The Dynamics of Mound Construction by *Microhodotermes viator*: termite herbivory and altered soil nutrient status drive plant community change in a karroid shrubland community.

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ABSTRACT

Aspects of the formation of earth mounds (termitaria), constructed by the harvester termite *Microhodotermes viator*, and their associated plant communities was studied. These aspects included the impact of mound size on vegetation pattern and plant species abundance, factors affecting the spatial distribution and establishment of mounds, the rate of change in mound size and carbon isotope studies of mound soils. Soil organic ^{13}C isotope values, extracted from mound soil horizons, ranged from -25.16‰ to -23.16‰ suggest a stable C^3 dominated shrubland in the region over the last c.4 000 years. ^{13}C isotope values from the basal calcritic layers, when corrected for fractionation, suggest a mixed vegetation composition consisting of C^3 shrubs and CAM shrubs/C^4 grasses, indicating a possible transition zone between xeric and mesic climatic conditions in the region of 4 000 years before present. A range of mound sizes (<1m to <30m diameter), were found in the landscape. A study of aerial photographs showed that large mounds increase in area at an average of 0.39% per annum. A sharp decline in the frequency of mounds >6m in diameter, relative to the smaller size classes, was recorded. This pattern was attributed to intense predation by the aardvark and various insect species on founder colonies, and interspecific competition between colonies for resources. Variation in vegetation dynamics with mound size could in part be explained by termite herbivory effects, and changes in soil nutrients resulting from mound construction. Plant species replacement occurred along a gradient of increasing mound size, with an overall pattern of increasing abundance of annuals and decreasing abundance of perennials as mound size increased. A continuum of species, differentially effected by termite herbivory and changing soil structure/nutrient conditions, was invoked to explain changes in species distribution and abundance. The status of *Microhodotermes viator* as a key-stone species is discussed, as well as the impact of this species on the conservation of biodiversity in the succulent Karoo.

1. INTRODUCTION

Earth mounds, up to 30m in diameter and 2m in height, are a conspicuous feature of the landscape of the south-western and western Cape Province, South Africa (Lovegrove and Siegfried, 1986, 1989). Extensive research from the last decade has concentrated primarily on the origin of these mounds, and their influence on the local habitat.

By studying the basal calcretized layers of eroded heuweltjies, Moore and Picker (1991) were able to end years of speculation by demonstrating that the harvester termite, *Microhodotermes viator*, was the sole agent responsible for mound construction. Earlier hypotheses had proposed alternative zoogenic and geological models for *heuweltjie* construction, the local name given these structures (see Cox *et al.*, 1987; Lovegrove and Siegfried, 1986, 1989; Moore and Picker, 1991). Foremost amongst these theories was the hypothesis that a combination of termite activity and mole-rat burrowing were responsible for mound construction (Lovegrove and Siegfried, 1986, 1989). Raised areas, resulting from termite activity, remained free from water-logging during the long winter rainfall season, which subsequently provided suitable conditions for mole-rat colonization. Other hypotheses included the effects of seismic activity and the collection of wind-blown sand at the bases of shrubs.

The altered soil and water conditions resulting from heuweltjie construction, support a distinctive on-mound vegetation community (Knight *et al.*, 1989; Midgley and Musil, 1990). *Heuweltjie* soils have increased clay and silt concentrations compared to off-mound soils, as well as enhanced macro- and micro-elemental concentrations (Midgley and Musil, 1990). These are all features of termite altered soils. The increased nitrogen concentrations and improved water status on-mound appear to result in conditions conducive to the success of deciduous plant forms. Furthermore, the erosion of nutrient-rich soil off mounds has been cited as a major factor driving vegetation change in the Karoo biome (Yeaton and Esler, 1990). The increased nutrient status of off-wash soils derived from *heuweltjies*, initiates the differential establishment of Mesembryanthemaceae species. These shrubs in turn provide micro-sites for the establishment of certain species of the shrubby Karoo guild (Yeaton and Esler, 1990). *Microhodotermes viator*, through the construction of heuweltjies, is therefore a major role player in the local ecosystem.

Although Moore and Picker (1991) alluded to the fact that some large mounds are active termitaria, the impression given by past literature is that *heuweltjies* are largely a stable feature of the current landscape. Broadly speaking, one of the aims of this study are to investigate the rate and dynamics of mound establishment and development. In particular, this study investigates the mound size-class distribution that exists in the landscape, and what the implications of this distribution are. This includes investigating the possible correlations of changes in plant diversity with changing mound size, and with unique guilds predominating on particular size classes. Furthermore, the impacts of termite herbivory on vegetation patterns and dynamics (a process as yet unstudied) is also examined. The temporal rate and scale of heuweltjie construction is also analyzed to provide further evidence for the dynamics of *M.viator* colonies, in space as well as time.

Through the use of carbon-isotopes, the study investigated the hypothesis that mounds of the largest size-class were constructed "during past periods of wetter climate and different vegetation" (Burgers, 1975; Merryweather, 1965), which will further help in understanding heuweltjie dynamics. Furthermore, these isotopes values will shed some light on what vegetation-types constitute the major dietary component of *M.viator*, another unknown aspect of the ecology of this species.

2. MATERIALS AND METHODS

2.1 Study site

Grazing land bordering the south-western edge of the Clanwilliam Dam was chosen as a study site (fig. 1). The vegetation, Clanwilliam Karroid Shrubland (Campbell, 1985), appeared to be only lightly grazed. Vegetation was thus minimally disturbed, representing a good approximation of the natural ecosystem. The study site consisted of shallow soils, derived from the superficial sandstone bedrock. This enhanced the visibility of smaller sized mounds and made identification of the various mound sizes more accurate.

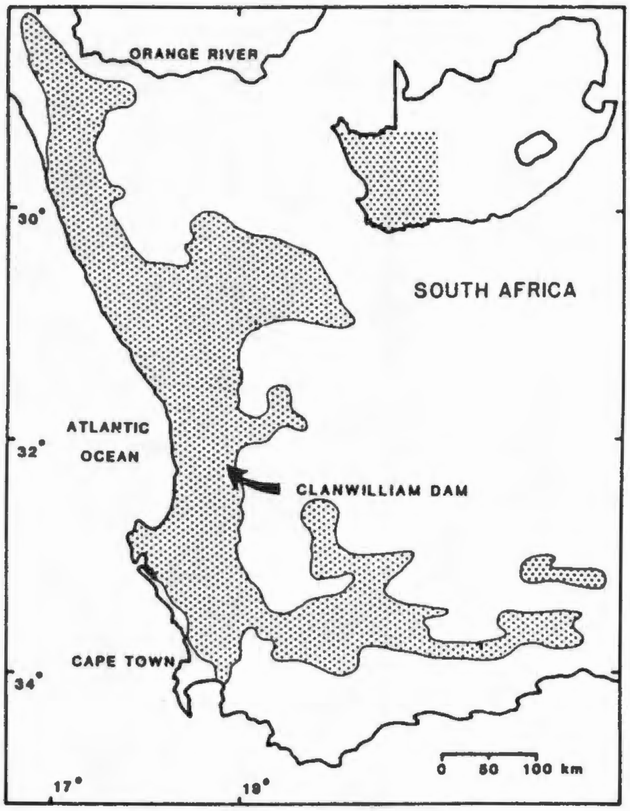

Fig. 1. Locality map of western Cape Province, South Africa, showing the study site at Clanwilliam Dam (modified from Moore and Picker, 1991). Stippled area shows distribution of *heuweltjies*, simplified from Lovegrove and Siegfried, (1986).

