Vegetation and Ant Dynamics in the Southern Karoo

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ABSTRACT

The aim of this thesis was to describe the structure and dynamics of ant and plant communities in the southern Karoo and to assess mechanisms of species coexistence in ant and plant communities. The role of species interactions in structuring natural communities was emphasised.

Diversity indices were used to determine the importance of habitat in maintaining ant species diversity. Ant species diversity was not predicted by measurements of plant species diversity or vegetation structural diversity. Ant species richness was correlated with vegetation structural diversity but not with plant species diversity. Ant species appeared to respond to aspects of vegetation height. Although vegetation complexity influences ant species richness, competitive effects, particularly of dominant ant species, appear to suppress sub-ordinate ant species influencing measures of richness and diversity.

Aggressive dominant ant species determine the distribution and abundance of sub-ordinate ant species. Interference competition for space was prevalent between dominant ant species and competitive success was a function of vegetation. It was not clear whether ants respond directly to physical conditions created by vegetation which then influences foraging activity or, alternatively, whether ants respond to productivity gradients which are affected by vegetation.

Understanding vegetation dynamics is critical to interpreting patterns of ant species distribution and abundance. A patchy habitat disrupts the competitive dominance of aggressive dominant species, removing the potential towards habitat monopolisation, and therefore maintaining ant species diversity. In the *Portulacaria afra* rangeland, *Pheidole* sp. 2 was superior in well-shaded microhabitats but *Messor capensis* nested successfully under woody shrubs and several ant species (*Tetramorium peringueyi*, *T. quadrispinosum*, *Monomorium alamarum*, *Ocymyrmex barbiger*) persisted on bare nutrient-rich patches. Rangeland dominated by grass would favour *Pheidole* sp. 2 at the expense of other ant species which would be unable to establish successfully.

There is no evidence supporting the notion that ant communities are at equilibrium. Rather, dominance hierarchies lead to the replacement of species over vegetation gradients with the tendency towards the aggressive acquisition and monopolisation of space. The coexistence of dominant ant species at study sites in the southern Karoo was a combination of territorial strategy and colonisation ability. In the *P. afra* rangeland most ant species escaped the severe competitive effect of *Pheidole* sp. 2 by persisting as fugitives on bare areas of local

disturbance where *Pheidole* sp. 2 was less successful. At Tierberg, competitively inferior ant species with a decentralised territorial system coexisted with competitively superior ant species in an unstable equilibrium by pre-empting newly available space through the lateral expansion of territories. Competitively superior species, however, replace the inferior competitor (yet, superior coloniser) in time.

Plant succession in the *Portulacaria afra* rangeland follows a deterministic pattern of cyclical replacement. No single mechanism adequately explains the coexistence of all plant species in this community. Nurse-plant effects were important for the establishment of *P. afra* and later-successional trees below woody shrubs and *P. afra* respectively. Soil moisture and nutrient levels below nurse plants were favourable for the successful establishment of seedlings but nurse plants also disrupt the inhibitory effect of grass on seedlings and young plants. Linked to the facilitative process is the directed dispersal of seeds by biotic vectors. Seed dispersal by ants and birds moves propagules away from the harsh competitive environment of established adult plants (particularly grass) to safe establishment sites below nurse plants. Complementary root systems of seedlings and nurse plants may facilitate the establishment of young plants but ultimately competition will reduce nurse plant vigour leading inevitably to the death of the nurse plant. At least two plant species (*Lycium cinereum* and *Psilocaulon absimile*) persist in the *P. afra* rangeland as fugitives on areas of local disturbance. The relatively cool and moist environment below *P. afra* clumps supports a variety of detritivorous taxa that enrich the soil. Once the *P. afra* clump collapses and dies, bare nutrient rich patches that favour the establishment of *L. cinereum* and *P. absimile*, ahead of the competitively superior grass component, remain. However, the replacement of the fugitive plant species by grass is inevitable as the soil nutrient levels decline.

The competitive superiority of grass controls the dynamics of the *P. afra* rangeland system. Disruption of the inhibitory effect of grasses by elevated nutrient levels (e.g. detritivore activity, ant nests) permits plant species to establish that would otherwise be unable to in the absence of disturbance. Degradation of the grass component by overgrazing at the *P. afra* rangeland site has the same effect as disturbance by soil-nutrient enrichment and results in an increase in plant species diversity. All stages of the cyclical process would be relatively uncommon in a grass dominated system because of the inability of plants to establish successfully in grass.

Strong feedback links exist between the ant and plant communities studied. Habitat patchiness maintains ant species diversity by disrupting dominance hierarchies. Ants maintain plant species diversity by moving seeds out of competitively harsh microhabitats into safe sites (often below nurse plants) for establishment. Soil nutrient enrichment (ant nests and various detritivore taxa) create disturbances which also facilitates plant establishment. Overgrazing by domestic stock causes the replacement of palatable by unpalatable plant species. Unpalatable plant species, released of suppressive effects, develop into a monospecific stand that inhibits the further establishment of seedlings. Loss of habitat patchiness results in habitat monopolisation by one (or two) dominant ant species. Habitat degradation therefore severs the complex feedback links between the plant community and the important invertebrate component (dispersal agents and detritivores) which disrupts the dynamic processes driving the system.

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DISCLAIMER

Unless acknowledgements are made to the contrary, the work in this thesis is my own. It has not been submitted to any other university.

HR Adie

H. R. Adie

Chapter 1: Introduction

1.1 MOTIVATION FOR THESIS

This dissertation examines the structure and dynamics of ant and plant communities in the semi-arid southern Karoo, South Africa. The motivation for this research was two-fold. Firstly, the Karoo region supports a productive small stock industry that depends on natural rangeland as its primary resource (Cowling 1986). Inappropriate stock management has resulted in severe rangeland deterioration such that the system is presently operating substantially below its former levels of production (Dean and Macdonald 1994). Ultimately, any rangeland research performed in this semi-arid region must address this problem of decreasing productivity. With this background, my interest and emphasis throughout the present study was to develop a theoretical understanding of ant and plant community dynamics. The research reported here was directed towards answering the questions "What mechanism permits the coexistence of ant species and what maintains plant species diversity in the southern Karoo?".

Existing conceptual models of Karoo vegetation dynamics treat the Karoo as two distinct systems; the winter rainfall region in the west and the summer rainfall region to the east (Milton and Hoffman 1994). The importance of grass to vegetation dynamics has been ignored or de-emphasised in rangeland models despite claims that the Karoo was a perennial grassland prior to the colonial introduction of domestic stock (Acocks 1953, Roux and Vorster 1983). The situation has not been improved by recent studies addressing Karoo rangeland problems (e.g. Yeaton and Esler 1990, Milton 1992, Esler 1993, Stokes 1994) because these studies have been done in the western shrub-dominated regions where grass is rare or non-existent. The transition from the winter to summer rainfall region is not abrupt and the complex east-west moisture gradient incorporating the Karoo region is gradual, covering an extensive area. Even if the extremes of this east-west gradient were dominated respectively by grass and shrubs, there is a broad transitional zone of interaction between these two plant components. I investigate plant community structure and dynamics in a grass-dominated system in the southern Karoo and speculate on pre-degradation environments in the region.

Ecological studies of ants in South Africa have concentrated on ant-plant interactions (Bond and Slingsby 1983, 1984, Slingsby and Bond 1985, Yeaton and Bond 1991, Dean and Yeaton 1992, 1993) and studies of ant community structure have been neglected. Elsewhere, ant community structure has been investigated in a variety of habitats (e.g. Room 1971, Majer

1976, Greenslade and Greenslade 1977, Andersen 1986*a*, 1992, Savolainen and Vepsäläinen 1988, Bestelmeyer and Wiens 1996). In these studies, ants were frequently sampled over some type of vegetation gradient but, in every case, the ants remain the focus of the research and seldom do the researchers have an explicit grasp of vegetation dynamics and its influence on ant community structure. I investigate ant community structure and the problem of ant species coexistence in the southern Karoo with an *a priori* understanding of vegetation structure and dynamics.

Disagreement over what constitutes a community and the definition of community structure has led to confusion among ecologists (Roughgarden and Diamond 1986). In this dissertation, I adopt Roughgarden and Diamond's (1986) concept of "limited membership" as evidence of community structure. I refer to an ecological community as a set of species about which an interesting question can be posed. Scale, too, has been a source of misunderstanding in the study of communities (Schluter and Ricklefs 1993, Bengtsson et al. 1994). In this research, I study how local processes, such as species interactions and dispersal patterns, influence the number of coexisting species. However, I use this understanding of local community dynamics, and the fact that the study was done at several sites of varying habitat over a broad geographical region, to speculate on regional patterns of plant species distribution in space and time.

1.2 COMMUNITY STRUCTURE AND SPECIES COEXISTENCE

1.2.1 Plant community structure

Few doubt the importance of competition in structuring plant communities (Goldberg and Barton 1992, Gurevitch et al. 1992, Bengtsson et al. 1994) but there is less consensus on the mechanisms permitting the local coexistence of species. One way plants overcome strong competitive effects to establish, is by using open spaces, created by disturbances, in which the influence of competitively dominant species is reduced or removed (Grubb 1977). The cause of disturbance and the scale at which it operates varies considerably (Pickett and White 1985). Plants, too, at the scale of the individual, can be considered as small-scale disturbances by altering local physical conditions or by disrupting the competitive superiority of dominant plant species. These positive interactions, or facilitation, lead to species coexistence and are important when considering plant community organisation and dynamics (Bengtsson et al. 1994, Bertness and Callaway 1994).

Nurse-plant effects, where neighbours modify the physical and/or biotic conditions, are common in harsh environments (Bertness and Callaway 1994) but they can also be expected in habitats where plant establishment is suppressed by competitively dominant species (e.g. in grasslands where the grass component obstructs the establishment of woody shrubs or trees). Nurse-plant effects initiate succession by facilitating the establishment of plant species, but frequently the facilitator is competitively displaced by the younger plant resulting in a predictable sequential replacement of species. This process has prompted the concept of cyclical succession (Yeaton 1978) and is well documented in arid and semi-arid regions (e.g. Yeaton 1978, McAuliffe 1988, Yeaton 1990, Yeaton and Esler 1990, Soriano et al. 1994).

Local population dynamics and species coexistence frequently rely on the effective dispersal of propagules (Hastings and Harrison 1994, Tilman 1994). What is the relative importance of dispersal to the success of nurse-plant effects? Is the spatial distribution of seeds with respect to nurse plants random, or are seeds moved to the effective nurse plant by some secondary biotic vector? The deterministic, cyclical processes described above seem to imply a more directed dispersal mechanism. In habitats where the effectiveness of primary seed dispersal mechanisms (e.g. wind, water) is reduced because of some structural feature of the vegetation (e.g. wind-dispersed seeds are trapped by grass, a competitively hostile microenvironment), secondary seed dispersal by biotic vectors might contribute to the effectiveness of facilitation. Biotic vectors would remove the seed from a competitively stressful microenvironment and place it in the vicinity of nurse-plants. Ants are effective secondary dispersers of seed in forests (Byrne and Levey 1993, Kaspari 1993) and their nests also provide high nutrient microenvironments that enhance seed germination and the establishment of plants (Beattie and Culver 1983, Dean and Yeaton 1992). In the Cape fynbos, ants move seeds of myrmecochorous plants away from the competitive influence of adult shrubs to nests that are positioned in open areas where young seedlings establish successfully (Yeaton and Bond 1991). In the northern Chihuahuan Desert, birds and rodents disperse the seed of *Opuntia leptocaulis* to sites below the canopy of *Larrea tridentata* where they establish (Yeaton 1978). Are these isolated incidents, or is there evidence that facilitation is closely coupled with directed secondary dispersal?

1.2.2 Ant community structure

Competition is considered the hallmark of ant ecology and has a pervasive influence on the organisation of ant communities (Hölldobler and Wilson 1990). Aggressive interference competition results in dominance hierarchies among ant species, the outcome of which is a well structured and predictable organisation of ant communities (e.g. Wilson 1971, Greenslade 1978, Savolainen and Vepsäläinen 1988, Andersen 1990, 1995). The common theme uniting these descriptive classifications is that ant communities are dominated by aggressive species that monopolise space by overt aggressive behaviour and influence the distribution and abundance of most subordinate ant species.

In spite of the widespread influence of interference competition on the organisation of ant communities, many community level studies implicitly assume that ant communities are at equilibrium and that niche differentiation among species, competing for a limited resource, accounts for their coexistence (e.g. Savolainen and Vepsäläinen 1988, Hölldobler and Wilson 1990, MacKay 1991). Partitioning along the following niche axes are frequently cited mechanisms accounting for the coexistence of ant species: daily and seasonal activity (Whitford and Ettershank 1975, Hansen 1978, Briese and Macauley 1980, Vepsäläinen and Savolainen 1990), habitat (Whitford et al. 1976, Greenslade and Greenslade 1977, Andersen 1986*b*), food resources (Davidson 1977*a*, Hansen 1978), foraging behaviour (Whitford et al. 1976, Davidson 1977*b*) and worker body size (Davidson 1977*a*, Vepsäläinen and Savolainen 1990).

Plant ecologists, dissatisfied with classical competition theory, have sought alternative explanations of very diverse plant communities resulting in a plethora of new theories (reviews in Auerbach and Shmida 1987, Silvertown and Law 1987, Bengtsson et al. 1994). Are there valid reasons to consider alternative theories to explain ant species coexistence? Are we justified in viewing ant communities as equilibrium communities? Several observations lead me to propose an alternative approach to understanding the structure and dynamics of ant communities. Firstly, ant communities are remarkably similar to marine invertebrate communities of the intertidal zone. In both systems, space is limiting and aggressive interference competition between dominant species results in competitive exclusion and the monopolisation of space. The adult stage of component species is generally sessile but individuals have a high reproductive output with equally high rates of dispersal. In marine invertebrates of the intertidal zone, species coexistence is disturbance mediated. That is, an external disturbance creates space by removing competitively dominant species and permits the colonisation of species with superior dispersal ability (Sousa 1979, Paine and Levin 1981). Is there evidence that ant communities might function in a similar manner? The influence of temperature and humidity on the distribution and abundance of ant species is well known (Hölldobler and Wilson 1990). In addition, vegetation can change temperature and humidity on a local scale (Bertness and Callaway 1994). This implies that vegetation might be important in structuring ant communities and, by altering ant species competitive abilities, drive ant community dynamics. Yet, ant community studies continue to focus on the ant and neglect the influence of vegetation on ant species distribution and abundance.

1.3 OBJECTIVES

The aim of this thesis is to understand patterns of ant species distribution and abundance in semi-arid Karoo rangelands with particular emphasis on mechanisms of species coexistence. Early in this study, it was evident that patterns of ant species distribution and abundance were difficult to interpret without understanding the structure and dynamics of the vegetation. Consequently, my objectives were extended to include aspects of rangeland structure and dynamics. Specifically, the objectives of this study were:

1. to describe patterns of ant species distribution and abundance at a shrub-dominated and a grass-dominated site in the southern Karoo (Chapter 2);
2. to test the relationship between ant species diversity and habitat complexity and to assess the value of diversity indices in explaining ant species diversity (Chapter 3);
3. to assess the relative importance of abiotic and biotic factors in influencing ant community structure (Chapters 3 and 4);
4. to test the importance of competition (interspecific and intraspecific) in determining ant species distribution and abundance (Chapter 4);
5. to assess mechanisms of ant species coexistence (Chapter 4);
6. to develop a descriptive model explaining rangeland dynamics in space and time and to speculate on the nature of vegetation change along a complex moisture gradient (Chapter 5);
7. to assess plant coexistence mechanisms with particular emphasis on facilitation and disturbance caused by nutrient enrichment (Chapter 5); and
8. to determine the importance of seed dispersal by biotic vectors (principally ants) in maintaining plant species diversity (Chapter 5)

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Chapter 2: The Karoo, study areas and ant species studied

2.1 THE KAROO

The Karoo region is situated in the south-west of southern Africa. Classified as arid or semi-arid, this extensive region is roughly one-third (427 000 km^2) of the land area of South Africa (Cowling 1986). The central interior is dominated by a massive highland plateau which gives way to areas of lower elevation to the west and south (Werger 1986). The southern and south-western limits of the Karoo are bordered by numerous mountain ranges referred to collectively as the Cape fold mountains. In the west, the Karoo extends to the coast.

The climate is influenced by the mountain ranges to the south and the position of the region relative to the Indian Ocean, the major source of moisture to the sub-continent (Tyson 1986, Werger 1986). The Karoo is characterised by low rainfall, the timing and reliability of which varies considerably (Cowling 1986). In the west, rainfall is predictable and associated with cyclonic frontal systems that develop in winter (Schulze 1972). The mountain ranges of the folded belt are a major barrier to these frontal systems preventing them from penetrating the interior. Rain in the summer rainfall region is of convective origin. The average rainfall decreases and becomes more variable westwards towards the winter rainfall region (Schulze 1972, Tyson 1986). Temperatures in the Karoo are extreme with large daily and seasonal fluctuations (Venter et al. 1986).

Dwarf shrubs dominate the Karoo vegetation but the diversity in topography and climate has resulted in considerable variation in vegetation types in the region. On the basis of rainfall and plant life form, the Karoo has been divided into two biomes in South Africa (Rutherford and Westfall 1986). Firstly, the Succulent Karoo incorporates the winter rainfall region and supports a rich and structurally diverse succulent flora. Woody shrubs, particularly asteraceous types, predominate in the second region, the Nama-Karoo, an area included in the summer rainfall region (Werger 1978, Rutherford and Westfall 1986). Grass is not widespread in the Karoo, except after favourable rainfall, but becomes more prevalent eastwards in the Nama-Karoo where shrubland grades into the grassland of the eastern Cape and Freestate (Roux and Vorster 1983, White 1983).

At present, almost all (99%) of the Karoo is privately owned and supports a small stock industry, the success of which is contingent on the state of the natural rangeland (Cowling 1986, Rutherford and Westfall 1986, Milton et al. 1992). Like most arid areas, this extensive region has had a history of mismanagement. A steady decline in stocking rates over the last 150 years indicates that the region is currently operating well below its potential (Dean and Macdonald 1994). The state of Karoo vegetation, prior to the colonial introduction of domestic stock, is unclear but theories considering pre-degradation environments have evoked controversy (Hoffman 1995) with some regarding the Karoo as a perennial grassland (Acocks 1953, Roux and Vorster 1983).

2.2 STUDY AREAS

The southern limit of the Great Karoo is dominated by mountain ranges belonging to the Cape folded belt (Bristow 1985). Running east to west, the Swartberg and Baviaanskloof ranges are rain shadows to the region causing the climate to become progressively dryer to the north and west. Numerous minor belts, sometimes only rocky ridges, dissect the region to the north of these two ranges. Between these minor belts the landscape is gently sloping or flat and it is on these gentle gradients that the study areas were situated. The climate of this general region is characterised by extremes in temperature and variability in the timing and amount of rainfall (Cowling 1986).

Most of the field work was done on two commercial farms in this southern Karoo region. The ant community research was initiated on the farm Tierberg (33° 07′ S, 22° 15′ E), located 25 km north-east of Prince Albert in a shrub-dominated region. A second farm in the Jansenville district, a grassland area approximately 230 km to the east of Tierberg, was studied for comparative purposes. This farm, Hillside (33° 06′ S, 24° 31′ E), was situated 25 km south-west of Jansenville (Figure 2.1).

The average annual rainfall recorded at Prince Albert is 169 mm (92 years) and the range for the region is from 100 mm to 300 mm (Venter et al. 1986). Most of the yearly average is likely to fall from February to May and the region is regarded as a transition between the summer and winter rainfall regions (Milton et al. 1992). The mean annual maximum temperature at the nearest long-term recording station, Beaufort West (32° 18′ S, 22° 40′ E, 49 years), is 25.2°C and the mean annual minimum temperature is 10.3°C. The climate is extreme with average highest monthly temperatures exceeding 35°C from October to March and average lowest monthly temperatures dropping below freezing from June to September (Weather Bureau 1986).

Tierberg farm is situated at the transition between the Succulent Karoo, Nama-Karoo and Succulent Mountain Scrub (Spekboomveld) (Milton et al. 1992). The farm is separated into

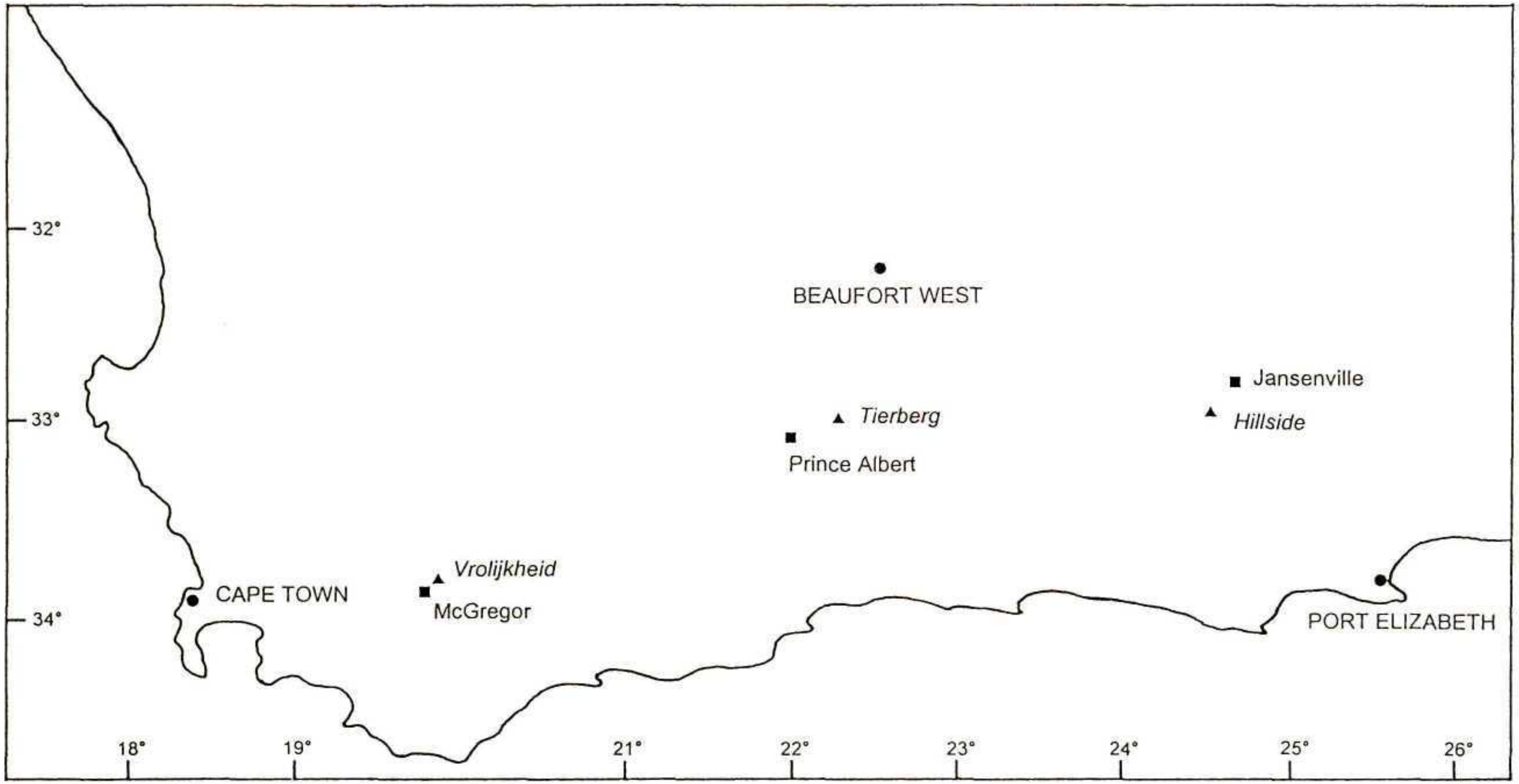

FIGURE 2.1: Map of the southern Karoo region showing towns and farms referred to in this thesis.

two distinct regions by a steep-sided rocky mountain belt (maximum altitude of 1124 m a.s.l.) which serves as a rain shadow, producing dryer conditions north of the belt. In this dissertation, I refer to areas north of the mountain belt as the Upper Tierberg rangeland and the lower altitude areas to the south as Lower Tierberg. The rangeland in both areas is shrub-dominated. Grass is non-existent and the ground between shrubs is bare. The major ant study area was located in the Upper Tierberg rangeland and all ant study sites were dispersed over a gently sloping south-facing hillside rising about 100 m in elevation over 6 km. On the plains, the vegetation is dominated by the succulent *Ruschia spinosa* Hartm. & Stüber and the woody shrub *Eriocephalus ericoides* (L. f.) Druce. Structurally, the vegetation is relatively homogeneous in appearance. Dissecting the plains are small drainage lines which, at lower elevations, are dominated by the woody shrub *Pteronia pallens* L. f.. *Pteronia pallens* is replaced by another woody shrub, *Galenia africana* L., in the drainage lines towards the top of the hillside. Later-successional tree species (e.g. *Grewia robusta* Burch., *Euclea undulata* Thunb., *Diospyros lycioides* Desf., *Maytenus polyacantha* (Sond.) Marais and *Rhus undulata* Jacq.) are distributed on the plains and in the drainage lines towards the top of the hillside. These tree species drop out on the plains at lower altitudes. Most of the ant experimental studies were done on, and in the vicinity of, an old abandoned airstrip (650 m × 40 m) situated at the foot of the gentle slope (± 850 m a.s.l.). Unlike the *Eriocephalus* dominated rangeland surrounding it, the airstrip is sparsely vegetated by an early successional asteraceous shrub, *Chrysocoma ciliata* L.

Relative plant species composition in the Lower Tierberg rangeland is distinct from the Upper rangeland. The Lower rangeland (± 780 m a.s.l.) is dominated by *P. pallens*, a woody shrub unpalatable to domestic stock and competitively dominant in the plant community. Succulent plants are more common in the Lower Tierberg rangeland with mat-forming species (*Malephora lutea* Schwant., *Brownanthus ciliatus* (Ait.) Schwant.) replacing *C. ciliata* as the important pioneer plant species. Later-successional trees are confined to the rocky mountain belts.

The unvarying rangeland vegetation described above is disrupted at regular intervals by nutrient-rich mounds, known locally as *heuweltjies*. *Heuweltjies* are approximately 1 m in height, up to 20 m in diameter, generally oval in shape and are understood to be the product of termite (*Microhodotermes viator* Latreille) activity (Lovegrove and Siegfried 1989, Milton and Dean 1990). The soil texture on *heuweltjies* is loamy compared with the hard compacted soil off mounds. They are very visible features of the landscape because the mound vegetation is dominated by succulent shrubs while the surrounding matrix is dominated by woody shrubs (Milton et al. 1992).

The Prince Albert district is no different from the rest of the Karoo in having a history of overgrazing by small livestock (Milton et al. 1992, Dean and Macdonald 1994). Tierberg farm is managed as a commercial enterprise with a stocking rate of Merino sheep, advocated by the Department of Agriculture and Water Supply, of 6 ha per small animal unit (Milton et al. 1992).

Rainfall increases eastwards and the mean annual rainfall at Jansenville (106 years) is 271 mm. Rain falls throughout the year although almost 60% of the yearly mean is expected from November to March. The average monthly maximum temperature at Jansenville (63 years) exceeds 35°C from September to April and exceeds 40°C from December to February. The average monthly minimum temperatures are less than 5°C from May to October and drop below freezing in June and July (Weather Bureau 1986).

The general vegetation type in the Jansenville district is Succulent Mountain Scrub or Spekboomveld (Acocks 1988). On Hillside farm, the vegetation is dominated by *Portulacaria afra* Jacq., an arborescent, succulent shrub known locally as spekboom. Hillside is unique because it has stands of *P. afra* growing on the plains, an unusual phenomenon in the arid parts of the southern Karoo. Later-successional trees, which are distributed on the mountain belts only further to the west, extend onto the plains at Hillside farm. *Portulacaria afra* forms distinct and discrete oval-shaped clumps of up 150 m^2 in area. Grass (mostly *Aristida* spp.) covers the ground between these clumps although a history of overgrazing has left large areas bare. Woody shrubs, particularly *Rhigozum obovatum* Burch., are common in these sparsely vegetated areas. Less common in the *P. afra* rangeland are slightly raised, oval-shaped mounds of variable size. These mounds, which will be referred to as nutrient-rich patches (hereafter NRP), show evidence of extensive mammal digging activity. Nutrient-rich patches are similar to *heuweltjies* in appearance, soil texture and plant species composition. Two plant species, *Lycium cinereum* Thunb. and *Psilocaulon absimile* N. E. Br., are common on NRP and rare elsewhere in the *P. afra* rangeland. *Portulacaria afra* is a highly palatable shrub and has been removed by grazing in extensive areas of the southern Karoo. The distribution of *P. afra* on the plains at Hillside farm is testimony to very conservative stocking rates in the past and at present Angora goats graze the rangeland infrequently.

Plant nomenclature follows Arnold and De Wet (1993) and Hartmann (1991). The term *mesemb* and *succulent* refer to succulent plant species belonging to the Mesembryanthemoideae and Ruschiodeae (Hartmann 1991).

2.3 DESCRIPTION OF ANT SPECIES

The following is a general description of the ant species encountered at Tierberg and Hillside during this study. This is an account of field observations and I make no attempt to quantify the points discussed or to discuss methodology. However, the patterns described here form the basis of the empirical work that follows in later chapters.

Following each species name is a measurement of body length and whether the species is monomorphic or polymorphic. Measurements refer to workers only and are taken from Arnold (1915-1924, 1926). Collection specimens of most species are housed in the South African Museum, Cape Town. The ant species described here are ordered in what I consider to be their level of importance in the ant community. The last few species were uncommon or known from a few observations only and are included for completeness only. I concentrated on distribution patterns of common ant species and how these corresponded to changes in vegetation or topography. Consequently, I emphasise the relative abundance of species along minor moisture gradients (e.g. from plains to drainage lines), large moisture gradients (e.g. from the Upper to Lower Tierberg rangeland) and major vegetation changes (e.g. shrub-dominated to grass-dominated systems). Many species present at the Tierberg study sites were also present in the *P. afra* rangeland. Observations of foraging and aggressive interactions between species were incidental.

Based on field observations of distribution, behaviour and feeding biology, I have assigned ant species to functional groups to simplify the ant community. I make no attempt to emulate classification systems used elsewhere (e.g. Greenslade 1978, Savolainen and Vepsäläinen 1988, Andersen 1990, 1995) because the classification has convenience value only.

2.3.1 Aggressive dominants

Aggressive dominant ant species are widespread and numerically dominant species. These ants are aggressive towards other ant species and appear to control the distribution and abundance of subordinate species.

Tetramorium peringueyi Arnold (4.4 - 4.6 mm, monomorphic). The most common ant species in the Upper rangeland at Tierberg, *T. peringueyi* is distributed in a variety of habitats ranging from bare or sparsely-vegetated areas to shrub-dominated rangeland. This species is mostly absent from drainage lines where it is replaced by *Anoplolepis steingroeveri*. *Tetramorium peringueyi* is uncommon on the plains of the Lower Tierberg rangeland. At Hillside, *T. peringueyi* is restricted to NRP and bare areas in the grassland. This species is strongly territorial and individuals moved experimentally to nest entrances of neighbouring colonies were attacked immediately. *Tetramorium peringueyi* has a single nest, positioned in the centre of its territory, with multiple entrances leading from it. The position of the nest with respect to vegetation varies according to habitat. On the airstrip, nests are frequently positioned on bare ground but in the adjacent *Eriocephalus* rangeland, nests are always positioned in the root systems of shrub clumps. Apart from overt aggression towards other ant species, *T. peringueyi* frequently allocates up to ten individuals to drop small pebbles down nest entrances of other species positioned in close proximity to their nests. An opportunistic forager, this species harvests seeds and scavenges dead and living animal matter. It is not active during the heat of the day.

Crematogaster melanogaster Emery (4.6 - 5.5 mm, monomorphic). *Crematogaster melanogaster* is common on the plains of the shrub-dominated rangeland of the Upper and Lower Tierberg but is absent from drainage lines. Unlike *T. peringueyi*, *C. melanogaster* is not distributed on open, bare ground and is absent from the *P. afra* rangeland at Hillside. This species has a territorial strategy that has been referred to as "nest decentralisation" (Hölldobler & Wilson 1990). Species with this territorial strategy have numerous "satellite" nests distributed throughout the territory. Nests of *C. melanogaster* are almost always positioned in the roots of woody shrubs and rarely on bare ground. Interference competition between *C. melanogaster* and *T. peringueyi* was observed on numerous occasions at one of the airstrip study sites. *Crematogaster melanogaster* becomes active earlier than *T. peringueyi* and workers of the former species surround nest entrances of the latter attacking them when they attempt to leave the nest. However, when *T. peringueyi* nests are located in the root systems of shrub clumps in the *Eriocephalus* rangeland, nests of *C. melanogaster* are rarely found in the vicinity of the *T. peringueyi* nest and consequently there is very little interaction between the two species. Although opportunistic on dead and living animal matter, *C. melanogaster* probably specialises on tending scale insects. The species forms semi-permanent trunk trails connecting "satellite" nests. *Crematogaster melanogaster* does not tolerate full sunlight and foraging activity declines as temperatures rise. This species is also nocturnal.

Anoplolepis steingroeveri Forel (2.7 - 7.0 mm, polymorphic). Unlike the previous two species, which are common on the plains, this species is confined to drainage lines and minor washes in the Upper Tierberg rangeland. This species has a similar distribution in the Lower rangeland but it is absent from the *P. afra* rangeland at Hillside. *Anoplolepis steingroeveri* has a territorial system similar to that described above for *C. melanogaster*. "Satellite" nests are almost always positioned in the root systems of plants. Probably the most aggressive ant encountered during this study, *A. steingroeveri* rarely coexists with either *C. melanogaster* or *T. peringueyi*. However, this aggressive behaviour does not extend to smaller ant species whose nests were frequently recorded in close proximity to those of *A. steingroeveri*. *Anoplolepis steingroeveri* is an extreme opportunist. It is highly predaceous but will also scavenge dead insects and tend scale insects. The species recruits rapidly and in large numbers to food sources and several individuals will co-operate in moving large prey items back to nests. Unlike most other ant species, *A. steingroeveri* is active over a wide range of temperatures.

Pheidole sp. 2 (2.5 - 5.0 mm, polymorphic). *Pheidole* sp. 2 is an uncommon species in the Upper rangeland where it is distributed in washes, often coexisting with *A. steingroeveri*. Overt aggression between the two species is frequent. *Pheidole* sp. 2 is rare on the plains of the Upper rangeland but common on the plains of the Lower rangeland where it coexists with *C. melanogaster*. However, superior numbers and the speed of recruitment of *Pheidole* sp. 2 overwhelmed *C. melanogaster* at fish baiting stations. *Pheidole* sp. 2 is the dominant ant species in the *P. afra* rangeland where its nests are most common in dense grass and below *P. afra* clumps. *Pheidole* sp. 2 has a decentralised territorial system and nests are usually positioned in well-shaded sites. Foragers of this species recruit rapidly and in high numbers to food sources. The species is aggressive towards other ant species and dominates food sources by numbers. *Pheidole* sp. 2 is granivorous, but like most other ant species in the southern Karoo, the species is opportunistic and scavenges both dead and living material. This species does not tolerate high temperatures and, of all the ant species encountered during this study, this species is the first to disappear underground as temperatures increase. Like *C. melanogaster*, it is also nocturnal.

