with an infrared gas analyser system (IRGA)(LI 7000, Li-Cor Biosciences).

Starting the trials, samples were removed from the oven, flushed with 20 seconds worth of humidified CO₂ free air and sealed with rubber stoppers. 0.2 ml of the headspace was extracted with a syringe and the sample vial placed back into the oven. The contents of the syringe were emptied into plastic piping (manifold) connected to the IRGA. The IRGA estimated the flux of CO₂ at a flow rate of 200 ml per minute. After the incubation (2 hrs) the vials were taken from the oven and 0.2 ml of the headspace extracted again and the CO₂ concentration determined on the IRGA. The rubber stoppers were again replaced with parafilm and vials returned to the oven for seven-day incubation. On day seven the samples were treated to the same procedure. Results are expressed as ml CO₂ g dry soil⁻¹ h⁻¹ (Vanhala, 2002).

Table 3.1. Methods and instruments used during soil analyses

| | Summary of method | Instruments Used | Reference |
|-------------------------|--|---|---------------------------|
| pH | Prepared a soil slurry with soil 1:2 deionised water. Solution was stirred and allowed to stand for 30 minutes before taking measurements. Used a reference electrode–Microprocessor meter, Hanna instruments. | pH meter, Hanna instruments | Bashour and Sayegh (2007) |
| Electrical conductivity | 1:5 soil solution water prepared with deionised water. Solution was stirred continuously for 30 minutes and allowed to stand for an hour before measurements were taken. | Conductivity meter- Model no. 441, Corning | Cookson (2002) |
| Total C | Digestion with elemental analyzer after Dry combustion | EA 3000 Series, EuroVector Instruments and software | Nelson and Sommers (1996) |
| Total N | Digestion with elemental analyzer after Dry combustion | EA 3000 Series, EuroVector Instruments and software | Nelson and Sommers (1996) |
| Available P | Bray 2, then analysed colorimetrically | | Bray and Kurtz (1945) |
| Particle size analysis | Rapid method | | Kettler et al., (2001). |

3.3.2.3. Nitrogen Mineralization

Ten *heuweltjies* were chosen at each site and soils were sampled to a depth of ten centimeters using steel tubes with a five centimeter inside diameter. Four composites were taken on and off each *heuweltjie* from the centre of the *heuweltjie* towards the edges on an east or west direction. The soils were then taken to the laboratory in plastic bags, where they were air-dried for two days and put through a 2mm mesh before being analyzed.

To test for the potential rates of ammonium production in soils, four grams of each sample were placed in 50 ml plastic vials. The vials were filled with enough deionised water to cover the soil and sealed with plastic stoppers disallowing the exchange of gases. These anaerobic conditions

prevented the production of nitrate such that only ammonium needed to be analysed (Binkley and Vitousek, 1989). The anaerobic technique is useful for detecting differences between sites (Binkley and Vitousek, 1989).

For initial concentrations of ammonium another four grams of each soil were placed in plastic vials. To extract the ammonium 20 ml of 2M KCl were poured into the vials. The vials were shaken at medium speed for an hour and centrifuged for five minutes, which allowed soil particles in suspension to concentrate at the bottom. The amount of ammonium in the clear extractant was determined colorimetrically by the indophenol blue method (Page et al., 1982). Phenate reacts with ammonia in the sample extractant in the presence of an oxidizing agent (Page et al., 1982) and results in a blue colour. A spectrophotometer (VIS 7200, Techcom) was used to measure the intensity of the resulting colour and the concentration derived from a standard equation. After the 10 days of incubation the rest of the samples underwent the same treatment. Net ammonium mineralization was the final concentration minus initial concentration in $\mu\text{g g soil}^{-1}$ for each soil sample.

3.3.2.4. *Phosphatase activity*

Acid and alkaline phosphatase activity was analysed following Tabatabai (1982). Soil samples were taken from on and off *heuweltjies* (following the same protocol as for N mineralization) and sieved with a 2 mm mesh sieve. The samples (two grams) were then weighed into 50 ml plastic vials, mixed with a solution of Toluene and *p*-nitrophenol and incubated at 35°C for an hour. CaCl_2 and NaOH were added to induce colour and stop the reaction. Controls were included in order to estimate the colour precipitation not coming from the phosphatases (Tabatabai, 1982). Samples were filtered and absorbance was estimated with a spectrophotometer set at 410 nm. The concentration was estimated with standards suggested by Tabatabai (1982). The results are presented as micrograms of nitrophenol released per gram soil per hour ($\mu\text{g } p\text{-NP g dry soil}^{-1} \text{ h}^{-1}$) (Bremmer and Tabatabai, 1969).

3.3.3. *Data analyses*

All data were normally distributed therefore *t*- tests of dependent variables were used to test for significant differences (Shapiro et al., 1968). For the soil water and temperature data, statistical tests were not performed because they were only recorded from one *heuweltjie* and non-*heuweltjie* site.

All statistical analyses were done on STATISTICA Version 8 (2007).

3.4. Results

3.4.1. Soil particle size analysis and volumetric soil water content

Within the three months of data collection, soil temperature and water levels differed between *heuweltjie* and interpatch soils (Fig 3.3). Water levels were similar for both soil types until April 15, 2009 when a rainstorm resulted in an increase in volumetric soil water content of both soils, but more so on the *heuweltjie* compared to the interpatch soils (Fig 3.3a). Temperature was always higher in the interpatch soils (Fig 3.3b). Overall, few significant differences were found in soil particle size distributions between *heuweltjies* and interpatches. Overall, *heuweltjie* soils had significantly higher silt content, lower sand content (not significant) and the same clay content as interpatch soils (Table 3.2). Only in WVR was a difference in clay content detected on and off *heuweltjies*.

3.4.2. Chemical soil properties

Overall, soil macro-nutrients were significantly higher ($p < 0.05$) on *heuweltjies* than interpatch soils, including C content, N content and P concentrations (Figs 3.4 a-f). The exception is P concentration in the Fynbos biome (JON and WGR) where at JON, *heuweltjies* had lower P (mg kg^{-1}) than the interpatches and at WGR *heuweltjies* and interpatches P (mg kg^{-1}) did not differ significantly (Fig 3.4 e). There was at least 1.5 times more N and twice as much C on *heuweltjies* as there was in the interpatch soils (Fig 3.4 b and d). The biggest difference in the C content of soil between *heuweltjies* and the interpatches was observed at the Succulent Karoo sites (TKRC and WVR) (Fig 3.4 c). The differences in the N content and P concentration showed a similar trend (Fig 3.5 a and e). TKRC *heuweltjie* soils had on average 0.22% N, 5 % C and 70 mg kg^{-1} P. This translates to 4 times, 6 times, 2 times higher N content, C content, and P concentration respectively than was found in the nearby interpatches (Figs 3.4 a, c and e and Figs 3.5 a-c).

Table 3.2. Physical features, vegetation type and management history at each study site.

| | Tierberg Karoo Research Centre | Worcester Veld Reserve | Jonaskop | Wiesenhof Game Reserve |
|------------------------------|---|---|--|---|
| Biomes ¹ | Succulent Karoo | Succulent Karoo | Fynbos/ Succulent Karoo ecotone | Fynbos |
| Vegetation Unit ¹ | Prince Albert Succulent Karoo | Robertson Succulent Karoo | Robertson Karoo/Breede Shale Renosterveld/North Sonderend Sandstone Fynbosbut sampled only Breede Shale Renosterveld | CapeWinelands Shale Fynbos |
| Dominant plant species | Interpatch: <i>Pteroniapallens</i> , <i>Ruschia spinosa</i> <i>Heuweltjies: Malephora lutea</i> , | Interpatch: <i>Pteroniapaniculata</i> <i>Heuweltjies: Euphorbiaspp.</i> | Interpatch: <i>Pteroniapaniculata</i> , <i>Dicerothamnusrhinocerotis</i> <i>Heuweltjies: Pteroniaincana</i> | Interpatch: <i>Dicerothamnusrhinocerotis</i> ., <i>Cliffortiasp.</i> <i>Heuweltjies: Cliffortiasp.</i> , <i>Dicerothamnusrhinocerotis</i> |
| Geology | Ecce shales/Dwyka tillites ² | Malmesbury shales ³ | Table mountain quartzite/Bokkeveld shales ⁴ | Malmesbury shale ¹ |
| Management History | Livestock grazing until 1987 | Livestock farming until 1935 | Light grazing | Game reserve/ tourist attraction |
| Conservation status | Protected, Long term research site | Protected, Department of Agriculture | Protected, CapeNature | Private property |
| Slope/Aspect | South Facing | South Facing | South Facing | North Facing |
| Rainfall (mm) | 169yr ⁻¹ (113 yrs) | 270yr ⁻¹ (125 yrs) | 575 yr ⁻¹ (9yrs) | 693 yr ⁻¹ (9yrs) |
| Average Tmin-Tmax (Winter) | 4.0 -18.3 | 7.8-18.4 | 7.6-17.8 | 10.4-18.0 |
| Average Tmin-Tmax (summer) | 16.0-32.4 | 16.0-30.4 | 15.1-28.1 | 17.0-27.7 |

¹Mucina and Rutherford, 2006, ²Milton et al., 1992; ³ Rahlao et al., 2008; ⁴ Agenbag et al., 2008.

JON *heuweltjies* had the lowest nutrient content of all the sites in this study. The %N is 1.4 times (mean = 0.21%) higher than that of interpatch soils (Fig 3.4 a and 3.5 a). There was no difference between the %C of the two soils and P concentration of *heuweltjies* soils was significantly lower than in the interpatches at this site (Figs 3.4 c and e). WGR *heuweltjies* on average contained 0.24 % N, 4 % C, and 4 mg kg⁻¹ P (Figs 3.4 a, c and e). No patterns were observed across a rainfall gradient for N and C contents of *heuweltjie* soil (Figs 3.9 a and b). However, P concentration decreased with increasing rainfall (Fig 3.9 c). The C/N ratio of *heuweltjie* soil had a mean of 18 and was significantly higher than that of surrounding interpatch soils (mean = 13) (Table 3.3). TKRC and JON were the sites where *heuweltjies* showed no difference in the C/N ratio. Electrical conductivity_{1:5} (μS cm⁻¹) varied between sites and was much higher on *heuweltjies* at TKRC ($t = 6.57$; $p < 0.001$) (Table 3.3 and Fig 3.5 d). The average pH (water) for all *heuweltjie* soils was 7.00 and significantly ($t = 5.46$; $p < 0.001$) higher than that of soil in the interpatches (5.89) (Table 3.3).

3.4.3. Biogeochemistry

3.4.3.1. Potential soil respiration

Generally, *heuweltjies* had higher soil respiration rates than surrounding soils, however, this was not consistent and, in most cases not significant. Only when data were pooled together, excluding site differences did *heuweltjies* show clear elevation in CO₂ flux ($t = 1.86$, $p = 0.041$) (Table 3.4). At both sample days *heuweltjies* showed higher respiration than their surrounding soils but on day one the difference was not significant. On the *heuweltjies*, respiration increased from day one to day seven ($p = 0.018$). Respiration of interpatch soils was highest in the first day and declined thereafter (Table 3.4). The sites demonstrate a diversity of results when it comes to CO₂ flux from day one to day seven (Table 3.4). On day seven, the flux of CO₂ was higher on *heuweltjie* soils than the surrounding soils at WVR ($t = 2.02$, $p < 0.05$). As for the Fynbos site, JON, respiration was highest in the first day of incubation and declined. The flow of CO₂ of *heuweltjie* soils at WGR was constant all throughout the incubation period.

3.4.3.2. Nitrogen mineralization

Laboratory incubation clearly shows that *heuweltjie* soils have potential for higher N mineralization (anaerobic). When pooled, Succulent Karoo (TKRC and WVR) *heuweltjies* soils also had much higher N mineralization than Fynbos (JON and WGR) *heuweltjies* ($F_{2, 37} = 11.43$, $p < 0.001$). Though lower in the *heuweltjies* of Fynbos these patches still had significantly higher N mineralization compared to interpatch areas. Nitrogen mineralization of interpatch soils did not

differ between sites (Fig 3.6). No relationships were found between soil C/N ratio and N mineralization (Figs 3.7 a and b). There were significantly positive relationships between soil N and fine soil particles (clay and silt) and N mineralization but only for Succulent Karoo sites (Figs 3.7 c-f).

3.4.3.3. Phosphatase activity

No significant differences were found between the two phosphatase types for interpatch soils ($t = 0.04$, $p = 0.97$). Alkaline phosphatases varied from 60.99 – 163.59 p -NP g dry soil⁻¹ h⁻¹ and acid phosphatases from between 47.02 – 78.61 p -NP g dry soil⁻¹ h⁻¹ ($t = 2.84$, $p < 0.01$) for *heuweltjie* soils. Succulent Karoo sites had higher alkaline phosphatases than acid phosphatases on the *heuweltjies* ($t = 8.68$; $p < 0.001$) but not so for Fynbos sites ($t = 0.39$; $p < 0.703$) (Table 3.5). At TKRC, *heuweltjies* showed higher phosphatase activity than the surrounding soils. Overall, there was low phosphatase activity in WVR. There was also no significant difference in the activity of either alkaline phosphatases or acid phosphatases between *heuweltjies* and the surrounding surface soil in WVR (Table 3.5). Interpatch and *heuweltjie* soils did not differ in the activity of acid phosphatases at JON however alkaline phosphatase activity was significantly enhanced on the *heuweltjies*. At WGR, it was the alkaline phosphatase activity that did not differ between *heuweltjies* and interpatch soils and acid phosphatases was significantly higher on the *heuweltjies*. There was a positive relationship between soil P and alkaline phosphatase activity and, a negative relationship between soil P and acid phosphatase activity in the interpatch soils of Fynbos sites.

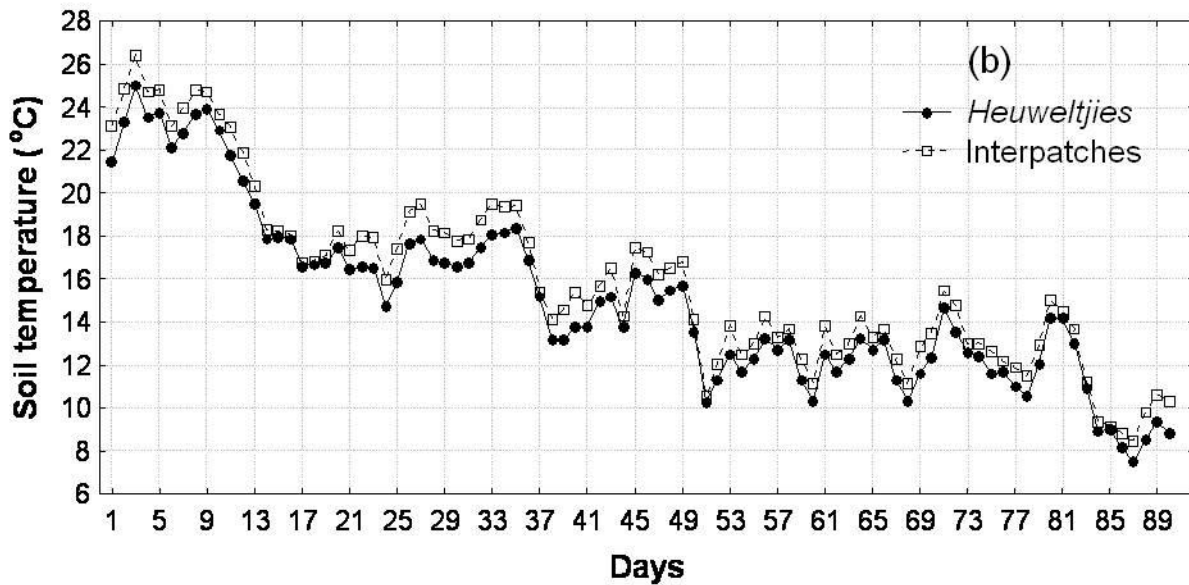
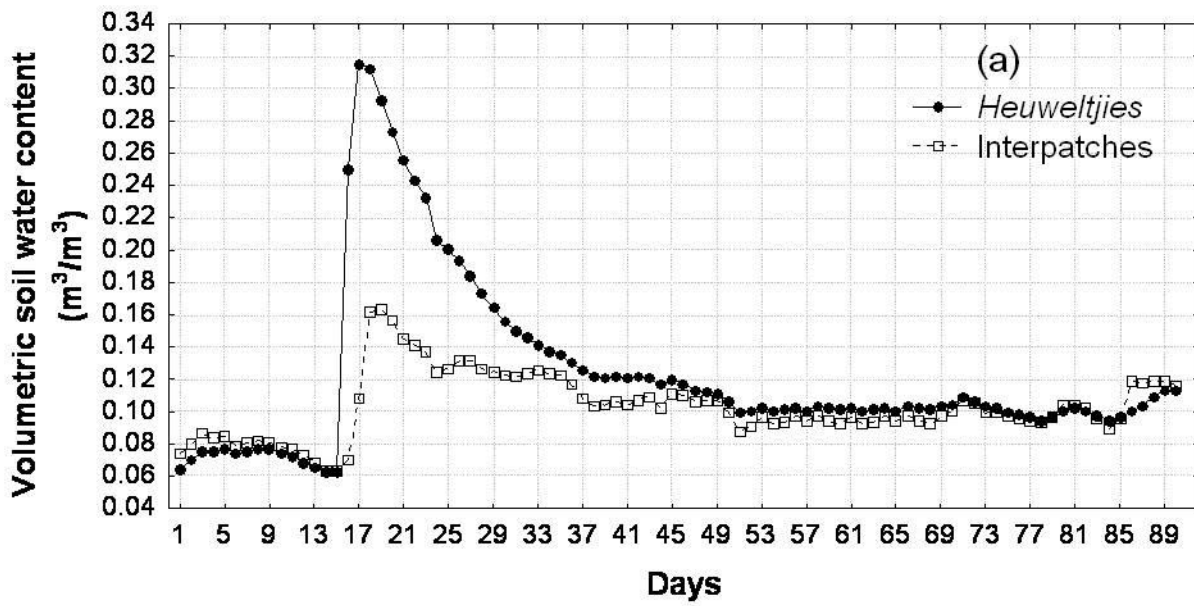


Fig 3.3. Volumetric soil water content (m^3m^{-3}) (a) and soil temperature ($^{\circ}\text{C}$) (b) on *heuweltjies* (solid) and the interpatch areas (open) at the Tierberg Karoo Research Centre. Parameters were monitored daily from 1 April 2009 – 30 June 2009.

Table 3.3. Mean (\pm SE) electrical conductivity (EC), C/N ratio, pH, %clay, %silt, % sand of soils (top 10cm) sampled from *heuweltjies* and adjacent interpatches in the study sites. Sites contain Succulent Karoo and Fynbos vegetation. Data represented from the driest (Tierberg Karoo Research Centre) to the wettest (Wiesenhof Game Reserve) site. The text in bold denotes significant differences (paired t-test).

| Site | Biome | Soil properties | <i>Heuweltjies</i> | Interpatches | <i>p</i> | <i>t</i> | <i>n</i> |
|--------------------------------|---------------------------------|--|--------------------------------------|--------------------------------------|------------------|-------------|----------|
| Tierberg Karoo Research Centre | Succulent Karoo | C/N ratio | 24.01 \pm 0.55 | 17.96 \pm 2.88 | 0.058 | 2.16 | 10 |
| | | EC_{1:5}(μS cm⁻¹) | 961.95 \pm 41.85 | 199.19 \pm 41.85 | <0.001 | 6.57 | 10 |
| | | pH (water) | 8.06 \pm 0.08 | 8.12 \pm 0.10 | 0.569 | -0.59 | 10 |
| | | % Clay | 16.90 \pm 1.75 | 21.07 \pm 1.71 | 0.224 | -1.33 | 8 |
| | | % Silt | 13.37 \pm 0.84 | 11.92 \pm 0.66 | 0.313 | 1.09 | 8 |
| | | %Sand | 69.73 \pm 2.39 | 67.01 \pm 1.71 | 0.510 | 0.69 | 8 |
| Worcester Veld Reserve | Succulent Karoo | C/N ratio | 19.57 \pm 1.24 | 11.47 \pm 1.17 | 0.001 | 4.50 | 10 |
| | | EC _{1:5} (μ S cm ⁻¹) | 240.37 \pm 41.85 | 202.21 \pm 41.85 | 0.519 | 0.86 | 10 |
| | | pH (water) | 7.22 \pm 0.22 | 4.34 \pm 0.56 | <0.001 | 12.29 | 10 |
| | | % Clay | 15.71 \pm 1.24 | 11.20 \pm 0.91 | 0.044 | 2.35 | 10 |
| | | % Silt | 23.83 \pm 1.85 | 20.30 \pm 1.06 | <0.001 | -23.86 | 10 |
| | | %Sand | 60.46 \pm 2.99 | 68.50 \pm 1.56 | 0.065 | -2.10 | 10 |
| Jonaskop | Ecotone(Fynbos/Succulent Karoo) | C/N ratio | 12.40 \pm 0.59 | 11.38 \pm 0.65 | 0.119 | 1.72 | 10 |
| | | EC _{1:5} (μ S cm ⁻¹) | 54.57 \pm 41.85 | 99.10 \pm 41.85 | 0.130 | -1.66 | 10 |
| | | pH (water) | 6.56 \pm 0.15 | 5.34 \pm 0.16 | 0.002 | 4.20 | 10 |
| | | % Clay | 12.73 \pm 0.60 | 12.45 \pm 0.87 | 0.784 | 0.28 | 10 |
| | | % Silt | 29.52 \pm 0.98 | 28.03 \pm 0.64 | 0.296 | 1.11 | 10 |
| | | %Sand | 57.75 \pm 1.10 | 59.51 \pm 1.00 | 0.222 | -1.31 | 10 |
| Wiesenhof Game Reserve | Fynbos | C/N ratio | 16.45 \pm 0.67 | 10.42 \pm 0.74 | <0.001 | 5.07 | 10 |
| | | EC _{1:5} (μ S cm ⁻¹) | 41.40 \pm 41.85 | 24.56 \pm 41.85 | 0.778 | 2.65 | 10 |
| | | pH (water) | 6.17 \pm 0.11 | 5.77 \pm 0.09 | <0.001 | 4.94 | 10 |
| | | % Clay | 10.12 \pm 0.59 | 12.35 \pm 3.00 | 0.545 | -0.66 | 5 |
| | | % Silt | 18.27 \pm 1.28 | 18.03 \pm 1.31 | 0.616 | 0.54 | 5 |
| | | %Sand | 71.61 \pm 1.76 | 69.63 \pm 2.42 | 0.600 | 0.57 | 5 |