2.2 Soil carbon-isotope analysis.

Three *heuweltjies* were manually excavated to a depth horizontal with the intermound ground level, or where a calcrete layer was encountered. Soil horizons at ten centimetre intervals were sampled. Following excavation of a ten centimetre layer, the entire face of the soil horizon was re-cleaned to avoid contaminating the underlying strata with soil from overlying strata. Care was taken to avoid sites showing bio-perturbation of the soil, which could result from termite and Aardvark (*Orycteropus afer*) activity or burrowing by rodents.

2.3 Preparation of soil samples for isotope analysis.

Samples were air-dried, then sieved [aperture of 2mm] to remove large organic fragments and other coarse material. The samples were transferred to conical flasks and dispersed in distilled water to remove particulate organic fragments (Stock *et al.*, 1993). Soil material was stirred vigorously and repeatedly, causing organic fragments to settle out on the water surface. This material was removed using a shortened suction pipette tube. The refined soil material was then settled out in aluminium sulphate solution, allowing the removal of excess water. The next step was to add 150ml of $5g.l^{-1}$ colgon solution to each flask. The flasks were then placed on a reciprocal shaker for 15 hours. This promoted the separation of different sized particles into separate fractions. After shaking, the soil sample was sieved using a 2μm-aperture sieve. The slurry containing the smallest particle fraction was collected and air-dried at 50°C in a forced convection oven. The dried soil sample was then broken up using a mortar and pestle.

(i) Organic soil samples.

From this soil, 100mg subsamples were weighed, to which 200μl of concentrated HCl (12M) was added to remove free carbonates. Following the methodology of Sofer (1980), samples were combusted in sealed quartz tubes, as described by Sealy (1986).

(ii) Inorganic soil sample.

For the inorganic soil sample, which weighed 0.1g, soil carbonates where converted to CO_2 using 100% phosphoric acid (McCrea, 1950). The soil sample and phosphoric acid where placed at the base and in the side arm of a reaction vessel, respectively. The reaction vessel was placed in a water bath at 25°C for 30 minutes before the two samples were mixed, facilitating the reaction. The reaction vessel was left in the water bath overnight to allow completion of the reaction.

The carbon dioxide that was formed in the quartz tubes and reaction vessel was collected using cryogenic distillation. $\delta^{13}C$ values were determined on a VG Micromass 602E mass spectrometer using a reference gas calibrated against six National Bureau of Standards isotope references. All isotope ratios are expressed relative to the Chicago Pee Dee Belemnite standard [$\delta^{13}C = ((R_{sample}/R_{PDB})-1) \times 1\,000$, where R is the ratio of ^{13}C to ^{12}C].

$\delta^{13}C$ values from calcrete samples (Picker, unpublished data) were corrected for fractionation, and used to provide an indication of the type of vegetation that was present at a period close to the initiation of mound formation (i.e. calcrete layers are formed at the base of earth mounds) (Moore and Picker, 1991). Fractionation occurs when organic material is transformed into inorganic material. Fractionation is expected to produce a change of between 10.2‰ and 12.3‰ (Quade *et al.*, 1989). By adding the difference between an organic and inorganic sample from the same soil horizon to the values obtained from calcrete samples, a true estimate of the $\delta^{13}C$ for calcrete can be calculated.

2.4 Investigating a chrono-sequence of mound size changes as inferred from aerial photography.

A chrono-sequence of aerial photographs were studied to estimate the rate at which *heuweltjies* increase or decrease in size. In the choice of suitable photographs, preference was given to those with the greatest clarity, and those which included a long time sequence (comparing 1945 with 1989 for example). Aerial photographs from south of the study site provided the first site (Grid reference: 32°13'30''S 18°52'00''E, Aerial photograph reference: Job 498/248 Strip 3/1157 and Job 226 Strip 5/04012). The second site was located on the west coast (Grid reference: 31°32'20''S 18°02'40''E, Aerial photograph reference: Job 11 Strip 18/729 and Job 498 Strip 1/1232). The selected aerial photographs were then enlarged to a scale of 1:3 000. The pairs of aerial photographs were then accurately calibrated. Particular *heuweltjies* were located on each map and their areas measured (n=50 for each study site). By comparing these areas, the change in size of individual *heuweltjies* during a certain time period could be estimated. Mound outlines were traced from the aerial photographs, and their areas calculated using an area meter.

2.5 Nearest neighbour analysis.

Aerial photographs were also used for nearest neighbour analysis of class 4 mounds. Distance from nearest neighbour and mound area were calculated from aerial photographs. If the combined mound area of neighbouring *heuweltjies* increases with increasing neighbour distance, then one can infer that there is a interspecific competitive effect between class 4 mounds. However, if there is no significant relationship between combined mound size and neighbour distance then one can infer that there is no interspecific competition between mounds.

2.6 Mapping the present day spatial distribution of *heuweltjies*.

Two grids were laid out in the field, and were mapped for *heuweltjies* of all size classes. The dimensions of the first grid were 50m x 40m, and the second 90m x 30m. The grids were sub-divided into 2m x 2m blocks, which were systematically excavated to ensure that any colonies present were located.

2.7 Size-class distribution as measured from field transects.

To obtain a representative size-class distribution, random transects were laid out at the Clanwilliam study site. Small and intermediate earth mounds within one metre either side of the transect tape were measured. Large *heuweltjies* were only included if the transect line passed through, or close to the middle of the mound.

2.8 Utilizing termite interactions to delimit colony boundaries.

Research by Coaton (1958, 1962) suggests that each colony has a single hive. Termites from different colonies display aggressive behaviour when they come into contact with each other (Coaton, 1958). These aggressive interactions are useful for delimiting the boundaries of individual colonies, which are questionable for mounds occurring in the intermound areas. In other words, it is difficult to distinguish between individual colonies in the intermound areas, as the physical features of these mounds are usually poorly developed. Aggressive interactions can help to distinguish between individual colonies. Two interaction tests were carried out between large mounds, while one interaction was performed across a single large mound. A number of interaction tests were performed between intermound colonies, and between intermound colonies and large colonies. For each interaction study, two termites served as the control, and were placed directly next to the foraging port from which they were collected. Two termites from a different colony were similarly treated, and any interaction (aggressive/non-aggressive) was noted.