2.3.2 Seed harvesters

These are ant species that harvest seeds when available but, like most ants species, they will scavenge animal material when the opportunity arises. These species are less common than, and subordinate to, the aggressive dominant species.

Messor capensis Mayr (6.0 - 11.0 mm, polymorphic). This species was studied on Tierberg before (Dean and Yeaton 1992, 1993*a*, 1993*b*, Milton 1992). A common species, *M.*

capensis is widely distributed on Tierberg and nests were located in most habitats except on the sparsely vegetated airstrip. Compared with the Tierberg study sites, nest density of *M. capensis* is greater in the *P. afra* rangeland. This species constructs large nest mounds (can exceed 2 m in length) that are almost always associated with a woody shrub species in the *P. afra* rangeland. *Messor capensis* is not an aggressive species and is subordinate to the aggressive dominant species at baiting stations. Typically, *M. capensis* is a specialist seed forager that forms long trunk trails leading to clumped sources of seed. This species does not tolerate high temperatures and forages in the early morning, later afternoon and night.

Pheidole sp. 1 (2.8 - 5.5 mm, polymorphic). This species is distributed on the sparsely vegetated airstrip in the Upper Tierberg rangeland where it is uncommon and subordinate to *T. peringueyi*. *Pheidole* sp. 1 is rare in the shrub-dominated *Eriocephalus* rangeland and was not recorded from the Lower Tierberg rangeland or the *P. afra* rangeland. Unlike *Pheidole* sp. 2, *Pheidole* sp. 1 has a single nest positioned in the centre of its territory. Nests are not associated with shrubs. In terms of general biology, this species is very similar to *Pheidole* sp. 2. Recruitment to food sources is rapid and by many individuals. *Pheidole* sp. 1 does not form trunk trails unless abundant resources are located. Although granivorous, it also scavenges dead and living animal material. *Pheidole* sp. 1 does not tolerate high temperatures and tends to be crepuscular and nocturnal in activity.

Monomorium havilandi Forel (2.5 mm, monomorphic). *Monomorium havilandi* is very common on the airstrip and, although less common, is also present in the Upper rangeland. This species is rare at Hillside where only one nest was found on a NRP in a degraded region of the *P. afra* rangeland. *Monomorium havilandi* has a single nest situated in the centre of its territory. Nests are always positioned in the open, away from vegetation. I regard this species as the most important harvester of mesemb seeds. Excavated nests yielded enormous quantities of mesemb seeds cached in chambers within 7 mm of the soil surface. *Monomorium havilandi* forms trunk trails to abundant food sources. Like other *Monomorium* species, this species tolerates higher temperatures than *T. peringueyi* and the *Pheidole* species.

Monomorium sp.-_*salomonis*-group (2.5 - 3.5 mm, monomorphic). This species will be referred to as ***M. salomonis*** in the text. *Monomorium salomonis* is common in the *Eriocephalus* rangeland and less common in the open habitat of the airstrip. This species was not recorded in the *P. afra* rangeland. Its single, centrally positioned nest was often located below the canopy of a shrub. The nest entrance of *M. salomonis* is recognised by a small, circular mound frequently decorated with minute plant parts. Like most of the other

Monomorium species, little is known of its feeding behaviour but it was observed harvesting mesemb seeds. This species is active over a temperature range similar to that of *M. havilandi*.

Monomorium macrops Arnold (1.5 mm, monomorphic). *Monomorium macrops* is a minute ant species recorded infrequently from the Upper and Lower rangeland at Tierberg. On the few occasions that nests of this species were found, they were near baiting stations indicating that most nests of this species probably went unnoticed. This species was observed moving the tiny seeds of the succulent *Ruschia dolomitica* (Dinter) Dinter & Schwant.

Monomorium alamarum Bolton (2.0 mm, monomorphic). Another tiny species that was only recorded from the *P. afra* rangeland. Nests were found by chance because this species never recruited to fish baiting stations. It was frequently observed foraging on NRP (nests were mostly found on NRP) where it harvested seeds of the mesemb *Psilocaulon absimile*.

2.3.3 Scavengers

These species are active at temperatures that just overlap with the upper range of the aggressive dominant species but they are unable to tolerate the extreme temperatures at which the thermophilic species are active (see below). These are aggressive species that were frequently observed preying on ants belonging to the aggressive dominant group. They scavenge dead and living material and are not known to harvest seeds.

Tetramorium quadrispinosum Emery (3.3 mm, monomorphic). This species is common in the *P. afra* rangeland where its nests are located in a range of habitats from dense grass to bare NRP. Nests are most common on the sparsely vegetated NRP. *Tetramorium quadrispinosum* is rare at Tierberg where only one nest was found in the root system of the shrub *Drosanthemum montaguense* L. Bol. in the Upper rangeland. This species has a single nest positioned in the centre of its territory. Although subordinate to both *T. peringueyi* and *Pheidole* spp. at the lower extreme of its temperature range, *T. quadrispinosum* preys upon both these species (even the *Pheidole* majors) at higher temperatures.

Monomorium australe Emery (3.3 - 3.8 mm, monomorphic). This is a widespread and variable species. *Monomorium australe* is particularly common on the airstrip at Tierberg and less common in the rangeland of the Upper and Lower Tierberg. It is a very aggressive species that recruits in such abundance to fish baiting stations that no other species is able to approach the bait. Few observations were recorded of *M. australe* away from baiting stations. This species was observed attacking and moving individuals of *Pheidole* sp. 2 back to its nest and dead individuals of *T. peringueyi* and *C. melanogaster* were recorded from the nest entrance of this species. This, and similar observations from the *P. afra* rangeland, suggest that the scavengers prey on aggressive dominants at the upper range of temperature tolerance of the dominant species. In the *P. afra* rangeland, nests of this species were only recorded in open, bare areas on NRP. It was observed carrying workers of *Pheidole* sp. 2 back to its nest during that period of overlap in activity when the aggressive dominant species are heat stressed.

2.3.4 Specialists

These are ant species with specialised foraging behaviours or that specialise on a particular food resource. The specialists are less common and submissive to the aggressive dominant species.

Ocymyrmex barbiger Emery (6.5 mm, monomorphic). *Ocymyrmex barbiger* is a common species at Tierberg (Upper and Lower rangeland) and the *P. afra* rangeland at Hillside. At Tierberg, nests of *O. barbiger* are distributed throughout the shrub-dominated rangeland but they are particularly common on *heuweltjies*. At the *P. afra* rangeland this species is confined almost exclusively to NRP and sparsely vegetated areas. Apart from bare ground, the silty texture of the soil of NRP and *heuweltjies* appears to be favoured as nest sites for *O. barbiger*. Nests are recognised by a volcano-shaped mound surrounding the entrance hole. *Ocymyrmex barbiger* is a thermophilic species that is active during the extreme heat of the day when most other ant species have disappeared underground. A solitary forager, the species preys on heat-stressed insects but was observed carrying the red fruits of *Lycium oxycarpum*, *L. cinereum* and *Atriplex semibaccata* R. Br. back to their nests. *Ocymyrmex barbiger* scavenges fish from baiting stations but is submissive and avoids contact with other ant species.

Ophthalmopone hottentota Emery (10.0 - 11.0 mm, monomorphic). A predator specialising on termites, the feeding biology of this species has been studied at Tierberg (Dean 1989). *Ophthalmopone hottentota* is common on Tierberg in the *Eriocephalus* rangeland and the airstrip. This species was not recorded from the *P. afra* rangeland. *Tetramorium peringueyi* was observed dropping small pebbles down the nest entrance of this species. Like most of the other specialist species, *O. hottentota* appeared to avoid overt confrontation with other ant species. A solitary forager and one of the few ant species that was never observed at fish baiting stations, it was active for most of the day.

Camponotus fulvopilosus De Geer (10.0 - 16.0 mm, polymorphic). *Camponotus fulvopilosus* is common in the shrub-dominated rangeland (Upper and Lower Tierberg) where nests are positioned in the root systems of shrubs. It was not recorded on the sparsely vegetated airstrip. This species is common in the *P. afra* rangeland. Although *C. fulvopilosus* behaves aggressively in the vicinity of its nest, it is submissive to, and avoids contact with, other ant species at baiting stations. *Tetramorium peringueyi* was observed dropping small pebbles down the nest entrance of this species at the *P. afra* rangeland. Although a solitary forager, this species does form small groups of five or six individuals that might be recruiting parties. *Camponotus fulvopilosus* is nectarivorous and was observed active at all times of the day.

Anoplolepis cf. *trimeni* Forel (2.5 - 3.2 mm, monomorphic). *Anoplolepis* cf. *trimeni* is very common at Tierberg where it is known from all habitats. Although nests of this species were found on NRP in the *P. afra* rangeland, *A.* cf. *trimeni* is not common in this habitat. Like *O. barbiger*, *A.* cf. *trimeni* is a thermophilic species and nests are always positioned in open areas away from vegetation. It is not clear what this species feeds on but observations of individuals on flowerheads suggest it harvests nectar or pollen. Like most other ant species, it was observed attacking and removing termites from termite nest entrances.

2.3.5 Rare or uncommon ant species

Acantholepis capensis Mayr (2.8 - 3.3 mm, monomorphic). Nests of this species are frequently located below rocks in the Lower Tierberg rangeland. *Acantholepis capensis* is uncommon in the Upper Tierberg rangeland and was not recorded from the *P. afra* rangeland. This is a nectarivorous species.

Aenictus rotundatus Mayr (2.3 - 3.8 mm, monomorphic). A nomadic species that was recorded once on Tierberg when a colony was attacked by *M. havilandi*. *Aenictus rotundatus* is very common in the *P. afra* rangeland where trails always lead into *P. afra* clumps.

Anochetus levaillanti Emery (5.2 - 6.0 mm, monomorphic). This is a specialist predator on, among other insects, fishmoths. It is uncommon on Tierberg where only two nests were located. *Anochetus levaillanti* is fairly common in the *P. afra* rangeland at Hillside.

Crematogaster sp.-_*liengmei*-group (monomorphic). On Tierberg, this is the only ant species known to nest in cavities of later-successional trees and arborescent shrubs (e.g. *R. obovatum*).

Leptothorax new sp. (monomorphic). Despite being a new species, this ant appears to be fairly common in the *Eriocephalus* rangeland at Tierberg. Individuals were rarely seen outside of their nest and most often their presence was known by recognising the nest entrance.

Monomorium sp. near *fastidium* Bolton (2 mm, monomorphic). This species was recorded once in the *P. afra* rangeland where foragers were attracted to bait placed below a *P. afra* clump.

Monomorium tchelichofi Forel (3.2 - 3.5 mm, monomorphic). The largest of the *Monomorium* species encountered in this study, this species is known from one nest only in the Upper Tierberg rangeland.

Plectroctena mandibularis F. Smith (14.5 - 16.5 mm, monomorphic). Only known from the *P. afra* rangeland, this is one of the few ant species, apart from *Pheidole* sp. 2, that nests under *P. afra* clumps. A slow and solitary forager, *P. mandibularis* specialises on millipedes and beetles.

Technomyrmex albipes F. Smith (2.2 - 2.5 mm, monomorphic). This species was recorded once in the *P. afra* rangeland where it was attracted to fish bait.

Tetramorium emeryi Mayr (3.5 mm, monomorphic). *Tetramorium emeryi* is very similar in appearance to *T. peringueyi*. It is uncommon in the *P. afra* rangeland where only two nests were located in dense grass.

2.4 DISCUSSION

Several general patterns emerge from the above commentary. Firstly, territories of aggressive dominant ant species were mutually exclusive, an observation that prompted the notion of ant mosaics following ant community studies in forest (Room 1971, Majer 1976, Jackson 1984). In this view, the dominant ant species form the core of the community and influence the composition and abundance of all other coexisting ant species (Hölldobler and Wilson 1990). Incidental observations at both study areas indicated that aggressive dominant ants were overtly aggressive towards each other suggesting that interference competition might be an important factor limiting the distribution of ant species. Although the aggressive dominants were competitively superior to subordinate species most of the time, the situation was reversed at higher temperatures when species belonging to the scavenging group preyed on them. Next, aggressive dominant species generally positioned their nests in the shade of shrubs and were active at lower temperatures. In contrast, subordinate species were active at higher temperatures and their nests were not necessarily situated in shaded sites. Nests of thermophilic ant species were only positioned on open, bare ground.

Where aggressive dominant ant species were distributed, they were numerically dominant in the ant community. Patterns of species replacement, however, were sharp and occurred over short distances (within metres from plains to washes). Species replacement over sharp gradients were not always associated with a concomitant change in vegetation structure. This was particularly evident in the relative change in ant species dominance from the Upper to Lower rangeland at Tierberg. Similar distribution patterns were evident in the *P. afra* rangeland except these operated at a smaller spatial scale. Almost all ant species, apart from *Pheidole* sp. 2, were located in sparsely vegetated areas (particularly NRP).

The following questions may be asked:

1. Is community membership limited and, if so, why?
2. What determines these patterns of distribution and abundance of ant species?
3. What are the relative importance of abiotic (e.g. vegetation) and biotic factors (competitive interaction) in influencing ant species distribution and abundance?
4. What promotes ant species coexistence (particularly amongst the aggressive dominant species)?

To answer these questions I will concentrate on the aggressive dominant species because they are common, widespread and their distribution patterns are immediately obvious. Furthermore, it is well known that dominant ant species influence the distribution and abundance of subordinate species (Room 1971, Majer 1976, Fellers 1987). In the following chapter (Chapter 3) I adopt a more traditional approach to the problem of understanding species diversity. Using diversity indices I investigate what aspects of the habitat (plant species diversity, plant structural diversity) influence ant species diversity. Because I found this approach unsuccessful, I emphasise species interactions in Chapter 4; specifically, the interaction between dominant species, how dominance relationships change in response to environmental gradients and the response of subordinate species to the dominant species.

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Chapter 3: Diversity patterns of ants and plants at a shrubland site in the southern Karoo

3.1 SUMMARY

Ant species distribution and abundance was sampled at eleven shrub-dominated sites on Tierberg farm in the southern Karoo to determine whether habitat influences ant species diversity. The study sites differed with respect to plant species composition, vegetation cover and vegetation structure. Ant species composition differed between sites but all sites were dominated by at least one ant species belonging to the aggressive dominant functional group. Ant species assigned to the seed harvesting and specialist foraging functional groups were present but scavenging ant species were not always represented at study sites.

Ant species diversity was not predicted by measurements of plant species diversity or vegetation structural diversity. Ant species richness was correlated with measures of vegetation structural diversity but not with plant species diversity. Although not explicitly addressed in this study, competition appears to influence ant community structure ultimately. The competitive affect of dominant ant species on other dominant and subordinate species suppresses ant species richness and diversity. Interference competition may account for non-significant associations between ant species diversity and vegetation structure.

3.2 INTRODUCTION

Habitat structural complexity has been correlated with species diversity in animal taxa as disparate as birds (MacArthur and MacArthur 1961, MacArthur et al. 1962, Recher 1969), lizards (Pianka 1967), small mammals (Rosenzweig and Winakur 1969), freshwater fish (Tonn and Magnuson 1982), plankton (Whiteside and Harmsworth 1967) and insects (Murdoch et al. 1972, Parmenter and MacMahon 1987, Parmenter et al. 1991). Generally, vertebrate diversity is not associated with plant species diversity. Certain invertebrate groups, in contrast, are influenced by plant species diversity (e.g. Murdoch et al. 1972, Parmenter and MacMahon 1987, Parmenter et al. 1991).

The relative importance of competition in structuring ecological communities dominated ecology in the 1980s (Schoener 1986). Studies of terrestrial arthropods generally documented weak or non-existent community patterns and questioned competition as a structuring force in communities (see Strong et al. 1984). In contrast, many studies that concentrated on terrestrial vertebrates found strong patterns in communities and advocated competition as the dominant ecological process (see Cody and Diamond 1975). Competition is a pervasive force in ant community organisation (Hölldobler and Wilson 1990) and its importance in structuring ant communities is not in question. However, much of the earlier work (dominated by studies of terrestrial vertebrates) investigating species diversity patterns assumed that communities were at equilibrium and that niche differentiation among species competing for a limited resource maintained species diversity. Ant ecology has inherited this paradigm and contemporary interpretation of mechanisms of ant species coexistence are influenced by it (e.g. Savolainen and Vepsäläinen 1988, Hölldobler and Wilson 1990, MacKay 1991). Ant communities, however, differ fundamentally in their structure from most other terrestrial animal communities in that non-equilibrial theories offer more robust explanations of species coexistence (Chapter 4). In this respect ant communities parallel plant and other sessile animal communities (e.g. marine invertebrates of the intertidal zone) in structure. Interference competition for space amongst dominant species leads inevitably to competitive exclusion. Therefore, the assumption that increased habitat complexity provides more opportunities for niche diversification and hence potentially more species does not necessarily hold true for ants.

The following questions may be asked:

1. What is the relative importance of competition and habitat in structuring ant communities?

2. Specifically, can ant species diversity be predicted by measurements of plant species composition or vegetation structure, or both?

The concept of species diversity has been confused by conflicting definitions (Hurlbert 1971). In this chapter, *species richness* refers to the number of species recorded in a known area and *species diversity* is a function of species richness and the evenness with which individuals are distributed among species.

3.3 STUDY SITES AND METHODS

Tierberg farm has been described in detail (Chapter 2). The ant study sites were distributed over a gently sloping, south-facing hillside, rising about 100 m in elevation over 6 km, in the Upper Tierberg rangeland. The study sites differed with respect to plant species composition, plant cover and vegetation structure so that I could determine whether any of these factors influenced ant species diversity (Table 3.1). Two sites (Barren and *Chrysocoma*) were located on an old, abandoned airstrip and an eleventh study site, where all the vegetation was removed, was positioned on the airstrip adjacent to the *Chrysocoma* site. All study sites were exposed to intensive, but never continuous, sheep grazing during the year.

3.3.1 Ants

A permanent 20 m × 20 m quadrat was established at all study sites except the Manipulation site where the quadrat size was 15 m × 15 m. Marking pegs were placed at 5 m intervals throughout the quadrat and used as baiting stations. Monitoring of ant species distribution and abundance began in October 1994. Only diurnal ant species were censused. Each site was monitored for one day with work starting shortly after sunrise and continuing into the hottest period of the day. Tinned fish was used as bait and placed at each marking peg to stimulate ant activity (most ant species including granivorous and nectarivorous species were attracted to the bait). I recorded the identity of all ant nests located within the permanent 20 m × 20 m quadrat and noted aggressive behaviour between individuals. Ant study sites were monitored every two months for the first year. Thereafter, the sites were censused in summer only because most ant species were inactive during the winter months. For each study site, an index of ant species diversity was calculated according to the formula $1/\sum p_i^2$ (MacArthur 1972), where p_i was the proportion of all ant nests found in the quadrat belonging to the i^{th} species.

TABLE 3.1: Descriptions of ant study sites at Tierberg, Prince Albert.

Study site	Slope inclination	Upslope direction	Location	Dominant plants	General comments
Manipulation	4°	59°	On airstrip	Cleared of all vegetation	No vegetation
Barren	3°	34°	On airstrip	*Chrysocoma ciliata*	Vegetation sparse, no erosion
Chrysocoma	4°	56°	On airstrip	*C. ciliata*, *Ruschia spinosa*	Slight sheet wash, woody shrubs present
Eriocephalus	4°	36°	Plains	*R. spinosa*, *Eriocephalus ericoides*	Vegetation typical of Tierberg rangeland
Ruschia dolomitica	0.5°	45°	On shale outcrop	*R. dolomitica*	*R. dolomitica* formed a dense ground cover
Lower *Ruschia*	3°	31°	In minor wash	*R. spinosa*, *E. ericoides*	Slight soil erosion
Upper *Ruschia*	2.5°	75°	On shale outcrop	*R. spinosa*, *E. ericoides*	Soil layer thin or non-existent
Lycium	4°	289°	In minor sheet wash	*Lycium cinereum*, *C. ciliata*	Slight sheet wash, silty soil layer
Pteronia	4°	28°	In drainage line	*Pteronia pallens*	Erosion, *P. pallens* inhibits other plant species
Galenia	5°	44°	In drainage line	*Galenia africana*, *C. ciliata*	Silty soil layer accumulates after rainfall
Rhus	6°	296°	On exposed shale band	Later-successional tree species	Severe erosion, very few shrubs

3.3.2 Vegetation

At each study site ten 5 m × 5 m sub-quadrats were randomly selected. The identity of all plant species located within these sub-quadrats was recorded and the height (*H*), length along the longest axis (*L*) and the greatest width at right angles to the length (*W*) measured. Shrub volume was computed as $\pi LWH/6$ and shrub cover as $\pi LW/4$ (Cody 1986). Diversity indices for the vegetation measurements were calculated with same index used to determine ant species diversity. Plant species diversity at each study site was computed with p_i referring to the total number of individuals of the i^{th} plant species expressed as a proportion of the total number of individuals of all species recorded in the ten 5 m × 5 m sub-quadrats. Plant volume diversity was calculated with p_i referring to the total volume of the i^{th} species expressed as a proportion of the total volume recorded for all plant species. Plant cover diversity was calculated in the same way except plant cover values were used. The two latter indices express a particular species contribution to total plant volume (or cover) and therefore yield a diversity measurement that is a combination of vegetation structure and plant species composition. Three additional measurements were calculated as the total number of plant individuals, the total plant volume (m^3) and the total plant cover (m^2) recorded in ten sub-quadrats at each study site.

Vegetation structural diversity was measured using a derivation of the MacArthur and MacArthur (1961) board measurements. A white board (60 cm × 50 cm) was divided into horizontal height profiles of 0 - 10 cm, 10 - 30 cm and 30 - 60 cm. Each height profile was further subdivided into three rows of equal height. The board was then vertically partitioned into ten 5 cm columns to give a total of 30 blocks for each height profile. Measurements were made by placing the board along the line made by two marker pegs at each of the 10 randomly selected sub-quadrats. With the observer positioned 5 m away, on the opposite side of the sub-quadrat, the number of blocks in each height profile intercepted by vegetation were counted. The observer's eyes were level with the particular height profile being measured. Where vegetation exceeded 60 cm in height, the 30 cm mark was raised to 60 cm above the ground to add a fourth horizontal layer. Two board measurements were recorded for each sub-quadrat yielding a total of 20 board measurements for each study site. Foliage height diversity was computed with p_i as the proportion of the total foliage that was in the i^{th} of the chosen horizontal layers. A final diversity index was calculated as the sum of all blocks intercepted by vegetation, irrespective of horizontal zone above the ground, in the ten sub-quadrats. Foliage profile diagrams for the 10 study sites were drawn with the horizontal layer on the ordinate and the proportion of the total foliage in the i^{th} horizontal layer (p_i) on the abscissa.

3.3.3 Analysis of diversity indices

Ant species diversity and ant species richness was regressed against the diversity indices computed for vegetation (species composition and structure) to determine whether any of these factors influenced ant community structure. I was not sure whether the ant assemblage recorded at the Manipulation site had stabilised following vegetation removal. These regression analyses were therefore performed with and without the Manipulation site datum.

3.4 RESULTS

3.4.1 Ants

Ant activity was influenced strongly by season. As a result, only the mid-summer censuses (January) were considered reliable. Apart from nest turnover, the general set of species present at each study sites did not vary over the two year monitoring period (Table 3.2). Aggressive dominant ant species were always present and most often this functional group was represented by two species. *Tetramorium peringueyi* and *Crematogaster melanogaster* were dominant at four study sites (*Chrysocoma*, *Eriocephalus*, *R. dolomitica*, Upper *Ruschia*) and both species were present at the Manipulation site prior to vegetation removal. Following plant removal, *C. melanogaster* abandoned the site and was not recorded again. *Crematogaster melanogaster* was absent from the Barren site which was dominated by *T. peringueyi*. The sites located in minor washes and drainage lines (*Lycium*, Lower *Ruschia*, *Rhus* and *Galenia*) were dominated by *Anoplolepis steingroeveri*. The *Pteronia* site, also positioned in a drainage line was dominated by *T. peringueyi*. However, after the first year, nests of *A. steingroeveri* which were previously absent from this site, increased in density at the *Pteronia* site. *Pheidole* sp. 2 coexisted with *A. steingroeveri* at three study sites. Overt aggressive behaviour was recorded between dominant ant species at all study sites.

Although the dominant ant species remained constant for the duration of the study, the presence of subordinate ant species and their nest density fluctuated. However, species belonging to the seed harvesting and specialist functional groups were always represented. Scavenging ant species (represented by *Monomorium australe* only in the Upper rangeland) were present at three study sites only.

TABLE 3.2: Ant species recorded in January 1997 at eleven ant study sites on Tierberg farm, Prince Albert. Values refer to number of nests within the 20 m × 20 m quadrat. Species are assigned to functional groups. The table is continued on the following page.

	Manipuln	Barren	Chryso.	Erioceph.	*Ruschia dolomitica*	Lower *Ruschia*	Upper *Ruschia*	*Lycium*	*Pteronia*	*Galenia*	*Rhus*
Aggressive dominant species											
Tetramorium peringueyi	5.3	2	5	2	1	-	2	-	2	4	-
Crematogaster melanogaster	-	-	1	1	1	-	1	-	-	-	-
Anoplolepis steingroeveri	-	-	-	-	1	1	-	1	1	1	1
Pheidole sp. 2	-	-	-	-	-	-	-	1	-	1	1
Seed harvesting species											
Pheidole sp. 1	-	-	2	-	-	-	-	-	-	-	-
Monomorium havilandi	3.6	5	3	-	-	22	-	-	-	-	-
M. salomonis	5.3	-	9	7	8	2	3	15	1	16	-
M. macrops	-	-	-	-	-	-	1	1	-	-	-
Scavenging species											
Monomorium australe	1.8	4	-	-	-	-	-	-	2	-	-

TABLE 3.2: continued from previous page.

	Manipuln	Barren	Chryso.	Erioceph.	*Ruschia dolomitica*	Lower *Ruschia*	Upper *Ruschia*	*Lycium*	*Pteronia*	*Galenia*	*Rhus*
Specialist species											
Ocymyrmex barbiger	-	-	-	1	1	-	-	-	-	4	1
Ophthalmopone hottentota	-	1	-	-	1	-	2	2	4	-	-
Camponotus fulvopilosus	-	-	-	-	-	-	3	-	1	2	2
Anoplolepis cf. *trimeni*	7.1	-	5	1	-	8	-	4	1	12	2
Uncommon species											
Acantholepis capensis	-	-	-	-	-	-	-	-	-	-	1
Anochetus levaillanti	-	-	-	-	-	-	1	-	-	2	-
Monomorium tchelichofi	-	-	-	-	-	-	-	-	-	4	1
Crematogaster liengmei	-	-	-	-	-	-	-	-	-	-	1

Ant species diversity was consistently high at the *Rhus* and Upper *Ruschia* sites (Table 3.3). Ant species diversity at the Manipulation site was high in January 1996 but declined in January 1997 because of a decline in species number. The Lower *Ruschia* and *R. dolomitica* sites consistently supported the lowest ant species diversity. The *Rhus* study site also supported the most ant species while the Barren and Lower *Ruschia* sites consistently supported the fewest ant species (Table 3.3).

TABLE 3.3: Ant species diversity recorded at eleven sites at Tierberg, Prince Albert in summer 1996 and summer 1997. Species richness for each site is in brackets. Ant species diversity was calculated with p_i referring to the proportion of all ant nests belonging to the i^{th} species.

Study site	January 1996	January 1997
Manipulation	5.84 (8)	4.33 (5)
Barren	2.78 (3)	3.13 (4)
Chrysocoma	4.69 (6)	4.31 (6)
Eriocephalus	2.77 (5)	2.57 (5)
Ruschia dolomitica	2.29 (5)	2.45 (6)
Lower *Ruschia*	1.76 (4)	1.97 (4)
Upper *Ruschia*	5.44 (6)	5.86 (7)
Lycium	2.73 (8)	2.32 (6)
Pteronia	4.84 (7)	5.14 (7)
Galenia	1.97 (5)	4.62 (9)
Rhus	6.86 (8)	7.14 (8)

3.4.2 Vegetation

The number of plant species at each site varied considerably with five species recorded at the Barren site and 17 species present at the Lower *Ruschia* site. Plant density was also lowest at the Barren site. The *Ruschia dolomitica* site, dominated numerically by *R.*

TABLE 3.4: Plant species richness, the total number of plant individuals, plant density and plant species diversity at eleven ant study sites on Tierberg farm, Prince Albert. Plant density is the average number of plants (± SE) in ten 5 m × 5 m sub-quadrats at each study site. Plant species diversity was calculated with p_i referring to the total number of individuals of the i^{th} plant species expressed as a proportion of the total number of individuals of all species recorded in ten 5 m × 5 m sub-quadrats.

Study site	Plant species richness	Total number of plants	Plant density	Plant species diversity
Manipulation	0	0	0	0
Barren	5	95	9.5 ± 1.74	2.21
Chrysocoma	7	476	47.6 ± 5.94	1.69
Eriocephalus	12	776	77.6 ± 4.43	2.74
Ruschia dolomitica	9	2667	266.7 ± 11.20	1.39
Lower *Ruschia*	17	585	58.5 ± 5.01	5.19
Upper *Ruschia*	15	686	68.6 ± 3.72	4.09
Lycium	14	463	46.3 ± 2.84	4.37
Pteronia	12	338	33.8 ± 3.94	3.88
Galenia	10	997	99.7 ± 4.60	2.68
Rhus	15	447	44.7 ± 3.20	2.56

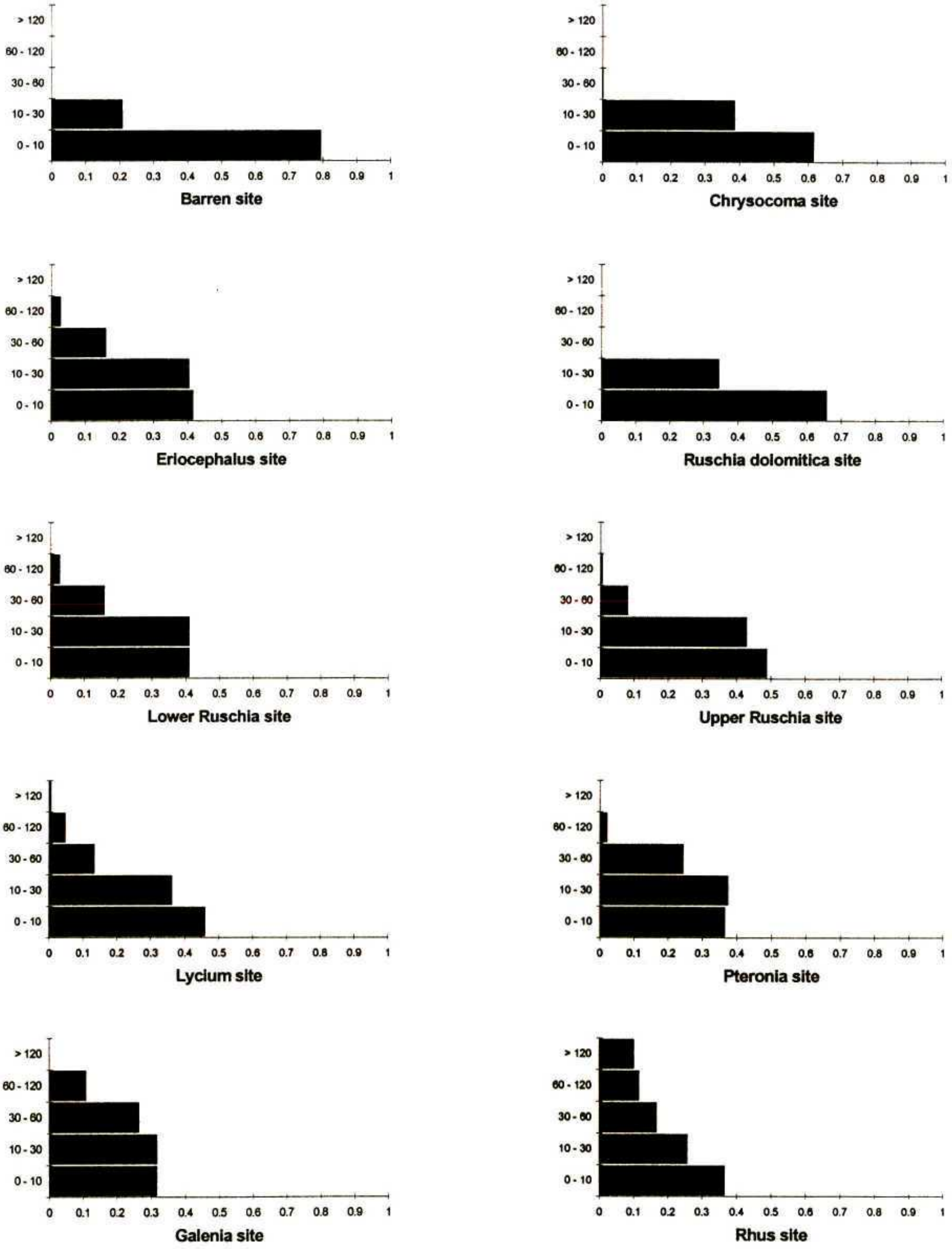
dolomitica, had the highest plant density followed by the *Galenia* site which was dominated by *G. africana* and *C. ciliata*. Plant species diversity was highest at the rangeland study sites (Lower *Ruschia*, *Lycium* and Upper *Ruschia* sites) and lowest at high disturbance sites (Barren, *Chrysocoma*, and *R. dolomitica* sites) which were dominated by early successional plant species (Table 3.4).

Vegetation structural diversity differed substantially at the ant study sites (Table 3.5, Figure 3.1). The sites with the most horizontal vegetation layers (*Rhus* site) and the densest vegetation (*Galenia* and *Pteronia* sites) were also the most structurally diverse. The two

TABLE 3.5: Foliage height diversity and total foliage at eleven ant study sites on Tierberg farm, Prince Albert. Foliage height diversity was computed with p_i the proportion of the total foliage that was in the i^{th} of the chosen horizontal layers recorded in ten 5 m × 5 m sub-quadrats. Total foliage is the sum of all blocks on the density board intercepted by vegetation, irrespective of horizontal zone, in the ten sub-quadrats at each site.