Table 3.3 (Continued) Mean (\pm SE) electrical conductivity, C/N ratio, pH, %clay, %silt, % sand of soils (top 10cm) sampled from *heuweltjies* and adjacent interpatches in the studysites. Sites contain Succulent Karoo and Fynbos vegetation. Data represented from the driest (Tierberg Karoo Research Centre) to the wettest (Wiesenhof Game Reserve) site. The text in bold denotes significant differences (paired t-test).

| Site | Biome | Soil properties | <i>Heuweltjies</i> | Interpatches | <i>p</i> | <i>t</i> | <i>n</i> |
|---------------|-------|--|--------------------------------------|--------------------------------------|------------------|-------------|-----------|
| Overall Means | | C/N ratio | 18.00 \pm 0.78 | 13.00 \pm 0.92 | <0.001 | 5.55 | 40 |
| | | EC_{1:5}(μS cm⁻¹) | 324.66 \pm 64.99 | 131.26 \pm 18.87 | 0.002 | 3.17 | 40 |
| | | pH (water) | 7.00 \pm 0.14 | 5.89 \pm 0.23 | <0.001 | 5.46 | 40 |
| | | % Clay | 14.25 \pm 0.71 | 14.15 \pm 0.97 | 0.932 | 0.08 | 33 |
| | | % Silt | 22.18 \pm 1.28 | 20.27 \pm 1.14 | 0.031 | 1.91 | 33 |
| | | % Sand | 63.58 \pm 1.49 | 65.59 \pm 1.04 | 0.257 | -1.15 | 33 |

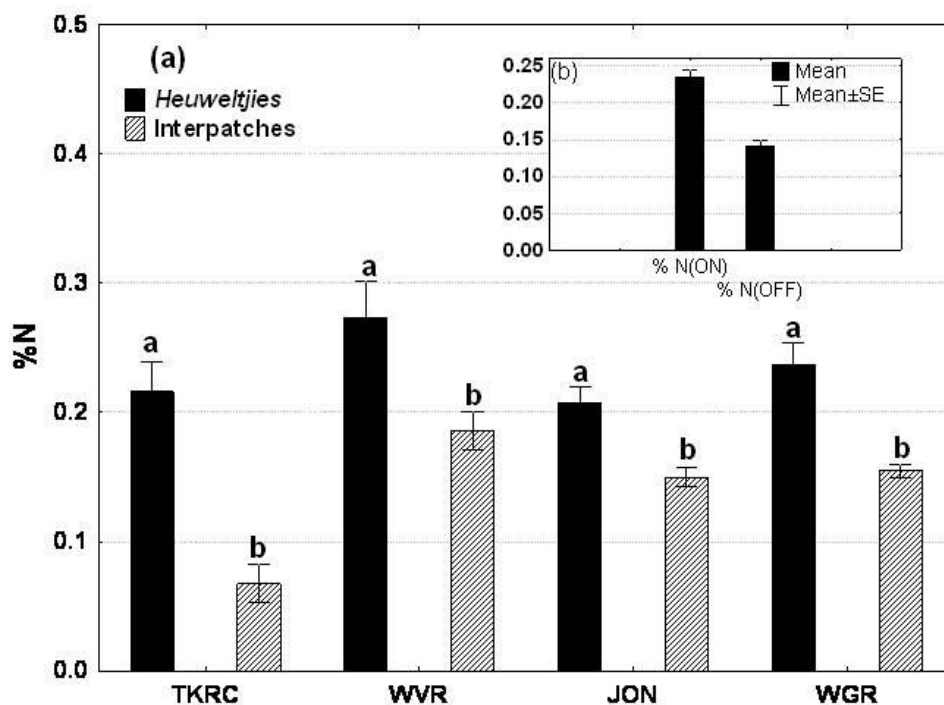


Fig 3.4. Mean (\pm SE) differences between %N (a), %C (c) and P (mg kg^{-1}) (e) of *heuweltjies* and interpatch soils at the all sites; the Tierberg Karoo Research Centre (TKRC), Worcester Veld Reserve (WVR), Jonaskop (JON) and Wiesenhof Game Reserve (WGR). Overall means (excluding site differences) for each variable on *heuweltjie* (ON) and interpatches (OFF) are also shown in each case; (b) %N, (d) %C, (f) P(mg kg^{-1}). Dissimilar letters denote significant difference at $p < 0.05$ analyzed using paired t-tests (comparisons were only made on the paired samples, *heuweltjies* and Interpatches, at each site and not between sites). TKRC and WVR are Succulent Karoo site, and JON and WGR Fynbos sites. Rainfall increases from TKRC to WGR.

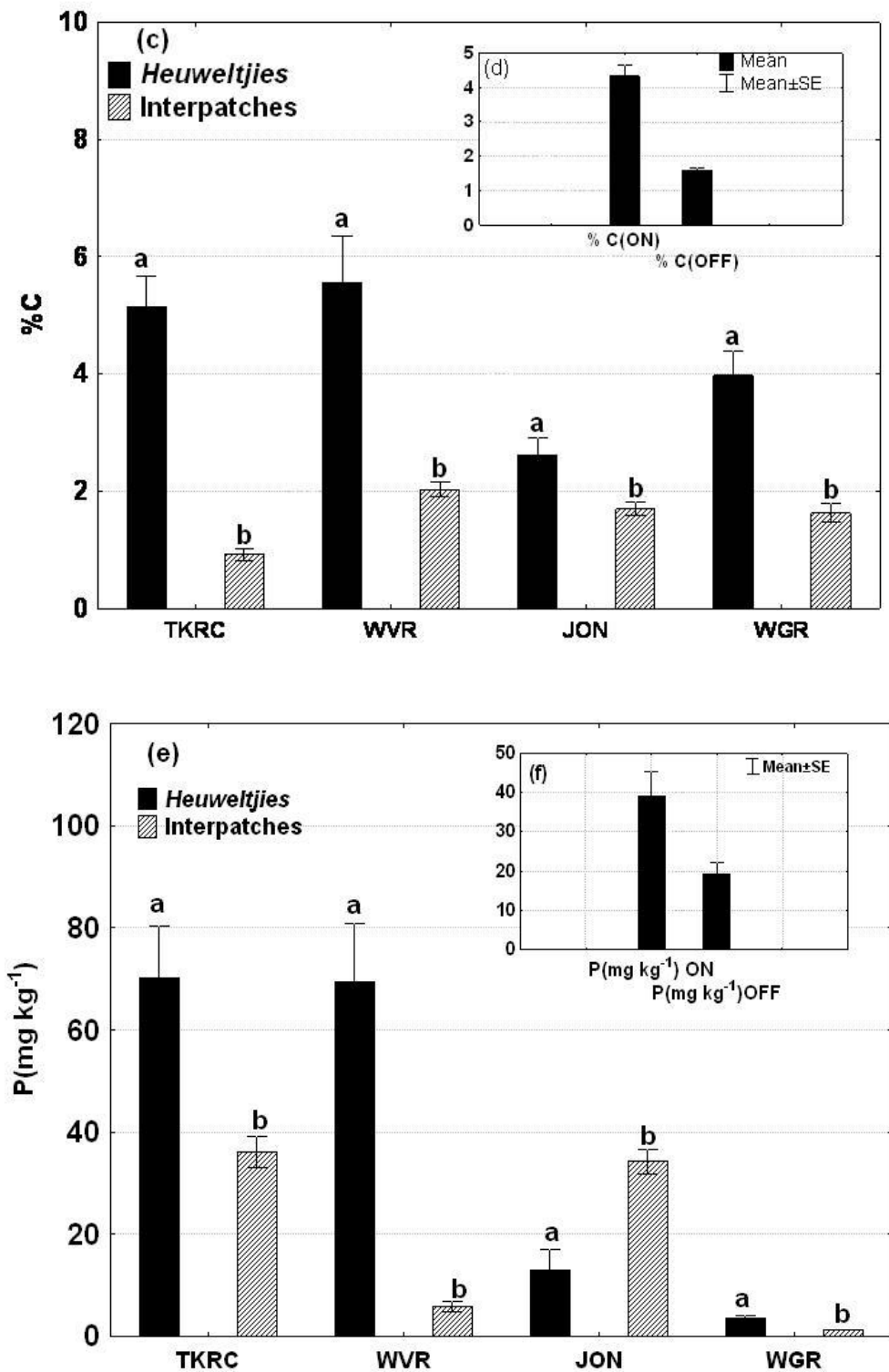


Fig 3.4 (Continued). Mean (\pm SE) differences between %N (a), %C (c) and P (mg kg^{-1}) (e) of *heuweltjies* and interpatch soils at the all sites; the Tierberg Karoo Research Centre (TKRC), Worcester Veld Reserve (WVR), Jonaskop (JON) and Wiesenhof Game Reserve (WGR). Overall means (excluding site differences) for each variable on *heuweltjie* (ON) and interpatches (OFF) are also shown in each case; (b) %N, (d) %C, (f) P(mg kg^{-1}). Dissimilar letters denote significant difference at $p < 0.05$ analyzed using paired t-tests (comparisons were only made on the paired samples, *heuweltjies* and Interpatches, at each site and not between sites). TKRC and WVR are Succulent Karoo site, and JON and WGR Fynbos sites. Rainfall increases from TKRC to WGR.

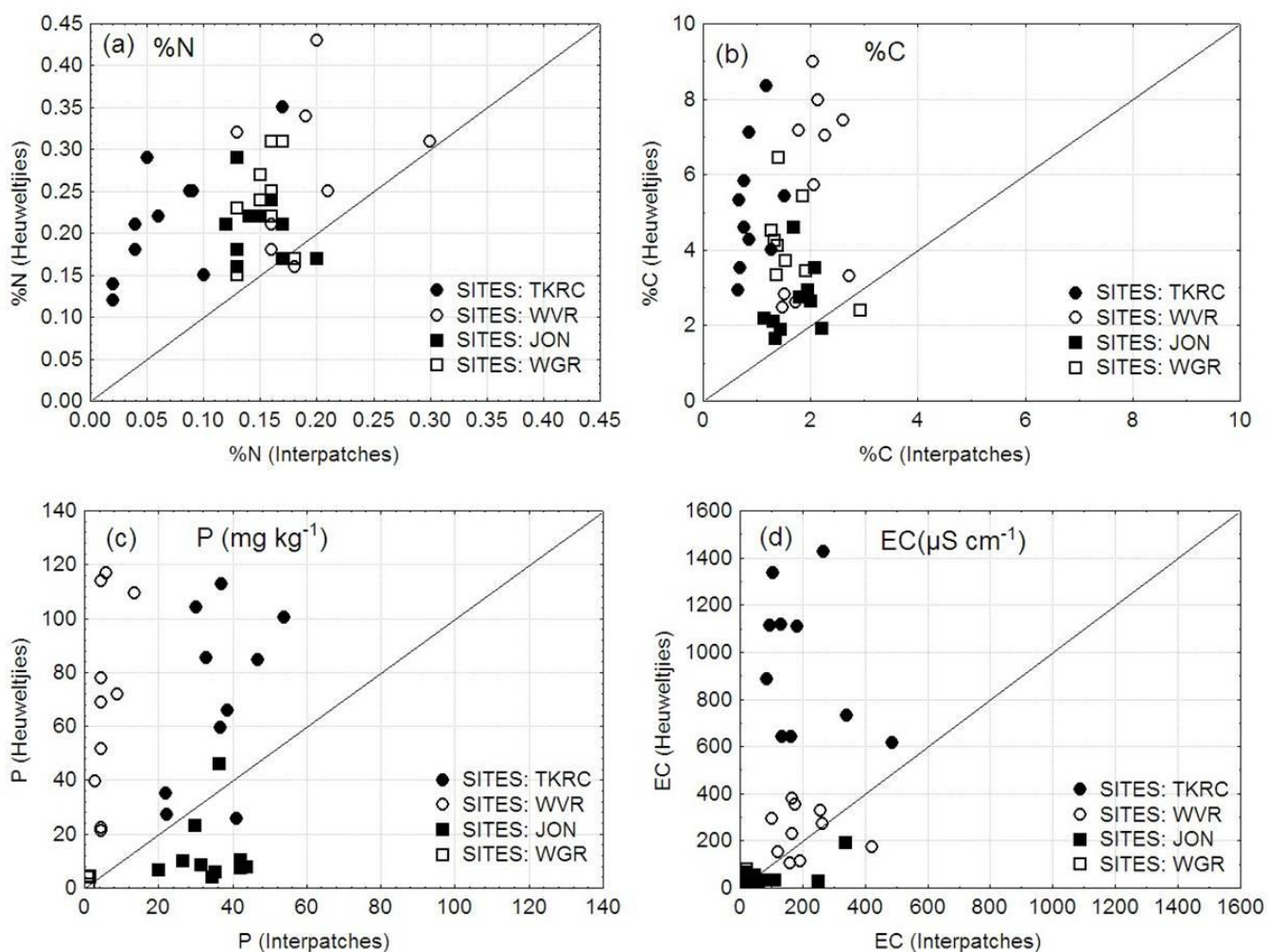


Fig. 3.5. Electrical conductivity and nutrient content of *heuweltjies* versus interpatches. Lines showing 1:1 relationships. Data represented for each study site. TKRC = Tierberg Karoo Research Centre, WVR = Worcester Veld Reserve, JON = Jonaskop, WGR = Wiesenhof Game Reserve. TKRC and WVR are Succulent Karoo, and JON and WGR Fynbos sites.

Table 3.4. Mean (\pm SE) potential soil respiration ($\text{ml CO}_2 \text{ g dry soil}^{-1} \text{ h}^{-1}$) for *heuweltjie* and interpatch soils at four sites across the south-western Cape. Results are represented with the driest site at the top and wettest the bottom. Significant differences were tested with paired t-test. Data were also pooled together to produce the matrix below showing means and p -values resulting from t-test. Significant p -values are in bold.

| | Day | <i>Heuweltjies</i> | Interpatches | n | t | P |
|--------------------------------|-----|-----------------------------------|-----------------------------------|-----------|-------------|--------------|
| Tierberg Karoo Research Centre | 1 | 6.32 ± 4.01 | 5.62 ± 3.28 | 5 | 1.24 | 0.453 |
| | 7 | 14.33 ± 8.83 | 3.74 ± 1.31 | 5 | 1.13 | 0.160 |
| Worcester Veld Reserve | 1 | 3.37 ± 0.98 | 3.01 ± 1.08 | 5 | 0.22 | 0.417 |
| | 7 | 4.09 ± 1.71 | 0.48 ± 0.24 | 5 | 2.33 | 0.040 |
| Jonaskop | 1 | 3.74 ± 0.23 | 6.36 ± 1.49 | 3 | -1.95 | 0.095 |
| | 7 | 0.59 ± 0.43 | 0.92 ± 0.32 | 5 | -0.66 | 0.273 |
| Wiesenhof Game Reserve | 1 | 5.26 ± 1.25 | 4.60 ± 0.88 | 5 | 0.36 | 0.388 |
| | 7 | 5.54 ± 1.60 | 1.96 ± 0.58 | 5 | 2.65 | 0.029 |
| Overall means | 1 | 4.78 ± 1.14 | 4.73 ± 0.98 | 18 | 0.02 | 0.490 |
| | 7 | 6.14 ± 2.40 | 1.77 ± 0.45 | 20 | 1.86 | 0.041 |

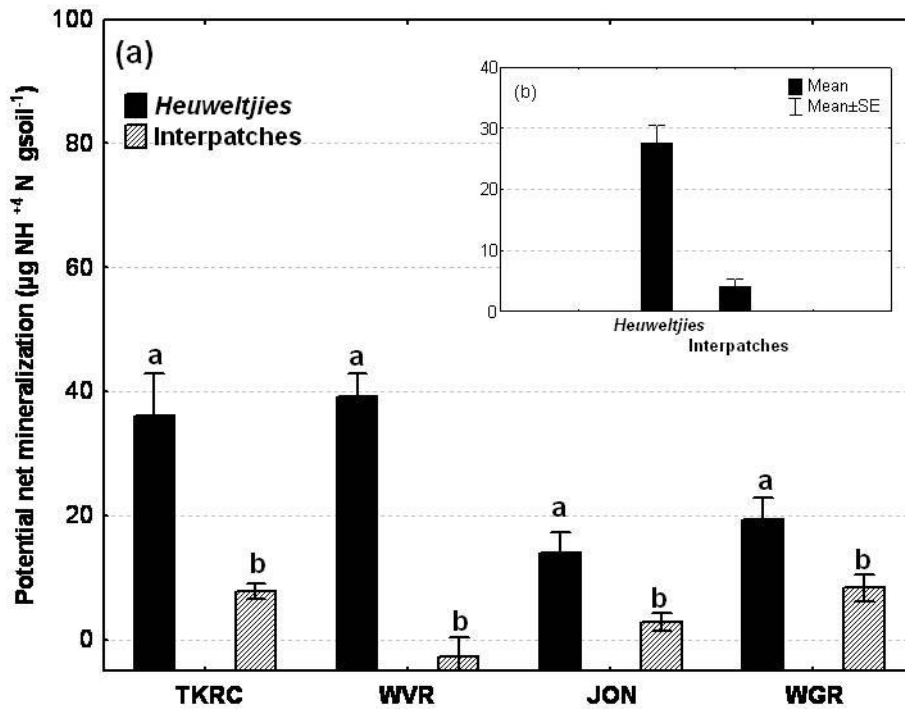


Fig. 3.6. Potential mineralization of ammonium for individual sites (a) and for pooled data (b) on and off *heuweltjies* soils. TKRC = Tierberg Karoo Research Centre, WVR = Worcester Veld Reserve, JON = Jonaskop, WGR = Wiesenhof Game Reserve. TKRC and WVR are Succulent Karoo, and JON and WGR Fynbos sites. Dissimilar letters denote significant differences at the $p < 0.05$ level. Differences tested using paired t -tests (comparisons were only made on the paired samples, *heuweltjies* and interpatches, at each site and not between sites).

Table 3.5. Phosphatase activity ($\mu\text{gp-NPg drysoil}^{-1} \text{h}^{-1}$) of individual sites and summarized means across all the sites (mean \pm SE) of *heuweltjies* and surrounding soils. Data were analysed with paired t -test and bold text represents significant differences $p < 0.05$.

| | Phosphatase | <i>Heuweltjies</i> | Interpatches | n | t | p |
|--------------------------------|-----------------|-----------------------|---------------------|-----------|-------------|------------------|
| Tierberg Karoo Research Centre | Alkaline | 242.86(25.26) | 49.26(5.35) | 8 | 7.32 | <0.001 |
| | Acid | 71.53(14.19) | 22.13(6.79) | 8 | 3.63 | 0.008 |
| Worcesterfeld Veld Reserve | Alkaline | 103.40(37.74) | 58.00(15.03) | 5 | 1.29 | 0.267 |
| | Acid | 20.15(6.43) | 13.86(8.98) | 4 | 1.22 | 0.308 |
| Jonaskop | Alkaline | 191.99(33.74) | 100.28(8.73) | 10 | 2.74 | 0.023 |
| | Acid | 35.25(5.50) | 50.29(5.43) | 5 | -1.99 | 0.117 |
| Wiesenhof Game Reserve | Alkaline | 60.57(10.40) | 12.34(1.97) | 5 | 3.93 | 0.017 |
| | Acid | 193.29(11.52) | 127.40(8.56) | 5 | 3.82 | 0.019 |
| Overall means | Alkaline | 163.59 (18.51) | 60.99 (7.04) | 30 | 5.83 | <0.001 |
| | Acid | 78.61(14.26) | 47.02(9.71) | 24 | 3.67 | 0.001 |

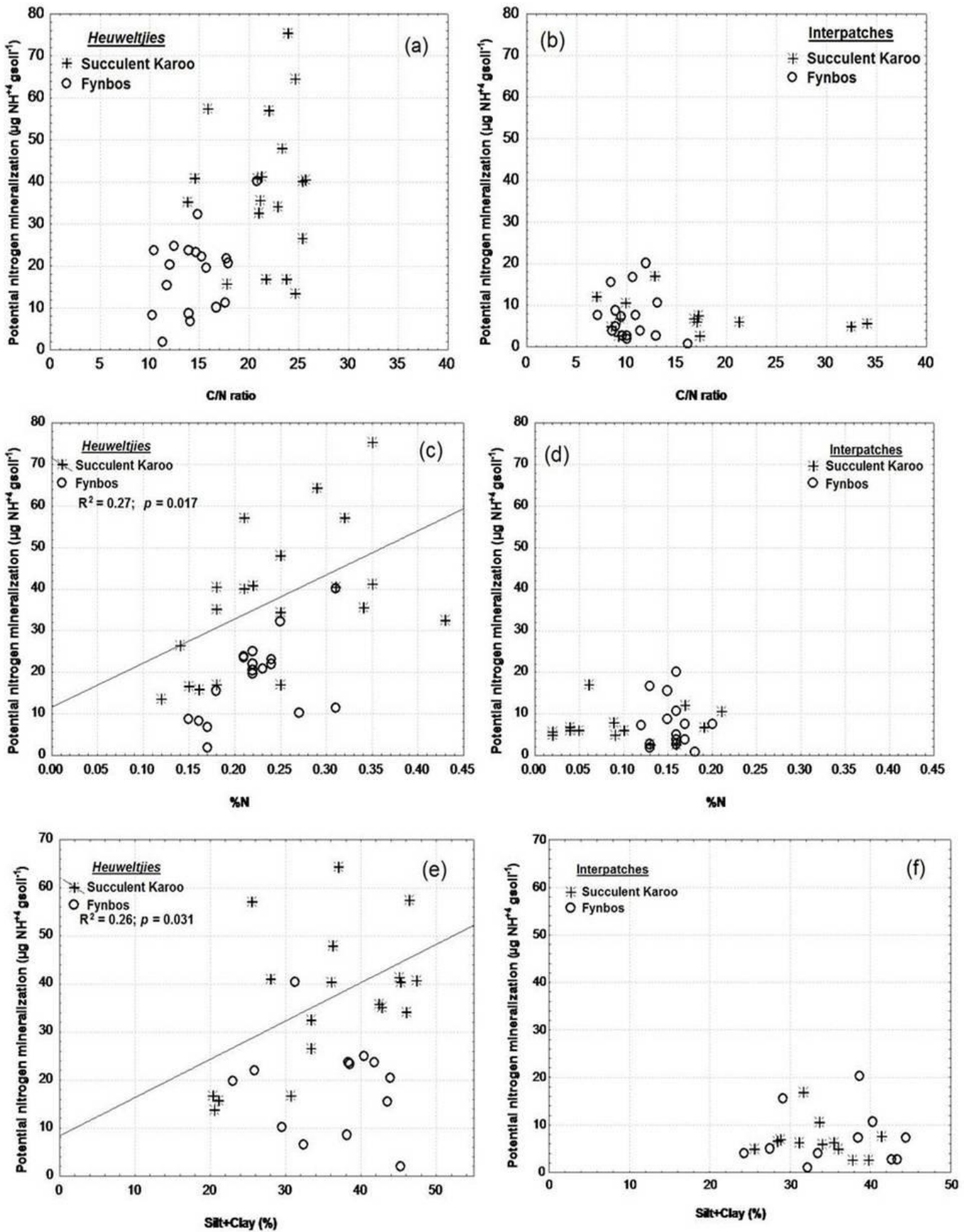


Fig 3.7. Scatter plots of potential nitrogen against some relevant soil properties (a-f) on and off *heuweltjies* for the Succulent Karoo and Fynbos sites pooled.