2.9 Vegetation studies

2.9.1 Plant species succession.

Vegetation change was studied by investigating species abundance on a gradient of increasing *heuweltjie* size. *Heuweltjie* size classes based on diameters included small (0 - 1m), small-medium (1 - 3m), medium (3 - 8m) and large mounds (> 8m). Species abundances from approximately ten *heuweltjies* of each size class were recorded. The percentage cover of each species was noted in the following manner:

(i) For perennial species the area covered by each individual plant was estimated. From the summed results of these measurements an estimate of percentage cover was calculated. *Heuweltjie* diameters were calculated from diameter (converted to radius) measurements taken in the field.

(ii) For annual species a visual estimate of percentage cover was recorded.

Unknown species were tagged in the field for later identification, which was done in the Bolus Herbarium (University of Cape Town).

2.9.2 Herbivory effects on Pteronia ciliata.

The condition of *P.ciliata* plants, based on the percentage of leaf-bearing branches in the canopy, was recorded for two different sites. The condition of five plants occurring within a one and five metre radius of the edge of class 4 *heuweltjie* were recorded. The underlying assumption behind these observations was that termite-grazing intensity decreases with increasing distance from the outer edge of a *heuweltjie*. These observations were recorded on the up-slope side of the *heuweltjies*, to minimize the possible effects that erosion of nutrient-rich soils off mounds might have (nutrient run-off is expected to be greater downslope than upslope).

3. RESULTS

3.1 Carbon isotope analysis.

Table 1. The $\delta^{13}C$ values from the soil profile of three earth mounds situated near Clanwilliam Dam, in the western Cape.

Soil Depth (cm)	H 1	H 2	H 3	H 4
0 - 10	- 25.16	- 23.21	- 25.11	-
30 - 40	- 23.61	-	-	-
80 - 90	-	- 24.74	- 24.19	-
* 80 - 90	-	- 13.31	-	-
+ calcrete	-	-	-	- 20.02

[* Denotes an inorganic carbon value. + Denotes a calcrete sample corrected for fractionation. The remaining values are organic carbon.]
H 1 - H 3 represents the three *heuweltjies* sampled. H 4 represents an average value of calcrete samples collected from eight different mounds (Picker, unpublished data).

Organic $\delta^{13}C$ values ranged from -25.16‰ to a high of -23.61‰ (Table 1). All data points were on the boundary of values typical of C3 vegetation [i.e. -26‰ to -30‰] (Farquhar, 1982). $\delta^{13}C$ values increased down the soil profile of two of the three *heuweltjies* sampled. The remaining *heuweltjie* (H3) showed a decrease in $\delta^{13}C$ carbon content in the 80-90cm soil horizon. The calcrete value was intermediate between the range typical of C^3 and C^4 vegetation types.

3.2 Aerial photography - Mound size change in recent time.

3.2.1 Site 1. *Heuweltjie* size increased by as much as 240% over a forty year period (fig. 2a), with an average increase of 57%. This is an increase in area of 1.4% per annum. Out of a sample of forty-two *heuweltjies* of varying size that were sampled, only five showed a decrease in size. *Heuweltjies* of the smaller size class showed a greater increase in area over the same time period than the corresponding *heuweltjies* of a larger size class. The density of cover vegetation showed a marked increase across the entire landscape during the period investigated. This could have resulted in an inflation of the area-change values [Plate 1 (a) and (b)], as vegetation was used to delimit *heuweltjie* boundaries on the aerial photographs.

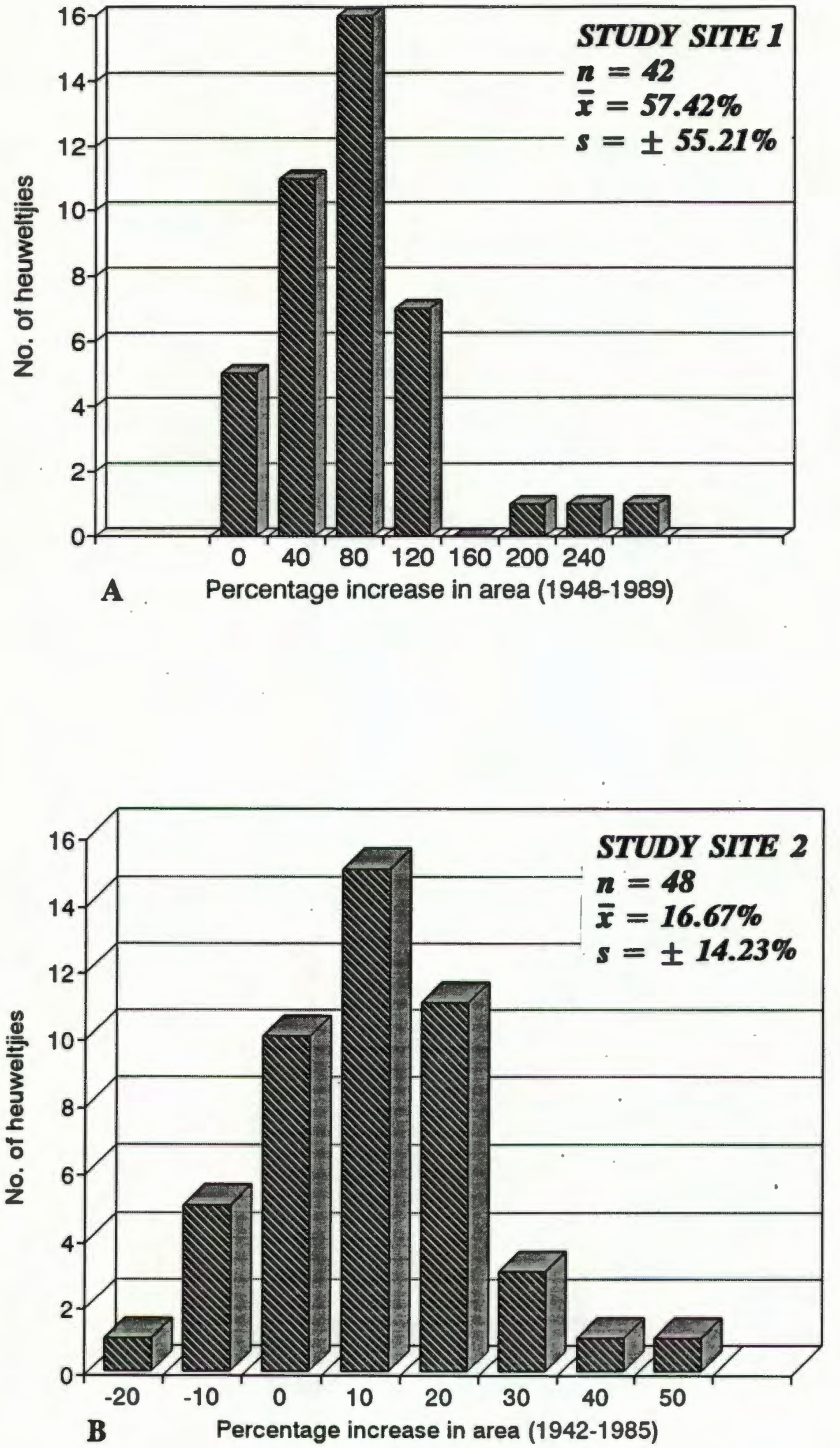

Fig. 2 (a) and (b). The number of *heuweltjies* showing various percentage changes in area. (a) = Study site 1, (b) = Study site 2.