Study site	Foliage height diversity	Total foliage
Manipulation	0	0
Barren	1.49	169
Chrysocoma	1.90	897
Eriocephalus	2.78	1436
Ruschia dolomitica	1.82	796
Lower *Ruschia*	2.79	1396
Upper *Ruschia*	2.34	1169
Lycium	2.79	1104
Pteronia	3.02	1479
Galenia	3.59	1907
Rhus	4.02	1520

airstrip study sites (Barren and *Chrysocoma*) along with the *R. dolomitica* site, positioned on a shale outcrop, were the least diverse habitats structurally (Table 3.5). Plant volume diversity was lowest at the *Chrysocoma* and *Pteronia* sites and highest at the Lower *Ruschia* and *Rhus* sites (Table 3.6). Plant cover diversity was lowest at the three sites dominated by pioneer shrubs (Barren, *Chrysocoma* and *R. dolomitica* sites). The *Rhus* site had the highest plant cover diversity (Table 3.7).



Barren site

Chrysocoma site

Eriocephalus site

Ruschia dolomitica site

Lower Ruschia site

Upper Ruschia site

Lycium site

Pteronia site

Galenia site

Rhus site

FIGURE 3.1: Foliage profile diagrams representing vegetation structural diversity at ten ant study sites at Tierberg, Prince Albert. Foliage diversity (i.e. the proportion of the total foliage in the i^{th} horizontal zone) is plotted along the abscissa. The horizontal zone (cm) above the ground is on the ordinate.

TABLE 3.6: Total vegetation volume, mean vegetation volume and plant volume diversity at eleven ant study sites on Tierberg farm, Prince Albert. Mean vegetation volume is the average plant volume (± SE) in ten 5 m × 5 m sub-quadrats at each study site. Plant volume diversity was calculated with p_i referring to the total plant volume of the i^{th} plant species expressed as a proportion of the total plant volume of all species recorded in ten 5 m × 5 m sub-quadrats.

Study site	Total vegetation volume	Mean volume (m^3) ± SE	Plant volume diversity
Manipulation	0	0	0
Barren	0.13	0.013 ± 0.004	2.23
Chrysocoma	2.17	0.217 ± 0.028	1.12
Eriocephalus	18.00	1.800 ± 0.099	2.89
Ruschia dolomitica	3.33	0.333 ± 0.035	3.75
Lower *Ruschia*	16.40	1.640 ± 0.164	4.52
Upper *Ruschia*	14.52	1.452 ± 0.167	3.85
Lycium	10.27	1.027 ± 0.224	3.21
Pteronia	26.09	2.609 ± 0.227	1.89
Galenia	42.79	4.279 ± 0.276	2.90
Rhus	32.14	3.214 ± 0.808	4.05

3.4.3 Analysis of diversity indices

Ant species diversity was not predicted by any of the vegetation indices used in this study (e.g. Figure 3.2, 3.3). Ant species richness, however, was significantly correlated (positively and linearly) with several vegetation indices in January 1997 but not in January 1996 (see Figure 3.4).

Ant species richness was positively associated with foliage height diversity in 1997 when the Manipulation site datum was included (Figure 3.5, $y = 4.01 + 0.86x$, $r = 0.6$, $p = 0.05$) and

TABLE 3.7: Total vegetation cover, mean vegetation cover and plant cover diversity at eleven ant study sites on Tierberg farm, Prince Albert. Mean vegetation cover is the average plant cover (± SE) in ten 5 m × 5 m sub-quadrats at each study site. Plant cover diversity was calculated with p_i referring to the total plant cover of the i^{th} plant species expressed as a proportion of the total plant cover of all species recorded in ten 5 m × 5 m sub-quadrats.

Study site	Total vegetation cover	Mean cover (m^2) ± SE	Plant cover diversity
Manipulation	0	0	0
Barren	1.35	0.135 ± 0.038	1.70
Chrysocoma	9.75	0.975 ± 0.103	1.14
Eriocephalus	87.86	8.786 ± 0.380	2.68
Ruschia dolomitica	59.04	5.904 ± 0.356	1.73
Lower *Ruschia*	73.13	7.313 ± 0.382	3.77
Upper *Ruschia*	73.45	7.345 ± 0.520	3.27
Lycium	42.81	4.281 ± 0.466	4.76
Pteronia	77.62	7.762 ± 0.432	2.57
Galenia	134.07	13.407 ± 0.552	3.48
Rhus	41.05	4.105 ± 0.765	6.82

excluded from the analyses ($y = 2.66 + 1.33x$, $r = 0.65$, $p < 0.05$). Similarly, there was a positive correlation between ant species richness and total vegetation volume with the Manipulation site included (Figure 3.6, $y = 4.81 + 0.09x$, $r = 0.75$, $p < 0.01$) and without the Manipulation site ($y = 4.76 + 0.09x$, $r = 0.74$, $p < 0.05$). Ant species richness was predicted by total foliage (i.e. the sum of vegetation profile measurements) with the Manipulation site datum (Figure 3.7, $y = 4.25 + 0.002x$, $r = 0.63$, $p < 0.05$) and without the Manipulation site datum ($y = 3.67 + 0.002x$, $r = 0.63$, $p = 0.05$).

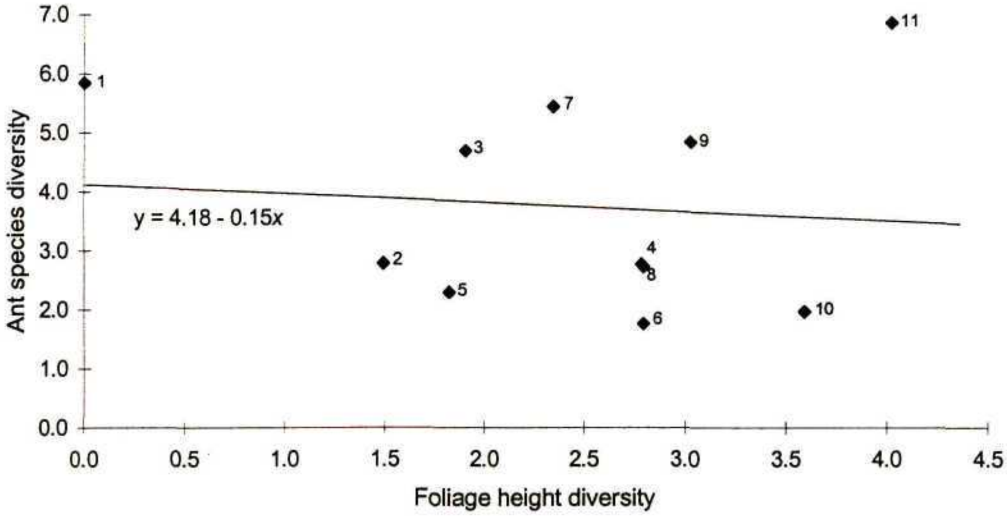


FIGURE 3.2: Ant species diversity recorded in January 1996 plotted against foliage height diversity at eleven study sites at Tierberg, Prince Albert. 1 - Manipulation site, 2 - Barren site, 3 - *Chrysocoma* site, 4 - *Eriocephalus* site, 5 - *R. dolomitica* site, 6 - Lower *Ruschia* site, 7 - Upper *Ruschia* site, 8 - *Lycium* site, 9 - *Pteronia* site, 10 - *Galenia* site, 11 - *Rhus* site.

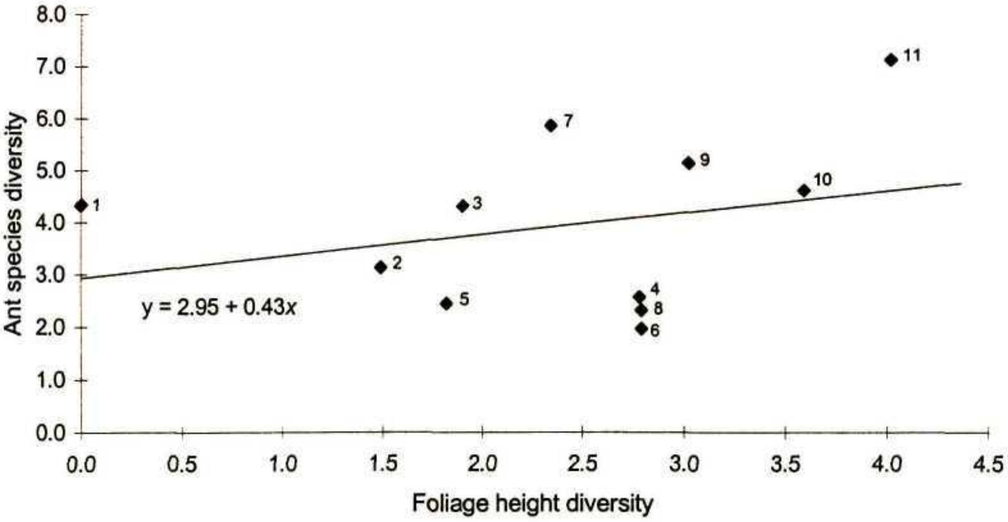


FIGURE 3.3: Ant species diversity recorded in January 1997 plotted against foliage height diversity at eleven study sites at Tierberg, Prince Albert. 1 - Manipulation site, 2 - Barren site, 3 - *Chrysocoma* site, 4 - *Eriocephalus* site, 5 - *R. dolomitica* site, 6 - Lower *Ruschia* site, 7 - Upper *Ruschia* site, 8 - *Lycium* site, 9 - *Pteronia* site, 10 - *Galenia* site, 11 - *Rhus* site.

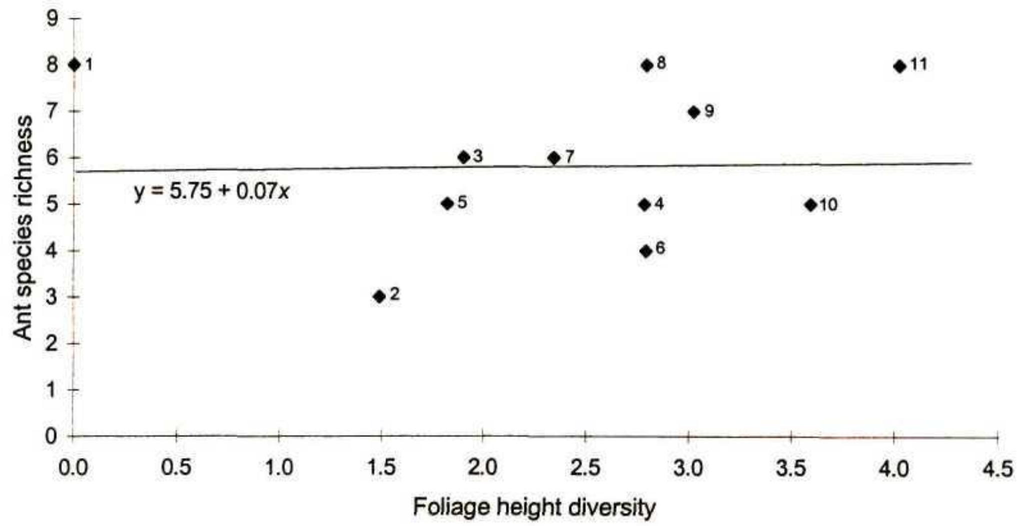


FIGURE 3.4: Ant species richness recorded in January 1996 plotted against foliage height diversity at eleven study sites at Tierberg, Prince Albert. 1 - Manipulation site, 2 - Barren site, 3 - *Chrysocoma* site, 4 - *Eriocephalus* site, 5 - *R. dolomitica* site, 6 - Lower *Ruschia* site, 7 - Upper *Ruschia* site, 8 - *Lycium* site, 9 - *Pteronia* site, 10 - *Galenia* site, 11 - *Rhus* site.

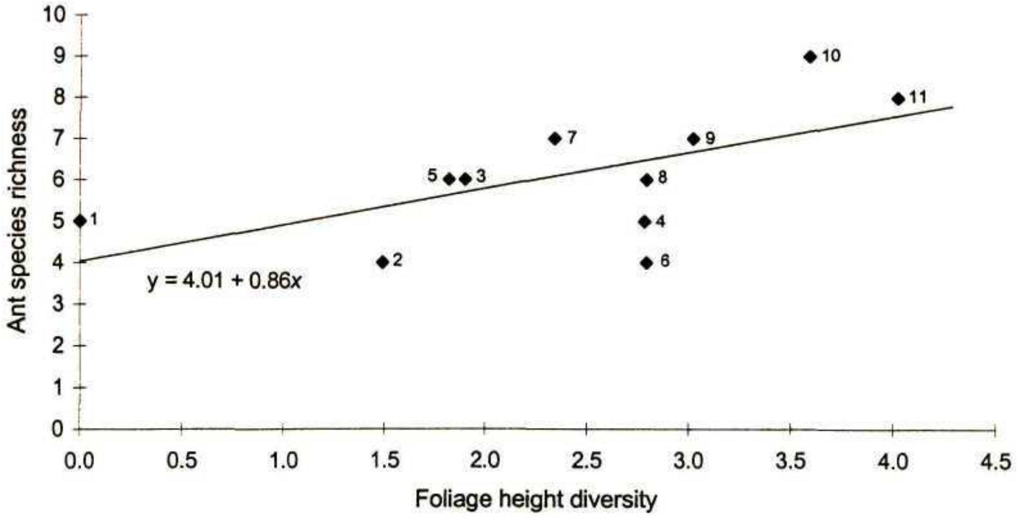


FIGURE 3.5: Ant species richness recorded in January 1997 plotted against foliage height diversity at eleven study sites at Tierberg, Prince Albert. 1 - Manipulation site, 2 - Barren site, 3 - *Chrysocoma* site, 4 - *Eriocephalus* site, 5 - *R. dolomitica* site, 6 - Lower *Ruschia* site, 7 - Upper *Ruschia* site, 8 - *Lycium* site, 9 - *Pteronia* site, 10 - *Galenia* site, 11 - *Rhus* site.

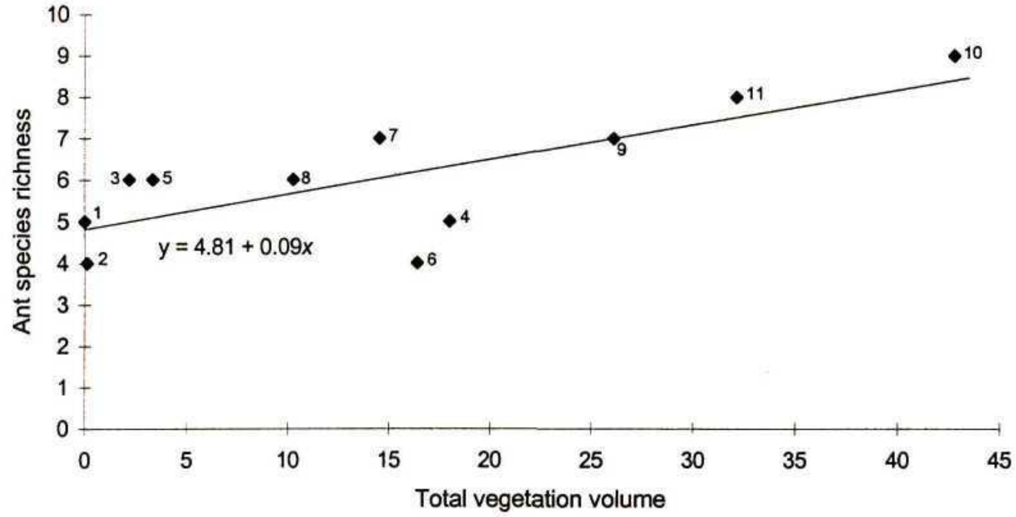


FIGURE 3.6: Ant species richness recorded in January 1997 plotted against total vegetation volume (m^3) at eleven study sites at Tierberg, Prince Albert. 1 - Manipulation site, 2 - Barren site, 3 - *Chrysocoma* site, 4 - *Eriocephalus* site, 5 - *R. dolomitica* site, 6 - Lower *Ruschia* site, 7 - Upper *Ruschia* site, 8 - *Lycium* site, 9 - *Pteronia* site, 10 - *Galenia* site, 11 - *Rhus* site.

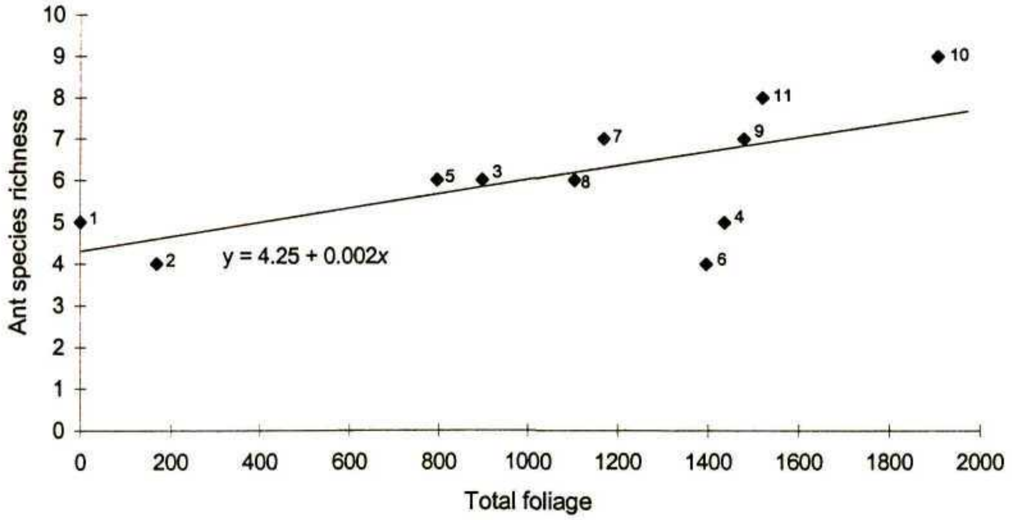


FIGURE 3.7: Ant species richness recorded in January 1997 plotted against the sum of the vegetation profile measurements at eleven study sites at Tierberg, Prince Albert. 1 - Manipulation site, 2 - Barren site, 3 - *Chrysocoma* site, 4 - *Eriocephalus* site, 5 - *R. dolomitica* site, 6 - Lower *Ruschia* site, 7 - Upper *Ruschia* site, 8 - *Lycium* site, 9 - *Pteronia* site, 10 - *Galenia* site, 11 - *Rhus* site.

3.5 DISCUSSION

Ant species richness at Tierberg was positively associated with three measurements of vegetation structure. Foliage height diversity and total foliage are direct measurements of vegetation structure. Although not a direct measurement of vegetation structure, total vegetation volume is similar to these indices because it incorporates an aspect of vegetation height. These results reject the notion that ant species richness or diversity are predicted by plant species composition and conform to earlier studies which correlate measures of animal diversity with vegetation structure.

That habitat complexity leads to increased ant species richness confirms what seems to be intuitively obvious. A structurally complex habitat permits more opportunities for niche diversification and hence more species. The two most structurally diverse study sites, *Rhus* and *Galenia*, supported three and two additional species respectively, that were rare elsewhere. The presence of *Crematogaster liengmei*, a species that nests in tree cavities, was almost certainly because of the additional tree component at the *Rhus* site. The depauperate Manipulation site, in contrast, lost *C. melanogaster* when all vegetation was experimentally removed. Presumably, *C. melanogaster* is unable to survive at the Barren site because of the very sparse ground cover. However, the Lower *Ruschia* site, which supported a low ant species richness, also had a foliage height diversity greater than the median value. Yet, the Lower *Ruschia* site supported the same number of ant species as the Barren site. The Lower *Ruschia* site was dominated by *Anoplolepis steingroeveri*, a highly aggressive ant species. Generally, *A. steingroeveri* excluded other ant species belonging to the dominant functional group but when *Pheidole* sp. 2 coexisted with it, overt interference competition between the two species was frequent and aggressive (*personal observation*). Is *A. steingroeveri* suppressing species richness at the Lower *Ruschia* site? It is well known that dominant ant species influence the distribution and abundance of subordinate ant species (Chapter 4, Room 1971, Majer 1976, Fellers 1987) and patterns of ant species diversity at the airstrip study sites support this contention.

Rangeland successional trends are evident on the airstrip and the adjacent *Eriocephalus* study site (Chapter 4). The sparse distribution of *C. ciliata* and the lack of woody shrub species suggests that the Barren site represents an early successional stage in the Upper Tierberg rangeland. The *Chrysocoma* site, with a greater plant cover and the presence of a woody shrub species (*E. ericoides*), represents the following successional stage in time. The

Eriocephalus rangeland, with four woody shrub species and a ground cover of *E. ericoides* of more than a third of the total cover, can be considered a later state in this successional trend. Patterns of ant species dominance vary predictably along this successional gradient (Chapter 4). The spatial distribution of *T. peringueyi*, in areas represented by the Barren and *Eriocephalus* sites, was regular, indicating that this species was competitively dominant at these sites. Although common at the *Chrysocoma* site, the spatial distribution of *T. peringueyi* was random and I suggest that this species is outperformed by *C. melanogaster* causing a reduction in the competitive superiority of *T. peringueyi* (Chapter 4). Ant species diversity at the *Chrysocoma* site was consistently higher than the Barren and *Eriocephalus* sites and ant species richness showed a similar, yet less pronounced, trend along the successional gradient. These patterns suggest that the competitive superiority of the dominant ant species (*T. peringueyi* in this case) suppresses ant species diversity (Figure 3.8). If this is so, we are unlikely to find linear associations between ant species diversity and any indices representing vegetation structure.

The habitat variation at Tierberg was not sufficient to alter the competitive dominance of *T. peringueyi* in favour of another species except in drainage lines. Although a new set of subordinate species may replace the assemblage associated with the previous dominant species, species richness and abundance may not necessarily show predictable change associated with the change in dominance relationships. A more profitable approach to the problem would therefore be to study dominance relationships, how they change in response to environmental gradients and the response of subordinate species to the dominant species. This approach is explored in the following chapter.

In this chapter I have shown that ant species richness is predicted by measurements of habitat complexity. Specifically, ant species appear to respond to some aspect of vegetation height. Ultimately, however, it seems that competitive interactions, particularly of the dominant ant species, determine the structure of the ant community. At the lower extreme of the vegetation structural gradient, certain ant species are excluded from the community because they appear unable to survive in that habitat. At some stage, although conditions may be conducive to survival, competitive interactions become important and species are excluded by the dominant ant species. At the upper extreme of the habitat gradient, species that are rare or uncommon elsewhere are facilitated by an increase in vegetation complexity. Clear patterns of ant distribution emerged from the census of the eleven study sites and these will be explored in greater detail in the next chapter.

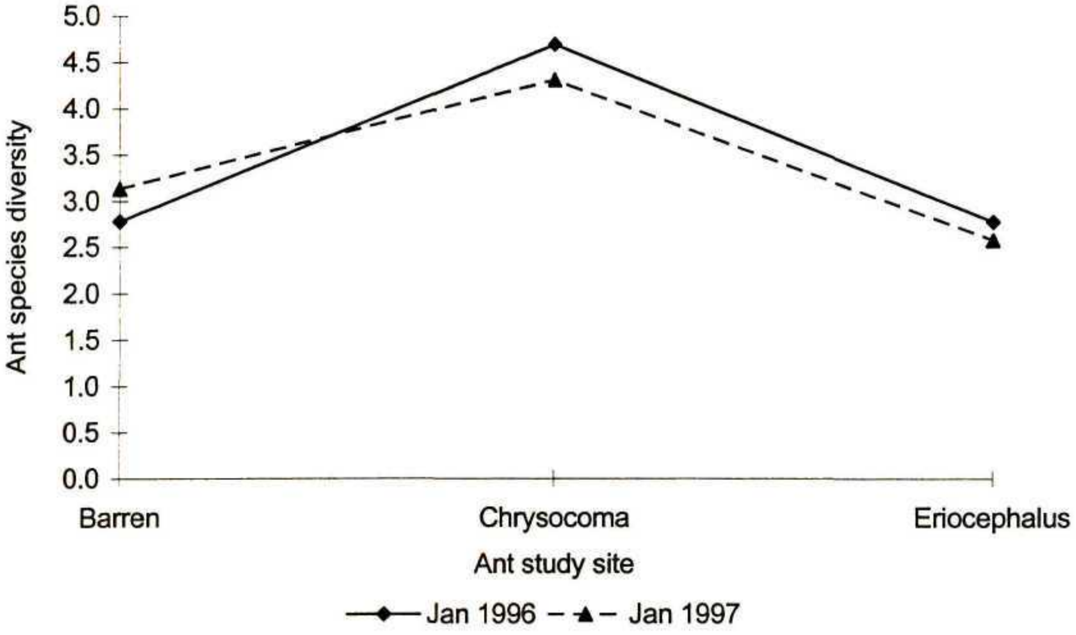


FIGURE 3.8: Ant species diversity at the Barren, *Chrysocoma* and *Eriocephalus* ant study sites. These three study sites represent a rangeland successional gradient. *Tetramorium peringueyi* had a regular spatial distribution at the Barren and *Eriocephalus* sites and was competitively dominant. *Crematogaster melanogaster* outperformed *T. peringueyi* at the *Chrysocoma* site where the latter species had a random spatial distribution.

3.5.1 Practical problems associated with the use of indices in the study of ant species diversity

Although the lack of significant associations of ant species diversity are adequately explained in the following chapter, it was not clear whether these patterns (or lack thereof) are a true representation of ant community structure in the southern Karoo or whether the data collected were inaccurate. Ant nests, particularly of the small cryptic species, were difficult to locate and I was never sure whether all nests at a study site were found. This might account for non-significant trends in species richness in summer 1996. The problem was compounded by ant species with a decentralised territorial system (*Crematogaster melanogaster*, *Anoplolepis steingroeveri*, *Pheidole* sp. 2). Although attempts were made to determine the size of their territories, I was unable to do so. Consequently, when these species were present at a study site, they were assigned an abundance value of one. It is not known how these sources of error affected the final calculation of diversity which is sensitive to changes in both species richness and evenness.

3.6 ACKNOWLEDGEMENTS

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Chapter 4: Dominance hierarchies in ant communities: different life histories and disturbance promote coexistence

4.1 SUMMARY

Ant species coexistence mechanisms were studied at two sites, a shrub-dominated rangeland and a *Portulacaria afra*/grass-dominated rangeland, in the southern Karoo. Ant communities have a predictable organisation resulting from intense interference competitive interactions. Dominance hierarchies, where aggressive ant species determine the distribution and abundance of subordinate species, were prevalent at both study sites. Interpreting patterns of ant community structure and dynamics requires an understanding of rangeland dynamics.

Tetramorium peringueyi was the dominant ant species on the plains of the *Eriocephalus* shrub-dominated rangeland. Disturbances disrupting the competitive dominance of *T. peringueyi* were absent at this site. *Tetramorium peringueyi* excluded all dominant ant species from its territory but the decentralised territorial strategy (multiple nests) of *Crematogaster melanogaster* facilitated the pre-emption of space not occupied by *T. peringueyi*. Different life histories (superior colonisation ability verses superior competitive ability) permit these two species to coexist in an unstable equilibrium.

Pheidole sp. 2 and *C. melanogaster* were dominant and excluded *T. peringueyi* from the *Pteronia pallens* shrub-dominated rangeland. *Pheidole* sp. 2 and *C. melanogaster* pre-empt available space by lateral expansion of existing colonies which inhibits the sexual foundation of new colonies.

At the *P. afra* rangeland site, *Pheidole* sp. 2 was dominant in well shaded microhabitats, such as under *P. afra* or in grass, but was outperformed by subordinate ant species on disturbed grassless areas. These disturbances are created by the death and subsequent collapse of *P. afra* clumps and their soils are rich in nutrients and organic materials. Nutrient rich patches serve as foci for the colonisation of subordinate ant species which persist on these disturbances as fugitives in the community. Local extinction of subordinate ant species by competitive exclusion is inevitable as grass colonises the disturbance and facilitates the invasion of *Pheidole* sp. 2.

4.2 INTRODUCTION

Ecologists, dissatisfied with the inability of classical competition theory to explain highly diverse communities, have responded with a wide variety of novel conceptual advances (Auerbach and Shmida 1987, Silvertown and Law 1987, Bengtsson et al. 1994). In opposition to traditional niche orientated models, which were originally developed for mobile animals, these alternatives stress the importance of environmental stochasticity (Sale 1977, Comins and Noble 1985, Warner and Chesson 1985), disturbance (Connell 1978, Huston 1979), life-history differences (Shmida and Ellner 1984), dispersal (Hutchinson 1951, Levin 1976, Tilman 1997) and facilitation (Bertness and Callaway 1994, Callaway 1995). The emphasis on dynamic processes and spatial heterogeneity permits the coexistence of trophically similar species but does not necessarily downplay the importance of competition in structuring communities.

Interference competition is widespread in ant communities and contributes significantly to their organisation (Fellers 1987, Hölldobler and Wilson 1990, Vepsäläinen and Savolainen 1990, Andersen 1992, Andersen and Patel 1994). In fact, the resulting organisation of ant assemblages is so predictable that several similar models based on competitive interactions have been developed to describe community structure (Wilson 1971, Greenslade 1978, Savolainen and Vepsäläinen 1988, Andersen 1990, 1995). Dominant ant species form the core of local communities and, through competitive interaction, they organise the distribution and abundance of subordinate species to form dominance hierarchies. Ant ecology has tended to concentrate on equilibrial coexistence mechanisms where species are self-limiting and any interactions between species are reduced before competitive exclusion is achieved (Hölldobler and Wilson 1990). The partitioning of daily and seasonal activity (Whitford and Ettershank 1975, Hansen 1978, Briese and Macauley 1980, Vepsäläinen and Savolainen 1990), habitat (Whitford et al. 1976, Greenslade and Greenslade 1977, Andersen 1983, 1986), food resources (Davidson 1977*a*, Hansen 1978), foraging behaviour (Whitford et al. 1976, Davidson 1977*b*) and worker body size (Davidson 1977*a*, Vepsäläinen and Savolainen 1990) are frequently cited mechanisms, among others, explaining the coexistence of ant species.

Certain assumptions of equilibrium communities have been challenged or do not hold for ant communities. Firstly, resource partitioning has been questioned on philosophical grounds unless there are *a priori* reasons for testing a particular niche axis (Silvertown and Law 1987). Differences between species do not necessarily reduce competition, permitting species coexistence. Secondly, stable limit cycles, which prevent competitive exclusion in equilibrium communities (Gilpin 1975) are not consistent with the dominance hierarchies that are so pervasive in ant communities.

Non-equilibrium theories of species coexistence have succeeded earlier niche orientated explanations of very diverse plant communities but, amongst animal communities, they appear to be limited to communities of sessile organisms. The importance of disturbance and dispersal in maintaining species richness in the intertidal zone is well known (Sousa 1979, Paine and Levin 1981) and the diversity of reef fish communities has also been explained by non-equilibrial conditions (Sale 1977). These communities, and the species belonging to them, have various attributes in common. Firstly, limited space combined with aggressive interference competition results in the tendency towards monopolisation by dominant species. Secondly, the adult stage is generally non-motile but species have a high reproductive potential supported by equally high dispersal rates. These are also attributes shared by ants. Given that vegetation structure influences the distribution and abundance of ants (Greenslade 1975, Majer 1976, Greenslade and Greenslade 1977, Andersen 1983, 1986), then ant community dynamics should track plant community dynamics. If this is so, do any of the non-equilibrial coexistence mechanisms referred to above apply to ant communities?

In this chapter I present a mechanism that explains how relative competitive strengths between competing ant species are altered leading to dynamic competitive hierarchies. I will argue that the outcome of competitive interactions are contingent on productivity gradients which are a function of the vegetation. Next, I will show that interspecific competition is widespread amongst ant species of communities in the southern Karoo and is ultimately responsible for community patterns. Finally, I will examine the observed community patterns in the light of current theories of species coexistence and demonstrate that disturbance and different life histories promote coexistence.

4.2.1 Ant functional groups

For convenience and to simplify the ant community, I have assigned ant species encountered during this study to functional groups. Although they are similar, I make no attempt to follow the classification systems used elsewhere (e.g. Greenslade 1978, Savolainen and Vepsäläinen 1988, Andersen 1990, 1995). The simple classification system that follows is based on field observations of distribution, behaviour and feeding biology (Chapter 2). It is descriptive and I make no assumptions of greater ecological interpretation although later I demonstrate general patterns that may have predictive qualities.

Aggressive dominants: These are species that are widely distributed, numerically common and strongly territorial. These species are overtly aggressive and dominate subordinate species that belong to other functional groups. This functional group is represented in my study by *Tetramorium peringueyi* Arnold, *Crematogaster melanogaster* Emery, *Anoplolepis steingroeveri* Forel and *Pheidole* sp. 2.

Seedharvesters: All seed harvesting species fall into this category but, like most ant species, they scavenge animal material when the opportunity arises. These species were less common than, and subordinate to, the aggressive dominant species. The functional group is represented by *Messor capensis* Mayr, *Pheidole* sp. 1, *Monomorium havilandi* Forel, *Monomorium* sp.-_*salomonis*-group and *Monomorium alamarum* Bolton.

Scavengers: These species were opportunistic foragers that scavenged on dead and living insect material and were never observed harvesting seeds. At higher temperatures, they were frequently observed preying on species belonging to the aggressive dominant group. The scavengers are represented by *Tetramorium quadrispinosum* Emery and *Monomorium australe* Emery in my study.

Specialists: These species have specialised foraging behaviours or specialise on a particular food resource. The specialists were less common and submissive to the aggressive dominant species. They are represented by *Ocymyrmex barbiger* Emery, *Ophthalmopone hottentota* Emery, *Camponotus fulvopilosus* De Geer and *Anoplolepis* cf. *trimeni* Forel in this study.

4.3 STUDY AREAS

Ant community patterns were investigated on two commercial farms in the southern Karoo, South Africa. The first study area was situated 25 km north-east of Prince Albert on the farm Tierberg (33° 07′ S, 22° 15′ E). The second farm, Hillside (33° 06′ S, 24° 31′ E), sited 25 km south-west of Jansenville, was approximately 230 km to the east of Tierberg. Two mountain ranges, the Swartberg and the Baviaanskloof, are situated to the south of Tierberg and Hillside respectively. These mountain ranges, which run parallel to each other, serve as rain shadows to the regions north of them.

Average annual rainfall at Tierberg is 169 mm (Prince Albert, 92 years) although the range is from 100 mm to 300 mm (Venter et al. 1986). Most of the yearly average is likely to fall between February and May, and the region is considered a transition between summer and winter rainfall regions (Milton et al. 1992). The mean annual maximum temperature at the nearest long term recording station, Beaufort West (32° 18′ S, 22° 40′ E, 49 years), was 25.2°C and the mean annual minimum temperature was 10.3°C. The climate is extreme with average highest monthly temperatures exceeding 35°C from October to March and average lowest monthly temperatures dropping below freezing from June to September (Weather Bureau 1986). Tierberg farm is separated into two distinct regions by a steep-sided rocky mountain belt (maximum altitude of 1124 m a.s.l.) which serves as a local rain shadow producing dryer conditions to the north of the belt. In this chapter, I refer to areas north of this belt as the Upper Tierberg rangeland and the lower altitude areas to the south as Lower Tierberg. The vegetation structure of the Upper Tierberg rangeland (± 850 m a.s.l.) was relatively homogeneous in structure and dominated by two plant species, the succulent *Ruschia spinosa* Hartm. & Stüber and the woody shrub *Eriocephalus ericoides* (L. f.) Druce. Two major study sites were established on an abandoned airstrip cut into the *Eriocephalus* rangeland. The greater part of the airstrip was sparsely vegetated with *Chrysocoma ciliata* L., an early successional asteraceous shrub. I refer to this site as the Airstrip site. A second study site was established to the western end of the airstrip where the density of *C. ciliata* was approximately seven times that occurring on the Airstrip site. Consequently, this second study area is referred to as the *Chrysocoma* site. The Lower Tierberg rangeland (± 780 m a.s.l.), also lacking spatial variability, was dominated by *Pteronia pallens* L. f., an unpalatable and competitively dominant woody shrub (Yeaton and Esler 1990). Tierberg farm was managed as a commercial enterprise with all the above rangeland grazed by Merino sheep.