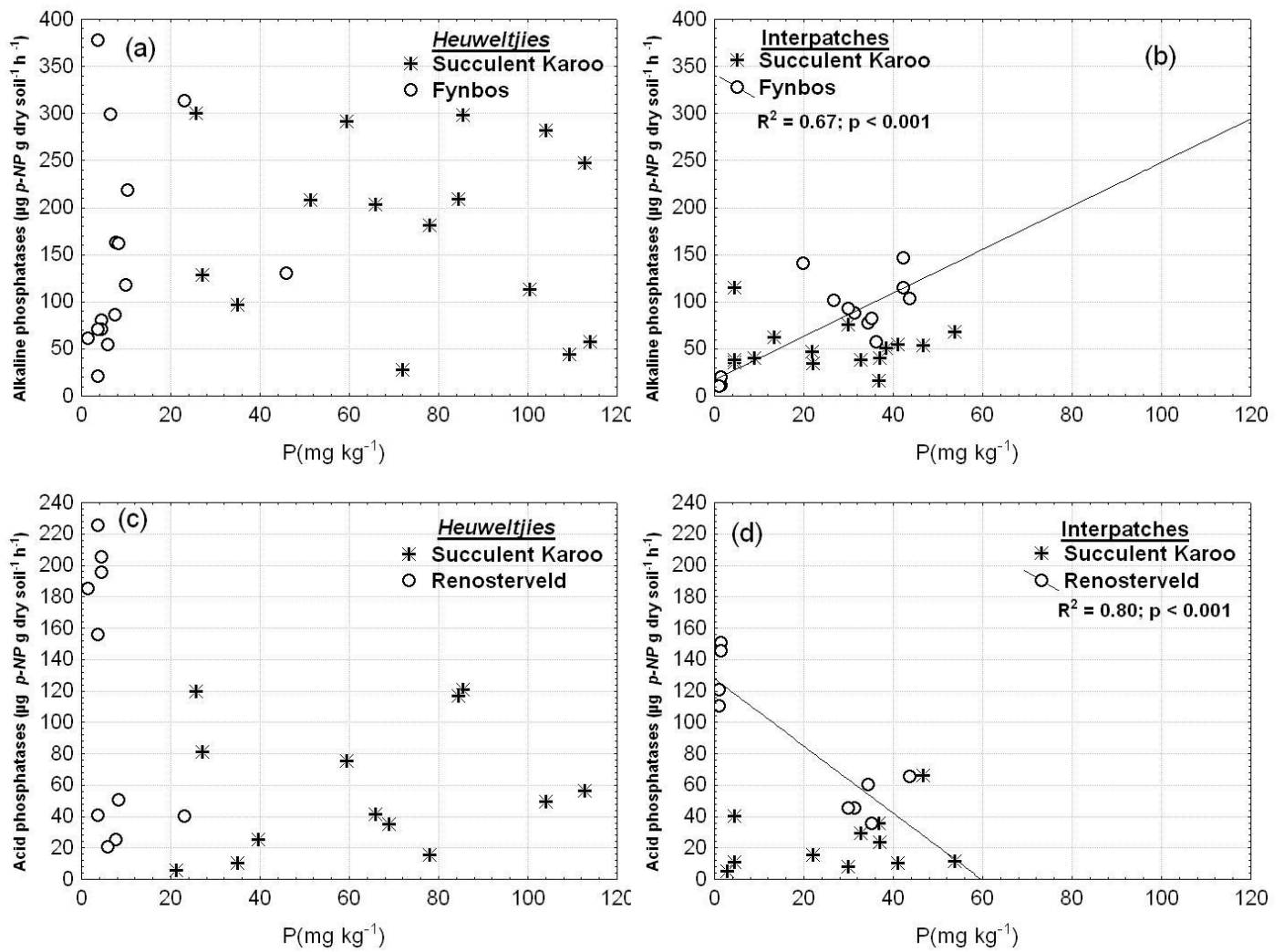


Fig 3.8. Regression analyses for Phosphatases (a-d) against some relevant soil properties on and off *heuweltjies* for the Succulent Karoo and Fynbos sites pooled.

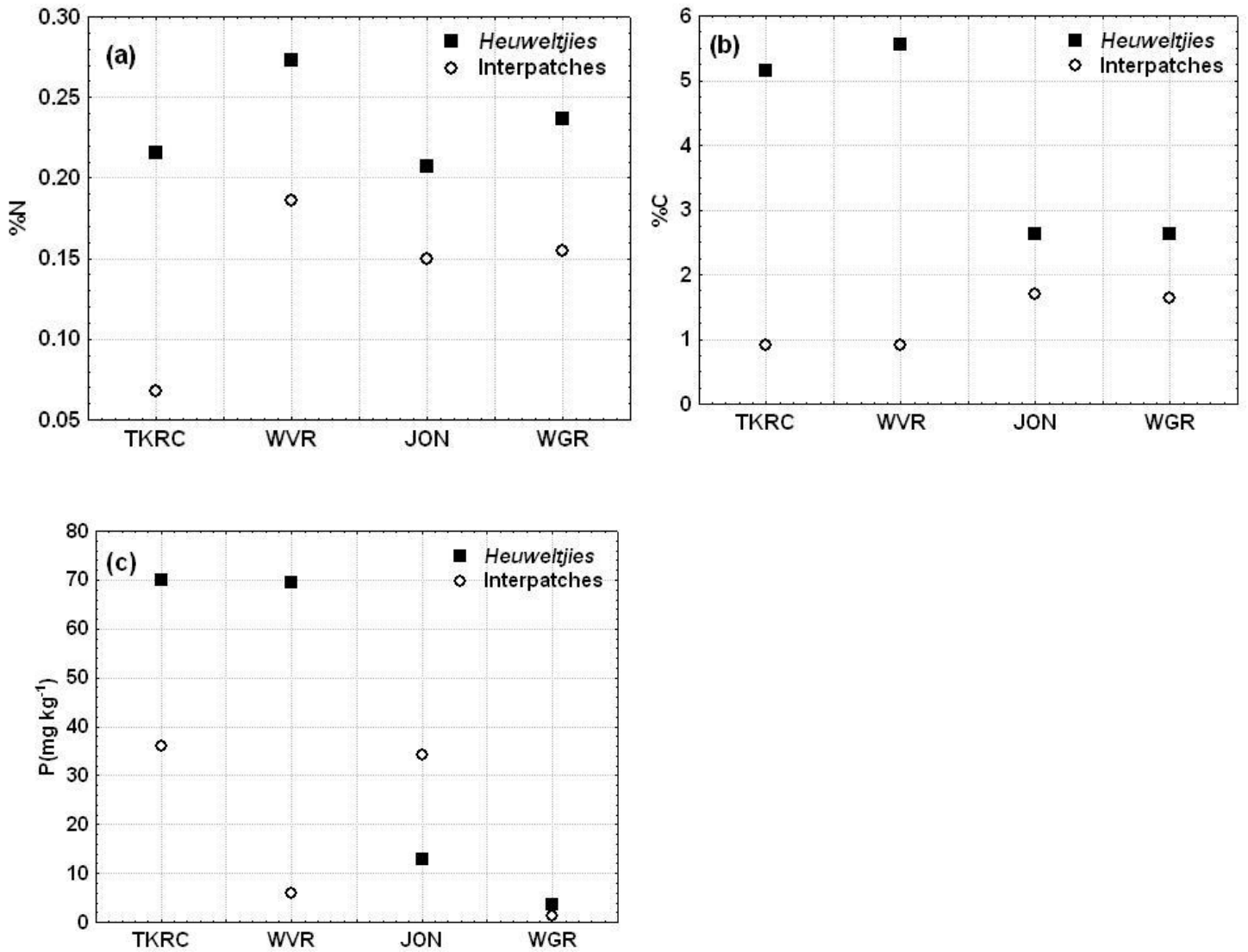


Fig 3.9. Scatterplots for sites against enrichment factors [a) nitrogen, b) carbon and c) phosphorus] with rainfall increase from left to right. TKRC = Tierberg Karoo Research Centre, WVR = Worcester Veld Reserve, JON = Jonaskop, WGR = Wiesenhof Game Reserve.

3.5. Discussion

3.5.1. Physicochemical properties

McClain et al., (2003) suggested that certain landscape features, such as topographical depressions and riparian zones are hotspots for biogeochemical activity. Hotspots play a very important role in landscapes as they are often visited and utilized extensively by large and small herbivores for their nutrient supplies, are the source of greenhouse gasses, and where they have different soil structure, they can also form a conduit for transfer of material aboveground and belowground (Le Maitre et al., 2007; Grant and Scholes, 2006; Lòpez-Hernández, 2001). Here I show that *heuweltjies* are nutrient enriched patches and also seem to be hotspots for nutrient cycling. The high accumulation of nutrients in soils of *heuweltjies* is in tune with other studies (Midgley and Musil, 1990; Milton et al., 1992; Ellis, 2002; 2004) and is typical of soils modified by termites. Lòpez-Hernández (2001) suggested that enrichment is due to the use of faecal material (frass) when cementing gallery walls and when building termitaria. It may also be due to the on-going collection of plant material for consumption and decomposition in the digestive systems of individual members of the colony and thus accumulation of organic matter in the mounds (Pomeroy, 1983). Similarly, *M. viator* uses plant material as the main source of food and the frass is incorporated into the soils above the nest (i.e. is part of the *heuweltjies*) (Coaton, 1958; Milton and Dean, 1990).

Thus far, studies on *heuweltjies* were mostly confined to the Succulent Karoo. My study included both the Succulent Karoo and the Fynbos and show differential enrichment in the two regions. From my results it is clear that vegetation type plays a role in the underlying accumulation/enrichment factors in the different regions. The P concentrations of *heuweltjies* soils were much higher than that of interpatch soils overall. Reports in the literature about the effects of termites on soil P are inconsistent. Lòpez-Hernández et al., (1989) showed a significant increase in all forms of soil P in *Nasutitermes ephratae* mounds compared to adjacent soils. On the other hand, Asawalam and Johnson (2007) reported no change or a decline in soil P from adjacent soil to mounds of *Cubitermes* and *Macrotermes* species respectively. These inconsistencies may also explain why differences were found between the Succulent Karoo and Fynbos sites in this study. Overall, the P concentrations for the two Fynbos soils were also considerably lower compared to the Succulent Karoo sites. Very low P levels are well documented for the Fynbos (Mucina and Rutherford, 2006), and are the result of the nutrient poor parent material. JON is the only site where the P of interpatch soils was higher than that of *heuweltjies*.

Agenbag et al., (2008) also analysed for soil P on and off *heuweltjies* at this site and found mounds to be enriched in terms of P. However, this author analysed the 14-31cm soil depth range and at these depths, *heuweltjies* could be indeed richer in P.

Meanwhile, organic matter seems to always increase from adjacent soils to mounds (Salick et al., 1983; Ackerman et al., 2007). The consistently higher C and N content of *heuweltjie* soils could have important repercussions for the host ecosystems. Apart from speeding up the rates of nutrient cycling (discussed later), it could also have consequences for vegetation composition and dynamics. The vegetation composition of termite mounds of North Eastern Australia differed greatly from that of adjacent soils because of a four times higher N content in mound soils (Spain and McIvor, 1988). The word hotspots has been used in relation to termite mounds in other ecosystems because of their high nutrient content and decomposition rates which affected distribution of plant species and consequently the feeding pattern of herbivores in such ecosystems (Loveridge and Moe, 2004; Grant and Scholes 2006, Freymann et al., 2010). The results of this study show that *heuweltjies* in the Succulent Karoo are, indeed hotspots for N, C, and P and possibly play a major role in animal movement, both native and domestic. The preference that sheep have for *heuweltjie* vegetation also supports the contention that these mounds affect the movement of animals (Armstrong and Siegfried, 1990). Further, as the enrichment of nutrients associated with Fynbos *heuweltjies* are considerably lower, and these changes were not associated with edaphic factors such as soil texture, this may be related to the increase in precipitation from the Succulent Karoo to the Fynbos. At WGR this may also be related to lateral movement of water as the sites were situated on a slope.

While both C and N content of topsoil on the *heuweltjies* were higher than interpatches, C/N ratio was also generally higher, suggesting more relative enrichment of C. Pomeroy (1977) studied large termite mounds in Uganda and showed that where mounds occur, the C/N ratio is either lower or higher than that of the surrounding soils depending on which species built the mounds. McComie and Dhanarajan (1993) also show the species specific nature of mound C/N ratio, with the mounds of *Cubitermes testaceus* showing lower and *Nasutitermes exitiosus* mounds showing much higher C/N ratio than their surrounding soils. The walls of *N. exitiosus* mounds were cemented with partially digested organic material. For *C. testaceus*, mounds were cemented with organic material in its advanced state of decomposition (McComie and Dhanarajan, 1993). *Heuweltjies* are never as large as the mounds

mentioned above such that studying the properties of mound walls is not feasible or possible (Coaton, 1962). However, termite frass (lightly digested organic/fecal material) is evident on *heuweltjies* in some areas (Midgley and Musil, 1990). The higher termite frass on *heuweltjie* soils is also shown in the next chapter of this study. This frass could be thought to have the same effect on soils as the organic material on *N. exitiosus* mounds (McComie and Dhanarajan, 1993) in that it (frass) leads to a higher C/N ratio on the *heuweltjies*.

The mean pH for the *heuweltjie* soils was 7.00 and higher than that of interpatch soils (5.89) as was shown by others (Midgley and Musil, 1990; Milton et al., 1992; Ellis, 2004; Herpel, 2008). The difference may have been brought about by the activities of the colony. Several studies have also shown that termites greatly modify the pH of the soil because of a, sometimes, extremely alkaline hindgut (Trapnell et al., 1976). Electrical Conductivity_{1.5}($\mu\text{S cm}^{-1}$) of *heuweltjies* soils is higher, and at TKRC twice that of interpatch soils. This was also observed by Milton et al., (1992) and Ellis (2002). Milton et al., (1992) connected it to higher saline conditions on the *heuweltjies* in their study area. It could also be due to a greater accumulation of ions in the *heuweltjie* soil solution, probably cations as shown by the higher pH. Enrichment of the *heuweltjies* in cations, though not determined in this study, was documented in several other studies (Ellis, 2002; 2004). The pH values at WVR might seem unusually low but they similar to what was reported by Cate (1966).

Texture of *heuweltjies* was slightly finer compared to the surrounding soils; due to the fact that *heuweltjies* had a higher silt content and lower sand content than nearby soils. However, clay, and sand fractions did not differ significantly from surrounding soils. This is in contrast with what was found by previous studies (Midgley and Musil, 1990; Milton et al., 1992). This study considered only the top 10 cm, the area of highest biological activity, and the earlier studies sampled at different depths. Evidence for modification of soil texture by termites is found in the literature (Sheikh and Kayani, 1982; Obi and Ogunkunle, 2009). The subterranean termites in Pakistan significantly increased the clay content of top soil in various ecosystems including natural forests and plantations (Sheikh and Kayani, 1982). Termite mounds had a coarser texture than the surrounding soils in a forest of Central Amazonia (Ackerman et al., 2007). Texture, being a stable ecosystem factor will affect other physicochemical properties as well as the biochemical activity.

From the above we see that *heuweltjies* have alkaline, saline, finer textured soils that retain more macronutrients (C and N) and possibly accumulate more cations than their surroundings. The higher available C and N and finer texture can lead to higher rates of biogeochemical cycling. Given enough soil water, while pH and electrical conductivity may affect certain aspects of microbial activity.

3.5.2. *Effect of heuweltjie properties on the soil respiration, nitrogen mineralization and phosphatase activity*

CO₂ efflux rates (potential soil respiration) of all soils were between 0.480-14.334 ml CO₂.g drysoil⁻¹.h⁻¹, with *heuweltjies* soils having higher rates than surrounding interpatch soils. The results presented here are within the range reported for forest soils by Vanhala (2002). However, at individual sites, soil respiration was significantly higher only for WVR and WGR after 7 days of incubation. Respiration of Fynbos soils remained the same, WGR, or declined, JON, from day 1 to 7. At all other sites and times the variation around the mean was very high, possibly due to microsite effects. Actual values were highest at TKRC, both in soils from the interpatches and *heuweltjies*. Also notable is that different sites responded differently when incubated for 1 day and for 7 days, with some sites showing a decline in CO₂ efflux at 7 days incubation. This may reflect differential availability of fast and slow (labile and recalcitrant) C associated with soils from different biomes and patch types.

Though this was a laboratory study, it is likely that a similar situation could be found under field conditions. Many studies suggest that soil water and soil temperature are highly influential in controlling soil respiration, and given the right soil conditions, this, along with higher C content of mounds clearly encourages higher turnover of C in these soils. Conant et al., (2000) found soil respiration to be highest under mesic conditions in semi-arid regions of San Francisco, those optimum for microbial activity. The higher soil water (and warm temperatures) of the Succulent Karoo and Fynbos soils of *heuweltjies* could similarly encourage higher CO₂ efflux. It is acknowledged that it is probably only the heterotrophic portion of respiration that was considered here, leaving out the important autotrophic respiration (Högberg and Read, 2006). However, this does not invalidate the observations made here as they demonstrate, at the very least, differences in decomposition rates. It must also be noted that water content of some *heuweltjie* soils is higher after a rainstorm. It is suggested, therefore, that it is only in these 'hot moments' that the CO₂ efflux of *heuweltjies* soils exceed that of interpatch soils. Anecdotal evidence suggests that *heuweltjies* may occupy as much as

25% of some landscapes. Thus, *heuweltjies* could make a significant contribution to the emissions of CO₂ at a landscape level.

Potential N mineralization followed a similar trend to soil respiration and was up to six times higher in the *heuweltjie* soils, a result not unfamiliar to termite mound soils. *Heuweltjies* N mineralization for Succulent Karoo soil is higher than that of Fynbos soils. C/N ratio of soils is unrelated to the N mineralization at either region. The results also show a positive relationship between N mineralization and soil N and N mineralization and fine soil particle content in the Succulent Karoo and this result disappears in Fynbos sites. These results suggest that it is the combination of the much higher N and finer texture of Succulent Karoo *heuweltjies* soils that lead to the accelerated N mineralization rates observed.

Ndiaye et al., (2004) showed a significant effect of termites on the N dynamics of savanna soils including increased level of denitrification (thus implying higher available N) and higher density of nitrifying bacteria. This is also a possibility with *heuweltjies* soils as they have much higher organic C that might encourage microbial growth. Laboratory incubated soils from *Nasutitermes ephratae* mounds also showed increased N mineralization compared to savanna soils (López-Hernández, 2001). Another laboratory study in the Negev desert showed that N mineralization declines in soils affected by harvester termite *Anacanthotermes ubachi navas* and, though not similar to the results of this study, it still demonstrates the impact that termites have on soil N dynamics (Zaady et al., 2003). C/N ratio seems not to be related to the N mineralization, in contrast to what was found by others (e.g. Emmett et al., 1998). Schimel and Bennett (2004) show that traditional ways of predicting N mineralization, such as C/N ratio are proving to be contradictory. Bengtsson et al., (2003) suggested that net mineralization and immobilization can be related more to soil respiration and ATP content than the C/N ratio. This lack of a relationship between N mineralization and C/N ratio could suggest that neither C nor N control N mineralization on the *heuweltjies* of the Succulent Karoo and Fynbos biomes. However, the weak but positive relationship between N and N mineralization for *heuweltjies* in the Succulent Karoo suggest otherwise. It is possible that the higher N on soils with high N mineralization is N from dissolved organic N which is readily converted to ammonium. Finer soil particles are associated with higher soil water, nutrients and biological activity that might encourage high N mineralization (Chapin et al., 2002).