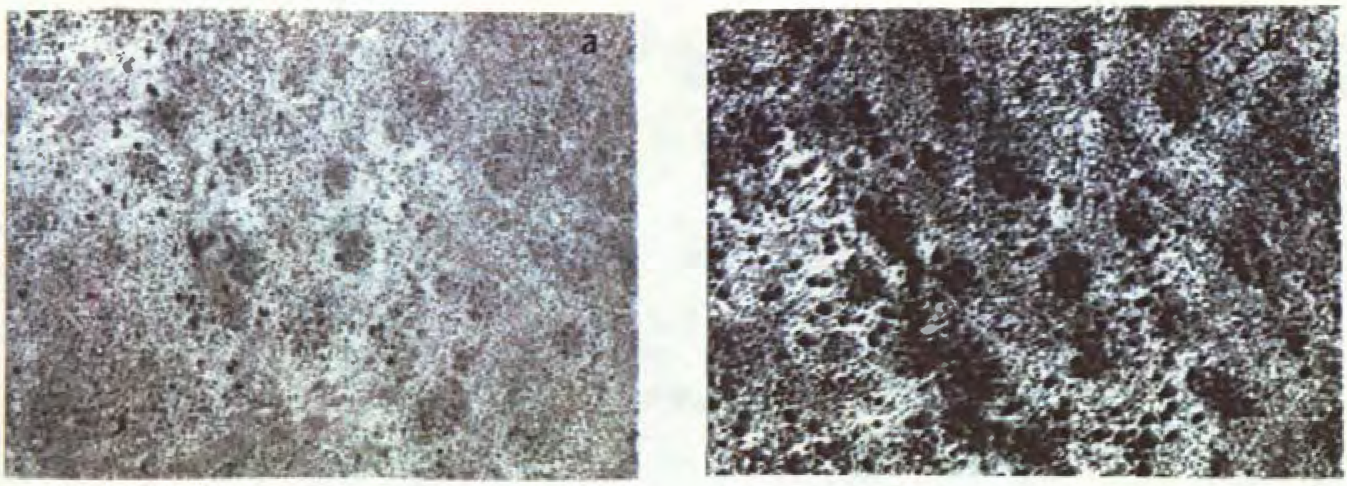

Plate 1 (a) and (b). Increase in vegetation cover during the study period (1948 - 1989). Because vegetation was used to delimit heuweltjie boundaries, mound size appears to have increased due to improved vegetation cover. This size increase is not necessarily due to an actual increase in physical size.
Map Scale 1:3 000.

Plate 2. Class 1 mounds. These mounds are not readily visible to the untrained eye. These founder colonies were commonly found at the base of shrubs such as *Pteronia ciliata*. This plate shows the site of the first grid, which is typical of the vegetation of the Clanwilliam Dam study site. The foreground is dominated by *P.ciliata*. A class 4 mound can be seen in the background.
(m = class 1 mound, c = class 4 mound)

3.2.2 Site 2. This locality was chosen because vegetation cover appeared to be constant over a forty year period, minimizing inaccuracy when measuring changes in *heuweltjie* area over time (i.e. vegetation was used to delimit *heuweltjie* boundaries). The maximum increase in area recorded was 58%, while the average change in area was an increase of 17 % (fig. 2b). This is an increase in area of 0.39% per annum. Six out of a sample size of fifty heuweltjies showed a decrease in size over the forty years, with a maximum decrease of -15% being recorded.

3.3 Heuweltjie size-class distribution at Clanwilliam study site.

Heuweltjies of the smaller size categories were found in far greater abundance than the corresponding larger classes (fig. 3). *Heuweltjies* in the size range of 0 - 2m were most common, with a marked decrease in abundance for *heuweltjies* larger than 5m in diameter (see Plates 2 to 4 for illustration of different size classes).

3.4 Nearest-neighbour analysis.

Nearest-neighbour analysis showed no significant relationship between combined neighbour areas and neighbour distance (fig. 4).

3.5 Spatial patterns of mounds.

The two grids (fig. 5a and 5b) show the spatial pattern of class 1 - 3 mounds, relative to class 4 mounds. Class 3 mounds are generally found in an area equidistant from neighbouring class 4 mounds (see Plate 2 - photograph of grid 1).

3.6 Heuweltjie-vegetation interactions.

The total number of species recorded increased with increasing *heuweltjie* size (fig. 6). Growth form abundance showed a continuum of change along a gradient of increasing heuweltjie size (fig. 7). The percentage cover of perennial species decreased with increasing *heuweltjie* size, while annuals showed an opposite trend of increased percentage cover with increasing *heuweltjie* size (Plate 5). Individual species of different growth forms showed varying trends in abundance on a gradient of increasing *heuweljtie* size. Species were placed in four broad categories, each of which showed a particular trend in cover abundance.