East of Tierberg the rainfall increases and the mean annual rainfall at Jansenville (106 years) is 271 mm. Rain falls throughout the year although almost 60% of the yearly mean falls from November to March. The average monthly maximum temperature at Jansenville (63 years) exceeds 35°C from September to April and exceeds 40°C from December to February. Average monthly minimum temperatures are less than 5°C between May and October and drop below freezing in June and July (Weather Bureau 1986). The dominant plant at the Hillside study site was *Portulacaria afra* Jacq., a succulent arborescent shrub known locally as "spekboom". *Portulacaria afra* is distributed on rocky mountain sides throughout its range in the more arid (western) parts of the southern Karoo. Hillside farm, however, is unique because *P. afra* is distributed on the plains. Later-successional trees, located only on the mountain belts at Tierberg, are also common on the plains. *Portulacaria afra* forms distinct and discrete oval shaped clumps of up to 150 m^2 in area (Chapter 5). Ground cover between these clumps alternates from bare ground to a dense cover of weedy grasses (*Aristida* spp.). Woody shrubs (especially *Rhigozum obovatum* Burch.) are common in these areas. Less common in the *P. afra* rangeland are slightly raised, oval shaped mounds of variable size but within a range of 14 m^2 to 90 m^2 (Chapter 5). These mounds, referred to as nutrient rich patches (hereafter NRP), show evidence of extensive mammal digging activity. *Lycium cinereum* Thunb. and *Psilocaulon absimile* N. E. Brown, a dwarf succulent shrub, are common on NRP. *Portulacaria afra* is a highly palatable shrub and has been grazed out in extensive areas of the southern Karoo. The *P. afra* rangeland at Hillside was conservatively stocked with Angora goats.

In the text I refer to ant species belonging to the *Monomorium* sp.-_*salomonis*-group as *M. salomonis*. To avoid confusion with certain ant genera (e.g. *Pheidole*), the *Portulacaria afra* and the *Pteronia pallens* rangeland study sites are referred to as the *P. afra* and the *P. pallens* rangeland sites respectively.

4.4 METHODS

Pitfall trapping and observations at baiting stations are methods frequently employed in the study of ant communities. These methods indicate dominant species and the relative activity of subordinate species but do not accurately show the distribution and abundance of ant species in space or their use of habitat. Selection operates at the level of the colony and, more specifically, on the nest position. Consequently, in my data collection I concentrated on quantifying the nest position in terms of habitat and the distribution of nests relative to each other.

4.4.1 Ant spatial distribution and nearest-neighbour distances on Tierberg

The spatial distribution of *Tetramorium peringueyi* on the Airstrip, *Chrysocoma* and *Eriocephalus* sites was determined using the Clark and Evans (1954) nearest-neighbour technique. Each study area was thoroughly searched until at least 20 nests of *T. peringueyi* were found. Nests of this ant species were recognised by multiple nest entrances that often cover an area exceeding 1 m in diameter. The calculation of nearest-neighbour distances (hereafter NND) by the Clark and Evans test is unbiased only when a boundary strip is included in the study (Krebs 1989). Consequently, a boundary strip of at least 20 m width, surrounding the initial area, was searched for *T. peringueyi* nests. The positions of *T. peringueyi* nests (in shade of shrub or in open) were recorded. Sample sizes of *T. peringueyi* nests on the *Chrysocoma* site were low because the site was unavoidably small. Neighbour distances of *T. peringueyi* to its three nearest conspecific neighbours were measured at the

Airstrip and *Eriocephalus* sites and to its first nearest conspecific neighbour at the *Chrysocoma* site. A nearest-neighbour distance measurement was disregarded if another nest lay between it and the focal nest. Following Clark and Evans (1954), the mean distance to nearest neighbour (*Ra*) was computed as $\Sigma r/n$ where r was the distance from each nest to its nearest neighbour and n the number of nests in the sample. The mean distance expected if the population was distributed at random (*Re*) was then calculated as $1/2\sqrt{p}$, where p was the number of nests per unit area. The ratio *Ra*/*Re* yields an Index of Aggregation (*R*). In a random distribution, $R = 1$. An aggregated spatial distribution has a value of 0 and a population with a regular or overdispersed spatial distribution has an R value close to 2. Thompson's (1956) method was employed to test for spatial patterning for the second and third nearest neighbour distances of *T. peringueyi* on the Airstrip and *Eriocephalus* study sites. Differences between the first three *T. peringueyi* distances to nearest conspecific neighbour (at each site separately) were tested by one-way analysis of variance. Finally, the distance of *T. peringueyi* to its first conspecific neighbour at each study site was compared using one-way analysis of variance.

Pheidole sp. 1 was common at the *Chrysocoma* site and rare at the Airstrip and *Eriocephalus* sites. As above, the Clark and Evans technique was used to determine the spatial distribution of *Pheidole* sp. 1 at the *Chrysocoma* site. Nearest-neighbour distances of *Tetramorium peringueyi* to *Crematogaster melanogaster* were also measured on the *Chrysocoma* site. While searching for *T. peringueyi* nests in the *Eriocephalus* rangeland, it appeared that *T. peringueyi* nests were regularly spaced. However, occasionally, nests of *Messor capensis* and *Pheidole* spp. (*Pheidole* sp. 1 and *Pheidole* sp. 2) were located in the area where I expected to find *T. peringueyi* nests. Consequently, the search for nests in the *Eriocephalus* rangeland was extended to include *M. capensis* and *Pheidole* spp.

Next, because *Messor capensis* nests appeared to be regularly spaced with respect to its nearest *Tetramorium peringueyi* neighbour in the *Eriocephalus* rangeland, 19 *M. capensis* nests were located by a random walk in the *Eriocephalus* rangeland. Dean (1991) reports that *M. capensis* colonies occasionally have subnests of up to 10 m apart. These colonies were disregarded if encountered. Neighbour distances to the three nearest *T. peringueyi* nests were measured. As before, a neighbour distance measurement was disregarded if another *T. peringueyi* nest lay between it and the focal *M. capensis* nest. This work was done shortly after the first spring rains (October 1996) when alates leave the nest to establish new colonies. Generally, new *T. peringueyi* nests were easy to identify. They almost always had a single nest entrance positioned in open bare ground and were frequently surrounded by *Crematogaster melanogaster* individuals. Further, *T. peringueyi* individuals belonging to new nests were smaller than those of established nests. Although new *T. peringueyi* nests were marked, they were not included in the analyses. A one-way analysis of variance tested for differences between the first three nearest neighbour distances of *M. capensis* to *T. peringueyi*. A t-test compared *M. capensis*/*T. peringueyi* first to third neighbour distances with *T. peringueyi*/*T. peringueyi* first to third neighbour distances respectively.

4.4.2 Ant removal experiments

Because *Messor capensis*, *Pheidole* spp. and *Crematogaster melanogaster* seemed to be replacing *Tetramorium peringueyi* occasionally at both the Airstrip and *Eriocephalus* sites, *T. peringueyi* nests were removed to test whether this species was competitively inhibiting the distribution of other ant species. Eighteen *T. peringueyi* nests at the Airstrip site and another 18 *T. peringueyi* nests in the *Eriocephalus* rangeland were experimentally removed using a commercially available organophosphate poison (Turmoil®, Bayer). Prior to nest removal, the distance from the focal (poisoned) *T. peringueyi* nest to nests of all other ant species within a radius of 12 m of the focal nest was measured. The Airstrip and *Eriocephalus* rangeland *T. peringueyi* nests were removed in November 1995 and March 1996 respectively. The poisoned nests were inspected regularly and poison reapplied to any nests where application was not successful. Both the Airstrip and *Eriocephalus* rangeland manipulations were censused in October 1996. To determine whether ant species responded to the removal of *T. peringueyi*, I compared the distance from the focal nest to the nearest nest of various ant species to the same distance before poisoning. If a species had multiple nests throughout its territory ("nest decentralisation" strategy, Hölldobler and Lumsden 1980), the distance to the nearest "satellite" nest was recorded. A response (positive or negative) was scored if the difference between before and after measurements exceeded 1 m. No change was recorded if this difference was less than 1 m. The response of ant species to the removal of *T. peringueyi* was tested using the Sign test (Siegel and Castellan 1988). I also compared the number of nests of ant species located within an 8 m radius of the focal nest before and after treatment. Changes in nest density were tested using the Sign test. Using related samples to test for differences before and after treatment permits the use of each nest as its own control (Siegel and Castellan 1988). Both experiments were censused a second time in January 1997 and at the same time a further 15 *T. peringueyi* nests were randomly located in the *Eriocephalus* rangeland and the distance to the nearest *C. melanogaster* nest was measured. A t-test was used to test for differences between these "control" measurements and the same measurements before and after poisoning. Poisoned nests were not inspected following the October census. Measurements where *T. peringueyi* had returned to previously poisoned nests were not included in the second set of analyses but the distances to nearest neighbours were recorded. I was unable to make similar "control" measurements on the Airstrip site because most of the *T. peringueyi* nests distributed on the Airstrip site had been poisoned earlier. The NND measurements of *T. peringueyi* to *C. melanogaster* in the *Eriocephalus* rangeland were tested against the same distance measurements recorded at the *Chrysocoma* site by a t-test.

4.4.3 Ant distribution in the Lower rangeland

The density of *Tetramorium peringueyi* and *Messor capensis* in the *P. pallens* dominated plains of the Lower rangeland was measured by counting the number of nests located in an area of 70 m × 70 m. There were no drainage lines or washes in the area where these measurements were recorded. The study area was sub-divided into 5 m × 5 m quadrats (marked by pegs) which were then thoroughly searched for nests of *T. peringueyi* and *M. capensis*. A fish bait was placed at each marker peg and in the centre of the quadrat to assist in the search for nests. In addition, the identity of the dominant ant species attracted to each baiting station (only the four corner stations) was recorded and expressed as a percentage of all the baiting stations in the study area. This gave an indication of the relative abundance of dominant ant species in the Lower rangeland.

Ant species distribution was censused on and off a cut strip of vegetation in the Lower Tierberg rangeland. In January 1994 a 15 m × 750 m strip (hereafter the bushcut) was cleared of *Pteronia pallens*. In a replicated experiment, the vegetation on the bushcut responded significantly to the removal of *P. pallens* compared with that off the bushcut (Yeaton, Adie and Ross, unpublished data). Ten 10 m × 10 m quadrats were laid out along the length of the cut strip. A second set (paired with the first) of ten quadrats were placed in the *P. pallens* rangeland immediately adjacent to the first set of quadrats. Using fish bait to encourage ant activity, nests of all ant species found in the study quadrats were recorded. The two most common ant species were *Crematogaster melanogaster* and *Pheidole* sp. 2. Unlike *Tetramorium peringueyi* which has a single, centrally positioned nest, both of these species have "satellite" nests that are distributed throughout their territory. Satellite nest entrances were counted to give an indication of the relative abundance of *C. melanogaster* and *Pheidole* sp. 2 within each quadrat. Each study quadrat was divided into four 5 m × 5 m quadrats of which one was randomly selected for vegetation measurements. The identity of each plant within this sub-quadrat was recorded and its length along the long axis (*L*) and the greatest width (*W*) at right angles to the length measured. Cover of each individual was then calculated according to the formula $\pi LW/4$ (Cody 1986). Fisher's exact test (Siegel and Castellan 1988) was used to test for differences in ant species distribution (row headings are ant species presence or absence) on and off (column headings) the bushcut. Differences in nest density of each ant species on and off the bushcut was tested using the Median test (Siegel and Castellan 1988). Next, I reduced the plant community to include only those species with a cover of more than 5% of the total plant cover. I used regression analysis to test for association between ant species nest density and plant cover (cover of each plant species and total cover). Finally, I regressed the nest density of *C. melanogaster* against the nest density of *Pheidole* sp. 2 on the 20 quadrats to test for association between these two ant species.

In the Lower Tierberg rangeland *Tetramorium peringueyi* was very sparsely distributed compared with its distribution in the Upper Tierberg rangeland. When *T. peringueyi* nests were located in the Lower Tierberg rangeland, the distance to its nearest *Crematogaster melanogaster* or *Pheidole* sp. 2 neighbour (whichever was closer) was recorded. This measurement was then compared with the same *T. peringueyi* NND measurements at the *Eriocephalus* and *Chrysocoma* (Upper Tierberg) study sites using the Kruskal-Wallis one-way analysis of variance by ranks test (Siegel and Castellan 1988).

4.4.4 Ant nest positions at Tierberg

Ten study sites, representing a variety of microhabitats, were selected in the Upper rangeland at Tierberg. At all sites, a permanent 20 m × 20 m quadrat was established and marker pegs placed at 5 m intervals throughout each study site. Fish baits were placed at marker pegs to stimulate ant activity and each quadrat was thoroughly searched for ant nests. The position (under shrub canopy, in open) of all ant nest entrances with respect to the nearest shrub was recorded. Next, I recorded the position of 50 random "nest sites" at each study site. Two points on a straight line on either side of a marker peg were selected. The random points were 1 m away from the reference point and the orientation of the line was taken to be the direction of the sun. The position (under shrub canopy, in open) of the random point with respect to the nearest shrub was recorded. For each ant species, a minimum sample size of 16 nests was required for data analysis and data from different study sites were not pooled. The Chi-square goodness-of-fit test (Siegel and Castellan 1988) was used to determine whether the nest positions of certain ant species deviated from random. Expected numbers were calculated as the product of the total number of nests found for a particular ant species and the relative frequency of that particular position (shaded or open) determined from the random points at each site.

4.4.5 Vegetation sampling of ant study sites

The ellipse-intercept survey method (Stokes and Yeaton 1994) was used to compare percentage shrub cover and shrub density at the Airstrip, *Chrysocoma*, *Eriocephalus* and *P. pallens* rangeland sites. Ten 20 m transect lines were laid out at each site with lines evenly spaced so that vegetation sampling included the whole area where ants were censused. The identity of each plant intercepted by the transect line was recorded and the length of the longest axis (L) and greatest width at right angles to the long axis (W) measured. Percentage vegetation cover at each site was calculated as $100(\pi/4l).\Sigma(L_i.W_i/TW)$ where l is the total length of the transect line, L and W are the axes of the i^{th} individual plant and TW is the effective transect width calculated as $L\left(2/\pi+(1-2/\pi).(W/L)^{1.45}\right)$ (Stokes and Yeaton 1994). Total shrub density at each site was calculated as $(1/l).\Sigma(1/TW)$ (Stokes and Yeaton 1994). I compared the relative proportion of early-successional (*C. ciliata*) and later-successional (woody shrubs) plant species at the Airstrip, *Chrysocoma* and *Eriocephalus* study sites because Yeaton and Esler (1990) have shown that the establishment of woody shrub species is facilitated by pioneer plant species and a change in their relative proportions gives an estimate of temporal change.

4.4.6 Ant distribution in the *P. afra* rangeland

Habitat preference of ants in the *P. afra* rangeland was quantified by recording their presence or absence in the following five habitats: under *P. afra* clumps, in dense grassland, on nutrient rich patches (NRP), in sparse grass (*Rhigozum obovatum* dominant) and in sparse grass where *Lycium cinereum* was dominant. Sparse grass was defined as bare ground up to approximately 20% cover. A distinction was made between the latter two sparse grass habitats because those dominated by *L. cinereum* represent old NRP (Chapter 5). The *L. cinereum* dominated grassy habitat differed from NRP in that mesembs (*Psilocaulon absimile*) were absent and there was no active mammal digging activity. Soil texture in these habitats, however, differed from those sparse grass areas dominated by *R. obovatum*. *Rhigozum obovatum* establishes in dense grass (Chapter 5). Consequently, in my operational definitions, this was the only shrub that was included as part of the dense grass habitat (100%

grass cover). Nutrient rich patches have been described before under Study Areas. Ants were sampled by placing fish bait at regular intervals within a quadrat of approximately 5 m × 3 m. Because presence or absence of ant nests was recorded, I did not adhere strictly to a particular quadrat size. If ant nests were located within ± 1 m of the quadrat and in the habitat sampled, they were recorded as present. Individuals attracted to baits that had nests outside of the predetermined habitat were ignored. Fifteen replicates of each habitat were sampled. Results from Tierberg indicated that ant communities were numerically dominated by one, and occasionally two, species. In the *P. afra* rangeland, the two aggressive dominant ant species were *Pheidole* sp. 2 and *Tetramorium peringueyi*. I combined the data from the two shaded sites and the three open sites and then tested for differences in ant species distribution with respect to shading against these two dominant species using the Chi-square test for 2 × 2 contingency tables (Siegel and Castellan 1988) or Fisher's exact test depending on the number of counts in the table. In addition, the dimensions of each NRP were recorded and their areas calculated according to Cody (1986). I used the Median test to determine whether the size of NRP influenced the probability that both *T. peringueyi* and *Pheidole* sp. 2 coexisted on NRP.

Nests of the thermophilic ant species *Ocymyrmex barbiger* were always located on bare ground away from dense vegetation. To test whether this species was unable to exist in shaded sites, a board (1 m × 1 m) was positioned so that the nest of *O. barbiger* was shaded for the duration of the day. The sample size for the experiment was nine and a further nine nests without manipulation were monitored as control. The boards were maintained in place for four weeks and then removed. Nests were then checked every day for four days following board removal to determine their status. A nest was recorded as abandoned if the nest was no longer active or if the nest entrance moved more than 45 cm (i.e. beyond the shading effect of the board) from the original nest entrance marked when the experiment was initiated. The response of *O. barbiger* to shading was tested using Fisher's exact test with column headings as shaded versus unshaded nests and row headings as number of nests remaining and number of nests abandoned after treatment.

4.4.7 Ant activity patterns

Ant activity patterns were determined over a four day period at the *Chrysocoma* site and adjacent *Eriocephalus* rangeland at Tierberg. On the first day ambient temperature and soil surface temperatures at three microenvironments (in the open, under *Chrysocoma ciliata*, under *Ruschia spinosa*) were recorded every 20 minutes from before sunrise until after sunset. Temperatures were recorded within a 15 m × 15 m area and measurements in each microenvironment were replicated four times. The probe of an electronic thermometer was inserted just below the soil surface. Preselected ant nests were monitored for activity over a period of five minutes following the recording of temperature measurements. At least three nests of each ant species were monitored and activity was recorded if it occurred in two nests. Prior to foraging, ants congregate at their nest entrance. Consequently, a species was recorded as active if it was observed foraging away from the nest or inactive if individuals were not observed, if individuals were excavating soil only, or if individuals were congregated at their nest entrance. Data were not collected on overcast days or after rainfall. After data collection on the first day, it was noted that only two species, *Ocymyrmex barbiger* and *Anoplolepis* cf. *trimeni*, were active during the hot period of the day. Activity of all other species ceased by mid-morning at a soil surface temperature of about 45°C. For the following three days temperature measurements were recorded every 15 minutes but only soil surface temperature in the open was recorded and no activity patterns were monitored over the heat of the day as it was known that only the two thermophilic species were active. The same procedure was used to determine ant activity patterns in the Lower rangeland and at the *P. afra* rangeland at Hillside. At the *P. afra* rangeland, soil surface temperatures (n = 3) were recorded on bare soil, in dense grass and inside *P. afra* clumps. Ant activity was monitored on bare to sparsely vegetated areas and inside *P. afra* clumps.

4.4.8 Overt aggression between ant species

During the course of collecting the above data I recorded numerous observations of aggressive encounters within and between ant species. These interactions are summarised.

4.5 RESULTS

4.5.1 Ant spatial distribution and nearest-neighbour distances on Tierberg

A total of 43 *Tetramorium peringueyi* nests were found at the Airstrip site of which 24 were located within a 30 m × 200 m quadrat. Only two nests of *Pheidole* sp. 1 were located in the same area and *Crematogaster melanogaster* was absent from this site. The mean distance to nearest conspecific neighbour of *T. peringueyi* was 11.6 m (SE 0.52). This distance was significantly more than the distance expected if the population was distributed at random ($z = 4.37$, $p < 0.001$). An Index of Aggregation of 1.47 indicates that the distribution of *T. peringueyi* tends towards regular on the airstrip (Table 4.1).

Twenty-three *Tetramorium peringueyi* nests were found in an area of 90 m × 95 m in the *Eriocephalus* rangeland. Two nests of *Messor capensis* and one each of *Pheidole* sp. 1 and

Pheidole sp. 2 were found in the same area. *Crematogaster melanogaster* was common in the *Eriocephalus* rangeland but was never observed in close proximity to nests of *T. peringueyi*. The mean distance of *T. peringueyi* to its nearest conspecific neighbour was 14.3 m (SE 0.57), significantly more than the distance calculated if the population had a random distribution ($z = 4.48$, $p < 0.001$). The Index of Aggregation was 1.49 indicating an overdispersed spatial distribution (Table 4.1).

TABLE 4.1: Spatial distribution of *Tetramorium peringueyi* and nest density of *Pheidole* sp. 1 at the Airstrip, *Chrysocoma* and *Eriocephalus* rangeland study sites at Tierberg, Prince Albert. The comparative nest density of *T. peringueyi* at the Lower Tierberg rangeland site is also presented. Nest densities are presented as the number of nests/1000m^2. Distances to nearest neighbours are presented as mean (± SE). *Ra* is the mean distance to nearest neighbour and *Re* is the mean distance expected if the population was distributed at random.

	Airstrip	*Chrysocoma*	*Eriocephalus*	Lower rangel.
Ra	11.6 m^a ± 0.52	7.2 m ± 0.81	14.3 m^a ± 0.57	-
Re	7.9 m	6.9 m	9.6 m	-
Index of Aggregation	1.47^b	1.04^c	1.48^b	-
Area of study site	6000 m^2	2070 m^2	8550 m^2	4900 m^2
Nest density: *T. peringueyi*	4	5.3	2.7	0.4
Nest density: *Pheidole*. sp. 1	0.3	5.3	0.1	-

[a] indicates a significant deviation from random at the 0.001 level.

[b] overdispersed spatial distribution.

[c] random spatial distribution.

The *Chrysocoma* study site was unavoidably small (27.5 m × 75.3 m) and sample sizes were consequently low. However, there are stark contrasts when compared with the other two study areas (Table 4.1). On average the nearest conspecific neighbour distance of *Tetramorium peringueyi* was 7.2 m (SE 0.81) and this value did not deviate significantly from the mean distance expected from a random distribution ($z = 0.28$, $p = 0.4$). An Index of Aggregation of 1.04 was close to the 1.00 expected from a perfectly random distribution. Unlike the other two sites, *Pheidole* sp. 1 was common at the *Chrysocoma* site but, like *T. peringueyi,* this species had a random distribution ($R = 0.91$). *Crematogaster melanogaster* was also common on the *Chrysocoma* site. Furthermore *Anoplolepis steingroeveri*, an aggressive ant species typically restricted to washes and drainage lines in the *Eriocephalus* rangeland, was present at the *Chrysocoma* site.

Mean values for the first three nearest conspecific neighbours of *Tetramorium peringueyi* on the Airstrip ($F = 18.9$, df = 71, $p < 0.001$) and the *Eriocephalus* rangeland ($F = 18.5$, df = 64, $p < 0.001$) differ significantly from each other (Table 4.2). Application of Thompson's (1956) method to the second ($z = 5.57$, $p < 0.001$) and third ($z = 5.68$, $p < 0.001$) nearest conspecific neighbour distances of *T. peringueyi* indicates a regular spatial distribution in the *Eriocephalus* rangeland. Similar results were obtained for the second ($z = 7.27$, $p < 0.001$) and third ($z = 10.03$, $p < 0.001$) nearest-neighbour distances of *T. peringueyi* on the Airstrip. These nearest neighbour distance values support the above Clark and Evans calculations that *T. peringueyi* was the dominant ant species on the Airstrip and in the *Eriocephalus* rangeland because its distribution is strongly overdispersed. The regular spatial distribution implies that intraspecific competition is important in the distribution of *T. peringueyi*. The first ($t = 3.56$, $p < 0.001$), second ($t = 1.87$, $p = 0.07$) and third ($t = 2.13$, $p < 0.05$) NND of the Airstrip *T. peringueyi* population were less than the same values in the *Eriocephalus* rangeland (Table 4.2). The nearest conspecific neighbour distance of *T. peringueyi* at the *Chrysocoma* site was

TABLE 4.2: Nearest conspecific neighbour distances of *Tetramorium peringueyi* at the Airstrip and *Eriocephalus* rangeland study sites at Tierberg, Prince Albert. The nearest *T. peringueyi* neighbour of *Messor capensis* at the *Eriocephalus* rangeland study site is also presented. Distances to nearest neighbours are presented as mean (± SE).

	T. peringueyi to *T. peringueyi* (Airstrip)	*T. peringueyi* to *T. peringueyi* (*Eriocephalus*)	Level of significance [a]	*M. capensis* to *T. peringueyi* (*Eriocephalus*)	Level of significance [b]
NND 1	11.6 m ± 0.52	14.3 m ± 0.57	$p < 0.001$	11.7 m ± 0.60	$p < 0.01$
NND 2	15.0 m ± 0.79	16.9 m ± 0.61	$p = 0.07$	15.7 m ± 0.76	$p > 0.1$
NND 3	17.5 m ± 0.70	19.5 m ± 0.59	$p < 0.05$	18.8 m ± 0.89	$p > 0.1$

[a] compares *T. peringueyi* to *T. peringueyi* NND between Airstrip and *Eriocephalus* sites (t-test).

[b] compares *T. peringueyi* to *T. peringueyi* NND with *M. capensis* to *T. peringueyi* NND at the *Eriocephalus* site (t-test).

7.2 m (SE 0.81), significantly less than the same measurements at the Airstrip and *Eriocephalus* sites ($F = 26.9$, df = 57, $p < 0.001$). This, together with the fact that *T. peringueyi/C. melanogaster* NND at the *Chrysocoma* site (2.7 m, SE 0.66) were significantly less than at the *Eriocephalus* rangeland (6.9 m, SE 0.46, $t = 5.35$, df = 24, $p < 0.001$) supports the above inference that there is a strong competitive interaction between *T. peringueyi* and *C. melanogaster*.

The mean values of the first three NND of *Messor capensis* to *Tetramorium peringueyi* in the *Eriocephalus* rangeland differed significantly from each other ($F = 21.6$, df = 56, $p < 0.001$). The first NND of *M. capensis* to *T. peringueyi* was significantly less than the same measurement of *T. peringueyi* to *T. peringueyi* in the *Eriocephalus* rangeland ($t = 3.16$, $p < 0.01$) but the second and third NND did not differ (Table 4.2). These data imply that *M. capensis* is overdispersed with respect to *T. peringueyi* and suggests competitive interactions between the two species. That *T. peringueyi* is itself overdispersed implies that *T. peringueyi* competitively inhibits the distribution of *M. capensis*. The competitive interaction, however, is not reciprocal and *M. capensis* permits new *T. peringueyi* nests to establish in relative close proximity to their nests. This probably explains the significant difference in the first NND.

4.5.2 Ant removal experiments

Three ant species were common enough to allow statistical evaluation of their response to the removal of *Tetramorium peringueyi*. *Monomorium havilandi* responded significantly to the removal of *T. peringueyi* on the airstrip (Sign test, $p < 0.01$, $n = 16$). Out of 18 nests poisoned, *M. havilandi* moved closer than the distance measured before poisoning on 14 occasions. Two nests did not change and two nests moved further away than the distance before poisoning. On average, nests of *M. havilandi* moved 3.6 m closer to the focal *T. peringueyi* nest after poisoning. The number of *M. havilandi* nests within an 8 m radius of the focal nest increased significantly following the removal of *T. peringueyi* on the airstrip (Sign test, $p < 0.01$, $n = 12$). The distribution of *M. havilandi* with respect to the poisoned nests did not change from the October to January census but there was change when comparing measurements before application with the January census (Sign test, $p < 0.001$, $n = 15$). Also on the Airstrip site, *Monomorium australe* moved closer to the poisoned nests when censused in January (Sign test, $p < 0.05$, $n = 13$) after showing no change in its distribution earlier.

In the *Eriocephalus* rangeland, *Crematogaster melanogaster* "satellite" nests moved significantly closer to the focal *Tetramorium peringueyi* nest after poisoning (Sign test, $p < 0.001$, $n = 16$). With the sample size reduced to 16 because of tied values, *C. melanogaster* nests moved closer on all 16 occasions. The number of *C. melanogaster* nests within an 8 m radius of the original *T. peringueyi* nest increased significantly (Sign test, $p < 0.001$, $n = 16$). The January census indicated further change from the October census. Although the sample size was reduced to ten because *T. peringueyi* had returned to five of the poisoned nests, *C. melanogaster* moved closer on nine occasions (Sign test, $p < 0.05$, $n = 10$). Of the five nests where *T. peringueyi* had returned after poison was no longer applied, *C. melanogaster* moved away from the occupied nest on four occasions and these new measurements did not differ from the "control" measurements (Wilcoxon-Mann-Whitney test, $z = -0.65$, $p = 0.52$, $n = 19$). "Control" measurements of *T. peringueyi* to *C. melanogaster* did not differ from the same measurements before the application of poison ($t = 1.12$, df = 24, $p = 0.27$) but the "control" measurements were significantly greater than the measurements recorded for the October ($t = -4.98$, df = 30, $p < 0.001$) and January ($t = -7.86$, df = 26, $p < 0.001$) censuses (Table 4.3). Clearly, *T. peringueyi* competitively inhibits the distribution of at least three ant species. These data support the inferences made earlier on the basis of distributional patterns.

TABLE 4.3: Mean distance measurement of *Tetramorium peringueyi* nest to its nearest *Crematogaster melanogaster* neighbour nest in the *Eriocephalus* rangeland at Tierberg, Prince Albert before application of poison to selected *T. peringueyi* nests and after application. After application (1) and (2) refer to measurements recorded in October and January, respectively. The before and "control" measurements are underestimates of the true value because on several occasions *C. melanogaster* was not recorded within 12 m of the focal nest.

	Mean NND ± SE (*n*)
Before application	7.6 m ± 0.41 (11)
After application (1)	3.9 m ± 0.38 (17)
After application (2)	2.1 m ± 0.38 (13)
"Control"	6.9 m ± 0.46 (15)

4.5.3 Ant distribution in the Lower rangeland

Two *Tetramorium peringueyi* and seven *Messor capensis* nests were located in an area of 70 m × 70 m in the *P. pallens* dominated Lower rangeland. The density of *T. peringueyi* decreased compared with its distribution at the Upper rangeland study sites (Table 4.1).

Unlike the Upper rangeland sites, *Pheidole* sp. 2 and *Crematogaster melanogaster* were numerically dominant at the Lower rangeland study site. These two species dominated 68% and 27.5% of baiting stations (n = 225) respectively. *Tetramorium peringueyi* and *M. capensis* were dominant at only three baiting stations each.

Supporting the above results, two ant species, *Pheidole* sp. 2 and *Crematogaster melanogaster*, were common at the bushcut manipulation site in the Lower Tierberg rangeland and very few nests of other ant species were found. Only two *Tetramorium peringueyi* nests were found on the 20 quadrats censused. In terms of presence and absence, neither *Pheidole* sp. 2 (Fisher's exact test, $p = 0.15$) or *C. melanogaster* (Fisher's exact test, $p = 0.53$) differed in their distribution between the bushcut and the adjacent *P. pallens* rangeland. However, *Pheidole* sp. 2 nests tended to be more densely distributed on the cut strip (Median test, $p < 0.05$). This was probably because of the increase in mat-forming mesembs, *Brownanthus ciliatus* (Ait.) Schwant. and *Malephora lutea* Schwant. (Yeaton and Adie, unpublished data), under which *Pheidole* sp. 2 tended to nest. Five plant species (*B. ciliatus*, *M. lutea*, *R. spinosa*, *Galenia fruticosa* (L. f.) Sond and *P. pallens*) had cover values exceeding 5% of the total. Ant nest density of *Pheidole* sp. 2 and *C. melanogaster* was not correlated to cover of these plant species or various combinations of them. The density of *Pheidole* sp. 2 was significantly and negatively correlated with the density of *C. melanogaster* ($y = -1.26x + 12.02$, $r = 0.93$, $p < 0.001$). While collecting these data, it was clear that territories of these two ant species were mutually exclusive. Where workers of both species recruited to the same fish bait, interactions were overtly aggressive with *Pheidole* sp. 2 tending to displace the other because of its ability to recruit large numbers of workers rapidly.

On average, the nearest *Crematogaster melanogaster* nest was 7.6 m (SE 0.66, n = 11) from *Tetramorium peringueyi* in the *Eriocephalus* rangeland. Nests of *T. peringueyi* were uncommon and hence difficult to find in the Lower Tierberg rangeland. On all but one occasion *Pheidole* sp. 2 was the nearest neighbour of *T. peringueyi*. Nearest-neighbour distances of *T. peringueyi* to *C. melanogaster* and *Pheidole* sp. 2 in the Lower rangeland were combined to yield an average NND of 3.9 m (SE 0.28, n = 8). Testing for differences between these measurements from the Lower rangeland, *Chrysocoma* and *Eriocephalus* sites indicated significant deviations from chance effects ($KW = 18.76$, df = 2, $p < 0.001$). A multiple comparison indicated that the Lower rangeland did not differ from the *Chrysocoma* site but that measurements recorded at both of these sites were significantly less than at the *Eriocephalus* site. Also, the *T. peringueyi* to *C. melanogaster* NND at the *Chrysocoma* site did not differ from the same measurements following poisoning at the *Eriocephalus* ($t = 1.71$, df = 26, $p = 0.1$) site indicating reduced competitive ability of *T. peringueyi* at the *Chrysocoma* site. Together with the relative rarity of *T. peringueyi* in the Lower rangeland, this implies that the competitive ability of *T. peringueyi* in the Lower rangeland was markedly reduced compared with the *Eriocephalus* rangeland.