Quite unexpected was the enhanced activity of phosphatases on the *heuweltjies*. Theoretically, a decline would have been expected because of the generally higher available P levels and pH conditions that are said to be optimum for P availability. It is possible that the increase in soil N caused a P limitation microorganisms (and plants). In several European ecosystems it has been found that relatively high N availability leads to P limitation (Sturner and Elser 2002). Thus P limitation then leads microorganisms to release phosphatase molecules in order to scavenge for more P in the soil. A study by Olander and Vitousek (2000) supports this by showing that addition of N can lead to increased phosphatase activity in N limited soils. Therefore, the increased N content of *heuweltjies* soils may be contributing to their increased phosphatase activity. Alkaline phosphatase activity was higher on the *heuweltjies* than the interpatch soils. There were also more alkaline phosphatases than acid phosphatases on the *heuweltjies*. Therefore, *heuweltjies* have higher phosphatase activity and much higher alkaline phosphatase activity than interpatch soils. This might be expected as alkaline phosphatases activity is usually higher in alkaline and neutral soils like that of *heuweltjies* (Dick et al., 2000).

The relationship between phosphatase and P is only evident in Fynbos and only in the interpatch soils. The positive relationship between P and alkaline phosphatases is not what was expected in accordance with past ecological studies. However, recent studies suggest that this relationship does not always hold (Bengtsson et al., 2003; Giardina et al., 2001). The higher soil respiration, N mineralization and phosphatase activity suggest that *heuweltjies* are indeed hotspots of biogeochemical processes. However, results for Succulent Karoo and Fynbos sites are somewhat different, which suggest a differentiation due to rainfall, soil pH or vegetation type. These differences are discussed further below.

3.5.3. Biogeographic trends

The expected trend of a decline in *heuweltjie* soil nutrients with increasing rainfall was observed for only P and not for C and N. The relationship with rainfall varied with each enrichment factor. Rainfall did not seem to explain the variation in soil N between my study sites; it increased from TKRC to WVR and then again from JON to WGR. However, soils of TKRC have inherently lower N than soils of the other sites (Milton et al., 1992) and soil N of interpatch soils of JON is slightly lower than that of WGR. Carbon content of soils increased from TKRC to WVR and remained the same between JON

and WGR. The P concentration of *heuweltjie* soils decreased with increasing rainfall as expected with rainfall/ enrichment factor relationships but even so the relationship is not perfect. I suggest that the number of sites that I sampled was too low for this relationship to surface.

Both the pH and the electrical conductivity of *heuweltjies* soils decreased with increasing rainfall. Studies show that soil of arid and semi-arid ecosystem (such as TKRC) tends to have a high pH. At the beginning stages of weathering, basic cations are released from rock minerals. Under high rainfall conditions, the basic cations are eventually leached from the soil. In arid environments, however, the basic cations accumulate and hydroxide bases form which leads to a high pH (Skujiņš, 1991). Similarly, low rainfall and high evapotranspiration in dry areas can cause the accumulation of salts, more soluble than Ca, in the soil (Chapin et al., 2002) leading to a high EC. Milton et al., (1992) also show the high soil pH and electrical conductivity on and off *heuweltjies* at TKRC.

When compared to *heuweltjie* soils in the Fynbos, Succulent Karoo soils had higher C, P, pH and EC. Studies on the boundaries between Fynbos and Succulent Karoo show that Fynbos vegetation coincides with lower soil nutrients and lower pH compared to Succulent Karoo. At Jonaskop, a Fynbos/Succulent Karoo ecotone, North Sonderend Sandstone Fynbos vegetation is found at the top of the mountain where the nutrients and pH are low (Agenbag et al., 2008). The lower P content of Fynbos soils may be explained by the low nutrient content of the underlying parent material, sandstone (Lechmere-Oertel and Cowling, 2001).

3.6. Conclusions

The termites can be considered as physical ecosystem engineers as they change the stocks of nutrients as well as rate of nutrient cycling in soils via the collecting and accumulation of plant material in the *heuweltjies*. Conditions for decomposition in the mounds are different from those of the surrounding surface soils. The activities and legacy of termite activity also seem to impact abiotic conditions such as the amount of soil water and the pH that affects the reaction rates of microbial processes (Gutiérrez and Jones, 2006). Conditions for heat transfer differ from site to site. This eventually leads to the acceleration of biogeochemical reactions on *heuweltjies* especially during high soil water levels making these sites hotspots with hot moments. Nutrients, especially C and P accumulate to a higher magnitude

on Succulent Karoo *heuweltjie* soils than Fynbos soils making the effects of the termite more pronounced on this biome. The balance of evidence on soil processes shown here are from laboratory studies where environmental conditions have been controlled. However, it is highly probable that these also apply in the field. These findings have important implications for management of climate change (because of higher CO₂ efflux from *heuweltjies*), for management of invasive alien plants (potentially have higher concentrations of available nutrients) and for restoration after mining and (over)grazing in the south-western Cape region and the Northern Cape province of South Africa.

3.7. References

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Chapter 4: A comparison of the growth form composition and ecophysiology of vegetation growing on and between *heuweltjie* patches

4.1. Abstract

Heuweltjies, termite mounds of *Microhodotermes viator*, are hotspots for soil nutrients and also biogeochemical hotspots, specifically for CO₂ efflux, N mineralization and acid and alkaline phosphatase activity. This enrichment in macronutrients and nutrient availability may have implications for plant function and vegetation distribution in the landscape. The aim of this study was to compare the structure (aerial cover) of plant functional types and selected cryptogams and the ecophysiology of selected common shrub species on *heuweltjie* patches with that of the interpatch areas. This was done to ascertain the role of these termites in cryptogam structure and vegetation structure and function in Succulent Karoo and Fynbos biomes. The aerial cover of plant functional types, cryptogams and selected physical attributes was determined within 1m² grids for *heuweltjies* and interpatches at four sites across a rainfall gradient in the south-western Cape region. Two of the sites were chosen for further ecophysiological analyses including xylem water potentials, stomatal conductance, leaf C and N isotope compositions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), foliar N and C/N ratio. In previous research to simulate elevated soil N levels on *heuweltjies*, interpatch areas were (10 years ago) fertilized (10g m⁻² of N twice every year), and I included these plots in my analyses. There were few differences in vegetation structure, including lower cover of non-succulent shrubs and lichens and higher cover of mosses on the *heuweltjies* with no trends along the rainfall gradient. Xylem water potential did not differ between *heuweltjies* and interpatches, whereas the stomatal conductance of interpatch vegetation was consistently higher than that of *heuweltjies*. However, this was the case only at the Succulent Karoo site, and specifically after the area received rainfall. *Heuweltjie* vegetation also had higher water use efficiency (higher $\delta^{13}\text{C}$) and leaves were nutrient enriched, particularly reflecting the elevated availability of soil N (the latter only at the Succulent Karoo site). N fertilization had positive impact on xylem water potential and on stomatal conductance but again, only after a rainstorm. These results show that activities of *M. viator* impact significantly on structure and ecophysiology of plants, and thus are major ecosystem engineers effecting ecosystem processes such as primary productivity and decomposition. However, the impact is less significant in the Fynbos, an important factor that needs to be taken into account in restoration efforts.

Keywords: Termitaria, biogeochemical hotspots, vegetation structure, ecosystem processes, plant ecophysiology

4.2. Introduction

The Succulent Karoo and Fynbos biomes are both exceptionally diverse vegetation types (Cowling et al., 1996; Richards et al., 1997a; Richards et al., 1997b; Lechmere-Oertel and Cowling, 2001; Desmet, 2007). Low stature and dwarf shrubs are the most dominant growth forms in the Succulent Karoo, while taller shrubs are characteristic of the Fynbos biome of South Africa. Plant relative abundance and distribution in the landscape is determined by rainfall and prevailing soils conditions (Esler and Cowling, 1993; Richards et al., 1997a). There are sharp boundaries between plant communities with sometimes a complete turnover in species composition (Cowling et al., 2003). The change in plant community composition is closely associated with changes in soil pH, N and P as well as climatic variables along the slopes and valleys of the Cape Floristic Region (Agenbag et al., 2008), showing the importance of microsite differences occurring over short distances. *Heuweltjies* in the Succulent Karoo and the Fynbos, provide another fine-scale landscape feature that can potentially influence turnover.

Heuweltjies, mounds of southern harvester termite *Microhodotermes viator*, cover vast areas of the south-western Cape region of South Africa, including the Succulent Karoo and Fynbos biomes and contribute considerably to the rich bio- and pedodiversity. Their soils are nutrient hotspots of C, N and P and have higher potential N mineralization, phosphatase activity and potentially higher efflux of CO₂ than their surroundings soils (see Chapter three). They, therefore, add to the heterogeneity of the landscape and may affect the distribution of the shrub communities (Knight et al., 1989; Cowling, 1990; Midgley and Musil, 1990). These ‘disturbance’ patches represent a dramatic change in the microenvironmental conditions which potentially have large impact on the composition and function of the vegetation.

Vegetation structure of *heuweltjies* was studied by previous authors (Knight et al., 1989; Midgley and Musil, 1990; Milton et al., 1992; Esler and Cowling, 1995); however, most of these studies were done at single sites and mostly in the Succulent Karoo biome. There is little information about *heuweltjie* structure and function in the Fynbos biome (Milton and Linder, 1980; Ellis, 2004; Muhl, 2008). Also,

none of the previous studies considered the important non-vascular component of the vegetation and cryptogams such as microbiological soil crust (MSC). MSC (including mosses, lichens, algae, and bacteria) are common in arid and semi-arid ecosystems such as the Succulent Karoo (Nash et al., 1977; Chen et al., 2007) and are known to photosynthesise and have the ability to fix N. They are the primary source of N in some ecosystems and influence many other ecosystem processes (Evans and Belnap, 1999). Soil factors such as clay content and pH have a particularly strong influence on MSC distribution (Eldridge and Greene, 1994; Review). Given that *heuweltjies* differ from the interpatches in physicochemical attributes and other soil properties it follows that the distribution of MSC may be affected by the presence of these mounds. This study will determine the role of *heuweltjies* in determining the structure of vascular plant communities and cryptogams (e.g. MSC). It is expected that *heuweltjies* will have higher cover of vascular plants because of their high nutrient status, and also higher cover of MSC because of their of fine textured soils (Eldridge and Greene, 1994).

Elsewhere in the world, nutrient hotspots are implicated in controlling the overstorey tree species composition in forests (Bump, 2008) and increasing the leaf quality of vegetation that makes for better grazing (Grant and Scholes, 2006). Hill et al., (2005) showed that, in the Shirley Basin, a morphotype of the shrub *Artemisia tridentata* associated with mima-like mounds exhibited greater photosynthesis per unit leaf area, higher stomatal conductance, xylem water potentials, water use efficiency, and higher flower production than the intermound morphotype. The mounds had better water and nutrient relations than intermound areas (Hill et al., 2005). *Heuweltjies* (at times referred to as mima-like mounds) could have the same impact on the vegetation in their host ecosystems. In some areas of the Succulent Karoo, *heuweltjie* vegetation dries out far more than interpatch vegetation during the dry season indicating possible differences in drought responses and in life histories in mound plants. Only one study (Midgley and Bösenberg, 1990) documented the xylem water potentials of *heuweltjie* vegetation. Apart from this, there are no available data on gas exchange and water relations of *heuweltjie* vegetation. However, as field observations suggest some differences in drought responses between *heuweltjies* and interpatch plants and it is suspected that *heuweltjie* plants will have differential ecophysiology, analogous to plants growing on other types of mounds (e.g. mima mounds).

In any terrestrial ecosystem plants play the role of primary producers, as they are entry points for materials and energy to the biotic component. Thus a change in plant community composition has far

reaching effects on ecosystem functioning. Leaf properties and leaf litter quality are some of the important ways in which plants (or plant traits) can influence ecosystem processes. C and N concentrations in plant tissue can either impede (low N concentrations) or enhance (high N concentrations) the growth and activity of microorganisms (Jonasson et al., 1999). High quality litter leads to higher decomposition, higher mineralization rates, and higher resource availability (Chapin, 2003; Martinez-Yrizar et al., 2007). Nutrient concentrations of plant tissue differ depending on the environment, allocation to parts of the plant, and the developmental stage of the species (Pearcy et al., 1989). A study at a single site in the Succulent Karoo showed higher nutrient tissue concentrations on the *heuweltjies* (Midgley and Musil, 1990) but there is no such study for Fynbos *heuweltjies*. As the mechanism of formation of *heuweltjies* in the Fynbos is similar to those in the Succulent Karoo, we expect plant tissues nutrient levels will reflect elevated soil nutrient availability, and be higher than that of the surrounding areas. Further, it is plausible that differences in soil conditions will lead to differences in plant community structure and plant ecophysiology (i.e. bottom-up controls of plant structure and function) (Lambers and Pooter, 1992).

Bottom-up and top-down controls such as edaphic factors and rainfall shape vegetation structure and affect plant ecophysiology in the ecosystem (e.g. Denyer et al., 2010). An accumulation of N at a microsite, for example, leads to higher plant growth affecting specific leaf area and stomatal conductance (Lambers et al., 1998). The result of interspecific competition then determines the vegetation composition of the site. Therefore, the measurements of plant properties such as C and N isotope composition ($\delta^{13}\text{C}$; $\delta^{15}\text{N}$), as well as stomatal conductance and foliar N concentrations can give an indication of the main factors that control plant ecophysiology and vegetation structure in an area. The differentiation in the edaphic properties of *heuweltjies* from their surrounding suggested that there maybe accompanying changes in plant ecophysiology and vegetation structure. This study will be testing this hypothesis.

A survey of plant community composition (including soil microbiota) of *heuweltjies* and interpatches was carried out across a rainfall gradient in the Succulent Karoo and Fynbos biomes. Two of the study sites, Tierberg Karoo Research Centre (TKRC) and Jonaskop (JON), were chosen for ecophysiological studies which tested the following hypotheses: 1) Are there differences in xylem water potential and stomatal conductance between *heuweltjie* and interpatch plants. 2) Are there differences in water use

efficiencies and N isotope values between *heuweltjies* and interpatch plants? 3) What is the impact of the addition of N on the xylem water potentials and stomatal conductance of interpatch vegetation?

4.3. Methods

4.3.1. Field sites and study species

For vegetation surveys, four sites were chosen, spanning a rainfall gradient in the south-western Cape of South Africa (see Table 3.2, Chapter three). Two sites are in the Succulent Karoo, Tierberg Karoo Research Centre (TKRC), and Worcester Veld Reserve (WVR), and two in the Fynbos biome, Jonakop (JON), and Wiesenhof Game Reserve (WGR). The rainfall ranges from 169 mm at the driest site, (TKRC), to about 700 mm at the wettest site (WGR) (refer to Fig. 3.2, Chapter three). Succulent Karoo sites have cool winters and warm to hot summers (many days above 30 °C) while Fynbos sites have a mild Mediterranean climate (see Table 3.2). *Heuweltjies* present at the sites are more or less evenly distributed and may cover at least ~3.4% and up to 25% of the landscape.

Ecophysiological studies were performed only at the TKRC (33°10' S, 22°17' E) and JON (33° 56' S, 19° 31' E) sites. Measurements at TKRC were carried out in 2007 (November) and 2008 (March and September) and included at least one occasion in autumn, and two occasions in spring. JON was sampled on only one occasion in February 2009. The most common species found both on and off the *heuweltjies* were chosen for ecophysiological measurements on *heuweltjie* and interpatch areas (10 each). *Pteronia pallens* (Fig. 4.1 a) and *Tripteris sinuata* (formerly *Osteospermum sinuatum*) (Fig. 4.1 b) were the sample species at TKRC, and *Pteronia paniculata* was the study species at JON (Fig 4.1c). All species are long-lived, non-succulent Asteraceaeous shrubs (see Table 4.1).

Pteronia pallens is an evergreen woody shrub which can grow from about 0.4 to 0.6 m high. Its shoots grow between May and August, developing buds in July and flowering in November (Milton, 1994). Plants have narrow, needle-like leaves of different sizes (long and short) with all the long leaves shed during dry spells and the individuals appearing to be dormant. *Tripteris sinuata* is broad-leaved and drought-deciduous. Individuals grow and flower opportunistically, whenever conditions become favourable (Milton et al., 2004). When it is dry, plants may lose all their leaves (Milton, 1992). Both *P. pallens* and *T. sinuata* are long-lived and widespread across TKRC with an average of ~3000 and

~6500 individuals per hectare respectively (Milton and Dean, 1990). The plants to be measured at each *heuweltjie* were chosen randomly but an effort was made to keep sizes of plants the same on and off the *heuweltjie*. *Pteronia paniculata* at JON is to a certain extent comparable to *P. pallens* at TKRC. *Pteronia* shrubs are extremely drought resistant particularly *P. paniculata* which can withstand long drought periods without any sign of wilting (Hoffman et al., 2009). It can also survive low xylem water potentials, even below -10 MPa (Jacobsen et al., 2007). All study species employ C₃ photosynthetic pathway (Table 4.1).

Fertilization experiments were set up in 1998 at TKRC where 10 g m⁻² of N and K were added to 25 m² plots twice every year (Fig 4.2). The purpose of this experiment was to test whether the interpatch vegetation will resemble *heuweltjie* vegetation following fertilization, thus implicating nutrients (N and potassium) in, the structuring of *heuweltjies*. Preliminary studies have already shown that differences in vegetation cover and reproduction between plots (Milton et al., unpublished data). The species that were measured on the *heuweltjies* and interpatches at the sites are also present on these plots and, therefore could be used for measurements.

4.3.2. Sampling

4.3.2.1. Vegetation structure surveys

Vegetation sampling took place between November 2008 and March 2009. The aim of the vegetation surveys was to ascertain the difference in structure (aerial cover of various vegetation types, various types of cryptogams and selected physical attributes) between *heuweltjies* and interpatch vegetation. The vegetation was therefore categorized into non-succulent shrubs, succulents and herbs and the aerial cover (%) of each estimated within 1 m² grids. Succulents included both leaf and stem succulents. Herbs were neither succulent nor woody, and included sedges, grasses, and ferns. Mosses, lichens, and cyanobacterial crusts were also considered and the cover of each was considered separately (cryptogams). Other variables such as stone, rock, litter, and termite frass cover were also measured in order to better detect structural differences. Stones were considered as any stone-like object on the soil surface that could be moved, and rocks were similar objects that could not be moved. Plant litter was dead plant material that was not rooted and was lying on surface of the soil. Termite frass could be identified by its powder-like, feather light, dark coloured form which distinguished it from the litter and the soil.

Three 1 m² grids were randomly placed on each *heuweltjie*. The interpatch sample grids were placed either east or west of the *heuweltjie*, in a stratified random manner. Aerial cover was estimated to the nearest 5%. The average for the three grids was taken as estimate of cover in 1 m². A *heuweltjie* was surveyed for two consecutive days. There were no significant differences between estimates made in day one and day two ($Z = 1.48$, $p = 0.138$; this was only done at TKRC).

4.3.2.2. *Ecophysiology of shrub species*

Xylem water potential was measured before dawn (around 5 am) and in the afternoon (about 13:00 hrs) with a pressure chamber (Model 1000, PMS instrument co.) during the same period as the stomatal conductance. However, this was not always possible due to the extremely low xylem water potentials encountered (requiring large amounts of gas, and very high pressure, which sometimes exceeded the capacity of the machine). At TKRC, the distance between the *heuweltjies* (and the period available for predawn measurements) prevented the measurement of plants on the same *heuweltjies* that were measured for stomatal conductance although that would have been ideal. Individuals growing in the interpatches were treated in the same way as the individuals on the *heuweltjies*. Stomatal conductance and xylem water potential measurements were also taken on *T. sinuata* and *P. pallens* plants growing on N and control plots at TKRC. This was at the same times as measurements on and off *heuweltjies*.

For stomatal conductance and xylem water potential measurements, individuals on and off *heuweltjies* were randomly chosen for measurements. Stomatal conductance was measured in the morning, afternoon and evening, between 7 am and 5:30 pm, after rains in November of 2007 and September 2008 and during a dry spell in March 2008 at TKRC (Fig 4.4 a and b). At JON, measurements were taken in late summer (February 2009). An average conductance was taken from three leaves of each individual. These individuals were marked during the first visit and used on every visit thereafter. A leaf porometer (Model SC-1, Decagon Inc.) was used for this purpose. Measurements were taken on the bottom side of the leaf with *T. sinuata* but this was not possible with *Pteronia spp.* because of their needle-like leaves. During measurements the needle-like leaves of *P. pallens* and *P. paniculata* were arranged to form a continuous surface by placing leaves together to cover the sensor aperture of the leaf porometer for a more accurate estimate of conductance (as recommended in the manual of the SC-1 Porometer, Decagon Inc, 2005). When it was dry, *T. sinuata* plants lost all their leaves and therefore could not be included in the measurements at these times.

Vapour pressure deficits (VPD) were calculated for Tierberg Karoo Research Centre using maximum daily temperatures and minimum relative humidity so as to estimate highest VPD that plants were exposed to. The calculations were as follows:

$$VPD_{\max} = SVP_{\max} * (1 - (RH_{\min}/100)) \text{ (modified after Howell and Donald, 1995)}$$

Where SVP_{\max} is the saturated water vapour pressure for the maximum air temperature, taken from a psychrometric chart. RH_{\min} is the daily minimum relative humidity. For Jonaskop, the same formula was used but using average air temperature and average relative humidity (data for the maximum temperature and humidity were not available).