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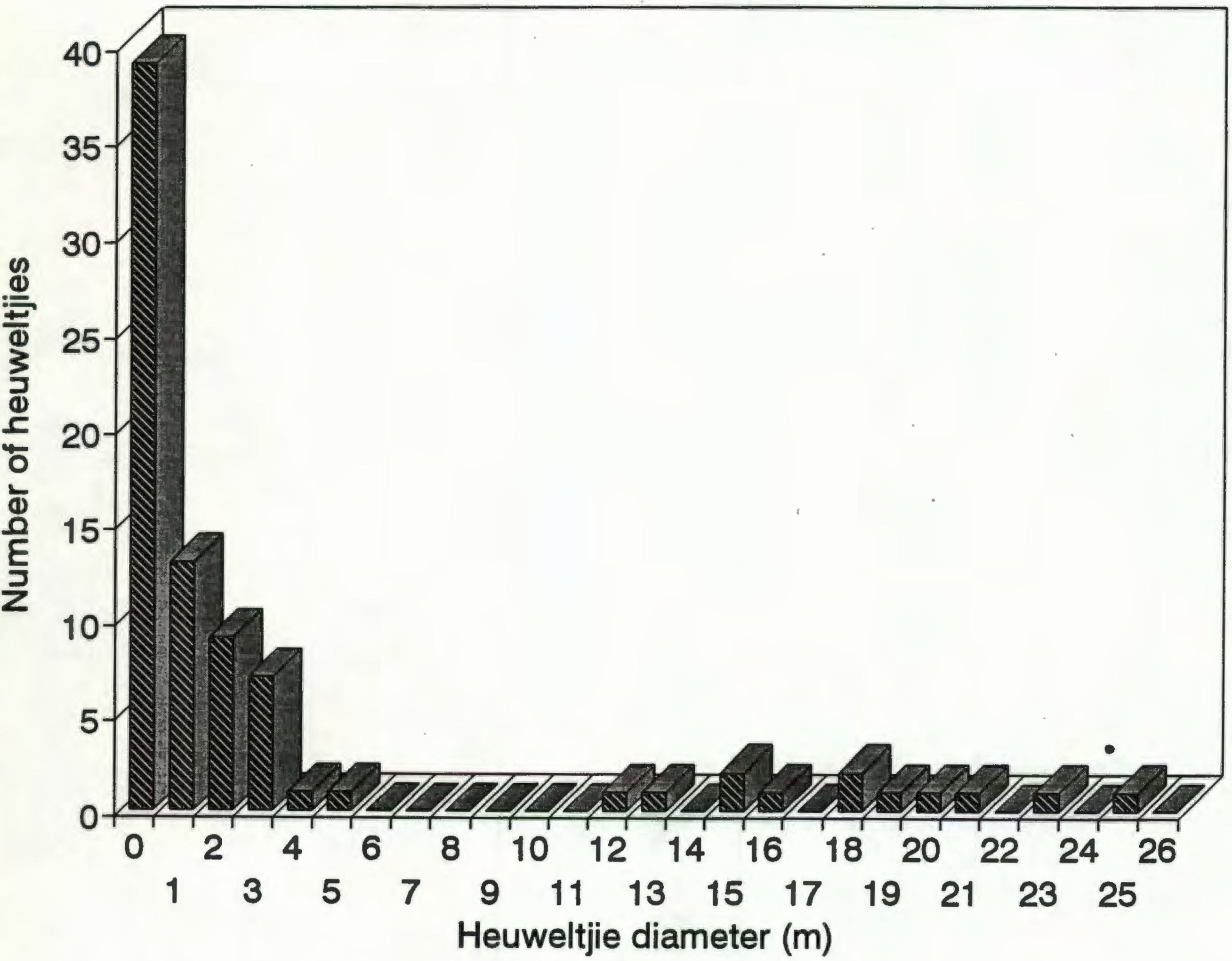

Fig. 3. The number of mounds recorded for different size classes.

Plate 3. Class 2 and 3 mounds. These size classes are characterized by the presence of perennial bushes, such as *Rhus incisa*. Size classes 2 and 3 are also physically distinct, being up to 0.5m in height. As these mounds increase in size, the percentage cover of perennial bushes such as *R.incisa* decreases, giving way to annual species.
(r = *Rhus incisa*).

Plate 4. A class 4 mound. These mounds are what are commonly referred to as *heuweltjies*, which have been the only size class considered in past studies. As can be seen, these mounds are highly distinctive features of the landscape. Note the increased abundance of annual plant species on-mound.

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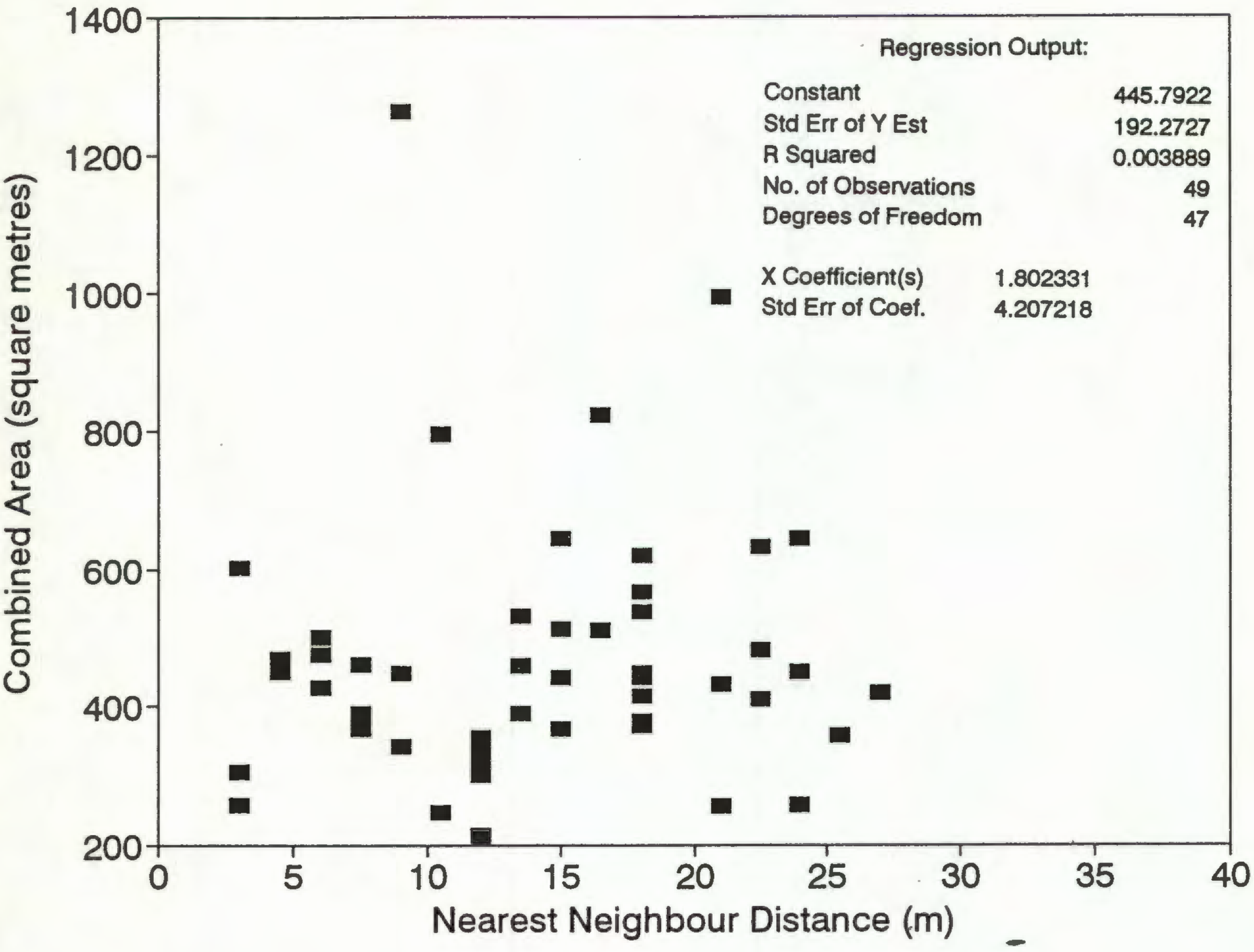

Fig. 4. Nearest-neighbour analysis of class 4 mounds, recorded from aerial photographs (for aerial photograph reference see study site 1).