4.5.4 Ant nest positions at Tierberg

Nests of most ant species recorded from study sites in the Upper Tierberg rangeland were not randomly positioned. *Pheidole* sp. 2 nests were positioned most frequently in the shade of shrubs (Site 6: $\chi^2 = 49.8$, $p < 0.001$, Site 11: $\chi^2 = 215.3$, $p < 0.001$). Likewise, nests of *Crematogaster melanogaster* were almost always positioned in the root systems of shrubs (Site 1: $\chi^2 = 75$, $p < 0.001$, Site 3: $\chi^2 = 13.4$, $p < 0.001$, Site 4: $\chi^2 = 40.1$, $p < 0.001$, Site 8: $\chi^2 = 32$, $p < 0.001$). *Anoplolepis steingroeveri*, which had a decentralised territorial strategy, also positioned its nests under shrubs (Site 2: $\chi^2 = 189.4$, $p < 0.001$, Site 7: $\chi^2 = 34.7$, $p < 0.001$, Site 11: $\chi^2 = 275.3$, $p < 0.001$). Although nests of *Monomorium salomonis* tended to be in shaded sites, this was not always statistically significant (Site 1: $\chi^2 = 29.4$, $p < 0.001$, Site 4: $\chi^2 = 1.1$, Site 7: $\chi^2 = 1.4$, Site 8: $\chi^2 = 2.7$, Site 11: $\chi^2 = 37.3$, $p < 0.001$). *Anoplolepis* cf. *trimeni* positioned its nests most frequently in the open at Site 2 ($\chi^2 = 7.5$, $p < 0.01$). Sample sizes were not large enough to test nest positions of *M. havilandi* and *Ocymyrmex barbiger*, both of which tend to position nests in the open away from vegetation. All 41 *Tetramorium peringueyi* nests located in the *Eriocephalus* rangeland were positioned in the root systems of shrub clumps. New nests ($n = 3$), however, were located in open ground. At the Airport study site, 16 *T. peringueyi* were positioned in the open and eight nests were associated with open canopied *Chrysocoma ciliata* shrubs.

4.5.5 Vegetation sampling of ant study sites

Percentage shrub cover and shrub density increased from the Airstrip to the *Chrysocoma* and *Eriocephalus* study sites (Table 4.4). Although the relative proportion of *C. ciliata* increased significantly at the *Chrysocoma* site, the proportion of early-successional shrub species at the Airstrip and *Chrysocoma* sites was the same. In contrast, woody shrub species were dominant at the *Eriocephalus* study site (Table 4.5). Shrub cover and density at the *P. pallens* study site in the Lower Tierberg rangeland was less than the *Eriocephalus* site but was greater than the Airstrip and *Chrysocoma* sites (Table 4.4).

TABLE 4.4: Percentage plant cover and plant density (plants/m^2) at the Airstrip, *Chrysocoma*, *Eriocephalus* and *Pteronia pallens* rangeland study sites at Tierberg, Prince Albert.

	Shrub cover (%)	Shrub density (plants/m^2)
Airstrip site	4.8	2.1
Chrysocoma site	13.1	3.4
Eriocephalus site	34.8	4.8
Pteronia pallens site	25.1	4.3

TABLE 4.5: The relative importance of early successional plant species (mesembs and *Chrysocoma ciliata*) and later-successional plant species (woody shrubs) at the Airstrip, *Chrysocoma* and *Eriocephalus* rangeland study sites at Tierberg, Prince Albert.

	Airstrip	*Chrysocoma*	*Eriocephalus*
Total shrubs	49	116	234
Relative proportion: *C. ciliata*	0.65	0.91	0.06
Relative proportion: mesembs	0.31	0.05	0.43
Relative proportion: woody shrubs	0.04	0.04	0.51
No. of woody shrub species	2	3	8

4.5.6 Ant distribution in the *P. afra* rangeland

Ant species in the *P. afra* rangeland showed clear distributional patterns relating to the degree of shading by vegetation (Table 4.6). *Pheidole* sp. 2 was the most common ant species in the *P. afra* rangeland and was recorded in all the habitats sampled. This species was particularly dominant in well-shaded habitats (*P. afra* clump, dense grass) where few other species were present. The distribution of *Pheidole* sp. 2 differed significantly from *Tetramorium peringueyi* (Fisher's exact test, $p < 0.001$), *T. quadrispinosum* ($\chi^2 = 4.3$, df = 1,

$p < 0.001$), *Ocymyrmex barbiger* (Fisher's exact test, $p < 0.001$), *Monomorium australe* (Fisher's exact test, $p < 0.01$) and *M. alamarum* (Fisher's exact test, $p < 0.001$). The decentralised territorial system of *Pheidole* sp. 2 enabled this species to "invade" bare areas, hence its commonness in unshaded sites. *Tetramorium peringueyi* was rare in well-shaded habitats and most common on NRP but this species was frequently distributed in both other unshaded habitats. *Tetramorium peringueyi* occupied the same habitats as *T. quadrispinosum* (Fisher's exact test, $p = 0.13$), *O. barbiger* (Fisher's exact test, $p = 0.11$), *M. australe* (Fisher's exact test, $p = 0.47$) and *M. alamarum* (Fisher's exact test, $p = 0.23$). Smaller NRP (less than the median size in this sample) supported either *T. peringueyi* or *Pheidole* sp. 2 but not both species (Median test, $p < 0.05$). This result confirms earlier findings of competitive interactions between aggressive dominant ant species. Ant species were most common on NRP (Table 4.6). *Ocymyrmex barbiger* and *M. alamarum* were most frequently recorded from unshaded sites and appeared to select nest sites in softer soils characteristic of NRP and ancient NRP. *Monomorium australe* was most common on NRP. Although most common on NRP, nests of *T. quadrispinosum* were also located in dense grass. I have shown elsewhere (Chapter 5) that *Messor capensis* nests more frequently beneath woody shrubs (*R. obovatum*, in particular) in the *P. afra* rangeland. Although nests of this species were uncommon on NRP, trunk trails of *M. capensis* lead directly to 13 of the 15 NRP sampled.

TABLE 4.6: The distribution of common ant species in five habitats at the *P. afra* rangeland, Hillside, Jansenville. Data represent the frequency a species was present in a habitat ($n = 15$). See text for habitat descriptions.

	P. afra clump	Dense grass	NRP	Sparse grass (*L. cinereum*)	Sparse grass (*R. obovatum*)
Pheidole sp. 2	15	15	9	8	7
Tetramorium peringueyi	0	4	13	10	8
T. quadrispinosum	0	5	10	1	4
Ocymyrmex barbiger	0	0	14	9	2
Monomorium australe	0	0	5	1	1
M. alamarum	0	0	8	6	1
Messor capensis	0	2	2	1	3

Experimental shading of *Ocymyrmex barbiger* nests caused nest abandonment. Six shaded and one control nest were abandoned after one month (Fisher's exact test, $p < 0.05$). Nests of *Pheidole* sp. 2 moved in under the shade of boards on two occasions and workers of this species were active throughout the day in this shaded environment. On three occasions new nests of *O. barbiger* were recorded from open sites in the vicinity of experimentally shaded sites but it was not possible to determine whether the shaded nests had moved to these new positions. Informal soil surface measurements recorded at 1300H showed the temperature in the shade of the board was 27.2°C while the corresponding measurement in the open was 60.5°C. In the following section I will show that *O. barbiger* only becomes active at ± 40°C.

4.5.7 Ant activity patterns

Activity patterns of ant species were strongly dependent on temperature although light may also be an important cue initiating and halting activity of certain species (Figure 4.1). Activity patterns between the Upper and Lower rangeland sites were similar and will be discussed together (Table 4.7). All species except the two thermophilic ants (*Anoplolepis* cf. *trimeni*, *Ocymyrmex barbiger*) had a bimodal activity pattern. *Crematogaster melanogaster* and *Pheidole* sp. 1 were active during hours of darkness before sunrise and after sunset suggesting that temperature was the most important cue halting their activity in the morning and initiating their activity in the afternoon. Most other species ceased activity in the late afternoon despite the soil surface temperature being well within their range of tolerance. This suggests that daylight and not temperature initiates activity in the morning and halts foraging in the late afternoon. *Tetramorium peringueyi* and *C. melanogaster* were active over a similar range of temperatures and were able to tolerate far higher temperatures than *Pheidole* sp. 2. Of the aggressive dominant species, *A. steingroeveri* was unusual in that it was active at high temperatures. Generally, the seed harvesting species tolerated slightly higher temperatures compared to the dominant species.

As before, ant species activity in the *P. afra* rangeland showed distinct temperature zonation with dominant ant species (*Pheidole* sp. 2, *Tetramorium peringueyi*) active at lower temperatures (Figure 4.2). These species were replaced, with a small zone of overlap, by the scavengers (*T. quadrispinosum*, *Monomorium australe*) which in turn were replaced by the true thermophilic species (*Ocymyrmex barbiger*). The seed harvesting species (*Messor capensis*, *Monomorium alamarum*) were active over a temperature range similar to the aggressive dominant species but were able to tolerate slightly higher temperatures. Ant activity in the *P. afra* rangeland differs from that at the two shrub-dominated study sites because vegetation cover modifies the environment which significantly alters ant activity patterns. For example, nests of *Pheidole* sp. 2 situated in the open were active for a short time in the morning with activity ceasing by about 37°C. Nests of the same species positioned in *P. afra* clumps were active the whole day despite maximum temperatures in the open exceeding 60°C. Corresponding soil surface temperatures below *P. afra* clumps did not exceed 30°C which was well below the critical temperature at which *Pheidole* sp. 2 became inactive (Figure 4.2). Whereas maximum soil surface temperatures in dense grass exceed the critical 37°C, this habitat would also allow *Pheidole* sp. 2 to extend its period of activity. Although similar temperature differentials were recorded in the Upper rangeland sites, shrubs do not provide the same area of cover as grass or *P. afra* and hence do not permit species to extend their activity in the same way.

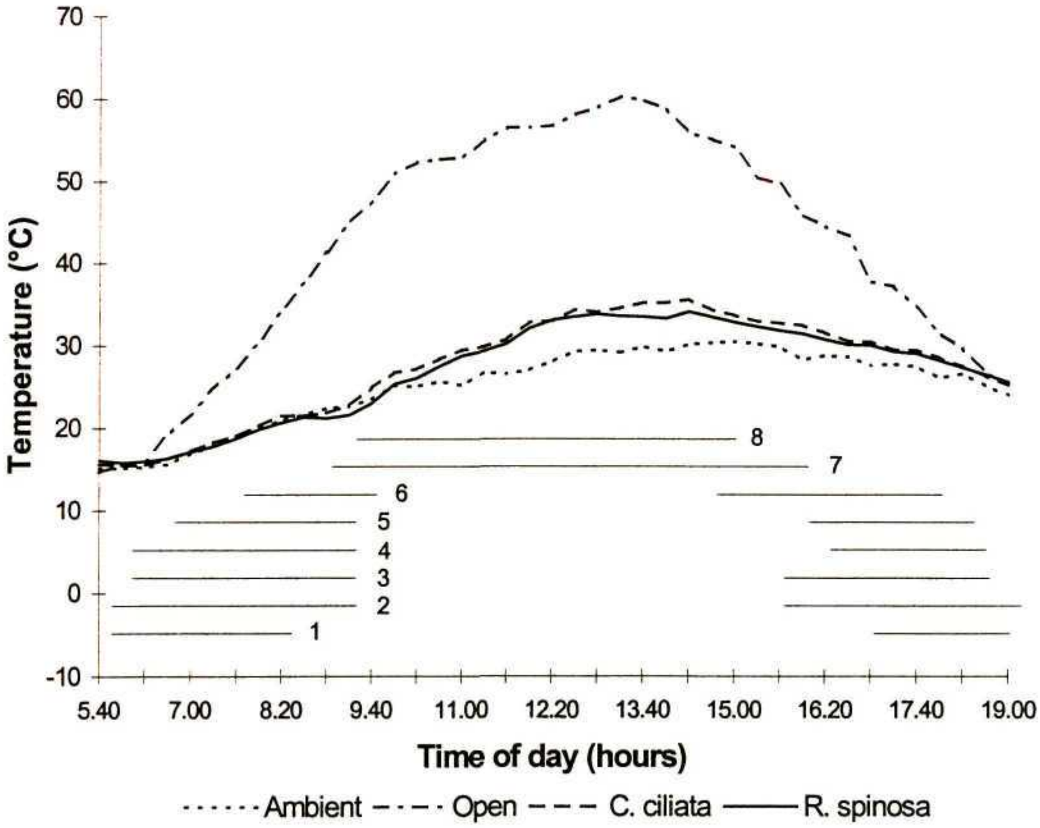

FIGURE 4.1: The change in temperature recorded at three microhabitats on one day at the *Chrysocoma* site, Tierberg farm, Prince Albert. Lines indicate the time ant species were active during the day. 1 - *Pheidole* sp. 1, 2 - *Crematogaster melanogaster*, 3 - *Tetramorium peringueyi*, 4 - *Monomorium havilandi*, 5 - *M. salomonis*, 6 - *M. australe*, 7 - *Anoplolepis* cf. *trimeni*, 8 - *Ocymyrmex barbiger*.

TABLE 4.7: Temperatures at which common ant species at Tierberg, Prince Albert were active. All species except *Ocymyrmex barbiger* and *Anoplolepis* cf. *trimeni* had a bimodal activity pattern. Temperatures in brackets are maximum temperatures at which those species were recorded as active. The range in tolerance to temperature of each species are not a true representation because measurements were recorded in summer only. Lower temperature measurements (bold) are therefore likely to decrease.

	Upper rangeland		Lower rangeland	
	AM (°C)	PM (°C)	AM (°C)	PM (°C)
Tetramorium peringueyi	**15.5** - 40.7	47.1 - **26.8**	**16.7** - 39.2	47.4 - **29.5**
Crematogaster melanogaster	**12.7** - 44.3	49.6 - **25.2**	**16.7** - 38.4	48.7 - **26.8**
Pheidole sp. 2			**16.7** - 37.9	39.2 - **29.5**
Pheidole sp. 1	**12.7** - 37.1	39.6 - **25.2**		
Anoplolepis steingroeveri	**16.8** - 53.0	52.3 - **34.4**		
Monomorium australe	27.2 - 50.9	53.2 - 31.5	27.9 - 50.5	51.5 - 32.4
M. havilandi	**15.5** - 44.3	44.7 - **26.8**		
M. salomonis	**16.8** - 44.3	46.4 - **29.7**		
Ocymyrmex barbiger	44.3 - (60.3)	(60.3) - 47.6		
A. cf. *trimeni*	41.3 - (60.3)	(60.3) - 44.7		

4.5.8 Overt aggression between ant species

The above results indicate that most ant species in the *P. afra* rangeland were distributed on NRP. It was here that many aggressive interactions between species were observed. Aggressive encounters between neighbouring *Tetramorium peringueyi* colonies were common. Active over a similar temperature range, this species was also involved in overt confrontation with *Pheidole* sp. 2. *Pheidole* sp. 2, however, was usually the winner of such interactions because of its ability to recruit many individuals very rapidly. Interference competition between *Crematogaster melanogaster* and *T. peringueyi* was observed on numerous occasions at the *Chrysocoma* site. Workers of *C. melanogaster* surrounded the nest entrances of *T. peringueyi* and attacked them when they attempted to leave their nest.

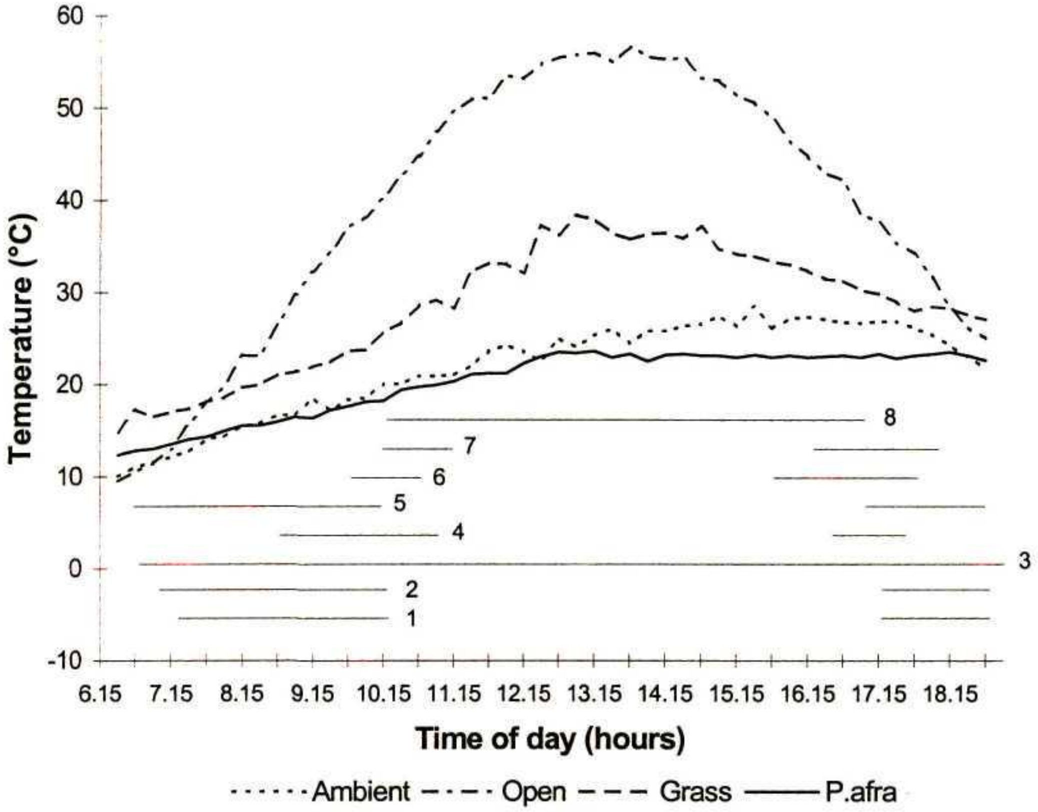

FIGURE 4.2: The change in temperature recorded at three microhabitats on one day at the *P. afra* rangeland site, Hillside farm, Jansenville. Lines indicate the time ant species were active during the day. 1 - *Tetramorium peringueyi*, 2 - *Pheidole* sp. 2 in the open, 3 -*Pheidole* sp. 2 under *P. afra*, 4 - *Monomorium alamarum*, 5 - *Messor capensis*, 6 -*T. quadrispinosum*, 7 - *Monomorium australe*, 8 - *Ocymyrmex barbiger*.

Tetramorium quadrispinosum was active at slightly higher temperatures than *T. peringueyi* and *Pheidole* sp. 2 (see previous section) but there was a zone of overlap when all three species were active. Despite the aggressive nature of *T. peringueyi* and *Pheidole* sp. 2, *T. quadrispinosum* (a more gracile species in appearance) was competitively superior at higher temperatures and was frequently observed attacking and removing individuals of the two former species (even the *Pheidole* sp. 2 majors) back to its nest. *Ocymyrmex barbiger*, a very submissive species, was also observed carrying *T. peringueyi* individuals back to its nest. A similar encounter between *Monomorium australe* (more heat tolerant) and *Pheidole* sp. 2 was recorded at Tierberg and on NRP in the *P. afra* rangeland. At Tierberg, *M. australe* was observed closing nest entrances of *Pheidole* sp. 2 with small pebbles but on another occasion it was seen excavating the nest entrance of *Pheidole* sp. 2 and removing individuals over a sustained period. Like *T. peringueyi*, *T. quadrispinosum* attacked conspecifics. Specialist ant species (such as *Camponotus fulvopilosus*, *O. barbiger*) avoided direct confrontation and at baiting stations these species were always subordinate to the aggressive dominants. However, *T. peringueyi* was frequently observed dropping small pebbles down nest entrances of certain specialist ant species (*C. fulvopilosus*, *Ophthalmopone hottentota*) that were positioned in close proximity to their nests. Conflict between *Ocymyrmex barbiger* conspecifics over a food resource appeared to be a ritualised confrontation with individuals standing head-on towards each other while antennae touched rapidly.

4.6 DISCUSSION

4.6.1 Ant community dynamics and structure

The results demonstrate that competition within the ant community studied is widespread. Dominant ant species control the distribution and abundance of several other ant species of various sizes and trophic levels. The frequency of overt aggressive encounters (intraspecific and interspecific) suggests that interference competition determines the outcome of competitive interactions.

The relative abundance of early-successional shrub species and woody shrub species indicates that temporal successional patterns at Tierberg can be inferred in space by the Airstrip, *Chrysocoma* and *Eriocephalus* sites. Dominance hierarchies of ant species are evident along this successional gradient. *Tetramorium peringueyi* was dominant at the Airstrip site where *Crematogaster melanogaster* was absent but was less successful at the *Chrysocoma* site where *C. melanogaster* was common. At the *Eriocephalus* site, where shrub cover and density was relatively high, *T. peringueyi* was dominant and *C. melanogaster* was present but not distributed in the vicinity of *T. peringueyi* territories (Table 4.8). Nests of *T. peringueyi* were not necessarily associated with shrubs at the Airstrip site but, at the *Eriocephalus* site, nests of *T. peringueyi* and *C. melanogaster* were always associated with shrub clumps. Ant community dominance in the Lower rangeland was shared by *Pheidole* sp. 2 and *C. melanogaster* at the expense of *T. peringueyi*, which was uncommon. The nearest non-conspecific neighbour distance of *T. peringueyi* in the Lower rangeland decreased significantly from that measured in the Upper rangeland indicating a reduced competitive ability of *T. peringueyi* in the Lower rangeland. Likewise, in the *P. afra* rangeland at Hillside, *Pheidole* sp. 2 was the dominant ant species and *T. peringueyi* was only present on sparsely vegetated NRP and bare regions (Table 4.8). Apart from *Pheidole* sp. 2, common ant species in the *P. afra* rangeland did not differ in their distribution from *T. peringueyi*. This does not imply that these species do not compete with *T. peringueyi*. Rather, these species, unable to outperform *Pheidole* sp. 2 in well shaded habitats, were distributed in open areas where *Pheidole* sp. 2 was less successful.

TABLE 4.8: Summary of distribution patterns of aggressive dominant ant species at Tierberg, Prince Albert and in the *P. afra* rangeland at Hillside, Jansenville.

	Airstrip	*Chrysocoma*	*Eriocephalus*	Lower rangeland	*P. afra* rangeland
Tetramorium peringueyi	Dominant	Present	Dominant	Rare	Sub-dominant
Pheidole sp. 2	Absent	Absent	Rare	Dominant	Dominant
Crematogaster melanogaster	Absent	Dominant	Sub-dominant	Sub-dominant	Absent
Anoplolepis steingroeveri	Absent	Present	Absent [a]	Absent [a]	Absent

[a] except in drainage lines and washes.

These patterns of ant species distribution indicate that ant community structure is controlled by dominance hierarchies which result in competitive exclusion and species replacement. Competitive ability appears to be altered by vegetation structure. In the discussion that follows, I will address two questions. Firstly, how can we account for the observed competitive hierarchies in each vegetation type? Secondly, despite evidence of widespread competitive interactions, how do ant species coexist in the communities studied?

4.6.2 Thermal tolerance, foraging activity and competitive superiority

Above-ground foraging activity of ants is constrained by soil-surface temperature (Bernstein 1974, Whitford 1978, Briese and Macauley 1980). Moreover, temperature and humidity within the nest are critical to egg production and the successful development of egg and larval stages (Brian and Brian 1951, Scherba 1959, Brian and Kelly 1967, Hölldobler and Wilson 1990). The importance of these physical conditions to the distribution and abundance of ants has led Hölldobler and Wilson (1990) to refer to ant species' tolerance to these conditions as that species' temperature-humidity (hereafter TH) envelope. Ants control below-ground conditions by nest location, nest construction, migration within nests and between multiple nests, as well as by regulation of metabolic heat where individuals cluster or remain dispersed within the nest (Hölldobler and Wilson 1990). However, there will be a critical TH level above or below which the colony will not reproduce or, further still, survive. *Myrmica rubra*, for example, survives but does not reproduce below 20°C (Brian 1973, Brian and Brian 1951). Ant colonies whose nests have TH conditions close to these critical regions will be competitively inferior to colonies whose nests fall within optimum TH conditions. Ants have no control over above-ground conditions.

4.6.2.1 Ant distribution in the shrub-dominated rangeland at Tierberg

Tetramorium peringueyi was the dominant ant species at the Airstrip and *Eriocephalus* sites where it had an overdispersed spatial distribution. The reason for the absence of *Crematogaster melanogaster* from the Airstrip site is not clear. This species scavenges insects opportunistically and also tends scale insects. The inferred plant successional gradient may represent a production gradient where a low shrub density, such as that at the Airstrip site, does not support a food resource adequate to sustain *C. melanogaster* or to allow it to compete successfully with *T. peringueyi*. Unlike *T. peringueyi*, *C. melanogaster* is not granivorous, a factor that might contribute to the success of *T. peringueyi* at the Airstrip site. *Chrysocoma ciliata*, an asteraceous shrub and the most abundant shrub at the Airstrip site, produces enormous quantities of seed that are harvested by *T. peringueyi* (*personal observation*). Alternatively, the shrub density at the Airstrip site may be too low to support *C. melanogaster*, a species whose nests are preferentially located in shrub root systems. *Crematogaster melanogaster* abandoned a site immediately after the vegetation was experimentally removed (Chapter 3). Without shading, nest TH conditions may be too extreme for the survival of *C. melanogaster*.

Although *T. peringueyi* had an overdispersed distribution at the Airstrip site, sparsely vegetated habitats such as this are not optimum for this ant species. This was evident at the *Chrysocoma* site where an increase in vegetation density permitted *C. melanogaster* to enter the system. *Tetramorium peringueyi*, inhibited by severe competition from *C. melanogaster*, was unable to maintain competitive dominance resulting in a random spatial nest distribution. *Tetramorium peringueyi* was only dominant at the Airstrip site because potential competitors (such as *C. melanogaster*) were less successful in low production (or high insolation) habitats. An increase in shrub density and shrub species richness will sustain increased productivity which will benefit both *T. peringueyi* and *C. melanogaster*. Yet, *C. melanogaster* was only able to persist in areas between the overdispersed nests of *T. peringueyi* and *Pheidole* sp. 2

was effectively excluded at the *Eriocephalus* site. Is it productivity alone that gives *T. peringueyi* the competitive edge in the *Eriocephalus* rangeland? At the *Chrysocoma* site, where *C. melanogaster* was competitively superior, nests of *T. peringueyi* were not necessarily associated with shrubs. In the *Eriocephalus* rangeland, however, established nests of *T. peringueyi* were only located in the roots of large mixed-species shrub clumps. Physical conditions (TH) in well shaded nests may be conducive to increased success in egg or larval production which indirectly leads to increased foraging success of the colony. I do not have data comparing the foraging activity of *T. peringueyi* colonies located in the open with colonies located in shrub root systems.

Numerous observations of overt confrontation at the *Chrysocoma* site suggest that *C. melanogaster* caused the reduction in competitive superiority of *T. peringueyi* at this site. *Pheidole* sp. 1, released from the inhibitory effects of *T. peringueyi*, consequently increased in abundance by an order of magnitude. Similarly, *Anoplolepis steingroeveri*, an aggressive ant species rarely observed out of drainage lines in the Upper rangeland, was able to successfully invade the *Chrysocoma* site. Alternatively, it might be argued that *Pheidole* sp. 1 and *A. steingroeveri* responded to the same production cues as *C. melanogaster*. The combined competitive effect of these three species would then reduce the competitive dominance of *T. peringueyi*. This seems less likely because one would then expect *Pheidole* sp. 1 and *A. steingroeveri* to be successful in the *Eriocephalus* rangeland.

Dominance hierarchies along this simple successional gradient illustrate the role of competition in ant species diversity. At the extremes of the gradient, where *T. peringueyi* was successful, few aggressive dominant ant species coexisted with it. Where *Crematogaster melanogaster* was able to achieve temporary dominance over *T. peringueyi* (at the *Chrysocoma* site), *Anoplolepis steingroeveri*, also an aggressive dominant species, was present and the seed harvester *Pheidole* sp. 1 increased in abundance. The coexistence of *C. melanogaster* and *A. steingroeveri* at the *Chrysocoma* site is likely to be unstable (both species are aggressive dominants) and a long term study might reveal the exclusion of *A. steingroeveri* by *C. melanogaster*.

Despite a difference in plant species composition, plant cover and shrub density at the Upper and Lower rangeland sites was similar. Distribution patterns of dominant ant species, however, were reversed. Although *T. peringueyi* was capable of nesting in the Lower rangeland, it was maintained at low densities by the competitive superiority of *Pheidole* sp. 2 and *C. melanogaster*. *Ruschia spinosa* and *Eriocephalus ericoides* were dominant plant species on the plains and *Pteronia pallens* was dominant in drainage lines in the Upper rangeland. *Pteronia pallens*, however, was dominant on the plains of the Lower rangeland. Stokes (1994) has shown that *P. pallens* dominated competition at high soil moisture levels but was outperformed by *R. spinosa* at lower levels at Tierberg. These vegetation patterns suggest that the ground moisture status changes dramatically on either site of the mountain belt separating the Upper and Lower rangeland sites. If this inference is correct, the Lower rangeland is likely to be a far more productive system compared with the Upper rangeland. *Pheidole* sp. 2 is a particularly aggressive forager. Once a resource is located by scouts, large numbers of workers are recruited to the food item rapidly. The foraging strategy of *Pheidole* sp. 2 is further enhanced by this species' decentralised territorial system. Costs incurred by the colony for the movement of a food item back to the nearest nest are considerably less than that of a central place forager (Hölldobler & Lumsden 1980). *Tetramorium peringueyi*, in contrast, is a solitary forager that also recruits to food sites but never with the numbers or the speed of *Pheidole* sp. 2. This strategy might be beneficial in a low production habitat but in a high production habitat, such as the *P. pallens* rangeland, *T. peringueyi* is outperformed by the extensive colonies of *Pheidole* sp. 2.

4.6.2.2 Ant distribution in the *P. afra*-dominated rangeland at Hillside

Tetramorium peringueyi and *Pheidole* sp. 2 are granivorous ant species that expand their trophic niche by foraging opportunistically on both dead and living insects. In the *P. afra* rangeland, *T. peringueyi* was active at, and tolerated, higher temperatures than *Pheidole* sp. 2 and both species separated very clearly by habitat in the *P. afra* rangeland (Table 4.6, Figure 4.2). The well shaded microhabitats (*P. afra* clumps, dense grass) were completely monopolised by *Pheidole* sp. 2. By inhabiting shaded (and therefore cooler, moister) habitats, this species extended its foraging activity to all day below *P. afra* clumps. *Tetramorium peringueyi*, despite being capable of nesting in dense grass, was excluded in these shaded regions by the competitively superior *Pheidole* sp. 2. *Pheidole* sp. 2, however, unable to tolerate higher temperatures, was less successful in sparsely vegetated areas because of a reduced foraging time permitting *T. peringueyi* and several other ant species (e.g. *T. quadrispinosum*, *Monomorium australe*, *M. alamarum*) to establish. Similar distribution patterns were observed in a Freestate grassland where *Pheidole* sp. 3 was dominant and *T. dichroum* Santschi was relegated to marginal disturbed areas (*personal observation*).

Nests of *Ocymyrmex barbiger*, an extreme thermophilic ant species, were found most frequently on NRP in the *P. afra* rangeland and never in dense grass (Table 4.6). In the grasslands of the southern Freestate, *O. barbiger* was also located on bare, flat areas (abandoned termite mounds) devoid of any vegetation (*personal observation*). *Ocymyrmex barbiger* seems to be physiologically incapable of nesting in shaded habitats and its absence from dense grass was not necessarily because of superior competitors such as *Pheidole* sp. 2. Nests positioned in open sites will heat faster and foraging activity will be initiated earlier than those colonies with nests positioned in shaded areas. The foraging time of shaded colonies would then presumably be reduced below a critical level that no longer supports the colony. The clear spatial distribution pattern observed at the *P. afra* rangeland site was lost at Tierberg. Nests of *O. barbiger* were distributed throughout the shrub-dominated rangeland because plants having the same shade properties as grass or *P. afra* were absent.

4.6.3 Mechanisms of species coexistence

4.6.3.1 Shrub-dominated rangeland at Tierberg

Tetramorium peringueyi and *C. melanogaster* do not differ in their distribution with respect to microhabitat in the *Eriocephalus* rangeland. Nests of both species were located within mixed-species shrub clumps. Similarly, the distribution between *C. melanogaster* and *Pheidole* sp. 2 in the Lower rangeland did not differ with respect to vegetation. Both pairs of species coexist despite intense competitive interactions between them. In addition, several other groups of subordinate ant species (e.g. specialists and seed harvesters) coexist with the competitive dominants.

The continued coexistence of *T. peringueyi* and *C. melanogaster* may result from different territorial strategies. Field observations indicate that the territories of *C. melanogaster* "fit in" (like pieces of a jigsaw puzzle) the space between the regularly dispersed territories of *T. peringueyi*. *Crematogaster melanogaster* has a territorial strategy that has been referred to as "nest decentralisation" (Hölldobler & Lumsden 1980). Unlike *T. peringueyi* which has a centrally positioned nest, "satellite" nests of *C. melanogaster* are decentralised through the area under its control. The benefit of this strategy is that large areas can be defended and resources exploited without the colony incurring the cost of movement from a distant point to a single central nest (Hölldobler & Lumsden 1980). The long-term success of any ant colony is contingent on its size and there is presumably a critical size below which net forager yield does not support the colony. The competitive dominance of *T. peringueyi* in the *Eriocephalus* rangeland forces any potential coexisting species into having an asymmetrical nest shape. *Crematogaster melanogaster* overcomes this problem because nest decentralisation permits an unusual territory shape that is not at the expense of territory size. This interpretation is supported by the almost total exclusion of *Pheidole* sp. 1 by *T. peringueyi* at the Airstrip site. *Pheidole* sp. 1 is competitively inferior to *T. peringueyi* on the sparsely vegetated airstrip. Presumably the critical minimum territory size of *Pheidole* sp. 1, also a central place forager, cannot be maintained in the face of severe competition by *T. peringueyi*. *Crematogaster melanogaster* may also be considered a fugitive species because its territorial strategy permits it to invade "enemy free space" (sensu Jeffries and Lawton 1984). This was evident by its rapid response to the experimental removal of *T. peringueyi*. Pre-emptive competition is important for competitively inferior species such as *C. melanogaster*. One would expect ant species with a decentralised territorial system to expand their territories through "vegetative" colonisation. By doing this, they pre-empt available space quicker than species that rely on colony foundation by sexual alates. *Crematogaster melanogaster*, therefore, is an effective coloniser but the regular spatial distribution of *T. peringueyi* indicates that the distribution of competitively inferior *C. melanogaster* is determined by *T. peringueyi*. By having different life histories (superior colonisation ability verses superior competitive ability) these two species coexist in an unstable equilibrium without niche differentiation (sensu Shmida and Ellner 1984).