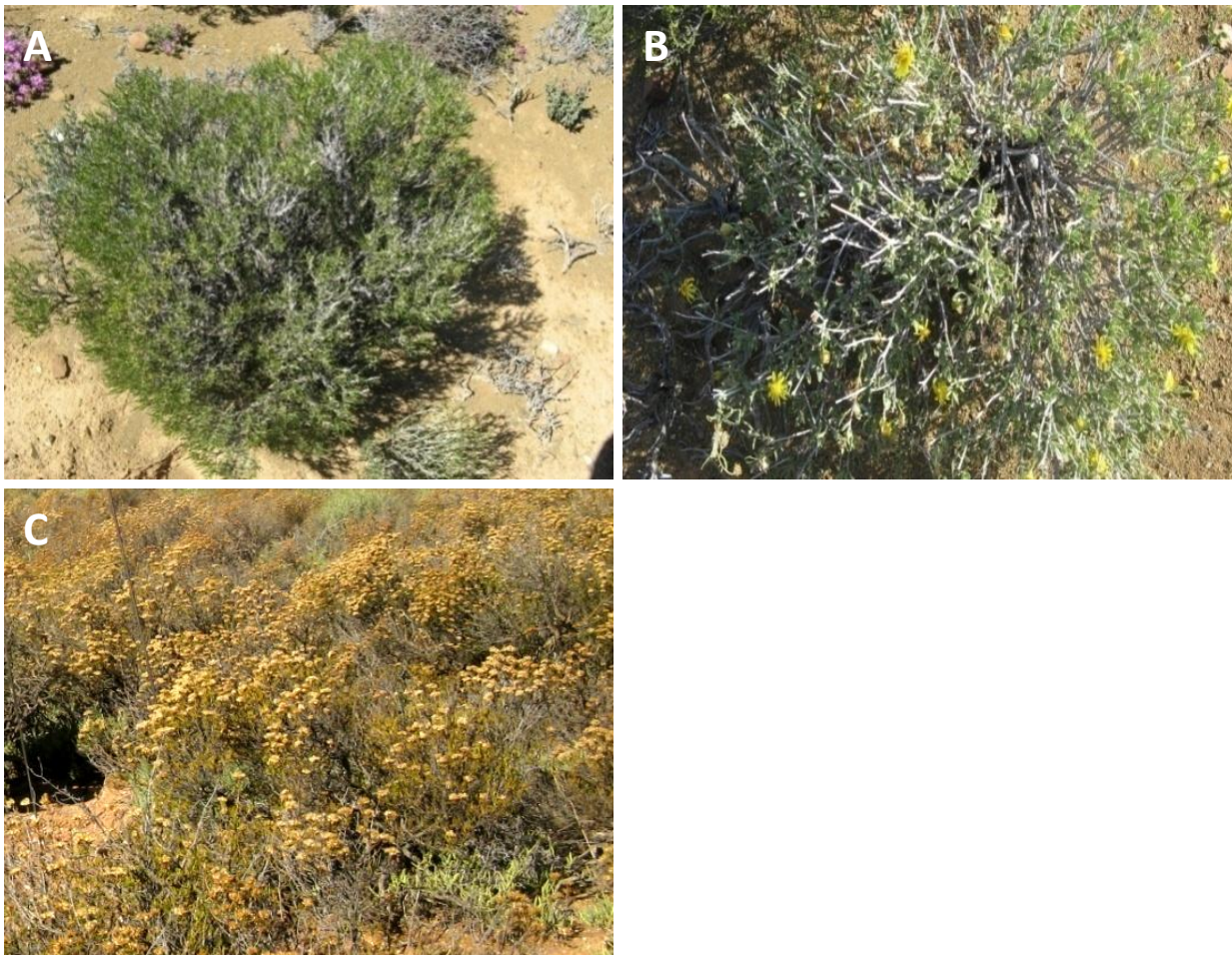


Fig 4.1. Photos of study species *Pteronia pallens* (A) and *Tripteris sinuata* (formerly *Osteospermum sinuatum*) (B) growing on and off *heuweltjies* at the Tierberg Karoo Research Centre and *Pteronia paniculata* (C) at Jonakop.

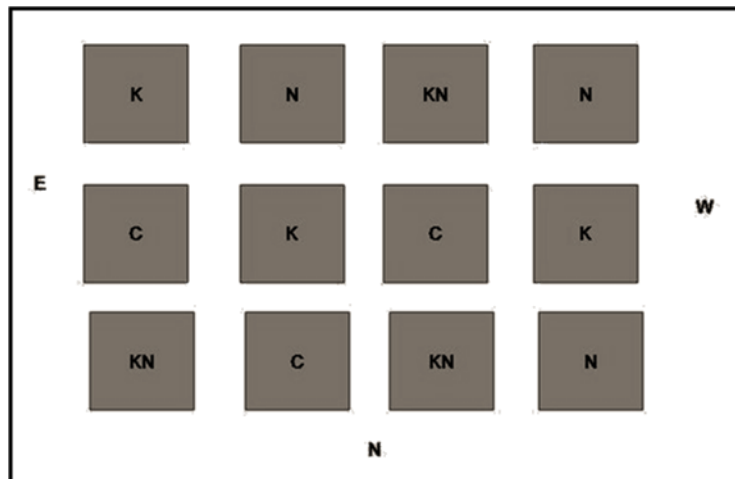


Fig 4.2. Layout of the fertilization plots at the Tierberg Karoo Research Centre. C = Control plots, N = Nitrogen plots, K = Potassium plots and KN = Potassium and nitrogen plots.

Leaves of one individual from each species on and off the *heuweltjie* were collected in the field, placed on paper bags and taken back to the laboratory where they were dried at 60-80 °C for four days. These were then ground and stored in a dry place at room temperature. A subsample was analysed for leaf nutrient content and stable C and N isotopes (Farquhar et al., 1984). During the analyses, micrograms of the sample were weighed into tin cups and enclosed. They were then combusted in a Flash EA 1112 elemental analyzer (Thermo Finnigan, Italy) and the gases passed to an isotope ratio mass spectrometer, Delta plus XP IRMS (Thermo Finnigan, Germany), via a Conflo III gas unit (Thermo Finnigan, Germany). Nitrogen is expressed in terms of its value relative to atmospheric N (reference) and C in terms of its value relative to Pee Dee Belemnite (reference).

For specific leaf area (SLA), 10 leaves (needles) were sampled from four individuals of *Pteronia spp.* on and off five *heuweltjies* at each site. Samples were collected in the morning (9:00-10:00 am) in September of 2008 at TKRC and February 2009 at JON. Leaves were collected, put into plastic bags, and taken to the laboratory where they were stored in the refrigerator below 4°C. Measurements of leaf area were taken with a leaf area meter (Li 3050C with transparent conveyer belt, LI-COR, USA). Thereafter leaves were dried at 60-80 °C for four days and weighed to the nearest 0.001 g. SLA is the ratio of leaf area to its dry mass (g cm^{-2}).

4.3.2. Data analysis

All aerial cover data, which showed a significant deviation from normal (Shapiro W at $p < 0.01$), were analysed with the Wilcoxon test. The average of the three estimates of each growth form on each *heuweltjie* was used in the statistical test. Ecophysiological data were tested either by paired t-test or by repeated measures ANOVA. All statistical analyses were done on STATISTICA 8.0 (2007) and 9.0 versions (2009) and Excel 2007.

4.4. Results

4.4.1. Vegetation structure

The vegetation surveys show few overall differences in vegetation cover between *heuweltjies* and interpatch areas (Table 4.2). The cover of mosses was 60% higher and lichen cover 537% lower on the *heuweltjies*. Non-succulent shrub cover was 26% lower on the *heuweltjies*. Apart from these, no other differences were found in the cover of vegetation between *heuweltjies* and interpatch areas. There was 40% more cover of plant litter and 640% more cover of termite frass on the *heuweltjies* compared to interpatch areas. There was also 88% less stone cover and 165% less rock cover on the *heuweltjie* patches.

No trends were observed across a rainfall gradient in the *heuweltjie* vegetation cover for all variables except non-succulent shrubs which increased with increasing rainfall (Table 4.2). Some similarities were found between sites of the same vegetation type in (Succulent Karoo or Fynbos) in terms of *heuweltjie* vegetation cover. Succulent Karoo sites (TKRC and WVR) had almost the same cover of succulent, non-succulent shrubs and cyanobacterial crust on their *heuweltjies*. Fynbos sites were similar only in the cover of succulents and non-succulent shrubs on their *heuweltjies*.

The highest cover of cryptogams was found at JON (Table 4.2). This was the only site where cover of cyanobacterial crusts of more than 10% was found both on the *heuweltjies* and in the interpatches. Mats of mosses were found under shrubs on the *heuweltjies* at this site (with an average cover of about 65%) and though cover was significantly reduced in the interpatches, it was still higher than moss cover at other sites. Lichens were equally high in cover in the WVR and JON interpatches. Herb cover was very low at TKRC and much higher at all other sites. The highest cover of succulents was found in the

Table 4.1. The characteristics of the study species at the Tierberg Karoo Research Centre from published work carried out here (*T. sinuata* and *P. pallens*). No information was available for Jonaskop (*P. paniculata*), and information was taken from publications of work done elsewhere. Plant height, density and volume are given as the mean (\pm SE).

| | <i>T. sinuata</i> | <i>P. pallens</i> L.f. | <i>P. paniculata</i> | References |
|--|--|---|-----------------------------------|---|
| Family | Asteraceae | Asteraceae | Asteraceae | - |
| Growth form | Drought-deciduous non succulent dwarf shrub, | Evergreen non succulent low shrub | Evergreen non succulent low shrub | - |
| Plant height (cm) | 10-50 | 40-70 | Unknown | Esler and Phillips (1994) |
| Canopy volume (CC X 10 ⁻³) | 91 \pm 1.2 | 104.0 \pm 11.1 | Unknown | Milton (1990) |
| Photosynthesis | C ₃ | C ₃ | C ₃ | Wand et al., (2001); Potts et al., 2009 |
| Leaves | Orthophyllous | Microphyllous | Microphyllous | - |
| Phenology | Grows and flowers opportunistically | Shoots grow in May-July; Buds in winter (July-Aug) and anthesis in spring (Sep-Oct) | Unknown | Milton (1995); Milton (1994); Milton et al., (1997) ; Milton et al., (2004) |
| Density per 100m ² | 65 \pm 4 | 30 \pm 22 | | Milton (1990) |
| Palatability | Palatable | Unpalatable (toxic) | Unpalatable (toxic) | Milton (1993); Saayman et al., (2009) |
| Microsites | On and off <i>heuweltjies</i> | On and off <i>heuweltjies</i> | On and off <i>heuweltjies</i> | - |

Table 4.2. Estimated mean (\pm S.E.) percentage cover of vegetation (dead or alive), soil biological crust and surface stone, litter, termite frass and rock cover on a 1 m² plot on and off *heuweltjies* across four sites in the south-western Cape. Data are represented from the driest (Tierberg Karoo Research Centre) to the wettest site (Wiesenhof Game Reserve). Tierberg Karoo Research Centre and Worcester Veld Reserve are Succulent Karoo sites and, Jonaskop and Wiesenhof Game Reserve are Fynbos sites.

| | Tierberg Karoo Research Centre | | Worcester Veld Reserve | | Jonaskop | | Wiesenhof Game Reserve | | Overall Means | |
|--------------------------|--------------------------------|--------------------------|--------------------------------|--------------------------|--------------------------------|--------------------------|--------------------------------|--------------------------|--------------------------------|--------------------------|
| | <i>Heuweltjies</i> (n = 10) | Interpatches (n = 10) | <i>Heuweltjies</i> (n = 10) | Interpatches (n = 10) | <i>Heuweltjies</i> (n = 10) | Interpatches (n = 10) | <i>Heuweltjies</i> (n = 10) | Interpatches (n = 10) | <i>Heuweltjies</i> (n = 40) | Interpatches (n = 40) |
| Cyanobacterial crust | 3.67 \pm 1.35 | 2.67 \pm 1.93 | 3.30 \pm 1.12** | 8.28 \pm 1.88 | 27.88 \pm 6.42 | 31.39 \pm 4.96 | 8.08 \pm 3.13 | 2.18 \pm 0.78 | 10.73 \pm 2.93 | 11.27 \pm 2.38 |
| Moss | 5.67 \pm 3.69 | 4.17 \pm 3.80 | 41.10 \pm 8.31 | 33.95 \pm 4.32 | 64.75 \pm 6.80** | 29.92 \pm 8.22 | 0.58 \pm 0.28 | 2.57 \pm 1.36 | 28.03 \pm 5.02* | 17.65 \pm 3.35 |
| Lichen | 2.83 \pm 1.08 | 2.75 \pm 2.57 | 0.08 \pm 0.08** | 22.03 \pm 6.23 | 4.42 \pm 2.89** | 21.83 \pm 3.95 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 1.83 \pm 0.80** | 11.65 \pm 2.57 |
| Herbs | 0.00 \pm 0.00 | 0.17 \pm 0.17 | 30.60 \pm 7.58* | 11.73 \pm 3.01 | 34.00 \pm 9.09* | 12.40 \pm 3.38 | 18.25 \pm 3.00** | 37.89 \pm 5.01 | 20.71 \pm 3.62 | 15.60 \pm 2.73 |
| Stem and Leaf Succulents | 30.92 \pm 4.75 | 22.58 \pm 3.22 | 35.27 \pm 5.92 | 36.40 \pm 3.82 | 2.92 \pm 2.56 | 6.17 \pm 2.01 | 7.42 \pm 3.75 | 2.02 \pm 0.58 | 19.23 \pm 3.12 | 17.40 \pm 2.59 |
| Non –succulent Shrubs | 10.17 \pm 3.11** | 32.17 \pm 4.56 | 13.70 \pm 4.17 | 16.18 \pm 1.40 | 38.98 \pm 6.58 | 38.17 \pm 5.17 | 42.67 \pm 3.42 | 46.98 \pm 5.41 | 26.48 \pm 3.18* | 33.39 \pm 2.79 |
| Dead plants | 9.67 \pm 1.73 | 5.91 \pm 0.87 | 7.92 \pm 3.15 | 9.85 \pm 2.60 | 15.38 \pm 5.01 | 19.17 \pm 2.91 | 6.33 \pm 1.39* | 2.70 \pm 0.66 | 9.87 \pm 1.49 | 9.72 \pm 1.40 |
| Litter | 39.83 \pm 4.24** | 15.58 \pm 1.99 | 51.13 \pm 4.11 | 40.51 \pm 5.22 | 69.98 \pm 4.01 | 64.75 \pm 5.08 | 49.83 \pm 5.53* | 32.05 \pm 3.39 | 52.70 \pm 2.78** | 38.22 \pm 3.47 |
| Termite Frass | 19.92 \pm 7.38* | 0.92 \pm 0.82 | 5.88 \pm 3.13* | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 4.42 \pm 2.58 | 3.18 \pm 2.13 | 7.55 \pm 2.35** | 1.02 \pm 0.59 |
| Stone | 15.48 \pm 5.90** | 51.58 \pm 3.03 | 37.83 \pm 3.25* | 55.95 \pm 2.71 | 33.17 \pm 6.59** | 57.25 \pm 4.58 | 36.75 \pm 4.33** | 67.65 \pm 4.69 | 30.81 \pm 2.88** | 58.11 \pm 2.08 |
| Rock | 0.58 \pm 0.43 | 2.08 \pm 1.03 | 0.71 \pm 0.48* | 12.93 \pm 3.57 | 0.00 \pm 0.00 | 0.00 \pm 0.00 | 15.58 \pm 4.80* | 29.57 \pm 5.12 | 4.22 \pm 1.57** | 11.12 \pm 2.41 |

Note: * and ** signify significant ($p < 0.05$) and highly significant ($p < 0.01$) differences between *heuweltjie* and interpatches vegetation tested with the Wilcoxon paired test

Succulent Karoo sites (TKRC and WVR). WVR was the site with the lowest cover of non-succulent shrubs. JON had the highest cover of dead standing material. Litter cover was high at all sites but also highest at JON. Termite frass were not found at JON and the highest cover was found at TKRC. Stone and rock cover were highest at WGR.

4.4.2. *Ecophysiology of non-succulent shrub species on and off heuweltjies at TKRC and JON*

4.4.2.1. *Xylem water potential and stomatal conductance*

No statistical tests were performed on *P. pallens* data because there were too few data points (Figs 4.3 a and b). Data, however, were displayed in order to show general trends and differences between species. There were no significant differences in the xylem water potentials between *heuweltjie* and interpatch plants for *T. sinuata* at TKRC in September 2008 ($F_{1,10} = 0.28, p = 0.608$) (Fig 4.3c) or *P. paniculata* plants at JON in February 2009 ($F_{1,5} = 1.25, p = 0.296$) (Fig 4.3 d). However, the trend was for higher predawn xylem water potential on the *heuweltjies* for plants growing at TKRC (Figs 4.3 a, b and c). The overall trend was for the midday water potential to be lower than predawn water potential at all sites, and for all individuals (Figs 4.3 c and b). However, predawn water potentials were significantly higher than midday water potentials only for *T. sinuata* in September 2008 and only on the *heuweltjies* [*T. sinuata*: $F_{1,10} = 19.82, p = 0.001$ (Fig 4.3 c); *P. paniculata*: $F_{1,8} = 13.41, p = 0.064$ (Fig 4.3 d)].

Stomatal conductance was highest in the morning and declined during the course of the day for all plants (Fig 4.4 a, c, d and e) with the exception of *P. pallens* at TKRC in March 2008 when stomatal conductance was uniform throughout the day (Figs 4.4 b). After rains (i.e. December 2007 and September 2008), conductance of interpatch plants was higher than that of *heuweltjie* plants ($F_{1,42} = 5.44, p = 0.025$) (Figs 4.4 a, c and d) at TKRC. For *T. sinuata* no significant differences were found in the stomatal behavior of *heuweltjie* plants compared to that of interpatch plants ($F_{1,14} = 1.37, p = 0.260$) in September 2008 (Fig 4.4 d). For *P. paniculata* at JON in February 2009, mean conductances were not significantly different between *heuweltjies* and interpatches ($F_{1,13} = 0.83, p = 0.778$; Fig 4.4 e). ANOVA shows significant differences between species and time of day and a significant interaction between time of day and species (Table 4.3). The weather conditions that prevailed at the study sites during sampling days are shown in Figs 4.5 a,b and c. Fig 4.5 b shows that March 2008 was the driest month of all sampling occasions at TKRC. December 2007 was the wettest for it had rainfall about 6

mm the day before measurements were taken (Fig 4.5 a). At JON, measurements were taken on a dry summer month and when VPD was relatively high (Fig 4.5 c).

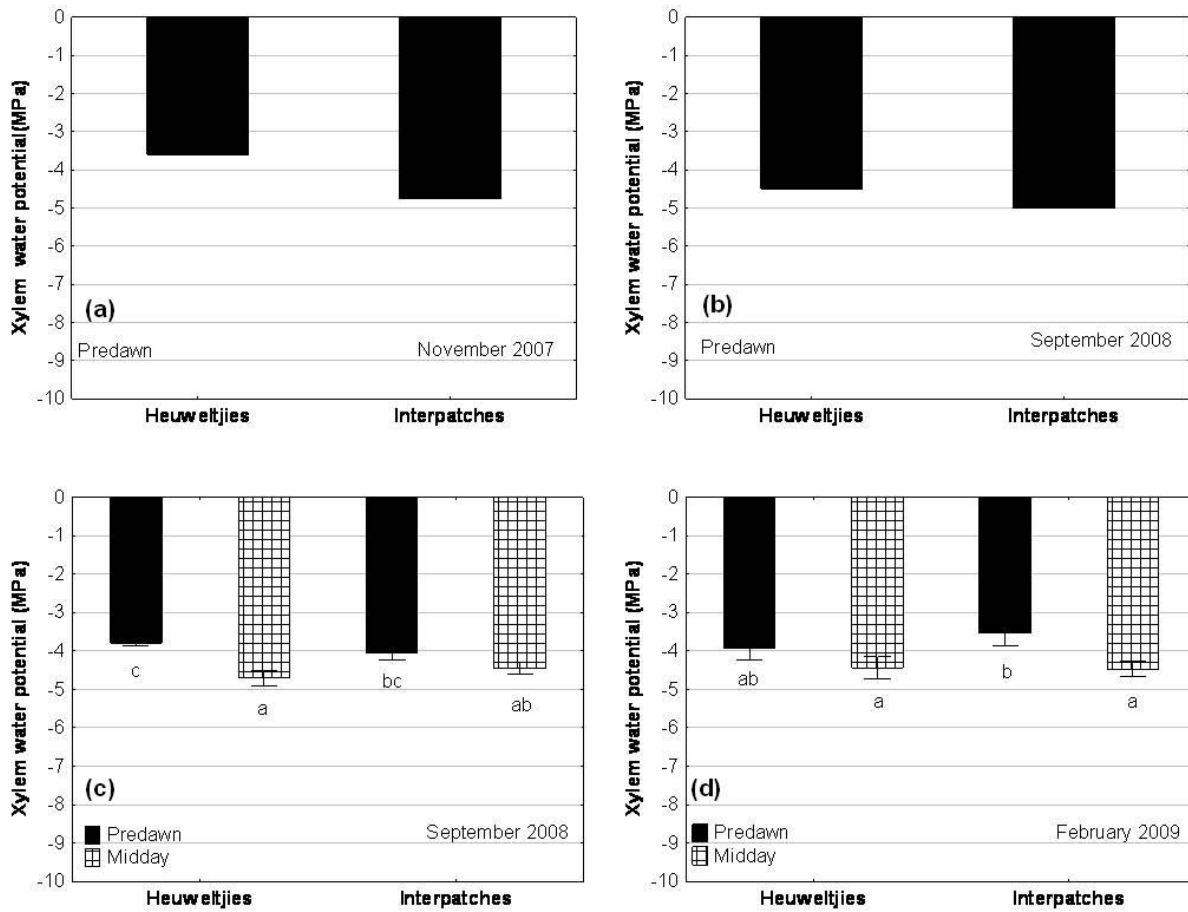


Fig 4.3. Predawn and midday xylem water potentials (Mean \pm SE) of *Pteronia pallens* (a) and (b), *Tripteris sinuata* (c) and *Pteronia paniculata* (d) growing on and off *heuweltjies* at Tierberg Karoo Research Centre and at Jonaskop in November 2007, September 2008 and February 2009. Standard errors were not calculated for *Pteronia pallens* (a) and (b) as only few data points were available.