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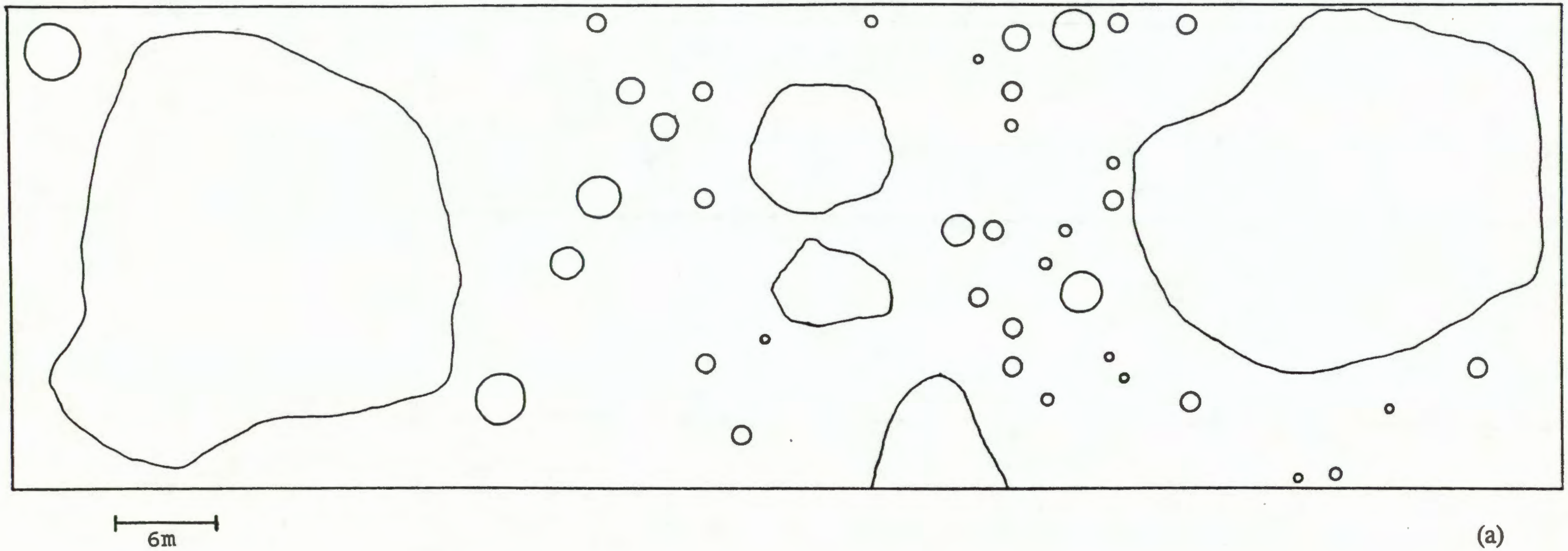

Fig. 5 (a) and (b). Maps showing the spatial distribution of various sizes of mounds, as recorded from two grids located above the southern bank of the Clanwilliam Dam, Cape Province.
(a) = Grid 1, (b) = Grid 2.

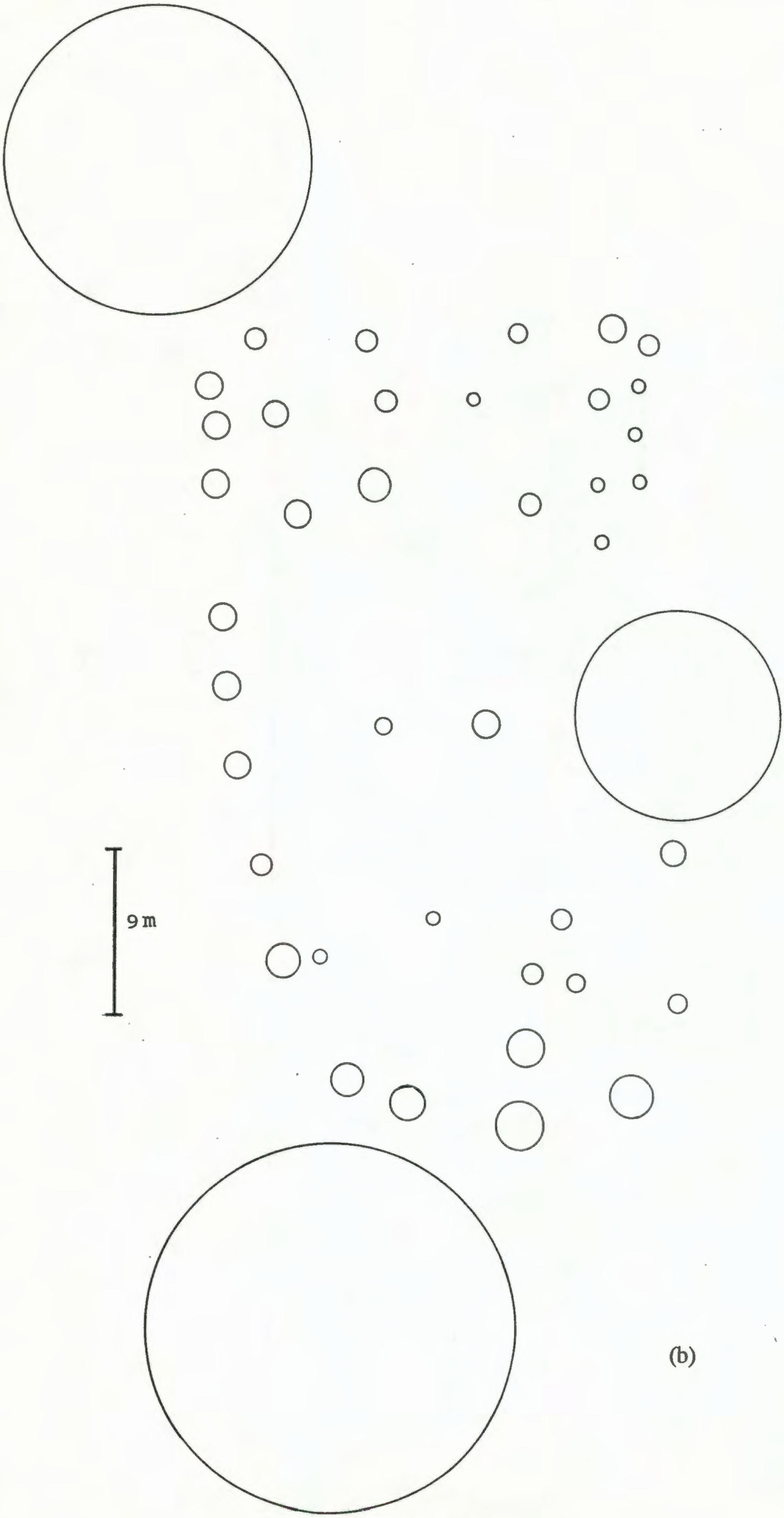
9 m
(b)

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Table 2. Species belonging to different categories, according to trends in species abundance with changing mound size.