Understanding why *Pheidole* sp. 2 and *C. melanogaster* coexist in the Lower rangeland is more difficult. Unlike the situation in the Upper rangeland where *T. peringueyi* (on the plains) and *A. steingroeveri* (in the drainage lines) achieved almost total competitive dominance, *Pheidole* sp. 2 and *C. melanogaster* were equally common in the Lower rangeland. Territory areas of these two species were mutually exclusive and field observations indicated direct interference competition. This implies that competition between these two species is reciprocal and symmetrical so that neither species is able to exclude the other. Also, both species have decentralised territorial strategies. Competition appears to be for space because, apart from the occasional *T. peringueyi* nest, the habitat was saturated by one or the other species. In plant communities, habitat patchiness offers qualitatively diverse opportunities for the establishment of plants by seed because the variability in habitat disrupts the competitive dominance and consequent monopolisation by any one species (Chapter 5). Widescale disturbance, such as that by overgrazing, results in competitive release, monopolisation and ultimately the competitive exclusion of plant species by a few dominant plant species. On Tierberg, germination and subsequent establishment of plant species in the Lower rangeland was reduced significantly by the inhibitory effect of *P. pallens* (R. I. Yeaton, unpublished data). I interpret the distribution of the dominant ant species in the Lower rangeland in the same way. Conditions produced by the total dominance of *P. pallens* in this habitat favour *Pheidole* sp. 2 and *C. melanogaster* resulting in their monopolisation of space in the Lower rangeland. Available space is likely to be pre-empted "vegetatively" by the nearest colony (either species) before the establishment of new colonies by sexual foundation. Majer (1976) reported similar observations in Ghana where the establishment of new colonies was rare because newly available space was usually compensated for by the lateral expansion of existing colonies. The de-emphasis of sexual foundation of colonies is further supported by the aggressive nature of both species and their saturation of the habitat which would contribute to the mortality of new queens. This might partially explain why *T. peringueyi* is uncommon in the Lower rangeland. The decentralised territorial strategy of these species facilitates the acquisition of new space, the maintenance of existing territories and their overall success.

In this study I have concentrated on the competitively dominant species because their dominance relationships influence the distribution and abundance of subordinate groups and are therefore the major force structuring the community (Room 1971, Majer 1976, Fellers 1987). Consequently, I can only speculate on mechanisms permitting coexistence of the specialist ant species (e.g. *Ocymyrmex barbiger*, *Anoplolepis* cf. *trimeni*, *Camponotus fulvopilosus*, *Ophthalmopone hottentota*). The data presented above shows that *T. peringueyi* inhibits the distribution of *Monomorium havilandi* and *M. australe*. *Tetramorium peringueyi* workers also drop pebbles down the nest entrance of *O. hottentota* and *C. fulvopilosus* when the nest entrances of the latter are too close to their nests (*personal observation*). Although speculative, the competitive dominance of *Pheidole* sp. 2 and *C. melanogaster* in the Lower rangeland may also explain the paucity of other ant species (particularly *Monomorium* species) in this habitat. The apparent importance of the dominant ant species in determining the distribution of these other groups of species leads me to suggest that members of the specialist functional group are opportunistic in their distribution. In other words, they establish where there are no competitive dominants to exclude them.

4.6.3.2 *P. afra*-dominated rangeland at Hillside

The *P. afra* rangeland plant community is dynamic in space and time with succession following a deterministic pattern of cyclical replacement (Chapter 5). Ultimately, the vegetation dynamics are determined by the grass component because of the tendency of grass towards monopolisation and exclusion of other species. The accumulation of nutrients below *P. afra* clumps creates open areas of local disturbance (NRP) once *P. afra* clumps break down. Certain plant species persist in the system as fugitive species on NRP (sensu Hutchinson 1951). These species are destined to local extinction through replacement by competitively superior grasses. Apart from disturbance, seed dispersal by various biotic vectors (ants, birds) is equally important in maintaining species richness in this system. Seed is removed by these dispersal agents from the inhibitory effects of grass-dominated sites to safer sites of establishment (Chapter 5).

The key to understanding ant community structure and dynamics at the *P. afra* rangeland lies with the above interpretation of the plant community dynamics. Coexistence mechanisms of ants in the *P. afra* rangeland parallel those observed in the plant community except that I de-emphasise the importance of dispersal in maintaining species richness. In natural communities where space is limiting, monopolisation by one dominant species is inevitable and vigorous interference competition prevents their replacement by other species (Sousa 1984, Yodzis 1986). However, disturbance that creates space and removes the competitively dominant species leads to local coexistence of species (Connell 1978, Sousa 1979, Paine and Levin 1981). In the *P. afra* rangeland, *Pheidole* sp. 2 was dominant and monopolised shaded habitats (*P. afra* clumps, grass) but was less successful in the open spaces created by NRP. The reduced competitive ability of *Pheidole* sp. 2 on NRP permits several other ant species (see Table 4.6) to displace it and to persist in the system as fugitives (sensu Hutchinson 1951) on the patches of local disturbance. However, like the plant species distributed on NRP, these competitively inferior ant species are destined to local extinction. As the nutrient status on the NRP changes in favour of the competitively superior grass component, so too are the local conditions altered in favour of *Pheidole* sp. 2.

Dispersal or recruitment limitation is an important factor determining local plant species composition (Tilman 1994, 1997). The *P. afra* plant community, where seeds are moved by biotic vectors to safe sites of establishment, is no exception (Chapter 5). Although dispersal is important for the regional persistence of fugitive species in a space limited system (Sousa 1984), dispersal does not appear to be a limiting factor in ant communities (Bernstein 1974). Ant colonies can produce enormous numbers of alate sexual forms which have high dispersal rates. Mortality caused by abiotic and biotic factors is very high at this stage (Hölldobler and Wilson 1990) and is probably more of a limiting factor in ant species distribution than their dispersal to safe sites.

Nutrient rich patches are regions of intense interference competition. How do the fugitive species coexist on these local patches? Generally, ants avoid or reduce interference competition by foraging at different times (Briese and Macauley 1980, Hölldobler and Wilson 1990). Ant activity on NRP was temperature dependent and there were very clear temporal replacement patterns associated with the functional groups. Aggressive dominant species (*T. peringueyi*, *Pheidole* sp. 2) were active at cooler temperatures but were replaced by species of the scavenging functional group (*T. quadrispinosum*, *M. australe*) at higher temperatures (Figure 4.2). Ant species belonging to these groups were overtly aggressive towards each other and the winner of inter-guild encounters was temperature related. Thus, aggressive dominant species outperform scavengers at lower temperatures when the aggressive dominants were competitively superior while the reverse occurred at higher temperatures. The scavenging species were replaced by specialist thermophilic species (*O. barbiger*) at very high temperatures. *Ocymyrmex barbiger* was also known to prey on species belonging to both functional groups that precede it in activity (*personal observation*). Of all the species coexisting on NRP, *O. barbiger* was probably the only species incapable (for physiological reasons) of existing in well-shaded habitats. Although ant species are presumably limited to activity at certain temperatures for physiological reasons, interference competition will serve to reduce the range in temperature that ant species are active, and to reinforce the temporal separation in activity. *Monomorium alamarum* was the only species belonging to the seed-harvesting functional group whose nests were frequently located on NRP. Generally, activity of this functional group overlaps with the aggressive dominants and the scavengers. *Monomorium alamarum*, compared with all the other fugitive species, was minute in size, a factor that might permit it to escape the competitive superiority of the other species distributed on NRP.

Because of the competitive dominance of ant species and the importance of vegetation in altering competitive abilities, patterns of species replacement are not gradual. An ant species will remain dominant in a system until a threshold (sensu Friedel 1991) in habitat change is reached. At that point, local conditions will favour a second ant species at the expense of the first. The competitively inferior species are then relegated to sub-optimal habitats unless they are able to coexist with the superior species through some mechanism. Hence, various species coexist on NRP in the *P. afra* rangeland but they are active at different temperatures and species coexistence results from temporal replacement. This argument can be extended to functional guilds where competitively superior aggressive dominant species occupy the optimum habitats (or, on a different scale, nest positions). Species belonging to this group were most successful at lower temperatures and, by inhabiting well-shaded habitats, their foraging time was extended considerably. Subordinate species (scavenging functional group) replace the dominant species in time because of their ability to tolerate higher temperatures. Although the species belonging to the scavenging functional group are capable of nesting below vegetation, they are relegated to sub-optimal habitats by the aggressive dominant species. Capable of tolerating higher temperatures, the scavenging group is competitively superior to the aggressive dominant species in these sub-optimal habitats The extreme thermophilic species, active at the highest temperatures, also exist in the most inhospitable habitats. These local replacement patterns can be extended to the regional scale in both space and time. Replacement patterns over a vegetation gradient (space) will parallel replacement patterns along a degradation gradient (time) and can be represented by simple state and transition models that parallel the change in vegetation (cf. Westoby et al. 1989).

4.6.4 Ants: non-equilibrium communities

Several generalisations result from the study of ant communities in the southern Karoo. Firstly, competition among, and between, ant species is widespread. Specifically, interactions between the aggressive dominant species (interference competition for space) determines the structure of ant communities. Secondly, understanding the structure and dynamics of the vegetation is the key to understanding ant community structure and dynamics. Thirdly, coexistence of aggressive dominant species is a consequence of non-equilibrial conditions. While differences in resource use almost certainly exist and would be easily measurable, they do not necessarily lead to ant species coexistence. However, niche differentiation (e.g. temporal separation in foraging, ant size differences, food specialisation) may explain the coexistence of subordinate species with the aggressive dominant ant species.

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Chapter 5: *Portulacaria afra* rangeland dynamics in the semi-arid southern Karoo, South Africa: the role of competition, facilitation, seed dispersal and soil nutrient enrichment

5.1 SUMMARY

The structure and dynamics of the *Portulacaria afra*-dominated rangeland in the southern Karoo, South Africa was studied. Plant species replacement patterns are cyclic and facilitated by nurse-plant effects. *Rhigozum obovatum*, a woody shrub that establishes in grassland and initiates the cyclical succession, facilitates the establishment of *P. afra*. Later-successional tree species, in turn, establish beneath *P. afra*. Conditions below *P. afra* clumps encourage the presence of detritivores that are responsible for soil nutrient enrichment. Bare nutrient-rich patches remain after the collapse of *P. afra* clumps. These sites of disturbance disrupt the competitive dominance of grass and permit *Psilocaulon absimile* and *Lycium cinereum* to persist as fugitive species. Seed dispersal by biotic vectors (birds and several species of ants) is important to these dynamic processes because propagules are removed from harsh physical conditions and the inhibitory effects of competitively dominant plant species to safe sites of establishment below nurse-plants.

Principles developed from the *P. afra* vegetation model were used to speculate on grazing induced vegetation change in the southern Karoo. Overgrazing by domestic stock severs the complex feedback links between the plant community and the important invertebrate component resulting in the loss of community patchiness and ultimately disrupts the dynamic processes driving the system.

5.2 INTRODUCTION

The relative importance of facilitation and interference competition in structuring plant communities is unclear (Bertness and Callaway 1994, Callaway 1995). In climatically extreme habitats such as deserts, plant establishment is not random and many plant species are unlikely to establish unless aided in some way by earlier colonising plant species. Mechanisms of facilitation are varied (Callaway 1995) but the outcome is a safe site for seed germination. Frequently, facilitation is followed by direct competitive interaction resulting in the displacement of the original nurse-plant (Valiente-Banuet et al. 1991*a*). These facilitative relationships and subsequent competitive interactions have been reported to establish a cyclical process in plant communities. Cyclical succession, at the scale of the individual, has been inferred from spatial patterns of species association and recruitment in semi-arid plant communities (Yeaton 1978). The colonisation of open spaces by certain species, or guilds of species, initiates a predictable sequential replacement of species that has been documented in the Sonoran Desert (McAuliffe 1988), the northern (Yeaton 1978) and southern Chihuahuan Desert (Yeaton and Romero M. 1986, Yeaton, *personal communication*), the Patagonian arid steppe (Soriano et al. 1994) and the southern African Karoo (Yeaton and Esler 1990) and Namib Deserts (Yeaton 1990).

The zoogenic influence on the above community-level cyclical processes has received scant attention. Apart from the obvious role of seed dispersal by various animal taxa, the concentration of nutrients by invertebrates has clear implications on successional processes by altering the relative competitive abilities of plants. In tropical forests, ants are responsible for the secondary dispersal of seeds to their nests (Byrne and Levey 1993, Kaspari 1993) which may improve the probability of seed germination and establishment (Roberts and Heithaus 1986, Levey and Byrne 1993). In fynbos, ants indirectly contribute to the fitness of certain plant species by moving seeds into open spaces which reduces interspecific plant competitive effects (Yeaton and Bond 1991). Harvester ants move prodigious quantities of seeds in deserts but it is not clear whether the ants affect the spatial distribution of plants (MacKay 1991). The concentration of nutrients in harvester ant mounds produces differences in plant species composition (MacKay 1991) and enhances seed germination and seedling survival on mounds (Beattie and Culver 1983, Dean and Yeaton 1992). Termites are reported to be the most important decomposers of plant material in semi-arid Australia (Holt 1987) and North America (Nutting et al. 1987, MacKay et al. 1989). Detritivores, in general, are a major source of energy in arid systems and soil enrichment through their activity alters plant community composition and affects community dynamics (MacKay et al. 1989, Polis 1991). Despite these important zoogenic effects on plant species distribution and abundance, the relative importance of these processes on community level dynamics remains unclear.

In this chapter, I investigate the importance of seed dispersal by harvester ants and soil nutrient enrichment by detritivores on successional processes in a semi-arid plant community. This research was prompted by the observation that later-successional trees have an extensive distribution on mountain slopes and on the plains below, in the semi-arid southern Karoo of South Africa. Closer inspection indicated that there was little or no new recruitment of any tree species, particularly on the plains, leading me to question how these later-successional trees established in the system. *Portulacaria afra* Jacq., a large clump-forming tree succulent, is the dominant plant species on the hill slopes of the eastern regions of the southern Karoo. The later-successional tree species coexist alongside *P. afra* on these slopes leading me to speculate that *P. afra* was responsible for facilitating the establishment of later-successional trees in the past.

This chapter contains several parts. First, I develop a predictive description of the dynamics of the *P. afra* rangeland and show that facilitation and competition are important processes in the organisation of this plant community. Second, I show that seed dispersal by harvester ants is responsible for the spatial distribution of *P. afra*, the dominant species in the plant community. Next, I demonstrate that the change in soil nutrient status through detritivore activity drives plant community dynamics and contributes towards maintaining species codominance in the system. Finally, using principles developed in this chapter, I speculate on the nature of the Karoo vegetation prior to the introduction of domestic stock and discuss the wider application of these principles to arid environments in general.

5.3 STUDY SITES

The semi-arid Karoo biome occupies roughly 35% (427 000 km^2) of the land area of South Africa and supports a profitable small stock industry (Cowling 1986). This study was done in the southern Karoo which lies south of the Great Escarpment in the central interior (Cowling 1986). The region is dissected by mountains, running east to west, belonging to the Cape folded belt (Bristow 1985). Two mountain ranges, the Swartberg and Baviaanskloof, act as rain shadows in the region. Strong moisture gradients exist with the climate becoming progressively dryer northwards and westwards from these ranges. Numerous minor belts, sometimes only rocky ridges, occur to the north of the two ranges. Between the minor belts the landscape is gently sloping to flat. The climate is characterised by extremes in temperature and variability in the timing and the amount of rainfall resulting in a vegetation that is adapted to arid conditions (Cowling 1986). *Portulacaria afra*, a tree-succulent which forms a dense thicket, is the dominant plant on the minor folded belts. Tree species, of which *Euclea undulata* Thunb. and *Pappea capensis* Eckl. & Zeyh. are the most common, are also distributed on the rocky slopes but rarely extend onto the plains except in the east where the rainfall is higher. The plains vegetation is dominated by dwarf shrubs.

Portulacaria afra has a wide distribution in the southern Karoo and eastern Cape. In the arid western areas, *P. afra* occurs on the rocky mountain slopes only. To the mesic east, however, *P. afra* extends off the slopes onto the flats. Still further to the east, where the grass component becomes dominant, *P. afra* is restricted to the large river valleys of the eastern Cape. Although *P. afra* produces enormous quantities of seed (*personal observation*), Stuart-Hill (1992) has de-emphasised the importance of sexual reproduction in favour of vegetative growth. Side branches of the plant bend downwards and initiate roots, producing a characteristic “apron” or “skirt” (Stuart-Hill 1992). Being heliophilic, the apron of *P. afra* is always located on the sunny, northerly sides of the clump (Von Maltitz 1991, *personal observation*). Removal of this apron, by overgrazing, causes the heavy succulent branches to collapse resulting in plant death (Stuart-Hill 1992). Overgrazing by domestic stock has led to local extinction of this important forage species in large areas of the southern Karoo and eastern Cape.

The common tree species (such as *E. undulata*, *Pappea capensis*, *Diospyros lycioides* Desf., *Maytenus polyacantha* (Sond.) Marais and *Rhus undulata* Jacq.) distributed on the rocky slopes of the southern Karoo are referred to as later-successional because they do not colonise open or bare areas. This implies that they require a nurse-plant for successful establishment. Indeed, several texts report that seedlings of certain tree species are rare or have never been found in the southern Karoo and eastern Cape (Midgley 1991, Van Breda and Barnard 1991, Von Maltitz 1991). Amongst others, these tree species are the dominant woody component in the Valley Bushveld of the eastern Cape (Acocks 1988).

The main study area was located 25 km south-west of Jansenville on Hillside farm (33° 06′ S, 24° 31′ E). This farm is unique because stands of *Portulacaria afra* grow on the plains, a rare phenomenon in the arid parts of the southern Karoo. Later-successional trees also extend onto the plains at Hillside farm. *Portulacaria afra* forms distinct and discrete oval shaped clumps of up to 150 m^2 in area. Pioneer grasses (mostly *Aristida* spp.), interspersed by bare patches, cover the ground between the *P. afra* clumps. Three woody shrub species (*Rhigozum obovatum* Burch., *Lycium cinereum* Thunb. and *Pentzia incana* (Thunb.) Kuntz) are common in these grassy areas. Less common in the *P. afra* rangeland are slightly raised, oval shaped mounds of variable size but within a range of 14 m^2 to 90 m^2 in area. These mounds, referred to as nutrient rich patches (hereafter NRP), show evidence of extensive mammal digging activity. *Lycium cinereum* and *Psilocaulon absimile* N. E. Br., a dwarf succulent shrub, are restricted to NRP in the *P. afra* rangeland. The *P. afra* rangeland study site was located on a slight (± 1°) north-facing slope. Hillside farm is presently managed as an Angora goat stud and the distribution of *P. afra* on the plains is evidence that this farm has had a history of low stock impact. A second study area, adjacent to the site described above but separated by a stock fence, was used for comparative studies. This second site, referred to as the Disturbed rangeland site, was positioned at the same level on the slope and had the same aspect as the *P. afra* rangeland site. *Portulacaria afra*, absent because of overgrazing, has been replaced by weedy, annual grasses at the Disturbed rangeland site. Mean annual rainfall (106 years, Jansenville) is 271 mm and falls throughout the year although almost 60% of the yearly mean falls from November to March. The average maximum temperature at Jansenville (63 years) exceeds 30°C from December to February while the hottest temperatures for the same period exceed 40°C. The average minimum temperatures for June and July are below 5°C and the coldest temperatures for the same months fall below freezing (Weather Bureau 1986). The second study site was at Boschfontein (33° 27′ S, 24° 03′ E), a farm located in the foothills of the Baviaanskloof mountains, 30 km south-west of Steytlerville and approximately 60 km south-west of Hillside farm. The climate at Boschfontein is similar to Hillside except near the mountain where conditions are cooler and wetter due to its elevation (S. W. Fitzhenry, *personal communication*). On Boschfontein, *P. afra* is distributed on the steeper north-facing slopes of the Baviaanskloof Mountains but does not extend onto the flats. Like Hillside, tree species extend off the rocky slopes and are common on the flats. Ground cover at this farm is dominated by grass. Both goats and sheep graze on this land.

One experiment examining mesemb seed dispersal by ants was done at Tierberg (33° 07′ S, 22° 15′ E), a farm situated 25 km NE of Prince Albert and approximately 230 km to the west of Hillside. Average annual rainfall at Tierberg is 169 mm (Prince Albert, 92 years) but the range is between 100 mm and 300 mm. Most of the yearly average is likely to fall between February and May, and the region is considered a transition between summer and winter rainfall regions (Milton et al. 1992). The mean annual maximum temperature at the nearest long term recording station, Beaufort West (32° 18′ S, 22° 40′ E, 49 years), is 25.2°C and the mean annual minimum temperature is 10.3°C. The climate is less extreme than the Jansenville district with average highest monthly temperatures exceeding 35°C from October to March and average lowest monthly temperatures dropping below freezing from June to September (Weather Bureau 1986). The vegetation at Tierberg is a shrub-dominated rangeland. Grasses and *P. afra* are absent. The seed experiment was performed in natural rangeland that was relatively homogeneous in structure and dominated by two plant species, the succulent *Ruschia spinosa* Hartm. & Stüber and the woody shrub *Eriocephalus ericoides* (L. f.) Druce. Tierberg farm is managed as a commercial enterprise with the above rangeland grazed by Merino sheep.

Plant nomenclature follows Arnold and De Wet (1993) and Hartmann (1991). The terms *mesemb* and *succulent* refer to succulent plant species belonging to the Mesembryanthemoideae and Ruschiodeae (Hartmann 1991). Ant nomenclature follows Arnold (1915-1924, 1926). Ant species belonging to the *Monomorium* sp.-_*salomonis*-group are referred to as *M. salomonis*. To avoid confusion with certain plant and ant genera, the *Portulacaria afra* rangeland study site is referred to as the *P. afra* rangeland site.

5.4 METHODS

5.4.1 Where do later-successional tree species establish?

Ten 20 m × 20 m quadrats were established in the *P. afra* rangeland at Hillside farm and all *P. afra*, *Rhigozum obovatum* and *Lycium cinereum* individuals within the quadrats were counted. *Portulacaria afra* clumps located on the quadrat boundary were disregarded if more than half their area fell outside a quadrat. The longest axis (L) and the greatest width at right angles to the long axis (W) of all *P. afra* clumps and NRP were measured and their cover calculated as $\pi LW/4$ (Cody 1986*a*). Next, because tree seedlings were never found in grass or on bare ground, the position of later-successional tree establishment was quantified as either within *P. afra* clumps or beneath woody shrubs. Differences in establishment between these microsites were tested with the Chi-square goodness-of-fit test (Siegel and Castellan 1988). Later-successional tree seedlings were individuals less than 50 cm in height without excessive stem thickening characteristic of older or overgrazed trees. The position of large later-successional trees with respect to *P. afra* clumps, open areas and NRP was recorded. In my operational definitions, open areas were defined as bare ground or ground with a grass covering. NRP were described earlier.

Another ten 20 m × 20 m quadrats were established in the Disturbed rangeland (separated from the *P. afra* rangeland site by a stock fence) and all large trees and *L. cinereum* and *R. obovatum* individuals counted. A thorough search for *P. afra* seedlings and later-successional tree seedlings was made. Differences in the density of large trees, tree seedlings, *L. cinereum* and *R. obovatum* between the *P. afra* rangeland and the Disturbed rangeland were tested by the Wilcoxon-Mann-Whitney test (Siegel and Castellan 1988).

5.4.2 Where does *Portulacaria afra* establish?

The establishment position of at least 50 *Portulacaria afra* seedlings in the *P. afra* rangeland at Hillside farm was quantified. Walking towards an emergent tree on the horizon, the position of all *P. afra* seedlings, located within 2 m on either side of the straight-line transect, was recorded. *Portulacaria afra* seedlings were defined as individuals less than 30 cm in height. As overgrazing can mask the age of smaller *P. afra* individuals, the stems of potential seedlings were checked to ensure that growth was not coppicing from the trunk of an old individual. Next, because I observed that *P. afra* appeared to be establishing preferentially under the woody shrub *Rhigozum obovatum*, the Chi-square goodness-of-fit test was used to determine whether the frequency of woody shrub nurse plants of *P. afra* occurred in the same proportion as woody shrubs in the rangeland. To determine the frequency of woody shrubs in the *P. afra* rangeland I recorded the identity of the nearest woody shrub encountered at 15 m intervals along a straight line walk in the *P. afra* rangeland. The exercise was terminated after 150 woody shrubs were counted. The product of the total number of *P. afra* seedlings found under woody shrubs, and the relative proportion of the specific woody shrub in the *P. afra* rangeland yields the expected numbers of that particular woody shrub as a nurse plant for *P. afra*.

Next, because the establishment of *P. afra* was most common beneath *R. obovatum*, I determined whether *P. afra* was displacing its nurse plant (*R. obovatum*) by regressing the area of *P. afra* individuals against the canopy area of the original *R. obovatum* nurse plant. Here I assumed that a negative relationship indicated that *R. obovatum* was displaced as the *P. afra* clump increased in size. The canopy area exposed to sunlight of *P. afra* and *R. obovatum* was determined by measuring the longest axis (L) of each canopy and the greatest width at right angles to the long axis (W). Cover of each individual was calculated according to the formula $\pi LW/4$ (Cody 1986*a*). The original nurse plant was taken as that *R. obovatum* individual closest to the thickest *P. afra* stems.

5.4.3 Where does *Rhigozum obovatum* establish?

Four microhabitats (bare ground, grass, under *Pentzia incana*, under *Portulacaria afra*) were searched for *Rhigozum obovatum* seedlings. Sampling areas were located, as before, by selecting an emergent tree on the horizon and walking towards it in a straight line. Because *R. obovatum* seeds are light and winged, seeds are likely to accumulate in a patchy distribution. To overcome this in the sampling procedure, the four microhabitats were located within one 5 m × 5 m quadrat and all seedlings found within a circle of 1 m diameter in each of the four microhabitats were recorded. Thirty 5 m × 5 m quadrats were searched for *R. obovatum* seedlings. The Chi-square test for $r \times 2$ tables tested for microhabitat differences in *R. obovatum* establishment with column headings the number of quadrats with or without *R. obovatum* seedlings and row headings the four microhabitats.

5.4.4 Vegetation patterns on nutrient rich patches

Twenty NRP were selected by means of a random walk in the *P. afra* rangeland. At each NRP the longest axis and the longest axis at right angles to the first axis was measured. All *Lycium cinereum* and *Rhigozum obovatum* individuals found on the NRP were counted and the presence or absence of the succulent *Psilocaulon absimile* was noted. Then, an area equal to the NRP was marked in the grass-dominated rangeland adjacent to the NRP and all *L. cinereum* and *R. obovatum* individuals counted and the presence or absence of *P. absimile* recorded. This control area never included *P. afra* clumps and, to avoid nutrient contamination from the NRP, was never down-slope of the NRP. Because the areas were matched, the Sign test (Siegel and Castellan 1988) was used to determine whether *L. cinereum* and *R. obovatum* differed in their distribution with respect to NRP. Fisher's Exact test was used to determine whether *P. absimile* was distributed on NRP more frequently than expected by chance. In the 2 × 2 contingency table, column headings were on the mound and in adjacent grassy area (control) and row headings were the presence or absence of *P. absimile*.

Seventy-six large later-successional trees of all species standing in the open (i.e. away from a *P. afra* clump) were located by a random walk in the *P. afra* rangeland. At each tree, I recorded whether the area surrounding the tree was raised (NRP are raised mounds), had evidence of mammal digging activity and whether grass and succulent plant species (*P. absimile* and *Mesembryanthemum crystallinum* L.) were present. Assuming that younger

NRP have well developed mounds and that the mound diminishes as the NRP ages, I tested for patterns of mesemb/grass replacement by a Chi-square test for $r \times 2$ tables. Column headings were young NRP (mound present under tree) and older NRP (mound absent under tree) and row headings were the presence of mesembs only, the presence of mesembs and grass and the presence of grass only. A Chi-square test for 2×2 contingency tables was used to test whether mammal digging activity (presence verses absence) differed on NRP of different ages in a similar fashion.

5.4.5 Is there an association between *Messor capensis* and the spatial distribution of *Portulacaria afra*?

At least 100 nests of the harvester ant *Messor capensis* Mayr were located in the *P. afra* rangeland and their positions (e.g. in grass, under woody shrub) noted. Next, because many *M. capensis* nests were positioned beneath *Rhigozum obovatum*, I tested whether *M. capensis* was nesting preferentially beneath this woody shrub. The Chi-square goodness-of-fit test was used to determine whether the frequency of woody shrubs under which *M. capensis* nests were found occurred in the same frequency as woody shrubs in the *P. afra* rangeland. As before, expected numbers were calculated by multiplying the total number of *M. capensis* nests found beneath woody shrubs with the relative density of the specific woody shrub in the *P. afra* rangeland.

To determine the *P. afra* seed moving ability of *M. capensis*, three nests of this ant species were chosen at random and monitored over a three-day period. The number of *P. afra* seeds returned to each nest by foraging individuals was recorded for 1 minute time intervals ($n = 10$ minutes for each nest).

5.4.6 Mechanisms of seed dispersal for *Psilocaulon absimile* and later successional tree species

Following rainfall at Tierberg and Hillside farms, I observed ants of the genus *Monomorium* harvesting mesemb seeds. Elsewhere (Chapter 4), I have shown that *Monomorium* spp. nest in open areas away from vegetation and are uncommon in the *P. afra* rangeland because of the dominance of grass and *P. afra*. Consequently, Tierberg farm was used as a model system to examine the dispersal of mesemb seeds by ants because of the dominance of succulent plant species and the commonness of *Monomorium* ant species at this site. The efficiency of ants as a vector of mesemb seed dispersal at Tierberg was observed directly by placing approximately 30 mesemb seeds in a small pile (± 1 cm^2) below the canopy of 30 *Ruschia spinosa* individuals. Seed piles were never within 3 m of each other.

Seeds of two succulent plant species, *Malephora lutea* Schwant. (approximate seed size: 1.1 mm × 0.9 mm × 0.9 mm) and *Drosanthemum montaguense* L. Bol. (approximate seed size: 0.8 mm × 0.5 mm × 0.5 mm), were used in this experiment because they differ in size. The seed size of *Psilocaulon absimile*, common on NRP in the *P. afra* rangeland, was slightly smaller than the seed of *D. montaguense*. I recorded the identity of the ant species visiting the seed station, the distance the seed was moved to the ant nest and the position of the nest with respect to the nearest shrub. Casual notes were made on the seed size selected by the various ant species. Seed piles were checked frequently over a two day period. Mesemb seeds are housed in hygrochastic capsules which require rainfall to open and release the seeds (Hartmann 1991). After heavy rainfall at the *P. afra* rangeland site, I recorded the identity of ant species harvesting seeds of *P. absimile*.

To determine whether birds were responsible for the dispersal of fruiting tree species in the *P. afra* rangeland at Hillside, a *P. afra* clump containing a fruiting tree species with an emergent canopy was randomly selected and all tree seedlings growing within the clump counted. Tree seedlings, conspecific to the emergent tree, were not considered because of the possibility of reseeding or coppicing from the larger individual. Next, a second *P. afra* clump, matched with the first in terms of cover, height and branch density but without an emergent tree, was selected in the general vicinity of the first clump. The number of tree seedlings located in the second *P. afra* clump were counted and compared with the number of seedlings found in the first clump using the Sign test once at least 30 paired clumps were inspected. Earlier results had shown that of all the later-successional trees, only *Maytenus polyacantha* established in sites other than a *P. afra* clump. The fruit of *M. polyacantha* is a hard capsule that splits to reveal three elaiosome-bearing seeds which are harvested by *Messor capensis* and *Pheidole* sp. 2 once the seeds fall to the ground. Seeds of *Maytenus polyacantha* were frequently found on the waste dumps of *Messor capensis* and surrounding the nest entrance of *Pheidole* sp. 2. Consequently, *Maytenus polyacantha* was not included in the above analysis but was tested separately. The rationale for this is that if this tree species was dispersed by a vector other than birds (e.g. an ant) then there should be no difference in the presence of seedlings below *P. afra* clumps with or without emergent fruit trees. Next, *Maytenus polyacantha* individuals bearing fruit were located by a random walk in the *P. afra* rangeland. If *Messor capensis* foragers were harvesting seeds from below the tree, their nest was located and the distance from the nest to the tree measured.

Thirty piles of approximately 70 *P. afra* seeds were placed at 20 m intervals in a straight line through the *P. afra* rangeland at Hillside. At each station, the seeds were scattered over an area of about 40 cm × 40 cm. The seed piles were inspected continuously over a two day period for seed removal by ants. I recorded the identity of the ant species, the distance the seed was moved to the ant nest, the position of the ant nest (e.g. in open, under shrub) and whether the nest had been damaged by mammal digging behaviour. Next, I placed piles of colour dyed *P. afra* seed close to the entrance of three *Messor capensis* nests. Once the seeds had been moved back to the nests, I gently excavated the nest and recorded the position of the dyed seeds.

5.4.7 Detritivores and soil nutrient enrichment

I observed that dead *Portulacaria afra* branches, accumulated beneath *P. afra* clumps, were infested with termites. The termite community in the *P. afra* rangeland was sampled by burying moist toilet rolls ($n = 11$ for each microsite) inside *P. afra* clumps, in NRP and in the grassy areas between *P. afra* clumps. The toilet rolls were inspected regularly for termite activity and termite specimens were collected for identification. Detritivores (millipedes [Pachybolidae: *Centrobolus* sp. Cook], snails [Urocyclidae: *Sheldonia* sp. Ancey] and giant earthworms [Microchaetidae: *Microchaetus* sp. Rapp]) were particularly active at the *P. afra* rangeland site following heavy rainfall but these taxa were inactive during hot, dry periods. Signs of their activity (faeces, worm castes) were common in the soil below the *P. afra* clumps. To test for the impact of all these detritivorous species on the soil nutrient status below *P. afra* clumps, 30 paired soil samples were collected from below *P. afra* clumps and from open areas between *P. afra* clumps. The two treatments will be referred to as *P. afra* soil and open soil respectively. Following Dean and Yeaton (1993), the soil was placed into pots organised in a systematic design (Hurlbert 1984) and three radish (*Raphanus sativus* L.) seeds were planted in each pot. After three weeks the young radish plants were weeded to one individual in each pot. Six weeks after the seeds were planted, plants were visually compared with photographs of various nutrient deficiencies (Skinner 1941). Plants with stunted or deformed leaves or without roots were defined as underdeveloped. Germination success and signs of nutrient deficiency between the two soil treatments were tested using the Chi-square test for 2 × 2 contingency tables or Fisher's exact test depending on the minimum value in the table.

5.4.8 Why is *Portulacaria afra* establishment more successful below woody shrubs?

To determine why *Portulacaria afra* establishment is more successful below woody shrubs, *P. afra* cuttings ($n = 21$) were planted into the following microhabitats: beneath adult *P. afra* clumps, under *Rhigozum obovatum* and in dense grass. To control for herbivory by domestic stock and wild animals, a second set of cuttings (paired with the first) was covered by wire cages. *Portulacaria afra* cuttings were obtained by removing the top 4 cm of new growth of an adult *P. afra* branch. A growth hormone was applied to the stem base and individuals were then planted into Speedling® trays and watered regularly. Root systems were produced after six weeks. Cuttings were transplanted into the field in early November and the results collected the following April. Mortality between caged (protected) and non-caged samples in each microhabitat was tested separately by the Chi-square test for 2 × 2 contingency tables. As no significant difference was found, these data were combined and establishment success of cuttings in each microhabitat was tested by the Chi-square test for $r \times 2$ tables with column headings the number of dead or alive cuttings and row headings the microsite in which seedlings were planted.