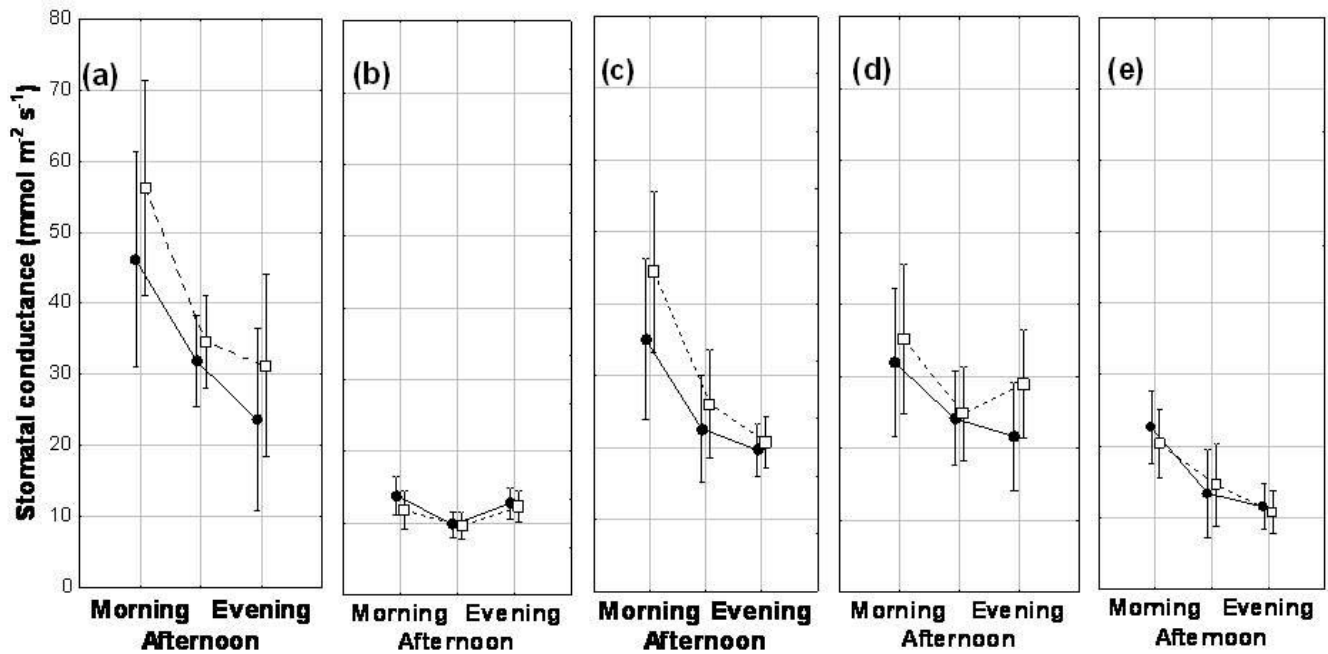


Fig 4.4. The morning, afternoon and evening means for stomatal conductance (\pm SE) of *Pteronia pallens* in December 2007 (a), March 2008 (b) and September 2008 (c) and *Tripteris sinuata* in September 2008 (d) growing on (solid circles) and off *heuweltjies* (open squares) at the Tierberg Karoo Research Centre (Succulent Karoo) and *Pteronia paniculata* at Jonaskop (Succulent Karoo/Fynbos) in February 2009 (e).

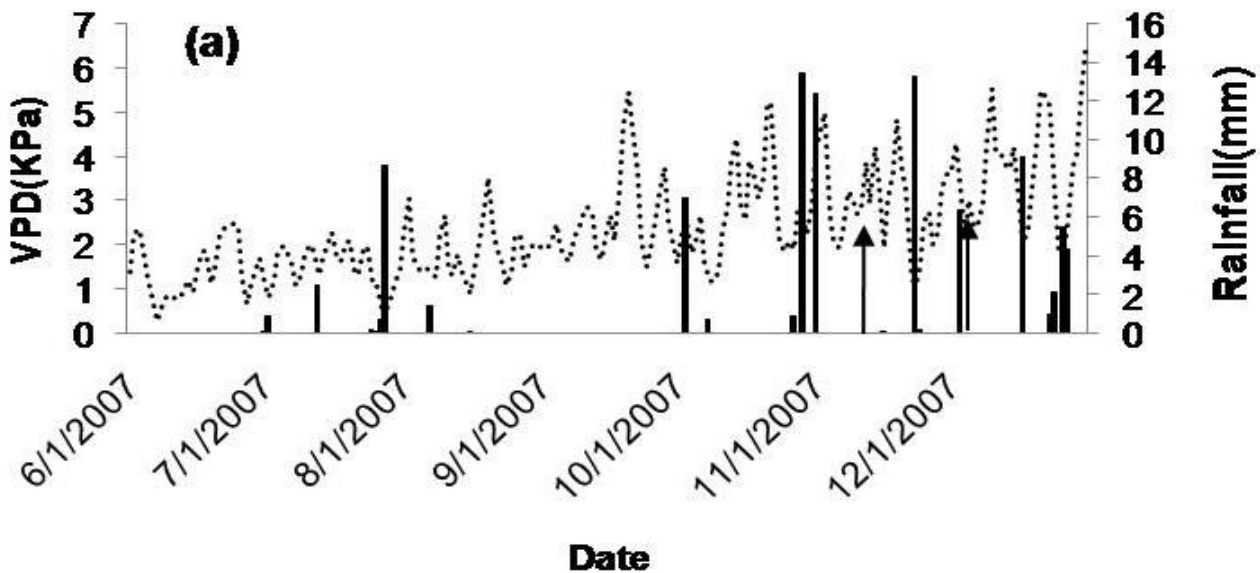


Fig 4.5. Rainfall (mm) and daily Vapour Pressure Deficit (VPD, Kpa) at Tierberg Karoo Research Centre between June 2007 to December 2007 (a) and between March 2008 to September 2008(b) and, at Jonaskop between September 2008 and February 2009. The sampling occasions are marked with arrows. Note differences in scale.

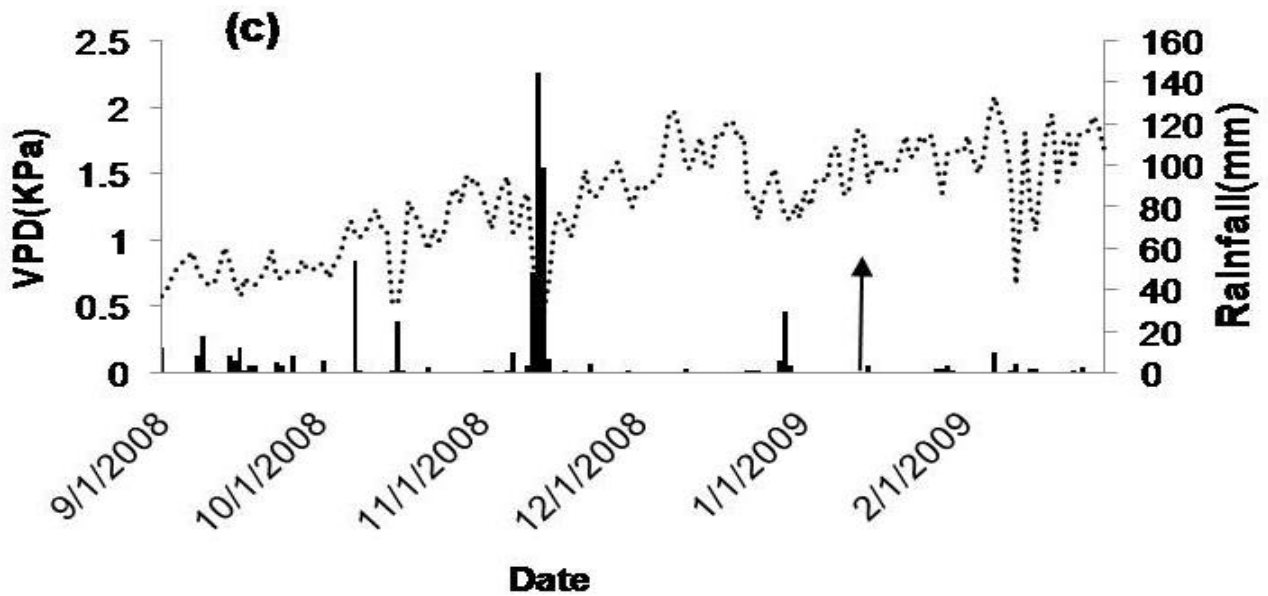
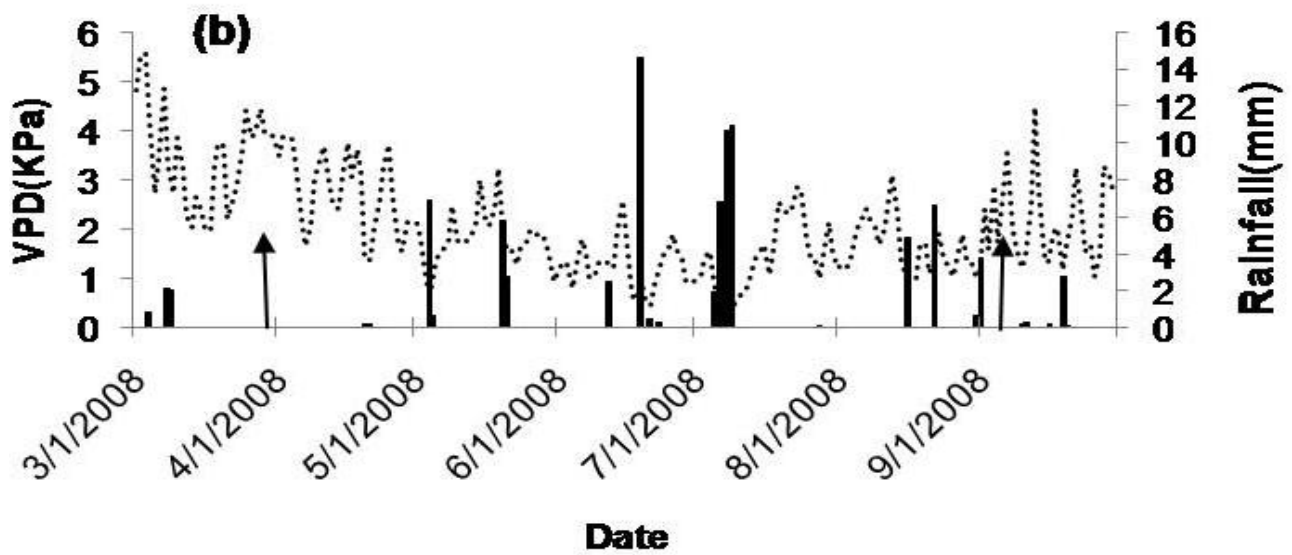


Fig 4.5 (Continued). Rainfall (mm) and daily Vapour Pressure Deficit (VPD, Kpa) at Tierberg Karoo Research Centre between June 2007 to December 2007 (a) and between March 2008 to September 2008(b) and, at Jonaskop between September 2008 and February 2009. The sampling occasions are marked with arrows. Note differences in scale.

Table 4.3. Three-way analysis of variance testing for the mean differences in stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) of *Pteronia pallens*, *Pteronia paniculata* and *Tripteris sinuata* growing on and off *heuweltjies* at the Tierberg Karoo Research Centre and Jonaskop. Microsite = *heuweltjies* or Interpatches; Time of day = morning, afternoon and evening.

| | Degr. of - Freedom | SS | MS | F | <i>p</i> |
|------------------------|--------------------|-----------------|-----------------|-----------------|------------------|
| Intercept | 1 | 85207.86 | 85207.86 | 1008.422 | <0.001 |
| Species | 2 | 4906.87 | 2453.44 | 29.036 | <0.001 |
| Microsite | 1 | 32.94 | 32.94 | 0.390 | 0.536 |
| Species*Microsite | 2 | 785.92 | 392.96 | 4.651 | 0.015 |
| Error | 44 | 3717.84 | 84.50 | | |
| Time of day | 2 | 3183.85 | 1591.93 | 15.828 | <0.001 |
| Time*Species | 4 | 1479.00 | 369.75 | 3.676 | 0.008 |
| Time*Microsite | 2 | 381.40 | 190.70 | 1.896 | 0.156 |
| Time*Species*Microsite | 4 | 430.07 | 107.52 | 1.069 | 0.377 |
| Error | 88 | 8850.71 | 100.58 | | |

4.4.2.2. Leaf chemical and isotopic composition

Carbon isotope composition of *heuweltjie* plants was higher (i.e. higher intrinsic water use efficiency) for *P. pallens* and *T. sinuata* at TKRC but not different for *P. paniculata* at JON (*P. pallens*: $F_{1,8} = 9.25$, $p = 0.016$; *T. sinuata*: $F_{1,7} = 28.46$, $p = 0.001$; *P. paniculata*: $F_{1,8} = 3.79$, $p = 0.087$). In addition, highest water use efficiencies were achieved by *P. pallens* plants and the lowest by *P. paniculata* (Fig 4.6 a), while drought-deciduous *T. sinuata* also showed low intrinsic water use efficiency. C/N ratio of leaf tissue was higher in the interpatches but only significant for drought-deciduous *T. sinuata* (*P. pallens*: $F_{1,8} = 4.18$, $p = 0.075$; *T. sinuata*: $F_{1,7} = 9.79$, $p = 0.017$; *P. paniculata*: $F_{1,8} = 0.14$, $p = 0.713$). C/N ratio of *heuweltjie* plants of *P. paniculata* at JON was 272 % and 582% higher than that of *P. pallens* and *T. sinuata* (at TKRC) respectively (Fig 4.6 b).

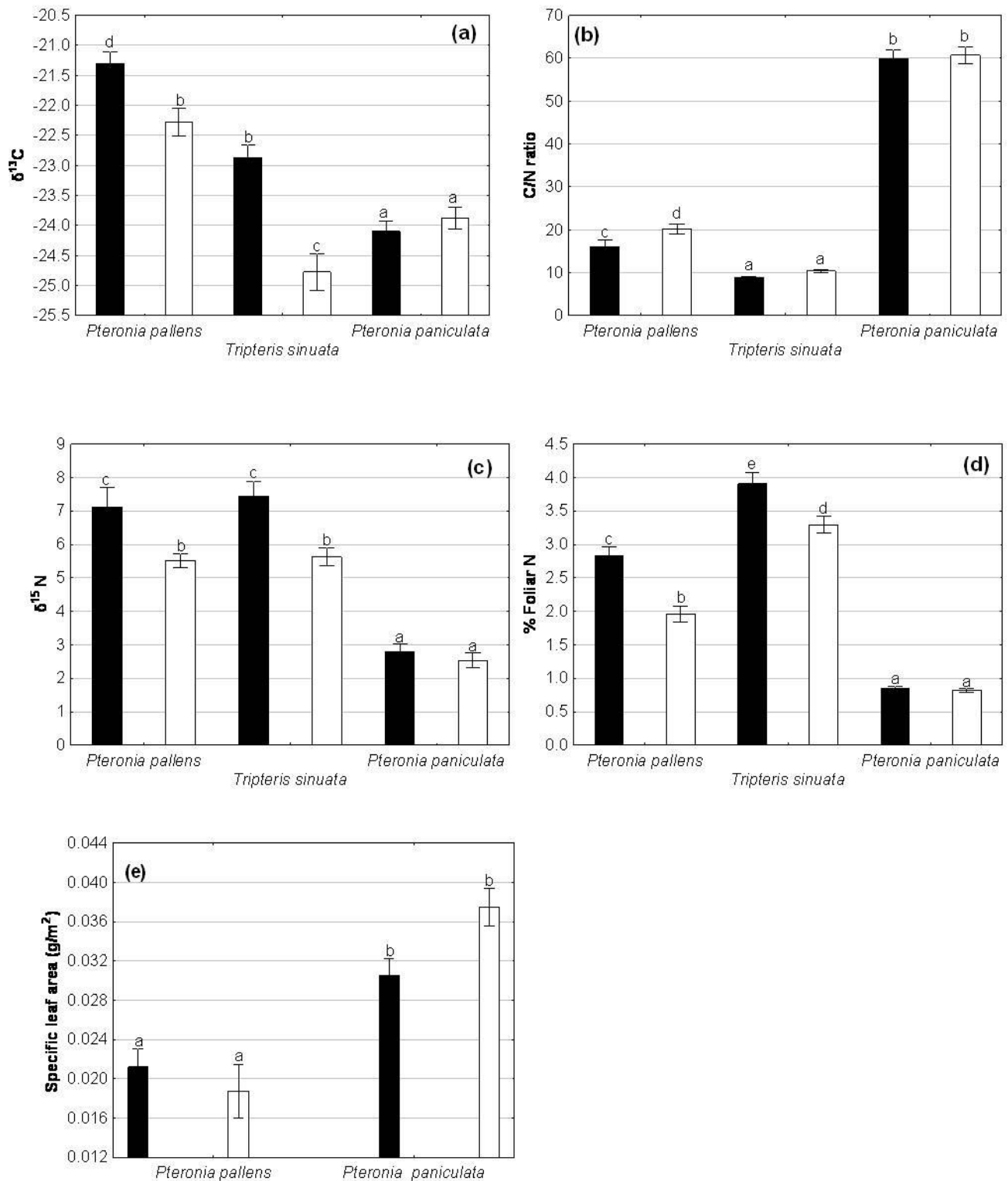


Fig 4.6. Mean (\pm SE) for carbon isotope composition (a), C/N ratio (b), nitrogen isotope composition (c), the leaf nitrogen content (d) and specific leaf area (e) for leaves of plants growing on the *heuweltjies* (solid bars) and in the interpatches (open bars) at the Tierberg Karoo Research Centre (*Pteronia pallens* and *Tripteris sinuata*) in the Succulent Karoo and Jonaskop (*Pteronia paniculata*) in the Fynbos biome. Significant differences were tested with repeated measures ANOVA and dissimilar letters denote statistically significant differences at $p < 0.05$.

Thus, the quality of leaf litter was lower at JON than TKRC as far as the species in this study are concerned. *Heuveltjie* plants were higher in $\delta^{15}\text{N}$ than plants growing in the nearby interpatches and more so for plants growing at TKRC compared to JON (*P. pallens*: $F_{1,8} = 7.96$, $p = 0.022$; *T. sinuata*: $F_{1,7} = 16.93$, $p = 0.004$; *P. paniculata*: $F_{1,8} = 1.48$, $p = 0.259$) (Fig 4.6 c). Foliar N was higher in the leaves of *heuveltjie* plants than those of the nearby interpatches and drought-deciduous *T. sinuata* showed the greatest accumulation (*P. pallens*: $F_{1,7} = 24.07$, $p = 0.002$; *T. sinuata*: $F_{1,7} = 5.66$, $p = 0.049$; *P. paniculata*: $F_{1,8} = 0.91$, $p = 0.369$) (Fig 4.6 d). Specific leaf area did not differ significantly between on and off *heuveltjie* plants for any of the species for which it was tested (Fig 4.6e) but was higher for plants at the site with higher rainfall (*P. paniculata*).

4.4.3. Ecophysiology of fertilized interpatch plants

Xylem water potentials were significantly higher in N than control plots for both *P.pallens* ($F_{1,4} = 44.64$, $p = 0.003$; Fig 4.7a) and *T. sinuata* ($F_{1,4} = 87.86$, $p < 0.001$; Fig 4.7b). Predawn water potentials were higher than midday water potentials for *T. sinuata* ($F_{1,4} = 18.86$, $p = 0.012$; Fig 4.7b). *P. pallens* plants growing on N plots showed a trend of higher stomatal conductance than plants growing in control plots but these were not statistically significantly different ($F_{1,10} = 2.10$, $p = 0.178$; Fig 4.8a). *T. sinuata* showed the opposite trend with plants growing in N plots having lower conductance ($F_{1,3} = 0.31$, $p = 0.618$; Fig 4.8b). Stomatal conductance of plants was lower during the dry periods (March 2008, Fig 4.9b) than after rains (November 2007, Fig 4.8a) ($F_{1,15} = 12.21$, $p = 0.003$) (Figs 4.8a-c). ANOVA showed a significant differences in stomatal conductance between species and differences depending on the time of day (i.e. morning, afternoon and evening) (Table 4.4). Conductance was generally high in the morning and at the end of the day (Figs 4.8 a-c).