↑ ↑ size ↓ ↑ size int no trend

Category 1	Category 2	Category 3	Category 4
Trachyandra muricata Senecio arenarius Cyanella hyacinthoides Aspalathus spp. Hermannia trifurca Schismus spp. Pteronia divaricata Protosparagus africana Euclea tomentosa Albuca altissima Galenia africana Stipa capensis Pentzia clava	Pteronia ciliata Nylandtia spinosa	Indigofera procumbens Euphorbia burmannii Rhus incisa Ruschia decurvans	Hermannia cuneifolia Tribolium atriculosum Athanasea trifurcata Montinia caryophyllacea Pentachistis spp. Tetragonia rosea

Category 1. These are species which show an increase in abundance with an increase in *heuweltjie* size, including both annual and perennial growth forms. Examples of this category include *Galenia africana*, *Stipa capensis* and *Pentzia clava* (fig. 8 and Plate 5).

Category 2. These are species which show a distinct decline in abundance with increasing *heuweltjie* size. Included in this category are perennials such as *Pteronia ciliata* and *Nylandtia spinosa* (fig. 9).

Category 3. This category consists of species which have a maximum level of abundance at intermediate *heuweltjie* size classes. Representative species include *Euphorbia burmannii, Rhus incisa* and *Ruschia decurvans* (fig. 10 and Plate 6).

Category 4. These are species which show no particular trend in abundance levels in relation

Plate 5. Typical vegetation of a class 4 mound. Note the hight percentage cover of annuals (including species such as *Stipa capensis* and *Pentzia clava*). *Galenia africana* is typically found on class 4 mounds, and also predominates on overgrazed, disturbed agricultural land. (g = *Galenia africana*)

Plate 6. *Ruschia decurvans*, (*Mesembryanthemaceae*) which has a maximum abundance on size classes 2 and 3.

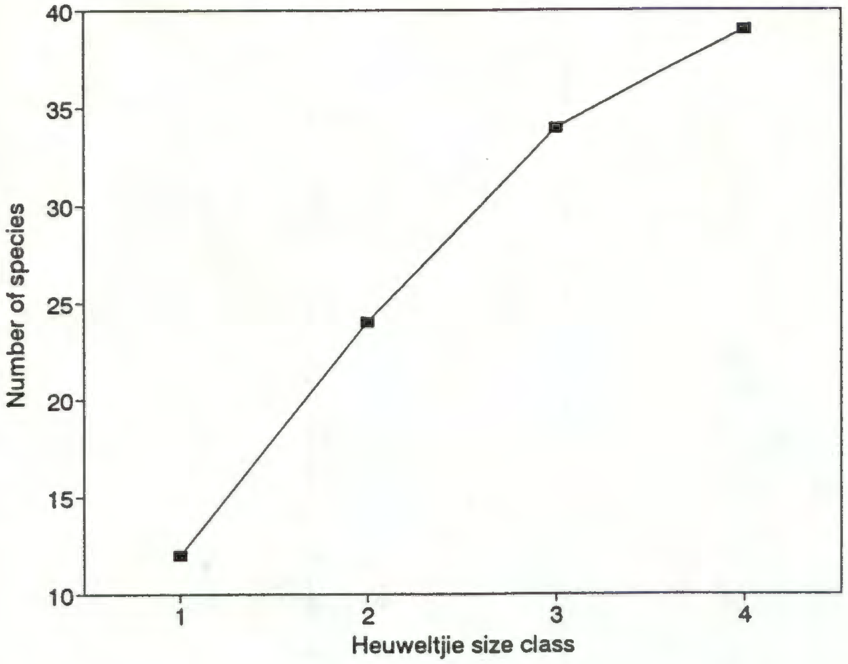


Fig. 6. The total number of species recorded verses an off-mound plot and a range of mound sizes.

[X-axis size-class categories: 1 = mound diameter 0 - 1m, 2 = mound diameter >1m - 3m, 3 = mound diameter >3m - 8m, 4 = mound diameter >8m.

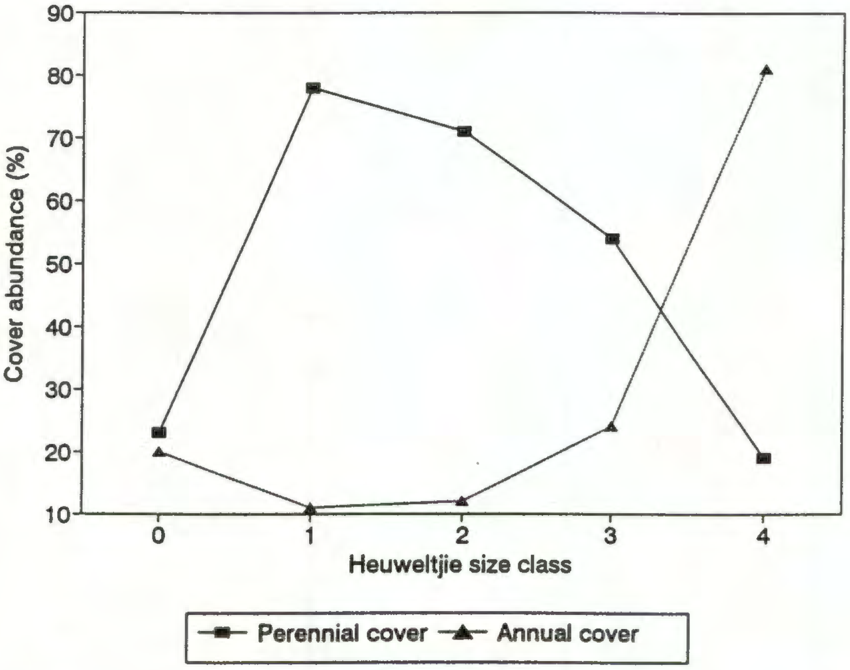


Fig. 7. The abundance (percentage cover) of annual and perennial vegetation verses an off-mound plot and a range of mound sizes.