5.4.9 Position of later-successional trees relative to *Portulacaria afra* clumps

Large individuals of *Pappea capensis* and *Boscia oleoides* (trunk diameters at ground level > 15 cm) were randomly located in the *P. afra* rangeland and the direction from the tree to the centre of the *P. afra* clump in which they established was recorded. Measurements from at least 50 trees were recorded and trees, for which the original nurse clump could not be clearly identified, were omitted from the analysis. The frequency that trees were positioned to the north (315° - 45°), east (45° - 135°), south (135° - 225°) and west (225° - 315°) of the parent *P. afra* clump was determined and tested against the null hypothesis that the position of large trees relative to their nurse *P. afra* clump is random using a Chi-square goodness-of-fit test (Siegel and Castellan 1988).

5.4.10 Soil erosion in the *P. afra* rangeland

To determine whether soil loss by erosion differed where *Portulacaria afra* was removed by overgrazing, I measured the distance from the soil surface to the exposed uppermost lateral root of 25 *Pappea capensis* trees in the *P. afra* rangeland and in the adjacent Disturbed rangeland. These differences were tested by a Student's *t* test (Zar 1984).

5.4.11 Growth patterns of large later-successional tree species

Many of the large later-successional tree species appeared to be leaning to the north. I measured the angle of the lean and the compass direction of the lean of 106 trees. At Hillside, *Boscia oleoides* (Burch. ex DC.) Tölken and *Pappea capensis* were chosen because all other tree species coppice at their base making the required measurements difficult. A plum-bob of 1 m length was attached to one end of a standard 1 m measuring stick. While holding the measuring stick horizontal, the plum-bob was brought up against the base of the tree. The distance from the plum-bob end of the measuring stick to the tree trunk was measured. Using trigonometric formulae, the angle of tree lean was calculated. The compass direction of the lean was recorded. The number of trees leaning in a north (315° - 45°), east (45° - 135°), south (135° - 225°) or west facing (225° - 315°) direction was determined and tested against the null hypothesis that tree species do not lean in any particular direction using a Chi-square goodness-of-fit test (Siegel and Castellan 1988). The above tree measurements were repeated at the Boschfontein study site (103 trees were measured) where *P. afra* is absent except on the slopes of the Baviaanskloof Mountains. On this farm, only the trees on the flats were measured so that the measurements could be compared with those at Hillside. A Chi-square test for $r \times 2$ tables was used to determine whether the frequency of tree orientation in the four compass directions differed between Boschfontein and Hillside.

5.4.12 Size-age distribution of later-successional trees in the southern Karoo

To determine the age distribution of later-successional trees, the basal diameters of *Euclea undulata* at various sites in the southern Karoo were measured. McAuliffe (1988) used a similar method to age *Larrea tridentata* and *Ambrosia dumosa* in the Sonoran Desert. *Euclea undulata* was selected because it has a wide distribution in the southern Karoo enabling a wide geographic scale for comparison. Because *E. undulata* is prone to coppicing, only coppicing individuals with a minimum of three stems were measured. The internal distance between the two outer most stems was measured at ground level. The number of *E. undulata* seedlings found was also recorded. Basal diameters of at least 100 *E. undulata* individuals were measured at three areas in the southern Karoo. Firstly, at Vrolijkheid Nature Reserve in the far west of the hypothesised distribution of *P. afra*. Next, basal diameters of *E. undulata* were measured in and out of a stand of *P. afra* on Tierberg farm. Finally, basal diameters of *E. undulata* were measured in a stand of *P. afra* on Hillside farm. Vrolijkheid Nature Reserve is located just outside McGregor, south of Robertson and approximately 150 km to the west of the present distribution of *P. afra*. Vrolijkheid does, however, have bush clumps of the trees that prompted this study. Basal diameters were divided into the following size categories: 0 - 10 cm, 10 - 20 cm, 20 - 40 cm, 40 - 80 cm, 80 - 160 cm and > 160 cm. Seedlings of *E. undulata* were placed into the smallest size category. Pair-wise differences between the above four *E. undulata* populations were tested by a Kolmogorov-Smirnov two-sample test (Siegel and Castellan 1988).

5.5 RESULTS

5.5.1 Where do later-successional tree species establish?

The mean *Portulacaria afra* clump size (including seedlings) measured in the 10 quadrats was 15.9 m^2 (SE 2.6) and clumps ranged in size from 0.005 m^2 to 238.2 m^2 (n = 131). On average, 12 *P. afra* clumps were located in a 20 m × 20 m quadrat (Table 5.1). Although *P. afra* seedlings were uncommon in the *P. afra* rangeland, they were never observed in the Disturbed rangeland. Nutrient rich patches were far less common than *P. afra* clumps with only six counted in ten quadrats. The average area of NRP was 30.2 m^2 (range 6.9 m^2 - 76.7

TABLE 5.1: Average density (± SE) of common plant species at the *P. afra* rangeland and adjacent Disturbed rangeland at Hillside. Results of Wilcoxon-Mann-Whitney test are presented (n = 10 for each site).

	P. afra rangeland	Disturbed rangeland	Statistical comparison
Portulacaria afra clumps [1]	12.1 ± 1.6	-	
P. afra seedlings [2]	1.1 ± 0.3	0	
Rhigozum obovatum	29.4 ± 3.8	31.7 ± 3.9	$z = 0.45^{NS}$
Lycium cinereum	8.3 ± 1.8	8.8 ± 1.2	$z = 0.42^{NS}$
Tree seedlings (in woody shrub)	0.5 ± 0.3	0.3 ± 0.3	$z = -0.87^{NS}$
Tree seedlings (in *P. afra* clump)	5.2 ± 1.0	0	
Large trees (in open and on NRP)	1.2 ± 0.5	2.0 ± 0.5	$z = 1.21^{NS}$
Large trees (in *P. afra* clump)	8.3 ± 1.5	-	

[1] Number of *P. afra* clumps excluding seedlings.

[2] Seedlings defined as plants less than 30 cm in height.

m^2). The density of *Rhigozum obovatum* and *Lycium cinereum* did not differ between the *P. afra* rangeland and the adjacent Disturbed rangeland. Although many more tree seedlings were found in the *P. afra* rangeland, the number of tree seedlings found outside of *P. afra* clumps did not differ between the *P. afra* rangeland and the Disturbed rangeland. Similarly, large later-successional trees were very common in *P. afra* clumps but the number of large trees positioned outside *P. afra* clumps did not differ between the *P. afra* rangeland and the Disturbed rangeland (Table 5.1). Like the *P. afra* rangeland, the only tree seedlings found in the Disturbed rangeland were *Maytenus polyacantha*, which had established beneath *R. obovatum*.

Fifty-seven later-successional tree seedlings were found in ten 20 m × 20 m quadrats in the *P. afra* rangeland. Seedlings were most frequently found in *P. afra* clumps (52 seedlings) and rarely beneath woody shrubs (5 seedlings of *M. polyacantha*) ($\chi^2 = 38.8$, df = 1, $p < 0.001$). Four individuals of *M. polyacantha* were found beneath *R. obovatum* and one seedling was located below the skeleton of *Lycium oxycarpum* Dun., a tree. Although *M. polyacantha* was also the most common tree seedling inside *P. afra* clumps, five other tree species were recorded within *P. afra* clumps at this study site (Table 5.2). Seedlings were never found in open or grassy microhabitats.

TABLE 5.2: The average number (± SE) of later-successional trees and seedlings located in *Portulacaria afra* clumps in ten 20 m × 20 m quadrats in the *P.afra* rangeland, Hillside. Tree counts do not include trees located on NRP (5 individuals) and in open, grassy habitats (7 individuals) and seedling counts do not include five *Maytenus polyacantha* seedlings located outside of *P. afra* clumps.

	Large trees	Tree seedlings
Boscia oleoides	0.1 ± 0.1	0
Carissa haematocarpa	0	0.1 ± 0.1
Diospyros lycioides	0.5 ± 0.17	0.8 ± 0.33
Grewia robusta	3.0 ± 0.73	0.2 ± 0.2
Lycium oxycarpum	2.8 ± 0.55	0
Maytenus polyacantha	1.1 ± 0.38	2.8 ± 0.88
Pappea capensis	0.5 ± 0.22	0.2 ± 0.13
Rhus undulata	0.3 ± 0.15	1.1 ± 0.31

Ninety-five large later-successional trees were located within ten sampling quadrats in the *P. afra* rangeland. More than 87% of these trees were found inside *P. afra* clumps and only five and seven individuals were distributed on NRP and in open sites respectively (Table 5.2).

5.5.2 Where does *Portulacaria afra* establish?

Fifty-six *Portulacaria afra* seedlings were found in the *P. afra* rangeland of which 52 were located below woody shrubs. The remaining four *P. afra* seedlings were located in grass (1), within the mesemb *Ruschia* sp. (2) and beneath *Lycium oxycarpum* (1). *Rhigozum obovatum* was the most common woody shrub (86 individuals) in the *P. afra* rangeland, followed by *P. incana* (41 individuals) and *L. cinereum* (23 individuals). Forty *P. afra* seedlings were found beneath *R. obovatum*. Seedlings of *P. afra* established significantly more often than expected under the canopies of *R. obovatum* and less often than expected under *P. incana* and *L. cinereum* (Table 5.3, $\chi^2 = 8.2$, df = 2, $p < 0.05$).

TABLE 5.3: The frequency that woody shrub species were used as nurse plants by *Portulacaria afra* in the *P. afra* rangeland at Hillside. Expected frequencies of woody shrub nurse plants were calculated as the product of the relative proportion of the specific woody shrub in the *P. afra* rangeland and the total number of *P. afra* seedlings found under woody shrubs in the *P. afra* rangeland.

	Relative frequency of woody shrubs	Observed numbers	Expected numbers
Rhigozum obovatum	0.573	40	29.8
Pentzia incana	0.273	8	14.2
Lycium cinereum	0.154	4	8

A significant negative linear correlation exists between the covers of *P. afra* and *R. obovatum* ($y = -0.05x + 0.53$, $r = -0.39$, $p < 0.01$, $n = 51$). As the *P. afra* canopy size increases, the canopy size of *R. obovatum* decreases.

5.5.3 Where does *Rhigozum obovatum* establish?

Seedlings of *Rhigozum obovatum* were uncommon and difficult to find. No *R. obovatum* seedlings were found in open ground and seedlings occurred in equal frequencies in the shaded sites (Table 5.4, $\chi^2 = 0.1$). More *R. obovatum* seedlings were found growing in grass and under *Portulacaria afra* than in *Pentzia incana*. *Rhigozum obovatum* is unlikely to establish successfully beneath *P. incana* because this is a small shrub with a very open canopy that permits high light levels below it. Earlier results show that *P. afra* outcompetes *R. obovatum* suggesting that successful establishment of *R. obovatum* is most likely in grass.

TABLE 5.4: The presence-absence of *Rhigozum obovatum* seedlings in 1 m diameter circles with respect to three shaded sites in the *P.afra* rangeland at Hillside. No seedlings were found on bare ground. The total number of seedlings found in each of these microhabitats is also shown.

	Quadrats with *R. obovatum*	Quadrats without *R. obovatum*	Total seedlings found
In grass	11	19	33
Under *Pentzia incana*	10	20	15
Under *Portulacaria afra*	11	19	37

5.5.4 Vegetation patterns on nutrient rich patches

One hundred and five *Lycium cinereum* individuals were located on 20 NRP and only 12 plants were counted in the adjacent control areas. With the sample size reduced to 18 because of tied values, *L. cinereum* was more abundant on NRP on all 18 occasions (Sign test, $p < 0.001$). *Rhigozum obovatum* was most common in the adjacent grassy area with 179 individuals counted compared with 35 individuals on NRP. This species was more abundant in the grassy areas on all 20 occasions (Sign test, $p < 0.001$). Likewise, out of 20 NRP measured, *Psilocaulon absimile* was present on NRP on 15 occasions and never recorded in the grassy areas adjacent to NRP (Fisher's Exact test, $p < 0.001$).

Seventy-six large later-successional trees were located in the *P. afra* rangeland. On 39 occasions there was evidence of a raised mound indicating the presence of a NRP surrounding the tree. Of the remaining 37 samples, 34 showed no evidence of a NRP (grass only, no raised mound, no mesembs, no mammal digging activity). The remaining three samples lacked an obvious raised mound but mesembs were present in the immediate vicinity of the later-successional tree indicating an intermediate age. While earlier results indicated that some *Maytenus polyacantha* trees establish outside *P. afra* clumps, the incidence of this was rare and I can reasonably assume that most trees in this sample established inside a *P. afra* clump. Succulent plant species establish on NRP first and are replaced by grasses as the NRP ages (Table 5.5). Mammal digging activity also declines as the NRP ages indicating a decline in productivity in the localised patch as the nutrient levels drop (Table 5.6, $\chi^2 = 21.9$, df = 1, $p < 0.001$).

TABLE 5.5: Distribution of the mesemb, *Psilocaulon absimile*, and grasses with respect to younger and older nutrient rich patches in the *P. afra* rangeland at Hillside. The presence of a raised soil mound below later-successional trees (n = 76) positioned in the open indicated a young NRP. Older NRP were inferred from the absence of a raised mound surrounding later-successional trees.

	Younger NRP	Older NRP
Mesemb only	2	0
Mesemb and grass	29	3
Grass only	8	34

TABLE 5.6: Incidence of mammal digging activity on younger and older nutrient rich patches in the *P. afra* rangeland at Hillside. Young and older NRP are defined in the text.

	Younger NRP	Older NRP
With mammal activity	27	5
Without mammal activity	12	32

5.5.5 Is there an association between *Messor capensis* and the spatial distribution of *Portulacaria afra*?

One hundred and three *Messor capensis* nests were found in the *P. afra* rangeland of which 77 were located beneath woody shrubs. The remaining nests were located in a variety of positions ranging from bare ground and grass covered areas to the sides of *P. afra* clumps.

The siting of nests beneath woody shrubs occurs more frequently than expected by chance when compared with all other nest positions combined ($\chi^2 = 25.3$, df = 1, $p < 0.001$). *Messor capensis* does not appear to select a particular woody shrub species to nest beneath (Table 5.7, $\chi^2 = 2.1$, df = 2).

TABLE 5.7: The frequency that woody shrub species were used as nest sites by *Messor capensis* in the *P. afra* rangeland at Hillside. Expected frequencies of woody shrub nest sites were calculated as the product of the relative proportion of the specific woody shrub in the *P. afra* rangeland and the total number of *M. capensis* nests found under woody shrubs in the *P. afra* rangeland.

	Relative frequency of woody shrubs	Observed numbers	Expected numbers
Rhigozum obovatum	0.573	48	42.4
Pentzia incana	0.273	15	20.2
Lycium cinereum	0.154	11	11.4

Foraging activity of *M. capensis* was restricted to specific periods of the day (early morning, late afternoon, at night). Activity during the hotter daylight hours was avoided. *Portulacaria afra* produces fruit in enormous quantities in early spring. The fruit, which is about 6 mm long, 4 mm wide and 3-winged, is manipulated with ease by *M. capensis*. Smaller ants in the *P. afra* rangeland were unable to carry the *P. afra* fruit (*personal observation*). The average number of *P. afra* fruit returned to the nest fluctuated considerably. However, an average of 20 fruit/minute (range 13 - 30 fruit/minute) were transported to the nest of *M. capensis* by foraging individuals. One extreme measurement was ± 90 fruit/minute recorded shortly before rainfall.

5.5.6 Mechanisms of seed dispersal for *Psilocaulon absimile* and later successional tree species

At Tierberg, three species of *Monomorium* ant regularly found seed piles and removed seed back to nests that were positioned in the open with respect to the nearest shrub (Table 5.8). After discovery by *Monomorium* spp., many individuals recruited to the seed pile and subsequent seed removal was rapid. Ten of the 12 seed piles found by *Monomorium macrops*

Arnold were located on the first morning of the experiment. *Monomorium havilandi* Forel, however, only started to find seed piles on the first afternoon. This experiment, therefore, is probably an underestimate of the seed dispersal capability of *M. havilandi*. Indeed, enormous quantities of mesemb seed were found stored in nests of this ant species (*personal observation*).

TABLE 5.8: Dispersal of mesemb seed by ants at Tierberg, Prince Albert. Dispersal distance and canopy to nest distance is average distance (± SE).

	Number of piles found	Dispersal distance (m)	Dispersal range (m)	Canopy to nest distance (m)
Monomorium macrops	12	0.74 ± 0.12	0.04 - 1.33	0.19 ± 0.06
M. salomonis	3	0.91 ± 0.67	0.18 - 2.55	0.15 ± 0.08
M. havilandi	7	2.96 ± 0.64	1.15 - 6.25	0.42 ± 0.09
M. australe	1	11.65	-	0.35
Tetramorium peringueyi	3	3.75 ± 0.65	2.65 - 4.9	0.09 ± 0.09
Not found	6			

Despite its minute size (± 1.5 mm long), *M. macrops* showed no difficulty in manipulating and moving the larger *Malephora lutea* seed. The larger *Monomorium salomonis* and *M. havilandi* did not discriminate in their choice of the two seed species. *Monomorium australe* Emery regularly found seed piles but did not remove seeds except on one occasion. *Tetramorium peringueyi* Arnold also found seed piles regularly but only started to remove seeds on the second afternoon. Only two to three individuals of *T. peringueyi* recruited to the seed pile and seed removal was slow. Following rainfall in the *P. afra* rangeland at Hillside, several ant species were observed harvesting seeds of *Psilocaulon absimile*. Although *Pheidole* sp. 2 and *M. australe* moved mesemb seed, the most active mesemb seed harvester at this site was *M. alamarum* Bolton and, to a lesser extent, *T. peringueyi*. In addition, *T. peringueyi* actively attempted to remove seeds from the capsules of *P. absimile*.

Thirty-seven matched pairs (*P. afra* clump with emergent later-successional tree species and adjacent clump of similar size without an emergent later-successional tree species) were searched for later-successional tree seedlings. This number was reduced to an effective sample size of 20 because of two ties and 15 matched clumps where no tree seedlings were found. Tree seedlings were more abundant in *P. afra* clumps containing an emergent fruit tree on 18 occasions (Sign test, $p < 0.001$). Seventy-four tree seedlings were located in clumps with an emergent tree and 26 seedlings were found in similar sized *P. afra* clumps without a large emergent tree (Table 5.9). The effective sample size of the presence of *Maytenus polyacantha* in *P. afra* clumps was reduced to 15. Seedlings of this tree species were more abundant in *P. afra* clumps with an emergent tree on nine occasions indicating that the presence of an emergent fruit tree has no affect on the distribution of *M. polyacantha* (Sign test, $p > 0.05$).

TABLE 5.9: The number of tree seedlings located below matched *Portulacaria afra* clumps with and without an emergent fruit tree ($n = 20$).

	P. afra with emergent tree	*P. afra* without emergent tree
Boscia oleoides	5	0
Carissa haematocarpa	2	0
Diospyros lycioides	8	2
Grewia robusta	7	4
Maytenus polyacantha	17	10
Pappea capensis	24	7
Rhus undulata	11	3

On average, *Messor capensis* moved seeds of *Maytenus polyacantha* a distance of 7.5 m (SE 1.03, range 3.1 m - 18.6 m) from below the fruiting tree back to nests. Intact seeds lacking elaiosomes were found on the refuge piles of all 23 nests studied. More than half (12) the nests were positioned below the shrub *R. obovatum*.

Although *T. peringueyi* and *Pheidole* sp. 2 were observed in the vicinity of *P. afra* seed piles, only *M. capensis* was responsible for removing these seeds back to nests. Twenty-one seed piles (70%) were located by *M. capensis* over a two-day period. Of these, 16 were located on the first morning and four on the second morning. Once a pile was located by scouts, workers were recruited and the seeds rapidly removed. On average, *M. capensis* moved *P. afra* seeds a distance of 7.5 m (SE 0.75, range 2.0 m - 16.5 m) back to nests. Evidence of mammal digging activity was present in 33% of the *M. capensis* nests and 67% of the nests were positioned below the woody shrub *R. obovatum*. Excavation of three *M. capensis* nests revealed seed storage chambers positioned in the mound above ground level. Nest disturbance by mammal (e.g. aardvark, fox, suricate) digging activity would spread seeds stored in the nest.

5.5.7 Detritivores and soil nutrient enrichment

Termites were present in only three toilet rolls, one from each microhabitat, buried in the *P. afra* rangeland (Table 5.10). Toilet rolls buried underneath *P. afra* clumps were at a more advanced stage of decomposition and invertebrates, particularly isopods and cockroaches, were present in all of these baits. Baits collected from the grass microhabitat were partially decomposed and, although dry, all had evidence of mycelia suggesting that fungi contribute to decomposition when moisture levels are higher. Minimal decomposition was evident in NRP, possibly because their soils, lacking vegetation covering, do not retain moisture and lack soil invertebrates. These results diminish the importance of termites as detritivores in this system. However, *Amitermes* Silvestri, a wood-eating termite, was responsible for the decomposition of dead *P. afra* branches below clumps.

TABLE 5.10: The fate of toilet rolls (*n* = 11 in each microhabitat) buried in three microhabitats in the *P. afra* rangeland at Hillside. Advanced decomposition refers to the almost total disappearance of the bait. In this case the remains of the toilet rolls were moist, invertebrates (e.g. isopods, cockroaches) were present and there was evidence of fungal activity. Those toilet rolls showing partial decomposition were dry when found but there was some evidence of fungal activity

	NRP[1]	Grass	*P. afra*[2]
Advanced decomposition (moist, inverts, fungus)	0	0	7
Partial decomposition (dry, fungus)	2	6	0
Termites present	1	1	1
No effect	6	4	0

[1,2] two and three toilet rolls respectively, were not found when the data were collected.

The radish bioassay was performed twice. Initially, an automatic sprinkler system producing a fine mist maintained soil moisture. The open soils drained poorly (because of a high clay content) and became waterlogged resulting in radish seeds germinating in only two pots. The *P. afra* soils were never waterlogged and germination success was 77% (Fisher's Exact test, $p < 0.001$). When the experiment was repeated, water was applied manually to ensure that soils were never saturated resulting in a 100% germination success for both treatments. Mortality at harvesting, six weeks after establishment, was 27% in the open soil and 30% in the *P. afra* soil.

Plants from both soil treatments showed signs of nutrient deficiencies. Significantly more radish plants in *P. afra* soils developed swollen roots than did individuals in open soils (Table 5.11, Fisher's Exact test, $p < 0.001$). Similarly, significantly more individuals had fully developed leaves in *P. afra* soils than in open soils (Table 5.12, Fisher's Exact test, $p < 0.001$). Retarded growth in roots and leaves indicates nitrogen and/or calcium deficiency. Soils collected from below *P. afra* clumps is more nutrient rich than the soils collected in open sites although leaves of 64% of plants in *P. afra* soils and 70% on open soils displayed extensive yellowing, a sign of nitrogen deficiency.

TABLE 5.11: The development of swollen roots on radishes grown in soil collected from below *Portulacaria afra* clumps and from the open areas between *P. afra* clumps.

	Open soil	*P. afra* soil
Root swollen	2	13
Root not swollen	20	8

TABLE 5.12: The development of leaves on radishes grown in soil collected from below *Portulacaria afra* clumps and from the open areas between *P. afra* clumps. Underdeveloped leaves were thin, stunted and deformed.

	Open soil	*P. afra* soil
Leaves fully developed	3	14
Leaves underdeveloped	19	7

5.5.8 Why is *Portulacaria afra* establishment more successful below woody shrubs?

Mortality of cuttings did not differ between protected (caged) and unprotected sites in the *Portulacaria afra* microhabitat ($\chi^2 = 0.12$, df = 1, $p > 0.05$), the grass microhabitat ($\chi^2 = 0.38$, df = 1, $p > 0.05$) and in the *Rhigozum obovatum* microhabitat (Fisher's Exact test, $p = 0.16$) (Table 5.13). This indicates that grazing by domestic or wild animals did not affect the success of cutting establishment for the duration of this experiment. Consequently, I combined these data and compared the success of cutting establishment in each microhabitat. Cuttings of *P. afra* established successfully significantly more often than expected below *R. obovatum* and less often than expected in the grass microhabitat (Table 5.14, $\chi^2 = 8.2$, df = 2, $p < 0.05$).

TABLE 5.13: Comparing establishment success of *Portulacaria afra* cuttings with and without protection from herbivores in three microhabitats in the *P. afra* rangeland at Hillside. Protected cuttings were covered by a wire cage. Each microhabitat was tested separately by 2 × 2 contingency tables.

		Alive	Dead
Portulacaria afra	Protected	14	7
	Unprotected	16	5
Grass	Protected	13	8
	Unprotected	10	11
Rhigozum obovatum	Protected	16	5
	Unprotected	19	2

5.5.9 Position of later-successional trees relative to *Portulacaria afra* clumps

The position of large *Pappea capensis* and *Boscia oleoides* trees relative to their original *P. afra* nurse plant was not random (Table 5.15, $\chi^2 = 47.7$, df = 3, $p < 0.001$). Large later-successional trees were positioned significantly more often than expected by chance to the south of the *P. afra* nurse plant and less often than expected to the sunnier northern and eastern sides. This indicates that the establishment of later-successional trees is most successful on the shadier sides of *P. afra* clumps.

TABLE 5.14: The establishment success of *Portulacaria afra* cuttings transplanted into three microhabitats in the *P. afra* rangeland at Hillside. Cutting mortality did not differ between protected (caged) and non-protected sites indicating that grazing by animals did not affect the success of cutting establishment for the duration of this experiment (Table 5.13). These data were combined and the success of cutting establishment in each microhabitat tested.

	Alive	Dead
Portulacaria afra	30	12
Grass	23	19
Rhigozum obovatum	35	7

TABLE 5.15: The position of large later-successional trees (*Pappea capensis*, *Boscia oleoides*) relative to their original *Portulacaria afra* nurse plant in the *P. afra* rangeland at Hillside.

	Tree numbers
North (315° - 45°)	0
East (45° - 135°)	7
South (135° - 225°)	33
West (225° - 315°)	11

5.5.10 Soil erosion in the *P. afra* rangeland

Despite the gentle gradient (slope angle ± 1°) on which the study sites were located, soil loss in the Disturbed rangeland (16.8 cm ± 1.4) was more than double the amount (7.2 cm ± 1.1) measured in the *P. afra* rangeland ($t = 5.46$, $n = 50$, $p < 0.001$). Bare shale, small stones and pebbles were exposed at the Disturbed rangeland site and not in the *P. afra* rangeland.

5.5.11 Growth patterns of large later-successional tree species

Twelve of 106 trees measured at Hillside were growing vertical to the ground and were disregarded from the analysis. Despite their establishment on the shadier sides of *P. afra* clumps, most trees grow towards the sunnier north and east-facing aspects at Hillside (Table 5.16, $\chi^2 = 18.9$, df = 3, $p < 0.001$). On Boschfontein, only four trees of 103 were growing straight and, as at Hillside, the direction of lean was to the north and east (Table 5.16, $\chi^2 = 14.1$, df = 3, $p < 0.01$). The tree populations at Hillside and Boschfontein did not differ in the frequency of direction that large later-successional tree species leaned ($\chi^2 = 1.07$, df = 3).

TABLE 5.16: The frequency that large later-successional tree species lean towards four direction categories in the *P. afra* rangeland at Hillside (n = 94) and in the rangeland at Boschfontein (n = 99).

	Hillside	Boschfontein
North facing (315° - 45°)	38	33
East facing (45° - 135°)	29	35
South facing (135° - 225°)	12	14
West facing (225° - 315°)	15	17

5.5.12 Size-age distribution of later-successional trees in the southern Karoo

Pairwise comparisons of size (age) distributions of the *Euclea undulata* populations from Vrolijkheid Nature Reserve and Tierberg indicate that there are no differences in the distribution of basal diameters of these trees away from *P. afra* clumps (Figure 5.1). Similarly, the *E. undulata* populations from Tierberg and Hillside measured in *P. afra* clumps did not differ in their size class distribution of basal diameters. The Vrolijkheid population in the open had significantly more individuals in larger size (age) classes than those in *P. afra* clumps at Tierberg (Kolmogorov-Smirnov two-sample test, $p < 0.01$) and Hillside (Kolmogorov-Smirnov two-sample test, $p < 0.05$) (Figure 5.2). Similarly, the *E. undulata* population measured out of *P. afra* vegetation on Tierberg had significantly more individuals in larger size (age) classes than those in *P. afra* clumps at Tierberg (Kolmogorov-Smirnov two-sample test, $p < 0.001$) and Hillside (Kolmogorov-Smirnov two-sample test, $p < 0.01$) (Figure 5.3).

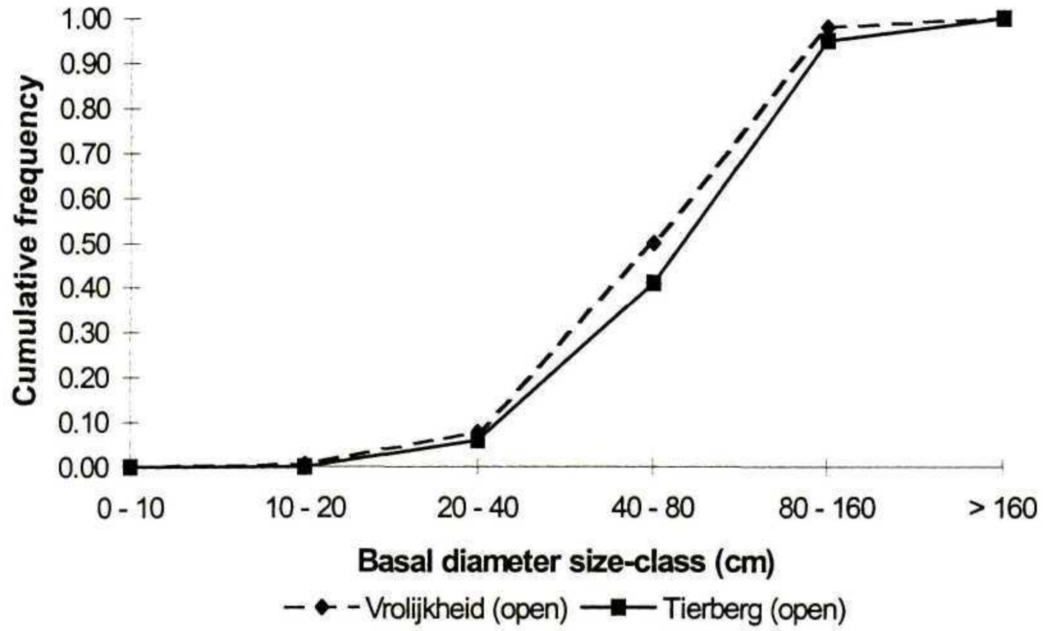

FIGURE 5.1: Size-class distribution of basal diameters of *Euclea undulata* populations measured outside of *Portulacaria afra* clumps at Vrolijkheid Nature Reserve, McGregor and Tierberg farm, Prince Albert.

5.6 DISCUSSION

5.6.1 Cyclical succession in the *Portulacaria afra* rangeland

Portulacaria afra is an evergreen tree-succulent that increases in cover by vegetative growth. The stems and leaves of this species are densely packed producing low-light levels and reduced temperatures within the clump (Chapter 4). *Portulacaria afra* produces an enormous amount of dead plant matter through leaf fall and the collapse of succulent stems. Being succulent, this "softwood" is rapidly decomposed by termite activity which, along with decomposition by other soil detritivores (millipedes, snails, earthworms), produces a raised mound of nutrient enriched soil below the *P. afra* clump. Both the physical and chemical properties of the soil below the *P. afra* clump are altered by this invertebrate activity. Such a plant species provides an ideal refuge for the germination and subsequent establishment of later-successional tree species. Almost all the later-successional tree species considered in this study produce fruit that are bird dispersed. The data indicate that later-successional trees (with the possible exception of *Maytenus polyacantha*) require the well-shaded microhabitat provided by *P. afra* for germination. Although these conditions are necessary for the initial

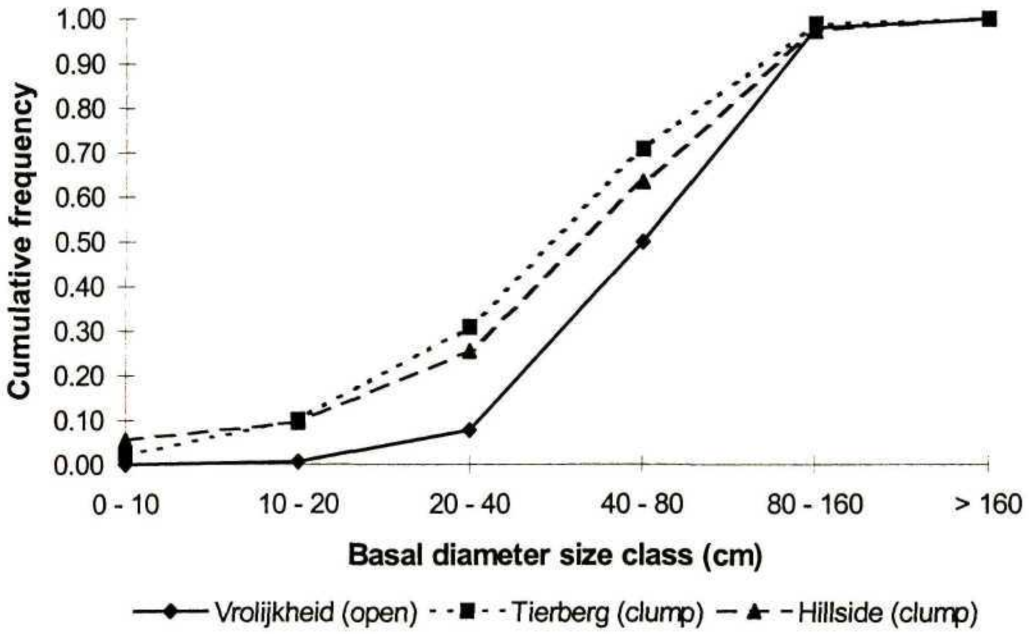

FIGURE 5.2: Size-class distribution of basal diameters of *Euclea undulata* populations measured outside of *Portulacaria afra* clumps at Vrolijkheid Nature Reserve, McGregor and within *P. afra* clumps at Tierberg farm, Prince Albert and Hillside farm, Jansenville.

establishment of tree species in these semi-arid rangelands, the low light intensity within the *P. afra* clump slows growth of the young tree. These trees respond by growing at an angle towards the sunnier northern and eastern sides of the clump. The direction of growth also depends on the position of seedling establishment within the *P. afra* clump. For example, seedlings germinating on the shaded side of the *P. afra* clump grow towards the south-west.