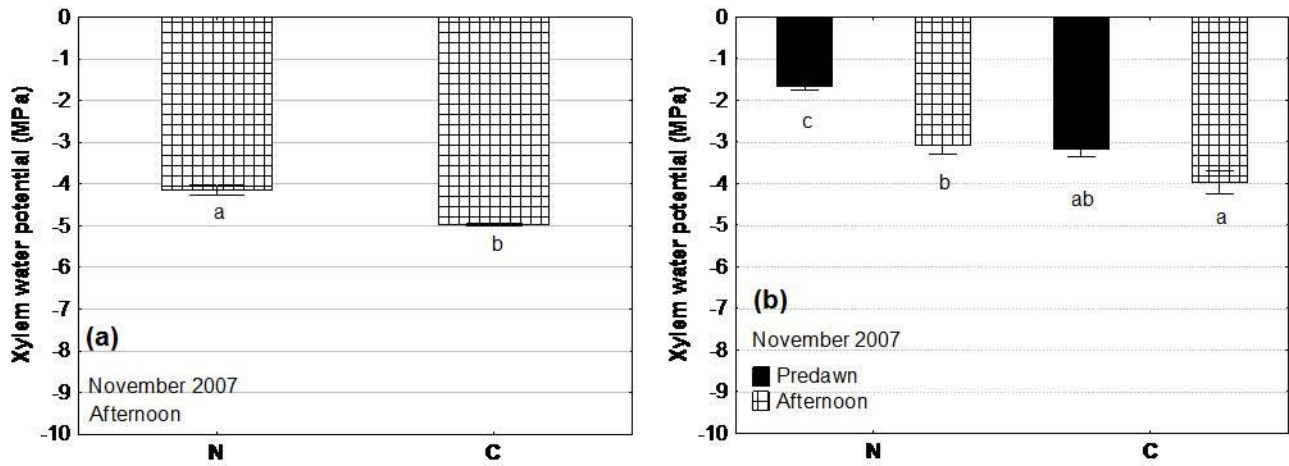


Fig 4.7. Midday water potentials of *Pteronia pallens* (a) and predawn and midday xylem water potential of *Tripteris sinuata* (b) growing on plots fertilized with 10 g m^{-2} of nitrogen (N) and control plots (C) at the Tierberg Karoo Research Centre in November 2007.

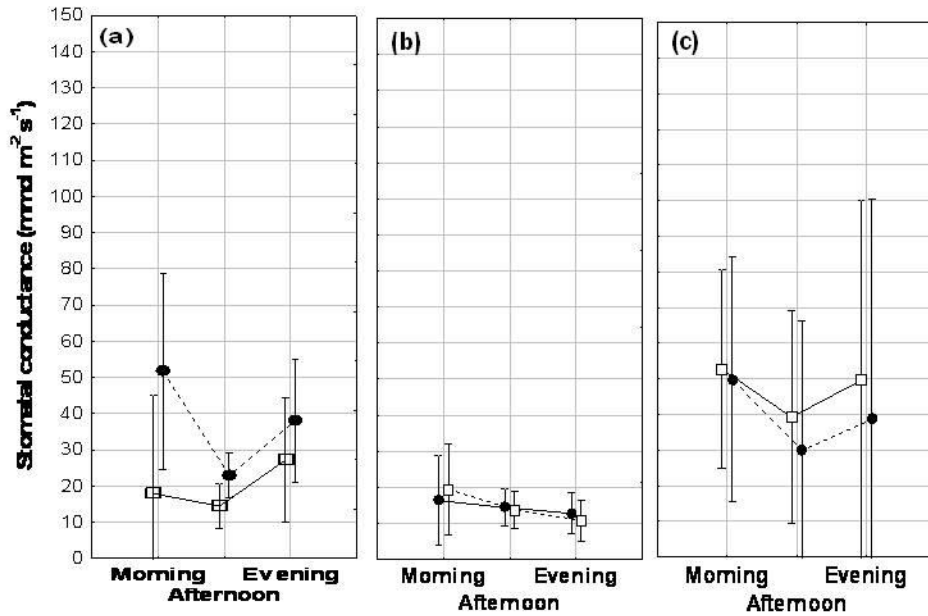


Fig 4.8. Means (\pm SE) of stomatal conductance for *Pteronia pallens* in November 2007 (a) and March 2008 (b) and, *Tripteris sinuata* in November 2007 (c) growing on nitrogen (solid circles) and control plots (open squares) at the Tierberg Karoo Research Centre.

Table 4.4.A three-way analysis of variance testing for mean differences in stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) of *Pteronia pallens* and *Tripteris sinuata* plants growing on fertilized plots at the Tierberg Karoo Research Centre. Plot = Nitrogen plots/Control plots; Time of day = morning, afternoon and evening.

| | SS | Degr. of - Freedom | MS | F | p |
|-------------------|-----------------|-----------------------|-----------------|---------------|------------------|
| Intercept | 50717.33 | 1 | 50717.33 | 131.06 | <0.001 |
| Species | 5627.56 | 1 | 5627.56 | 14.54 | 0.002 |
| Plot | 3.20 | 1 | 3.20 | 0.01 | 0.092 |
| Species*Plot | 821.16 | 1 | 821.16 | 2.12 | 0.167 |
| Error | 5417.64 | 14 | 386.97 | | |
| Time | 1435.51 | 2 | 171.76 | 5.41 | 0.010 |
| Time*Species | 94.31 | 2 | 47.15 | 0.36 | 0.704 |
| Time*Plot | 193.65 | 2 | 96.83 | 0.729 | 0.491 |
| Time*Species*Plot | 10.60 | 2 | 5.30 | 0.340 | 0.961 |
| Error | 3717.31 | 28 | 132.76 | | |

4.5. Discussion

4.5.1. Vegetation structure

Heuweltjie patches, as nutrient and biogeochemical hotspots in the Succulent Karoo and Fynbos landscapes were expected to differ substantially in vegetation form and function from the surrounding interpatch vegetation. Knight et al., (1989) supported this notion when they showed that deciduous and succulent shrubs dominated *heuweltjies* in the Clanwilliam area. Midgley and Musil (1990) also found deciduousness to be favoured on the *heuweltjies* in the Worcester/Robertson valley. However, the results of my own surveys revealed only few differences in vegetation composition between *heuweltjies* and interpatches. This included the cover of moss, lichen and non-succulent shrubs species. Further, rainfall did not have an effect on either the magnitude of the difference in cover between *heuweltjies* and interpatches or whether *heuweltjies* had higher or lower vegetation cover than interpatch areas. Vegetation type seemed to affect the cover of succulents and non-succulent shrubs on the *heuweltjies*. My results did not capture important life history characteristics such as deciduousness, and vegetation structural attributes such as plant height and the spatial arrangement of individuals. However, visual inspection of the *heuweltjies* suggest these aspects are important in distinguishing

heuweltjies from surrounding interpatch areas, as are differences in species composition. It is recommended that these aspects be considered for future studies.

This study took a novel approach by investigating cover of functionally important cryptogams such as mosses, cyanobacterial crusts, and lichens. Where lichens were found, their cover was always higher on the interpatches, while mosses were most likely to be found on the *heuweltjies*. In arid Australia and Utah, the distribution of soil microbiota was found to be affected by soil properties. Mosses were dominant in soils with higher clay content, pH and soil water content. Also, they were associated with soils of calcareous and limestone origin (Anderson et al., 1982; Downing, 1992). These conditions are comparable to the conditions on the *heuweltjies* observed by this and other studies (Midgley and Musil, 1990; Milton et al., 1992; Ellis, 2002). Lichens are confined to areas of low disturbance (off *heuweltjies*). They prefer much the same high clay soils as mosses, only they grow much slower and thus are outcompeted (Cornelissen et al., 2001; Honegger, 1993). Mosses and lichens have different effects on the soil on which they grow. Whereas lichens photosynthesize and fix N, which adds significantly to the N inputs in some ecosystems, mosses insulate the soil and retain water, causing cool, anaerobic conditions that slow down decomposition (Chapin et al., 2002). N and P that are retained in the peat caused by the moss mats affect vascular plant growth (Chapin et al., 2002). This could be the case at JON, where the highest cover of moss mats were found on *heuweltjies*.

The cover of non-succulent shrubs on *heuweltjies* and interpatches differed greatly at TKRC and this affected overall results, whereas no differences were found for other sites. This study did not differentiate between deciduous and evergreen shrubs perhaps this is where more differences may have been detected. Furthermore, the succulent and non-succulent growth forms include a variety of species with differing life histories (Esler and Cowling, 1995; Milton and Dean, 1999) and it may be more valuable to consider the actual identity of species growing on and off *heuweltjies*, as mentioned before. At TKRC, *heuweltjies* were dominated by *Psilocaulon utile* and *Malephora lutea*. In most cases, these species were restricted to the *heuweltjies* and other cases they were the only species present on the *heuweltjie*. *M. lutea* is a succulent halophyte (Milton et al., 1994) and is thus able to survive the relatively more saline environment of *heuweltjies* at TKRC. In the interpatches, the most prominent species were *Ruschia spinosa*, a slow growing and hardy succulent (Esler and Phillips, 1994), and *Rhinephyllum spp.* at TKRC. Similar results were found by Milton et al., (1992) at this site.

Pteronia pallens and *Tripteris sinuata* occur both on and off the *heuweltjies*. The reason why these species are able to survive on the *heuweltjies* at TKRC may be partly due to their ability to store fructans in their vacuoles thus increasing osmotic potential (Van der Heyden, 1992). Adjusting the osmotic potential maintains the gradient in water potential between soil and plant, allowing it to take up water even under the low soil water potentials of saline soils (Chapin et al., 2002). At JON, *heuweltjies* were dominated by the shrub species *Pteronia incana*, with stands that cover the whole *heuweltjie* in places. *Pteronia incana*, native to the Succulent Karoo has invaded parts of the Eastern Cape (Kakembo et al., 2007). It, therefore, possesses the characteristics typical of invasive species which allow it to thrive in the eutrophic conditions on the *heuweltjies*. In addition, invasive *P. incana* was shown to colonise, dominate, and finally outcompete grasses in drier parts of the landscape in the Eastern Cape Province (Kakembo et al., 2007). This shows the ability of this species to withstand the dry conditions such as those existing on *heuweltjies* at certain times of the year. The only growth form affected by rainfall (i.e. across the rainfall gradient investigated) was the non-succulent shrubs but this was probably due to the simultaneous decline in the cover of succulent shrubs from Succulent Karoo to Fynbos. The succulent component of the vegetation was higher in the Succulent Karoo; not surprising as this vegetation is defining characteristic of the biome.

The differences in the cover of physical variables between *heuweltjies* and interpatches (i.e. lower cover of stone and rock and higher cover of termite frass and plant litter on the *heuweltjies*) could have important implication for the ecology of the landscape. Consistency in the lower cover of stones on *heuweltjies* throughout all sites is evidence of the disturbance by the termites during the formation of the mounds. Cox et al., (1987) studied the distribution of stones in mima mounds in the Columbia Plateau and demonstrated that perturbation can cause a decline in the large stone fraction on mounds as observed for *heuweltjies*, possibly due to a long history of disturbance. Termites must also have avoided rocky areas during nest construction. The cover of termite frass shows that not all the sites had active *heuweltjies* at the time of sampling. Thus, properties of these *heuweltjies*, including soil properties, might be because of positive feedbacks from the vegetation growing there and historical enrichment of past activity, however, climatic variables such as high rainfall may equal out any differences in the absence of termites. The higher litter on the *heuweltjies* is probably from the harvesting activities of the termites. Also, litter production is known to be effected by soil fertility and soil water retention which are both high on *heuweltjies* (see Chapter three) (Facelli and Pickett, 1991). Fynbos *heuweltjies* seemed to be less active than those in the Succulent Karoo. This lack of disturbance

may have major repercussion for vegetation structure and needs further attention. Whether this is a reflection of a different climate is unclear.

4.5.2. *Ecophysiological differences between heuweltjies and interpatch plants*

Xylem water potentials of *heuweltjie* plants were not different from that of interpatch plants. Predawn water potentials were higher than midday water potentials as is seen for some shrubs in semi-arid ecosystem (Syvertsen et al., 1975). Succulent Karoo and Fynbos plants had similar values, with average values between -3.5.0 MPa and -5.0 MPa for all plants. The trend for *P. pallens* at TKRC was higher predawn xylem water potential on the *heuweltjies* in November 2007. This could be explained by high soil water availability for it had rained about 12.4 mm 11 days before measurements were taken. It was shown in previous chapters that *heuweltjies* soils retain more water (for longer) than interpatch soils (see Fig 3.3a, Chapter three). However, there could be a discrepancy between water content and water potential in *heuweltjie* soils. Water potential gradients drive the movement of water from the soil to the plant (Lambers et al., 1998). Soil water potential is effected by a number of factors including soil salinity. The accumulation of salts (especially in the Succulent Karoo) increases the osmotic component of water potential and decrease overall soil water potential (Chapin et al., 2002). The lower soil water potential then leads to a complementary decline in plant water potential, and may explain why the water potential *heuweltjies* plants is not improved by their higher soil water content. The xylem water potential of *heuweltjie* plants was much lower in September 2008 probably because of lower soil water (and lower soil water potentials). It had only rained 4 mm, 6 days before this sampling occasion. At this sampling time water content of *heuweltjie* soils might have equated with that of nearby interpatch areas (Fig 3.3a, Chapter three). This was also evident with *T. sinuata*, as there were no significant differences between the water potentials of *heuweltjie* and interpatch plants of this species in September 2008. At JON, xylem water potentials of *P. paniculata* varied little between *heuweltjie* and interpatch plants and plants appeared to be more water stressed on the *heuweltjies* before dawn in late summer of 2009. This suggests that the finer texture of *heuweltjie* soils is making it more difficult for plants to take up water during dry periods. Midgley and Bösenberg (1990) studied xylem water potential on and off *heuweltjies* at the Worcester Veld Reserve. Their study included two of my study species and their results are within the same range as the current study.

Overall, *heuweltjie* plants had lower stomatal conductance compared to interpatch plants. At TKRC, March 2008 had been the driest month of all sampling occasions; hence, stomatal conductance was lowest and did not differ between sites. September 2008 was wetter, and VPD had dropped and plants responded by increasing their stomatal apertures. December 2007 was probably the month with the highest soil water and stomatal conductance was concomitantly high regardless of the high VPD. Conductance was higher in the morning than any other time of the day except for *P. pallens* in March 2008. This trend is probably due to these plants in arid areas taking advantage of relatively favourable conditions early morning, but closing their stomata when less favourable conditions prevail in the midday and afternoon. In addition, when seasonal dry conditions prevailed (such as in March 2008) stomatal conductance was low, regardless of the time of day. At JON, the conductance of *P. paniculata* plants in February 2009 was almost as low as those of *P. pallens* in March 2008 and did not differ between *heuweltjies* and interpatches.

Differences in stomatal conductance between the months suggest that conductance could be correlated to soil water. Deciduous species are known to achieve higher stomatal conductance than evergreen species, however, this was not the case with *T. sinuata*. Literature shows ability for *T. sinuata* to achieve far greater stomatal apertures than was recorded in this study. Bowie (1999) measured values as high as $0.499 \text{ mol m}^{-2} \text{ s}^{-1}$ under controlled, well-watered conditions. This implied that shortage of water is the main reason for the conservative behaviour exhibited by this species. Data for *P. pallens* shows that *heuweltjies* are potentially more water stressed than interpatch plants. This is also supported by the large drop in xylem water potential values on *heuweltjies* between November 2007 and September 2008. Previous studies have shown that competition is fierce on *heuweltjies* compared to the surrounding interpatches (Riginos et al., 2005). In the Succulent Karoo are a number of opportunistic species who will take full advantage of high soil water conditions (Midgley and Moll, 1993; Milton et al., 2004). *T. sinuata* is one such species but on the *heuweltjies* it is most likely outmatched by more vigorous growth forms such as annuals and forbs which appear in abundance after rain (Milton, 1990). *P. paniculata* had low conductance because it was measured at the end of summer when Fynbos vegetation is at its driest, as is also shown by the prevailing weather conditions at the time of sampling (Cowling et al., 2003). At these times, *P. paniculata* is probably experiencing strong competition from more competitive species such as *P. incana* on the *heuweltjies*. This effect was also evident in the predawn xylem water potentials of *heuweltjie* plants at this site.

Water use efficiency (as measured by leaf $\delta^{13}\text{C}$) of *heuweltjie* plants was significantly higher than that of interpatch plants for *P. pallens* and *T. sinuata* but not *P. paniculata*. The water use efficiency (WUE) results correspond well with those of stomatal conductance. They also show that plants on the *heuweltjies* at TKRC are experiencing a water shortage in the longer-term.

The link between soil water and plant water use efficiency is well known (Dudley, 1996; Tsialtas et al., 2001). However, there is also a link between soil nutrient availability and leaf $\delta^{13}\text{C}$. Bender and Berge (1979), for example, showed that plants of timothy grass (*Phleum pratense*) that were fertilized with N had more positive $\delta^{13}\text{C}$ values. Brueck (2008) reviewed the relationship between N and WUE and showed that they are positively related. Livingston et al., (1999) supports this by showing that in C_3 plants there is a negative relationship between WUE and N use efficiency (NUE). This means that increased N supply to plants increase their water use efficiency (Livingston et al., 1999), as can be seen on *heuweltjies*. This also explains the differences observed between *P. pallens* and *P. paniculata* as the latter grows in a site with higher average rainfall. Also *P. paniculata* leaves were collected in the late summer, under drought conditions when there was little possibility of new growth, and when old leaves are nutrient poor (Chapin et al., 2002). The observed differences between drought-deciduous *T. sinuata* and evergreen *P. pallens* at TKRC demonstrate the higher productivity of deciduous species compared to evergreen. The $\delta^{13}\text{C}$ values for *T. sinuata* shows that this species is probably not achieving its full potential in terms of productivity on the *heuweltjies* as result of water stress. Wand et al., (2001) reported values between -30.2 and -27.8 for *T. sinuata* plants growing under controlled, well-watered conditions. Wegner et al., (2003) used the plant C/N ratio as a surrogate for NUE. If we look at the C/N ratios values for this study, we see that these results also correspond with Livingston et al., (1999).

Improved N dynamics can be seen from the foliar data with the lower C/N ratio, higher $\delta^{15}\text{N}$ and higher foliar N in *heuweltjie* plants. The aggregate leaf quality of *P. pallens* was significantly higher (lower C/N ratio) on *heuweltjies* than the interpatches. The quality of plant litter is the main factor controlling decomposition. There are differences in the rates of decomposition caused by the inclination of litter to decompose. For example, leaves from high nutrient sites, such as *heuweltjies*, decompose more rapidly than leaves from nutrient-poor sites such as the interpatch areas (Chapin et al., 2002). The higher decomposition also goes hand in hand with higher N mineralization of *heuweltjie* soils as shown in previous chapters (see Chapter three). C/N ratio of *T. sinuata* was lower than that of *P. pallens* but did

not differ between *heuweltjies* and interpatches. This result supports the known fact that deciduous leaves decompose faster than evergreen leaves (Chapin et al., 2002). For *P. paniculata* C/N ratio was much higher than that of other two species but also did not differ between microsites. This implies that at N dynamics at TKRC (Succulent Karoo) are different from those at JON (Fynbos). $\delta^{15}\text{N}$ values were higher for *heuweltjie* plants for all species, but lowest for *P. paniculata*. Foliar N differed only for plants at TKRC with much higher values on the *heuweltjies*. $\delta^{15}\text{N}$ values are known to be higher in plants that grow faster and capture more N (Dunn et al., 2006). It is indicative of elevated availability in soils, which supports the finding in Chapter three (see also Dawson et al., 2002). The lower available N found in the Fynbos biome on the *heuweltjies* is also reflected in lower foliar $\delta^{15}\text{N}$ values, foliar N values and higher C/N ratios (overall, for *P. paniculata*). Additionally, the mean annual rainfall is one of the primary controls on soil and plant $\delta^{15}\text{N}$ (Amundson et al., 2003). High $\delta^{15}\text{N}$ are often associated with plants growing in dry environments (Schulze et al., 1998; Swap et al., 2004). Therefore, recorded values support those shown for water use efficiency and leaf N. The higher leaf N content of *heuweltjies* provide better conditions, under relatively high soil water potential, for a higher maximum photosynthesis, as shown by positive relations between leaf N and photosynthesis in number of studies (Green and Mitchell, 1992; Vaitkus and McLeod, 1995).

In summary, *heuweltjies* are, therefore, patches with vegetation that has a low stomatal conductance after rain, compared to plants in nearby interpatch areas. The leaves of *heuweltjie* species also have higher aggregate quality (low C/N ratio), higher photosynthetic potential (high foliar N) with rapid turnover of N (high $\delta^{15}\text{N}$). The increased N availability of their soils increases their water use efficiency (high $\delta^{13}\text{C}$) and may decrease their nutrient use efficiency (low C/N ratio). But these patterns are most clear in the site with the lowest rainfall, in the Succulent Karoo. For the plants growing at JON some of these patterns disappear either because of the increased rainfall or the age of the evergreen leaves.

4.5.3. Effect of nitrogen on the plant ecophysiology of fertilized interpatch plants

When the plants of interpatch areas at TKRC were fertilized with 10g N m^{-2} the results were a decrease in water stress (higher xylem water potential) and greater variation in stomatal conductance. The positive response of xylem water potential to N, at high water levels is an interesting result. With a potential increase in leaf area and the decline in root/shoot ratio brought on by higher N availability one

would expect increased water stress (Nobel et al., 1989). However, the improvement of predawn xylem water potential and midday xylem water potential with increasing N availability is not unheard of (Hillerdal-Hagströmer et al., 1982; Brix and Mitchell, 1986). Green and Mitchell (1992) suggest that this may be a common feature with plants that grow under water and N deficient conditions, as is the case with my study site (Milton et al., 1992). Plants on N plots tended to have higher stomatal conductance though this was not significant. Stomatal conductance may be affected more strongly by water availability than nutrients but nutrients are also important, as we have seen earlier. Fertilization leads to higher conductance (at elevated CO₂ and water levels) in wheat (Li et al., 2004) and lower conductance in poplar species (Yin et al., 2009). When there is any resource limitation it is likely that conductance will increase with increasing availability of that resource (Chapin et al., 2002; Pearcy et al., 1987) just as P deficiency had increased the sensitivity of stomata to water stress in cotton plants (Radin 1984).

The response of these plants to N fertilization shows that, were it not for the high water deficiency, *heuweltjie* plants would have improved growth (higher stomatal conductance and xylem water potentials) as a result of their higher N availability at this site. It is thus primarily soil water that controls the vegetation structure of the mounds in the Succulent Karoo and they are dominated by succulents which are better equipped to deal with water shortages, though salinity may also play a role.

4.6. Conclusion

This study has shown that *heuweltjies*, which are nutrient and biogeochemical hotspots, affect the distribution of the soil cryptogamic community. The distribution of other growth forms is little affected by the presence of *heuweltjies*. No significant impact of rainfall could be detected, and biome type (Succulent Karoo or Fynbos) had little effect. The properties of *heuweltjie* vegetation in the Succulent Karoo are different from those in the Fynbos. The ecophysiology of *heuweltjie* plants in the Succulent Karoo differed substantially from that of interpatch plants with differences in stomatal conductance and leaf nutrient properties. Leaf quality of *heuweltjie* plants is high and with the higher litter content, the repercussions for ecosystem processes could be great. The growth of *heuweltjie* vegetation in the Succulent Karoo is constrained by the availability of water. For the interpatch plants, nutrients are probably the most limiting factors. The addition of N to this vegetation improves water relations, including xylem water potentials and stomatal conductance. The higher foliar N and higher $\delta^{15}\text{N}$ show

the high N supply in soils and is having an impact on N dynamics of this vegetation. There is potentially a bottom-up effect. Fynbos *heuweltjie* plants differ little from their surrounding interpatch plants in all the aspects that were studied. There was some indication of N stress in all Fynbos plants. It may be that strong competition with other species caused my study species to fail to take advantage of high soil N on the Fynbos *heuweltjies*. These differences in the properties and behaviour of *heuweltjies* vegetation between Succulent Karoo and Fynbos biomes need to be taken into account in the management and restoration of these hotspots.

4.7. Referencess

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Chapter 5: Synthesis and Conclusions

5.1. Introduction

Results presented on soil properties and processes, vegetation, and cryptogamic communities associated with *heuweltjies* suggest that they are hotspots for ecosystem function within Succulent Karoo and Fynbos biomes, and may further act as keystone resources in these relatively resource-poor environments. *Heuweltjies* were found to have higher pH and electrical conductivity (related to salinity) and elevated levels of N, C, and P in their soils than the soils of interpatch areas. *Heuweltjie* soils also had higher silt content and seem to have higher soil water content after rain (only determined at one of the Succulent Karoo sites). They are hotspots for CO₂ efflux, N mineralization, and phosphatase activity. Vegetation structure of *heuweltjies* differed from that of the interpatches only in the cover of the soil cryptogams. The ecophysiology of the *heuweltjie* plants differed from that of interpatch plants in the Succulent Karoo. Common species had lower stomatal conductance, higher water use efficiency, higher foliar N, higher $\delta^{15}\text{N}$ and lower C/N ratio on *heuweltjies*.

It was also discovered that there are differences between *heuweltjies* of the Succulent Karoo and Fynbos, especially in the magnitude of nutrient accumulation, and in the ecophysiology of plant biota. Along the rainfall gradient considered here, *heuweltjies* differ both in soil and vegetation properties. The effect of rainfall in influencing ecological functioning on and off the *heuweltjies* seems to be indirect through its role in leaching nutrients and salts from soils. At the specific sites chosen for this study, these leaching effects may have been enhanced at three sites, (two of which were in the Fynbos), where *heuweltjies* were situated on a slope. As a result, this synthesis will proceed by first discussing the overall findings separately for Fynbos and Succulent Karoo. It then goes further to consider what these results mean for knowledge regarding ecosystems processes in these biomes. Then, the significance of the findings for restoration, management, and global change are discussed. Lastly, recommendations are made for future research.

5.2. Succulent Karoo

The differences in soil properties and processes and vegetation structure and ecophysiological traits between *heuweltjies* and the interpatch area are unambiguous in the Succulent Karoo. This may be related to the eutrophic soils (Fey et al., 2010), commonly associated with semi-desert areas, and the effect of drought stress which occurs for long periods in this biome. Though productivity is generally low for the biome (Dean and Milton, 1999), plant material which is high in N (Chapter four), and phosphorus (Milton, 1993) is collected by termites, digested, and the excreta (frass) produced enriches the soil of the *heuweltjies* in the Succulent Karoo. While some organic matter collected remains undigested, the net result is of a patch within the landscape that is enriched in C, N, and phosphorus (in the topsoil). This enrichment is perpetuated in the Succulent Karoo by the continuing activity of the termites (more frass), whereas *heuweltjies* in the Fynbos generally showed less activity (less frass).

Soil processes are affected disproportionately on *heuweltjies*. Potential N mineralization and levels of CO₂ efflux associated with *heuweltjie* soils (indicating higher activity of microbes) are higher. Though these two processes were carried out under controlled conditions in the laboratory, the results are consistent with elevated N and C cycling on *heuweltjies* (and supported by higher $\delta^{15}\text{N}$ values and more labile C in the form of frass). They are also consistent with the contention that *heuweltjies* in the Succulent Karoo more closely resemble the hotspots for biogeochemical processes as envisaged by McClain et al., (2003). The punctuation of dry periods by rainfall is likely to increase biogeochemical activity, and more so on the *heuweltjies* (hot moments, McClain et al., 2003).

Topsoil properties in the Succulent Karoo are heterogeneous and *heuweltjies* contribute significantly to this patchiness (Herpel, 2008, see also Chapter three of this study). The high animal activity, specifically pedoturbation on *heuweltjies* leads to a finer soil texture; this, along with increased soil salinity may well play an important role in structuring plant and animal communities within these patches. My study shows this structuring effect as salinity (EC) of surface soils was negatively correlated with the cover of mosses and shrubs (Fig 5.1 a and b). The combined effect of higher soil organic matter and finer soil texture may also affect ecohydrology of *heuweltjies*, as was found in this study where soil water content differed in space (on and off *heuweltjies*) and time (dry periods and rainstorms). Medinski et al., (2010) made a detailed study of the effect of soils on the distribution of important life forms in the arid and semiarid regions of South Africa (Succulent Karoo) and also

showed that both soil electrical conductivity and texture play an important role. In the current study *heuweltjie* soils had higher silt content than surrounding interpatch soils. This accumulation of fine material may encourage faster rates of N mineralization, thus increasing the bioavailability of N to the vegetation (see Chapter three). This effect is probably more apparent following a rainstorm when the soil water content of *heuweltjies* reaches its peak. The N availability in soils then affects the growth and productivity of the vegetation including an increase in the foliar N content (Fig 5.2)

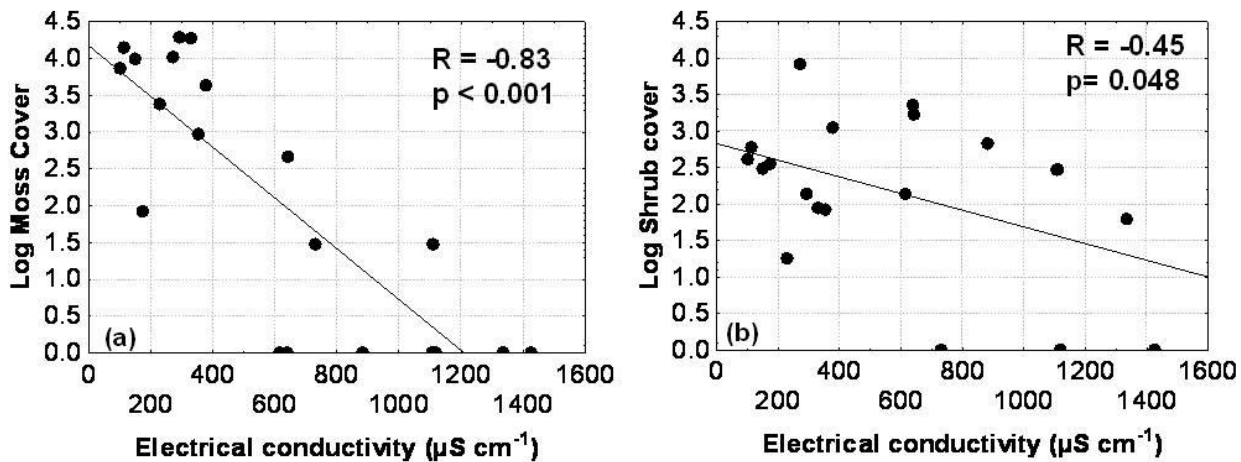


Fig 5.1. Relationship between soil electrical conductivity and cover of mosses (a) and shrubs (b), on *heuweltjies* in Succulent Karoo.

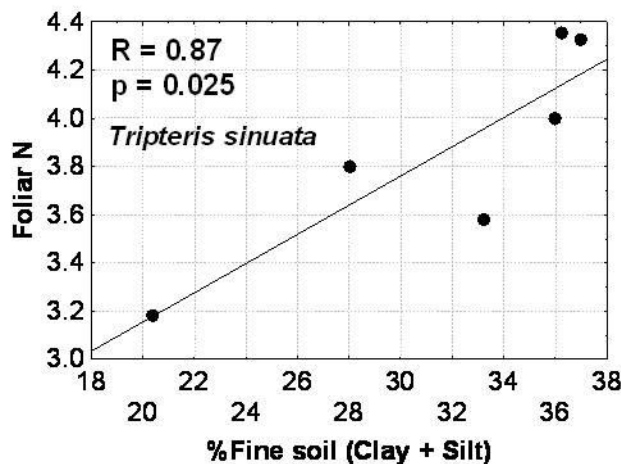


Fig 5.2. Describes the relationship between fine soil content and the foliar N content of *Tripteris sinuata* plants growing on *heuweltjies* in Succulent Karoo.

The cover of succulents was found to be higher on *heuweltjies* of the Succulent Karoo compared to the interpatch areas (see Chapter four of this study). This may be because succulents are able to withstand both the saline conditions and long-term low water content of *heuweltjie* soils (Ogburn and Edwards,

2010). Previous studies in the Succulent Karoo have shown clear dominance by annuals and drought deciduous species on the *heuweltjies* and state that disturbance and higher nutrient requirements are the reasons for this trend (Knight et al., 1989; Midgley and Musil; 1990; Esler and Cowling, 1995). However, it appears from the results of this study that drought avoidance and drought tolerance is part of the explanation. Water is the main resource limiting plant productivity on the *heuweltjies*. In Chapter four, *heuweltjie* plants were shown to have higher intrinsic water use efficiency (higher $\delta^{13}\text{C}$) and lower stomatal conductance compared to surrounding vegetation. The stronger competition for water will then favour drought-avoiders such as annuals and drought-deciduous species as observed by aforementioned studies.

5.3. Fynbos

The Fynbos sites have higher rainfall than the Succulent Karoo sites, a fact that has implications for soil nutrients. Fynbos *heuweltjies* had relatively nutrient poor soils (Chapter three; see also Fey et al., 2010) with significantly lower C contents, P concentrations and salinity levels compared to Succulent Karoo *heuweltjies*. The lower P concentrations of Fynbos *heuweltjie* soils compared to those of the Succulent Karoo and to those of the Fynbos interpatches follow the general trend of extremely low P in Fynbos soils. The steeper slopes of the sites selected in the Fynbos may have also contributed, as over time P levels may have been lowered by both vertical and lateral movement of water in the soils.

In general, the potential for N mineralization was lower for these sites compared to the Succulent Karoo; this is clear from both the N mineralization results and the foliar $\delta^{15}\text{N}$ results obtained. Although this study measured N mineralization under ideal conditions in the laboratory and not *in situ* conditions, this difference is nevertheless significant. However, results presented here show that although potentially higher on the *heuweltjies*, N mineralization in this biome did not appear to result in higher foliar N in the vegetation as is the case with the Succulent Karoo *heuweltjies*, where the study species was concerned. This may be related to competitive effects for scarce resources of individual plants on *heuweltjies* in the Fynbos. At least one plant species is present (*P. incana*) that is invasive in other South African biomes, suggesting an enhanced competitive ability, and the ability to outcompete other biota such as mosses when N levels are low. To support this contention, the C/N ratio of the leaves in the Fynbos was generally found to be strikingly higher than in the Succulent Karoo, although more results showing the differences in ecological stoichiometry of plants in these biomes are needed.

Inter- and intra-specific competition on the *heuweltjies* can also go some way in explaining the results for soil P that were discussed earlier. There is evidence of low uptake of both ammonium and nitrate by some species in the Fynbos (Stock and Lewis, 1984). These types of plants may be disadvantaged on the *heuweltjies* and are outcompeted by more vigorous growers. The turnover of N, as denoted by the $\delta^{15}\text{N}$ of the vegetation was low for the study species (*P. paniculata*) suggesting that this species may be a slow growing, nutrient efficient species (see Chapter four of this study). It is also possible that since nutrients are so limiting, the plants of this biome invest energy into reabsorbing nutrients from leaves prior to senescence (especially such conditions of strong interspecific competition and low resource availability), thus resulting in lower litter quality both on and off *heuweltjies*. *Pteronia paniculata* drops some of its leaves during dry periods, such as those prevailing during sampling.

In general, Fynbos plants had a lower water use efficiency than Succulent Karoo plants (inferred using $\delta^{13}\text{C}$), showing that water is less limiting in this biome. However, this was not reflected in a higher stomatal conductance and higher xylem water potential as one would have been expected; this may be due to the fact that these measurements were taken during a dry spell, as mentioned before. There was no difference in water use efficiency of *P. paniculata* between *heuweltjies* and interpatch areas, again showing that differences, this time in terms of ecohydrology, between *heuweltjies* and interpatch areas seem to be relatively minor. It is recommended that more studies be carried out to investigate ecophysiological attributes of *heuweltjies* and interpatch areas in the Fynbos, especially where common species, such as *P. paniculata* occurs.

5.4. Implications for ecosystem and landscape processes

Le Maitre et al., (2007) suggested that *heuweltjies* are patches where resources are conserved within the landscape of the Succulent Karoo. Results presented in Chapter three and four showed higher nutrient resources within topsoils and plants of *heuweltjies*, and supports the idea of resource conservation. The high soil process rates mean that nutrients are turned over faster than in the interpatches (also demonstrated by the higher foliar $\delta^{15}\text{N}$). The higher N content of leaves, in turn, enhances the quality of litter and leads to a positive feedback that maintains these hotspots within the Succulent Karoo biome. The low rainfall also minimizes the possibility of leaching. Following a rainstorm, water is absorbed and retained for a longer period on *heuweltjies* than the interpatches. The water is used conservatively by the vegetation (higher water use efficiency) which furthers the saving of

resources. Some nutrients are, however, exported from *heuweltjies*; the extensive use of *heuweltjie* plants by animals means that nutrients are transferred to other areas in the landscape (e.g. via dung deposition).

The model presented by le Maitre et al., (2007) is of less significance for the Fynbos biome. With the increase in rainfall in the Fynbos, drought stress is less of a factor and nutrients become more limiting. Here, nutrient cycling is only slightly enhanced over the interpatches; this may be due to vertical (and lateral) leaching of nutrients from topsoils in addition to competitive effects (explained above), which also diminish the differences between the *heuweltjies* and the non-*heuweltjie* areas. Fynbos is characterized by the slow decomposition because of low litter quality (high C/N ratio) and low litter production (Mitchell et al., 1986). Other processes such as N mineralization may be also slowed significantly as a result (Chapin et al., 2002). The C/N ratio of the *heuweltjie* vegetation was not shown to differ from that of interpatch plants in this study, although the litterfall on *heuweltjies* was significantly increased (or increased as result of deposition by termites). This is further evidence that nutrients are limiting on the *heuweltjies*, as it is in the interpatches. The vegetation of these *heuweltjies* will contribute fewer nutrients to the landscape than the Succulent Karoo. The overall impact of these *heuweltjies* on the hydrological processes of the Fynbos biome remains unclear.

5.5. Restoration and management

The Succulent Karoo is threatened by climate change, overgrazing, ostrich farming, mining and illegal collection of plant and animals. As a result of their high grazing quality, *heuweltjie* plants are the first to go following overgrazing (Esler et al., 2006). Even though literature has shown that simply resting the veld will improve plant diversity on *heuweltjies* in the Succulent Karoo, this process takes a long time (Rahlao et al., 2008) and might not be possible in cases of extreme overgrazing. In these extreme cases, *heuweltjie* vegetation communities might need to be reestablished. This study has highlighted some of the key biogeochemical and ecophysiological aspects that influence the growth and survival of *heuweltjie* plant communities. The contribution of *heuweltjies* to landscape processes was also shown and this emphasises the importance of restoring these mounds after degradation. The differences that were shown between Succulent Karoo and Fynbos *heuweltjie* plants will also have to be taken into consideration when considering reestablishment.

This study has shown that *heuweltjies* have higher bioavailability of plant nutrients including often-limiting N. It is possible that even under cultivation *heuweltjies* will retain higher availability of nutrients. If so, different agricultural practices might need to be applied in the case of *heuweltjies*. For example, though as the *heuweltjie* vegetation in the Fynbos is limited by nutrients, using nitrogenous fertilizer on these plants might not be necessary, or indeed, wanted, as higher productivity of, for example in *Vitis vinifera*, reduces wine quality (Shange et al., 2006). In the Succulent Karoo, it might be a disadvantage as it will lead to N saturation which will eventually lower the productivity of the vegetation as other nutrients become increasingly limiting (Gress et al., 2007).

Strip-mining can remove all soils to a depth of up to 30 m. Even though these soils are stored and eventually returned to their natural environment, natural pedo-heterogeneity associated with landscapes with *heuweltjies* is not recreated. The soils become homogenized (Prinsloo, 2005). This process removes all *heuweltjies*, possibly for good. *Heuweltjies* cover extensive areas of the Succulent Karoo and of the current protocols on restoration and rehabilitation of the biome few make mention of them (Beukes and Cowling, 2003; Anderson et al., 2004; Blignaut and Milton, 2005). Rehabilitation of land by land-use managers needs to consider the structure and function of *heuweltjies* and their role within the landscape (Botha et al., 2008).

The base-poor parent material of most Fynbos soils prevents the formation of *heuweltjies* in this biome except in the base-rich parent material of the Fynbos–Renosterveld vegetation type (Picker et al., 2007). Given that this is a smaller area compared to the Succulent Karoo the chances of them being completely removed (and lost) by human disturbance in the Fynbos are greater. Another major issue for Fynbos *heuweltjies* is the potential effect of alien plant invasions (Muhl, 2008). Especially concerning is the potential invasion of legumes on *heuweltjies*, for these plant can increase the soil N and C content; this has the potential to cause additional pressure on native *heuweltjie* plants that are poor competitors.

5.6. Recommendations for future studies

Soil disturbances by termites foraging on or small mammals constructing burrows on *heuweltjies*, especially in the Succulent Karoo, is an issue that needs to be addressed, for it could also influence the

results that were observed by this study. As this study has shown differences in the composition of soil cryptogams between *heuweltjies* and interpatches, it would be useful to study soil microbial biomass and diversity between the two microsites as baseline information for restoration. It may also be interesting to know what happens when *heuweltjies* are cultivated and genetic differences are removed within the plant community; how will the productivity of cultivars be affected by the presence of *heuweltjies*? And, will the ecophysiology of *heuweltjie* plants be the same or different from interpatch plants? Invasion by alien shrubs such as *Atriplex lindleyi* in the Karoo and, grasses and legumes in Fynbos could affect ecosystem processes and therefore this issue needs some attention. The impact of *heuweltjies* on the hydrological processes of the Fynbos biome is another issue that needs to be addressed, in order to fully appreciate the effects that *heuweltjies* have on the hydrology of the landscapes of this biome. Finally, ecologists need, together with land-use managers, devise a strategy whereby *heuweltjies* can be returned to the landscape following human destruction. For without this, the Succulent Karoo and Fynbos biomes can never truly be restored.

5.7. References

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Appendix A

Table A1: The water holding capacity , at 100%, for soil that were used in a soil respiration experiment. In all cases the t-test results represent comparison between *heuweltjies* and interpatches .

| | Tierberg Karoo Research Centre | | Worcester Veld Reserve | | Jonaskop | | Wiesenhof Game Reserve | | Overall | |
|----------|--------------------------------|--------------|------------------------|--------------|--------------------|--------------|------------------------|--------------|--------------------|--------------|
| | <i>Heuweltjies</i> | Interpatches | <i>Heuweltjies</i> | Interpatches | <i>Heuweltjies</i> | Interpatches | <i>Heuweltjies</i> | Interpatches | <i>Heuweltjies</i> | Interpatches |
| N | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 20 | 20 |
| Mean | 33.75 | 28.44 | 31.68 | 22.98 | 53.57 | 46.07 | 37.93 | 32.93 | 39.23 | 32.60 |
| SD | 3.34 | 2.78 | 8.58 | 5.91 | 9.36 | 3.83 | 5.80 | 3.49 | 11.00 | 9.55 |
| Median | 35.53 | 27.42 | 35.99 | 21.82 | 50.38 | 48.14 | 40.95 | 32.33 | 37.54 | 30.85 |
| Min | 29.73 | 26.52 | 18.52 | 15.82 | 45.99 | 69.49 | 30.30 | 29.62 | 18.52 | 15.82 |
| Max | 37.16 | 33.34 | 38.46 | 31.92 | 39.86 | 49.25 | 43.28 | 37.62 | 69.49 | 49.25 |
| Perc.25 | 30.60 | 27.12 | 27.50 | 20.82 | 48.15 | 44.93 | 33.19 | 29.78 | 31.90 | 26.82 |
| Perc. 75 | 35.71 | 27.78 | 37.92 | 24.52 | 53.85 | 48.15 | 41.95 | 35.30 | 44.63 | 28.74 |
| SE | 1.49 | 1.24 | 3.83 | 2.64 | 4.19 | 1.71 | 2.59 | 1.56 | 2.45 | 2.13 |
| <i>t</i> | 3.84 | | 1.36 | | 1.88 | | 1.64 | | 3.45 | |
| <i>p</i> | 0.018 | | 0.243 | | 0.133 | | 0.174 | | 0.002 | |