The vigour of *P. afra* might be reduced by the shading effect of large trees (Von Maltitz 1991). It is difficult to determine whether *P. afra* is competitively displaced by later-successional trees. Being heliophilic, *P. afra* tends to grow away from the shading effect of emergent trees as well as themselves. Trees growing within *P. afra* clumps were often surrounded by an open area (*personal observation*). In many cases this was due to a shading effect but trampling by animals browsing on the tree canopy can create the same effect.

Detritivores greatly modify the physical structure of soil and lead to its enrichment relative to adjacent soils (MacKay et al. 1989, Polis 1991). I have shown elsewhere (Chapter 4) that soil surface temperatures inside *P. afra* clumps remain below ambient throughout the day. This cooler environment reduces the loss of soil moisture and encourages the presence of

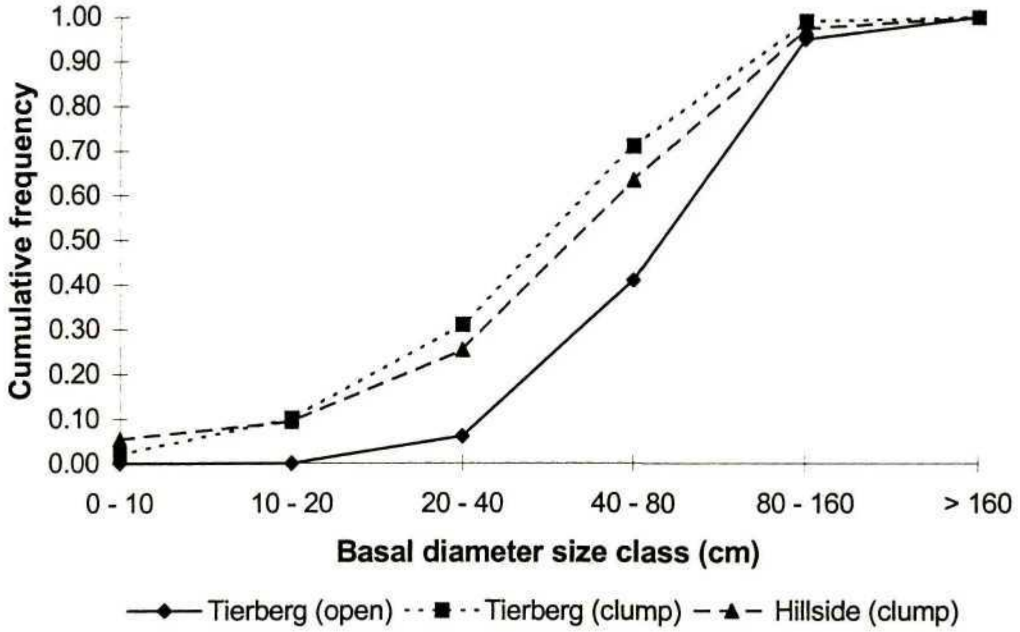

FIGURE 5.3: Size-class distribution of basal diameters of *Euclea undulata* populations measured outside of *Portulacaria afra* clumps at Tierberg farm, Prince Albert and within *P. afra* clumps at Tierberg and Hillside farm, Jansenville.

detritivores such as isopods, cockroaches and collembolans. Elevated soil moisture levels also stimulates decomposition by fungi. Furthermore, earthworms (*Microchaetus* sp.), millipedes (*Centrobolus* sp.) and snails (*Sheldonia* sp.) were very active in the *P. afra* rangeland following rainfall but these taxa remain buried in the soil below *P. afra* clumps during dry periods (*personal observation*). Dead *P. afra* branches that accumulate below clumps were rapidly reduced by the termite *Amitermes* sp. Apart from nutrient enrichment, the accumulated affect of these detritivores greatly modifies the physical structure of the soil. Unlike the hard, crusted open soils which have a high clay content, soils below the *P. afra* clump are rich in organic matter and have a loamy texture.

The heavy succulent branches of *P. afra* collapse and die once the vegetative apron has been removed by overgrazing (Stuart-Hill 1992). Larger (older) clumps appear to start thinning from the centre, possibly a consequence of self-shading. Whatever the cause, the collapse and subsequent decomposition of the clump creates a bare mound of nutrient enriched soil. At Hillside farm, *Psilocaulon absimile* and *Lycium cinereum* were the first plant species to colonise these NRP. These pioneer species were replaced by grass on older NRP. The *P. afra* rangeland at Hillside farm lost its palatable perennial grasses to overgrazing. I can therefore only speculate that perennial grasses would outcompete *P. absimile* and *L. cinereum*. Although this study did not concentrate on grasses, clear replacement patterns were evident on NRP. *Enneapogon scoparius* Stapf was the first grass species to invade NRP and coexist with *P. absimile*. *Aristida adscensionis* L. was more common on older NRP where it coexisted with *P. absimile* and *E. scoparius*. *Aristida congesta* subsp. *barbicollis* (Trin. & Rupr.) De Winter was the dominant grass species in the *P. afra* rangeland. This non-palatable grass replaces all other plant species on NRP. The presence of *Aristida* spp. is evidence that this rangeland was heavily overgrazed in the past (Tainton et al. 1985, Van Oudtshoorn 1991).

How does *Rhigozum obovatum* establish in the *P. afra* rangeland? Recruitment of *R. obovatum* appears to be infrequent to rare in the southern Karoo (Van Breda and Barnard 1991, J. H. J. Vlok, *personal communication*). In the more arid areas to the west of Hillside farm, *R. obovatum* is distributed on rocky slopes and, on the plains, this woody shrub occurs in drainage lines only. This distribution suggests that *R. obovatum* requires reasonably moist conditions for establishment. In the present study, two untypically wet seasons preceded data collection. As a result, although uncommon, *R. obovatum* seedlings were found relatively easily once it was known where to find them. Apart from high moisture conditions, grass seems to be important for the successful germination and establishment of *R. obovatum*. Little is known about the competitive interactions between grasses and shrubs (Wondzell and Ludwig 1995). Water uptake by grass after rainfall is more rapid than shrubs (Knoop and Walker 1985, Williams and Hobbs 1989, F. Smith, *personal communication*) and shrubs require exceptionally high moisture levels to establish in semi-arid grassland (Harrington 1991). Brown and Archer (1989) showed that a reduction in grass biomass increased *Prosopis glandulosa* seedling mortality implying that grass may facilitate the initial establishment of *P. glandulosa* and that competitive effects with grass are less important at the seedling stage. *Rhigozum obovatum* probably requires grass cover for its initial establishment (grass will maintain a high soil moisture) but thereafter will be in direct competition with grass for moisture. Only under unusually high moisture conditions, where moisture is no longer limiting, will *R. obovatum* successfully outcompete grass. Although *R. obovatum* seedlings were frequently located in *P. afra* clumps, this woody shrub is displaced by *P. afra*. However, if the dense canopy of the *P. afra* clump has started to collapse, *R. obovatum* will establish successfully.

How does *P. afra* establish in this plant community? *Portulacaria afra* seedlings were found most frequently beneath woody shrubs, particularly *R. obovatum*. The dense canopy of *R. obovatum* provides shade during the hot summer months, but being deciduous, it loses its leaves in winter. Not only does this protect the *P. afra* seedling from the extreme summer temperatures, but it allows *P. afra* to exploit the weaker winter sunlight. The woody stems and branches of *R. obovatum* also protect the young *P. afra* individual from herbivores. Thus, *R. obovatum* would seem to provide the ideal microsite for the establishment of *P. afra* seedlings.

Indirect evidence that the harvester ant, *Messor capensis*, is responsible for the spatial distribution of *P. afra* has been presented. Nests of *M. capensis* were positioned preferentially beneath woody shrubs. Although most nests of this ant species were beneath *R. obovatum*, *M. capensis* does not select this woody shrub preferentially to nest under. *Messor capensis* foragers move enormous quantities of *P. afra* fruit back to their nest sites. Although *M. capensis* is a seed predator, seeds cached by this ant species are "lost" in the soil when nests are disturbed by digging mammals (Dean and Yeaton 1992). Elevated soil nutrient levels on nest mounds will contribute to successful germination and establishment of seeds (Dean and Yeaton 1992, 1993). Disturbance by mammals may facilitate *P. afra* establishment because seedlings cannot emerge if germination occurs deeper than 2 cm below the soil surface (Whiting 1991).

Portulacaria afra displaces its nurse plant, *R. obovatum*, by competitive interaction. The densely packed stems and leaves of *P. afra* shade woody shrubs growing within the clump unless the shrub maintains its canopy above the *P. afra* clump. However, by doing this, the ratio of stem thickness to stem height of *R. obovatum* decreases resulting in stems that are more susceptible to breakage. Dead or dying stems of *R. obovatum* were common in many of the larger *P. afra* clumps. Individual *R. obovatum* plants were uncommon within the very largest *P. afra* clumps.

I have used inferential and experimental evidence to provide a predictable description of the dynamics of the *P. afra* rangeland in the southern Karoo (Figure 5.4). The organisation of the *P. afra* rangeland is not random. The plant community represents a dynamic mosaic of various shrub species, grass and patches of nutrient rich soil which all offer different microhabitats for plant establishment. Earlier successional plant species facilitate the establishment of later successional plants by providing microhabitats that buffer the extreme climatic conditions, reduce the competitive effect of dominant plant species and lesson the threat of herbivory. Once established, the later successional plant displaces its facilitator by competitive interaction. Seed dispersal by biotic vectors (birds and several species of ants) and soil nutrient enrichment by detritivores are important in these dynamic processes.

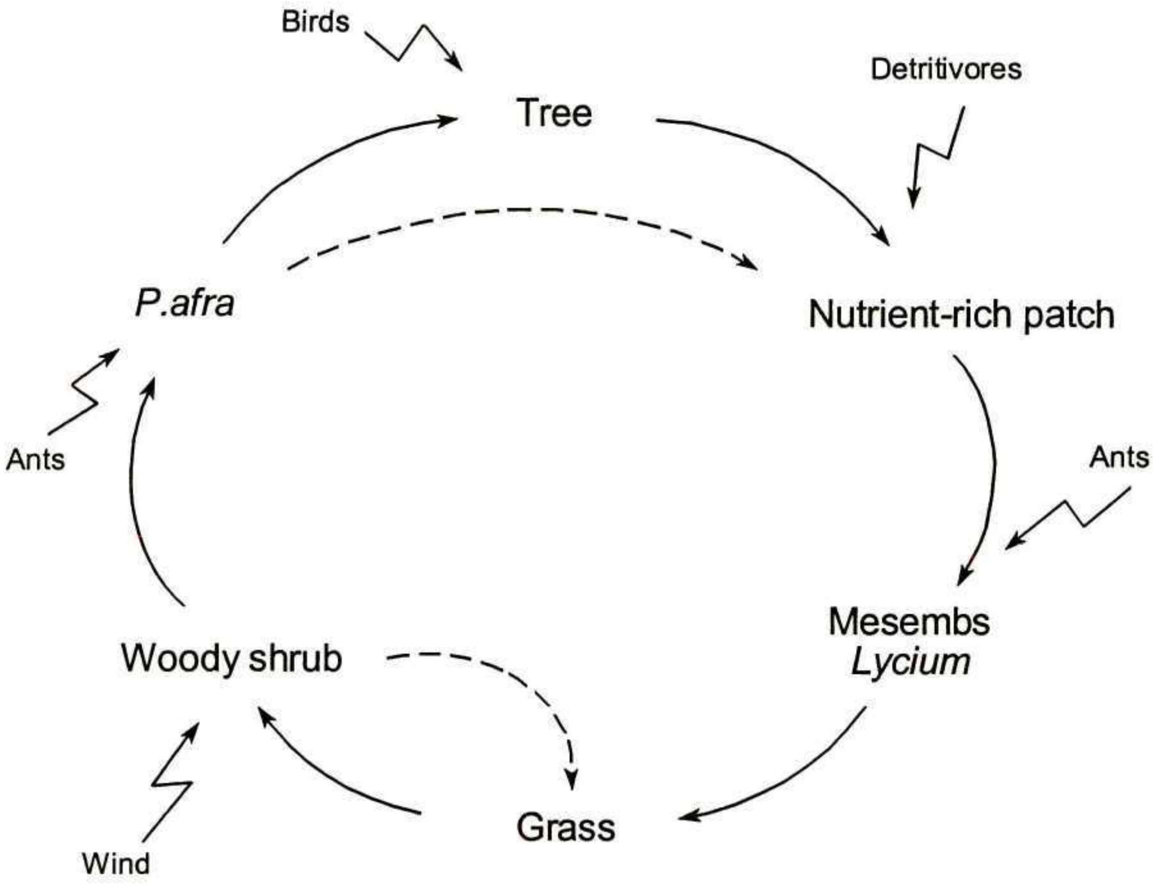

FIGURE 5.4: Cyclical replacement of major plant species and their postulated dispersal mechanism in the *P. afra* rangeland at Hillside farm, Jansenville.

5.6.2 What maintains plant species diversity in the *P. afra* rangeland community?

Disturbance promotes species coexistence in natural communities by removing competitively superior species and creating open space (Connell 1978, Paine and Levin 1981). These local patches serve as foci for the establishment of competitively inferior species (Sousa 1984). In the *P. afra* rangeland, nutrients are concentrated in discrete patches that are dynamic in space and time. Their presence prevents the complete monopolisation by grass and permits two plant species, *Lycium cinereum* and *Psilocaulon absimile*, to persist in the system as fugitive species (Hutchinson 1951). Both these species, however, are destined to local extinction by the superior competitive ability of grass. Detritivores, the agents of soil nutrient enrichment, are not persistent on NRP resulting in the steady decline of nutrient levels. The change in soil characteristics shifts the competitive balance in favour of grasses which invade the NRP and prohibit any further establishment of either *L. cinereum* or *P. absimile*.

At the scale of the individual, each successive plant in the cyclic process has a complementary root system suggesting that species coexistence of certain plant species might be promoted by differences in life form which effect different nutrient and water uptake strategies (cf. Cody 1986*b*). Although complementary root systems may contribute to the successful establishment of plants by reducing root competition with their respective nurse-plants, competitive interactions between these plant species are deterministic and the outcomes predictable, indicating that resource partitioning is not an appropriate concept explaining species coexistence in this plant community. Small-scale disturbances, such as an ant nest or an established shrub, reduce the competitive superiority of grasses and permit the establishment of later-successional species. In this way, *R. obovatum* and *P. afra* facilitate the establishment of *P. afra* and later-successional tree species respectively. Not only does facilitation ameliorate harsh physical conditions (Bertness and Callaway 1994) but the nurse-plant also reduces the competitive ability of dominant plant species allowing establishment of competitively inferior species.

Local population dynamics and disturbance-mediated coexistence are frequently contingent upon dispersal mechanisms (Hastings and Harrison 1994, Tilman 1994, 1997). Seed dispersal by biotic vectors in the *P. afra* rangeland is as important to maintaining diversity as the disturbance itself. Ant species (e.g. *Tetramorium peringueyi*, *Monomorium alamarum*) that harvest mesemb seeds are themselves fugitive species on NRP (Chapter 4). Following rainfall, enormous quantities of mesemb seeds are harvested and cached in storage chambers within 20 mm of the soil surface (*personal observation*). These nests would be frequently disturbed, causing seed burial, by the repeated mammal digging activity on NRP. Likewise, the dispersal of *P. afra* seed by ants and later-successional tree fruit by birds moves these propagules away from the inhibitory influence of grass to safe sites beneath shrubs. Yeaton and Bond (1991) explained the coexistence of two competing overstory shrubs in the Cape fynbos of South Africa in the same way.

Disturbance does not account for the continued coexistence of *R. obovatum* in this plant community. *Rhigozum obovatum* is a critical component to the dynamics of this community because it initiates the cyclic process that maintains all other plant species in the system. The rarity of seedlings and young plants indicates that establishment is episodic and I have suggested earlier that the successful establishment of *R. obovatum* is contingent on exceptionally high rainfall events, when moisture is not limiting, to overcome the competitive dominance of grass. Provided it can overcome the initial inhibitory effects of grass, *R. obovatum* will be maintained in the community by its deep root system. There is no evidence that seeds of *R. obovatum* are dispersed by biotic vectors or that this shrub establishes on some type of disturbance such as an ant or termite nest. I speculate that the continued coexistence of *R. obovatum* (and all the plants following) is made possible by unpredictable events of recruitment ("storage effect" of Warner and Chesson 1985, Chesson 1986). The age-class structure of the *R. obovatum* population could not be determined by inferential techniques because all plants of this palatable species were severely overgrazed.

Do the general principles described above apply to arid and semi-arid systems elsewhere? Nurse facilitation and competition govern coexistence patterns and determine plant community structure in arid systems (McAuliffe 1988, Valiente-Banuet et al. 1991*a*, 1991*b*). However, the zoogenic influence on these processes is less clear. In the northern Chihuahuan Desert, *Opuntia leptocaulis* replaces *Larrea tridentata* which colonises open ground (Yeaton 1978). Rodents create the disturbance responsible for the mortality of *O. leptocaulis* and both birds and rodents deposit *O. leptocaulis* seeds beneath *L. tridentata*. McAuliffe (1988) describes similar patterns in the Sonoran Desert where *Larrea tridentata* replaces *Ambrosia dumosa* but he did not document any zoogenic effects in this simple two-species community. Similar patterns were found in a species-rich plant assemblage in the Sonoran Desert (McAuliffe 1988). Likewise, cactus recruitment in central Mexico was facilitated by trees (Valiente-Banuet et al. 1991*a*, 1991*b*). In the species rich southern Karoo, species belonging to a woody shrub guild recruit inside mat-forming succulent shrub species (Yeaton and Esler 1990). Yeaton and Esler (1990) argue, as I have in this chapter, that soil changes initiated by termite activity set up small-scale environmental gradients which favour different plant species. More recently, Yeaton (*personal communication*) has studied similar cyclic patterns in the species-rich southern Chihuahuan Desert of the Mexican states of San Luis Potosi and Zacatecas. As in *P. afra* rangeland, harvester ants (e.g. *Pogonomyrmex rugosus*, *P. barbatus*) set up the cyclic process by "losing" seeds, which subsequently germinate in the waste heaps at the edge of their nest mounds.

5.6.3 The *Portulacaria afra* vegetation model: what are the implications on Karoo vegetation prior to introduction of domestic stock?

Portulacaria afra is a palatable shrub that is prone to overgrazing by domestic stock (Stuart-Hill 1992). Yet, the *P. afra* population at the Hillside study site was in a healthy condition despite the abundance of weedy *Aristida* grasses, a clear sign of overgrazing (Tainton et al. 1985, Van Oudtshoorn 1991). I have emphasised cyclical succession at the scale of the individual. Understanding competitive interactions at this scale permits me to predict landscape-level patterns and the above paradox can be effectively interpreted by application of state-and-transition models (Westoby et al. 1989). In the absence of overgrazing by domestic stock, the superior competitive ability of grasses would control the dynamics of this system by inhibiting the establishment of *Rhigozum obovatum*, resulting in a grass-dominated system where *P. afra* and trees would be uncommon. Perennial grasses, however, were lost in the southern Karoo as a consequence of overgrazing but, on Hillside, that initial period of mismanagement was not sustained long enough to completely remove *R. obovatum* and *P. afra*. The loss of competitively superior grasses created space for the colonisation of less vigorous, weedy species such as *Aristida congesta*. *Rhigozum obovatum*, released from the competitive effects of perennial grasses, subsequently increased in abundance permitting further establishment of *P. afra* and later-successional trees. In contrast, both the perennial grass component and *P. afra* was lost when domestic stock were first introduced into the Disturbed rangeland at Hillside. Although *R. obovatum* increased to the same density as the *P. afra* rangeland, *P. afra* (and therefore, the later-successional trees) is absent from this community because it never recovered from that initial period of overgrazing. These rangelands, therefore, have been driven into different states depending on their early grazing pressures.

The impact of overgrazing by domestic stock in the southern Karoo increases westwards because of the interactive effects of moisture and grazing (Stokes 1994). I have used inferential techniques to show that certain tree species that presently have a discontinuous distribution with *P. afra* would have established within clumps of this species. There is no new establishment of *Euclea undulata* where populations of this tree species do not co-occur with *P. afra*. I have also speculated from the vegetation model presented above that *R. obovatum* requires perennial grass to facilitate its establishment. The present distribution of later-successional trees and *R. obovatum* suggests a pre-degradation distribution of *P. afra* and perennial grasses that would have extended far further to the west than at present. Presently, relict populations of perennial grass species are found across the region. This idea is not new and has stimulated considerable research and comment (e.g. Roux and Vorster 1983, Hoffman and Cowling 1990, Palmer et al. 1990, Dean and Macdonald 1994, Milton and Hoffman 1994, Hoffman 1995). Grazing alters the plant species composition of grassland and, world-wide, the general trend is one of replacement of perennial grass species by unpalatable grasses and woody shrubs (Humphrey 1958, Walker et al. 1981, Bahre and Shelton 1993, Archer 1996).

Does this interpretation offer a new insight into the much debated origins of *heuweltjies* (Lovegrove and Siegfried 1986, 1989, Milton and Dean 1990, Moore and Picker 1991)? *Heuweltjies* are nutrient-rich mounds approximately 1 m in height, up to 20 m in diameter, generally oval in shape and are believed to have been formed by the activity of *Microhodotermes viator* Latreille, a termite (Lovegrove and Siegfried 1989, Midgley and Musil 1990, Milton and Dean 1990). They are visible features on the landscape because the mound vegetation is dominated by succulent shrubs while the surrounding matrix is dominated by woody shrubs (Milton et al. 1992). Throughout their distribution, *heuweltjies* are distributed on both rocky slopes and plains and it is not unusual to find later-successional trees located on *heuweltjies* (*personal observation*). Yeaton and Esler (1990) have argued that the nutrients concentrated in these mounds are the forces driving the plant community dynamics of the shrubland they studied. In this chapter I have been careful to separate NRP (found in the *P. afra* rangeland) from *heuweltjies* (found in the succulent Karoo). Although similar in terms of appearance and the presence of certain plant species, the two formations differ in that *M. viator* is absent from NRP. Active *heuweltjies* (i.e. occupied by *M. viator*) show sustained termite activity and hence nutrient enrichment. Nutrient rich patches, in contrast, lose their biotic activity once the *P. afra* clump collapses and the high shade, high moisture microenvironment is lost. In time, nutrients are leached from NRP resulting in colonisation by grass.

Ant community structure is indirectly determined by vegetation. The replacement of grass by shrubs and the consequent loss of ground cover alters competitive abilities in favour of new ant species which then become dominant (Chapter 4). Termite distribution and abundance appear to be influenced in exactly the same way (Haverty and Nutting 1975, Pomeroy 1978, Crawford 1981). *Amitermes* sp. was the common termite species in the *P. afra* rangeland where grasses and *P. afra* were dominant. *Microhodotermes viator*, however, was rare in this rangeland but common in severely degraded rangeland (lacking ground cover) adjacent to the *P. afra* rangeland (*personal observation*). If the predictions from the above vegetation model are correct and the *P. afra*/grass rangeland extended further to the west prior to the introduction of domestic stock, then the distribution of *M. viator* would have been considerably reduced. Has *M. viator* invaded the Karoo from the fynbos following the degradation of the *P. afra*/grass rangeland in the west? *Microhodotermes viator* is very common in the fynbos of the southern and south-western Cape (Coaton and Sheasby 1974, 1975). The present distribution of *M. viator*, however, extends north, north-east and east of the fynbos into typical Karoo shrub-dominated rangeland. The implication here is that *heuweltjies*, at least in the more eastern parts of their distribution, are relatively recent additions to the landscape. Although *M. viator* may have invaded NRP accounting for the presence of later-successional trees on *heuweltjies*, the origins of *heuweltjies* and NRP are independent. Further to the west, in the winter rainfall region, production gradients would differ from that in the east and *M. viator* may have been present in that region for a longer time period. This implies that *heuweltjies* in the west of their distribution are older which might account for their larger size (Lovegrove and Siegfried 1989). *Heuweltjies* in the Clanwilliam district have been dated to 4000 years (Moore and Picker 1991).

The implications of the loss of *P. afra* and grass from the Karoo plant community are serious and far reaching. The relatively shallow but extensive root system of *P. afra* maintains soil stability (Coates Palgrave 1984). There is evidence of reduced soil loss in the *P. afra* rangeland compared with adjacent degraded areas where root systems of later-successional trees are exposed to a depth of almost 40 cm. Erosion in the southern Karoo is exacerbated by the hilly topography created by the folded mountain belt. Efforts to improve ground cover by encouraging the establishment of palatable plant species are compounded by unstable and low quality soils. The affect of soil loss on edaphic fauna is unknown. Widescale soil erosion following vegetation change has been reported in semi-arid regions of south-western United States, Mexico and Australia (Bahre and Shelton 1993, Melville 1994, Wondzell and Ludwig 1995). The consequences of reduced vegetation cover and soil loss on the hydrological cycles in the Karoo are beyond the scope of this chapter but one can speculate that ground water supplies would be adversely affected.

5.6.4 The zoogenic influence on arid-zone plant community dynamics

The decline in perennial grass and its replacement by a woody component as a consequence of overgrazing is a world-wide phenomenon (Walker et al. 1981). In southern

Africa, the Karoo is no exception. The question now is whether we can manage these rangelands to attain their former levels of production. Management and rehabilitation of disturbed systems can only be attempted once their dynamics are understood.

I have argued that animals, particularly invertebrates, are an important factor to consider when attempting to understand plant community dynamics. The patterns produced by animals, however, are difficult to detect in degraded systems. Semi-arid plant communities are sensitive to overgrazing and once disturbed, dynamic patterns are lost or become masked. At Hillside, due to its previous landuse history of relatively low grazing pressure, these dynamic patterns are evident on the plains. The role of various ant species and nutrient releasing detritivorous taxa on the spatial distribution of plants is clear at this site. The response of these semi-arid plant communities to large-scale disturbance, such as overgrazing, can be described as rapid and irreversible, resulting in the local extinction of many plant and animal species. Plant species, mainly unpalatable ones, released from the inhibitory effects of other superior competitors become dominant. The harmful consequence of this effect is that the complex feedback links between the plant community and the important invertebrate component are severed. This in turn results in the loss of community patchiness and ultimately disrupts the dynamic processes driving the system.

5.7 ACKNOWLEDGEMENTS

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Chapter 6: Conclusions

The aim of this thesis was to describe the structure and dynamics of ant and plant communities in the southern Karoo and to assess mechanisms of species coexistence in ant and plant communities. I placed particular emphasis on the role of species interactions in structuring natural communities.

6.1 ANT COMMUNITY STRUCTURE

Diversity indices were used to determine the importance of habitat in maintaining ant species diversity in the southern Karoo. Ant species diversity was not predicted by measurements of plant species diversity or vegetation structural diversity. Ant species richness, however, was correlated with measures of vegetation structural diversity but not with plant species diversity. Ant species appeared to respond to aspects of vegetation height. Although vegetation complexity influences ant species richness, competitive effects, particularly of dominant ant species, appear to suppress subordinate ant species influencing measures of richness and diversity. This may account for the lack of association between habitat and ant species diversity. Diversity indices did not adequately address the questions posed at the start of the study. Consequently, I concentrated on interactions between dominant ant species and how their competitive performance changes with respect to vegetation.

I concentrated on dominant ant species because they were common, widespread and their distribution patterns were clear. Also, aggressive dominant species determine the distribution and abundance of subordinate ant species. Interference competition for space was prevalent between dominant ant species and competitive success was a function of vegetation. However, it is not clear whether ants respond directly to physical conditions created by vegetation which then influences foraging activity or, alternatively, whether ants respond to productivity gradients which are affected by vegetation. For example, *Pheidole* sp. 2 foragers with nests positioned under *Portulacaria afra* clumps were active for the duration of the day while individuals with nests positioned in the open were not active for 7 hours during the hot period. This appears to support the first option but it fails to explain why *Tetramorium peringueyi* was dominant in the Upper rangeland at Tierberg but was outperformed by *Pheidole* sp. 2 and *Crematogaster melanogaster* in the Lower rangeland. The difference in plant species composition between the Upper and Lower rangeland sites at Tierberg implies a productivity gradient to which the ants might respond.

Understanding vegetation dynamics is critical to interpreting patterns of ant species distribution and abundance. For example, a patchy habitat disrupts the competitive dominance of aggressive dominant species, removing the potential towards habitat monopolisation, and therefore maintaining ant species diversity. In the *P. afra* rangeland, *Pheidole* sp. 2 was superior in well-shaded microhabitats but *Messor capensis* nested successfully under woody shrubs and several ant species (*Tetramorium peringueyi*, *T. quadrispinosum*, *Monomorium alamarum*, *Ocymyrmex barbiger*) persisted on nutrient-rich patches. However, woody shrubs, *P. afra* (and therefore NRP) all established in this system successfully because overgrazing by domestic stock reduced the competitive ability of grass. A system dominated by grass would favour *Pheidole* sp. 2 at the expense of other ant species in the community which would be unable to establish successfully.

There is no evidence supporting the notion that ant communities are at equilibrium. Rather, dominance hierarchies lead to the replacement of species over vegetation gradients with the tendency towards the aggressive acquisition and monopolisation of space. The coexistence of dominant ant species at study sites in the southern Karoo was a combination of territorial strategy and colonisation ability. In the *P. afra* rangeland most ant species escaped the severe competitive effect of *Pheidole* sp. 2 by persisting as fugitives on bare areas of local disturbance where *Pheidole* sp. 2 was less successful. At Tierberg, competitively inferior ant species with a decentralised territorial system coexisted with competitively superior ant species in an unstable equilibrium by pre-empting newly available space through the lateral expansion of territories. Competitively superior species, however, replace the inferior competitor (yet, superior coloniser) in time.

6.2 PLANT COMMUNITY STRUCTURE

Plant succession in the *P. afra* rangeland follows a deterministic pattern of cyclical replacement. No single mechanism adequately explains the coexistence of all plant species in this community. Nurse-plant effects were important for the establishment of *Portulacaria afra* and later-successional trees below woody shrubs and *P. afra* respectively. Soil moisture and nutrient levels below nurse plants were favourable for the successful establishment of seedlings but nurse plants also disrupt the inhibitory effect of grass on seedlings and young plants. Linked to the facilitative process is the directed dispersal of seeds by biotic vectors. Seed dispersal by ants (seed predators) and birds moves propagules away from the harsh competitive environment of established adult plants (particularly grass) to safe establishment sites below nurse plants. Complementary root systems of seedlings and nurse plants may facilitate the establishment of young plants but ultimately competition will reduce nurse plant vigour leading inevitably to the death of the nurse plant. At least two plant species (*Lycium cinereum* and *Psilocaulon absimile*) persist in the *P. afra* rangeland as fugitives on areas of local disturbance. The relatively cool and moist environment below *P. afra* clumps supports a variety of detritivorous taxa that enrich the soil. Once the *P. afra* clump collapses and dies, bare nutrient rich patches that favour the establishment of *L. cinereum* and *P. absimile*, ahead of the competitively superior grass component, remain. However, the replacement of the fugitive plant species by grass is inevitable as the soil nutrient levels decline.

The competitive superiority of grass controls the dynamics of the *P. afra* rangeland system. Disruption of its inhibitory effect by elevated nutrient levels (e.g. detritivore activity, ant nests) permits plant species to establish that would otherwise be unable to in the absence of disturbance. Overgrazing by domestic stock at the *P. afra* rangeland site has the same effect as disturbance by soil-nutrient enrichment and results in an increase in plant species diversity. All stages of the cyclical process would be relatively uncommon in a grass dominated system because of the inability to establish successfully in grass.

6.3 ANTS AND VEGETATION: TIGHTLY LINKED COMMUNITIES

Strong feedback links exist between the ant and plant communities studied. Habitat patchiness and high plant species diversity maintains ant species diversity. Ants, as seed dispersal agents, maintain plant species diversity by moving seeds out of competitively harsh microhabitats into safe sites (often below nurse plants) for establishment. Soil nutrient enrichment (ant nests and various detritivore taxa) create disturbances which also facilitate plant establishment. Overgrazing by domestic stock causes the replacement of palatable by unpalatable plant species. Unpalatable plant species, released of suppressive effects, develop into a monospecific stand that inhibits the further establishment of seedlings. Loss of habitat patchiness results in habitat monopolisation by one (or two) dominant ant species. Habitat degradation therefore severs the complex feedback links between the plant community and the important invertebrate component (dispersal agents and detritivores) which disrupts the dynamic processes driving the system.

6.4 FUTURE RESEARCH

I have concentrated on developing a theoretical understanding of ant and plant community dynamics. Ultimately, rangeland research in the southern Karoo must focus on applied issues.

First, Karoo rangelands are operating substantially below their former levels of production. Can these degraded systems be successfully rehabilitated? Second, the grasslands situated along the west-east moisture gradient are still vulnerable to degradation and invasion by a woody component (trees and shrubs). Can we predict when a vegetation state is approaching a threshold to change? Finally, addressing the former problems will contribute towards understanding (and predicting) the expected change in vegetation, due to global warming, along the west-east moisture gradient. Specifically, I propose research to address the following questions:

1. Is the reintroduction of palatable, perennial grasses into the southern Karoo a viable and practical option? Although a long-term plan, palatable grasses will improve productivity and reduce soil erosion. Research would need to address the absence of perennial grass seed in rangelands, the potential problem of grass seed predation by ants and herbivory by domestic stock. Sites such as Hillside farm, Jansenville, are suited to experimental studies because of the well established annual grass ground cover.
2. Is the reintroduction of *Portulacaria afra* into the more arid regions of the southern Karoo a viable and practical option? Also a long-term plan, *Portulacaria afra* is a highly palatable forage plant with similar soil retaining properties as grass. This plant species is easily propagated by cutting and its succulence and CAM metabolism makes it drought tolerant. I have initiated replicated experiments (November 1996) in the Upper and Lower rangeland at Tierberg where cuttings (4 cm long) were planted in different microhabitats simulating nurse plants.
3. What is preventing woody shrub invasion into the perennial grasslands of the southern Freestate and Eastern Cape? Research would focus on the relative importance of shrub seed availability and dispersal verses the competitive ability of perennial grasses.
4. What are the germination and establishment requirements of *Rhigozum obovatum*? This woody shrub species is a palatable forage plant but its establishment is rare. Research would focus on moisture requirements, establishment success in annual verses perennial grasses and especially the role of grasses in facilitating its establishment. I expect perennial grasses inhibit the establishment of *R. obovatum*, except at exceptionally high moisture conditions when moisture is no longer limiting, but that perennial grasses are necessary to maintain soil moisture status required for establishment.
5. Is the breakdown of the grass component facilitating the range expansion of *Microhodotermes viator*? If *Trinervitermes* sp. is being replaced by *M. viator* where the

grass component has been disrupted, is the affect of *M. viator*, on the already disturbed rangeland, destructive? Research into termite community structure should focus on the influence of vegetation on termite distribution and abundance and the factors altering the relative competitive ability of termites. I expect competitive interactions, mediated by vegetation differences, structure termite communities in the same way that ant communities are structured.