[X-axis size-class categories: 0 = off-mound plot (3m x 3m), 1 = mound diameter 0 - 1m, 2 = mound diameter >1m - 3m, 3 = mound diameter >3m - 8m, 4 = mound diameter > 8m]

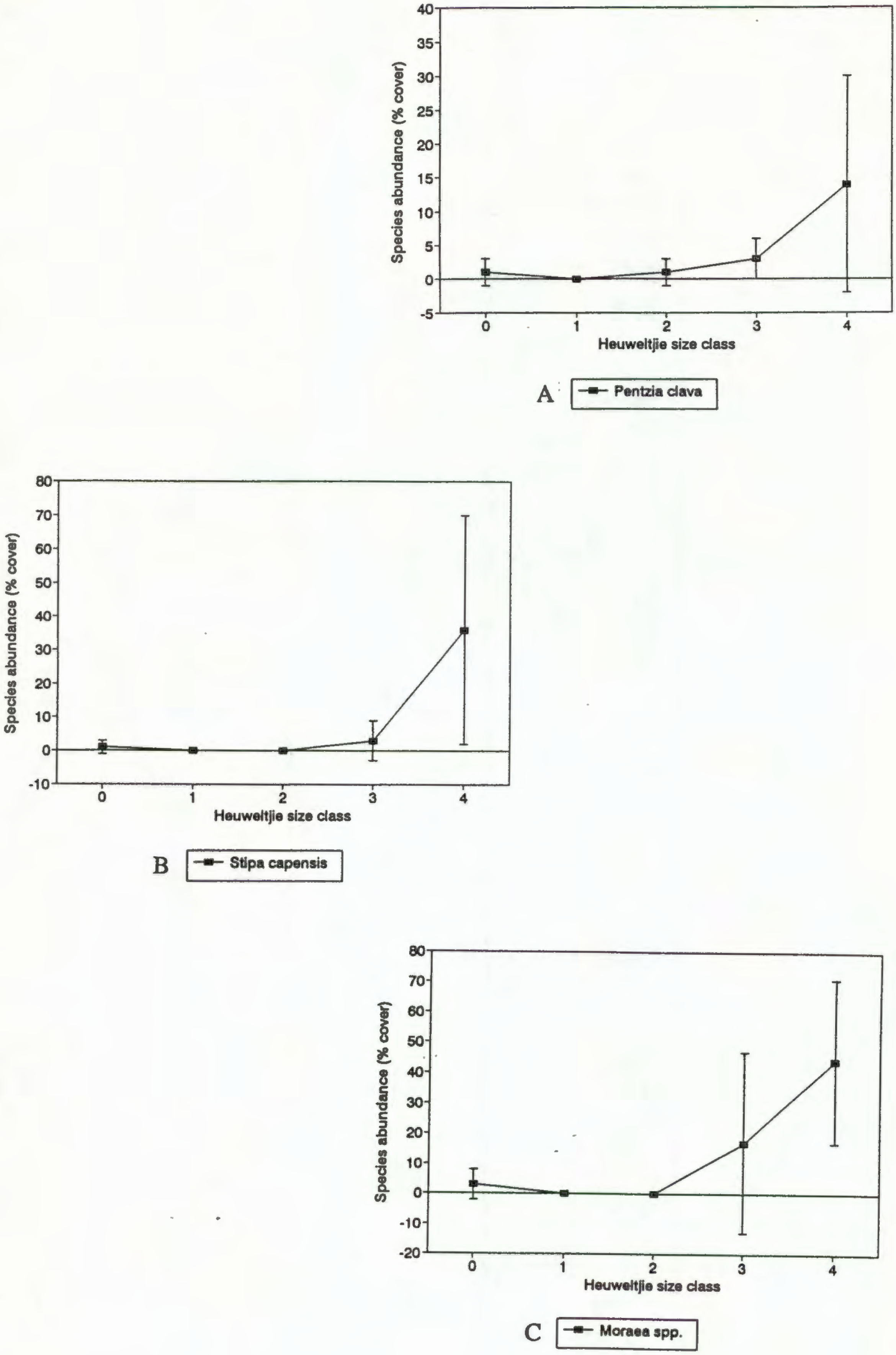
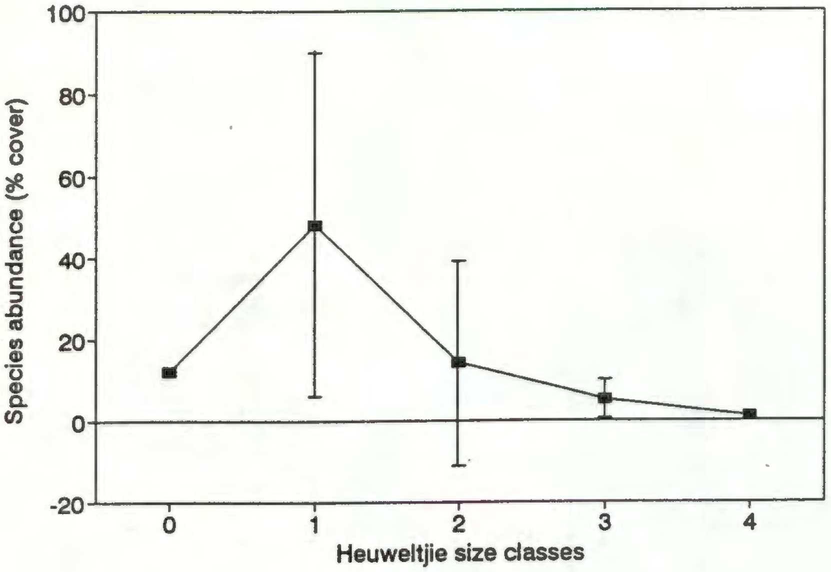


Fig. 8. Abundance values (percentage cover) verses an off-mound plot and a range of mound sizes, for plant species showing a rapid increase in abundance at size class 4. A = *Pentzia clava*, B = *Stipa capensis*, C = *Moraea spp.*

[X-axis size-class categories: as above]



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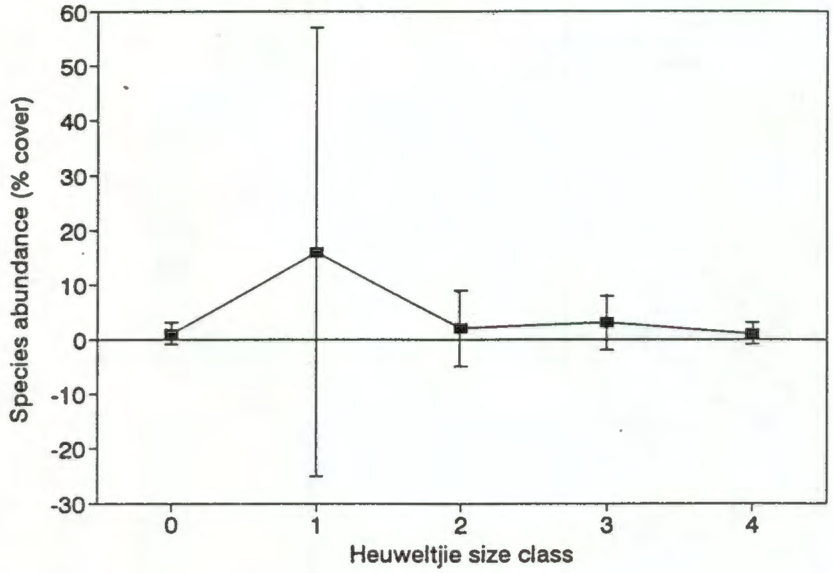

B

Fig. 9. Abundance values (percentage cover) verses an off-mound plot and a range of mound sizes, for plant species with decreasing abundance with increasing mound size. A = *Pteronia ciliata*, B = *Nylandtia spinosa*,

[X-axis size-class categories: as above]

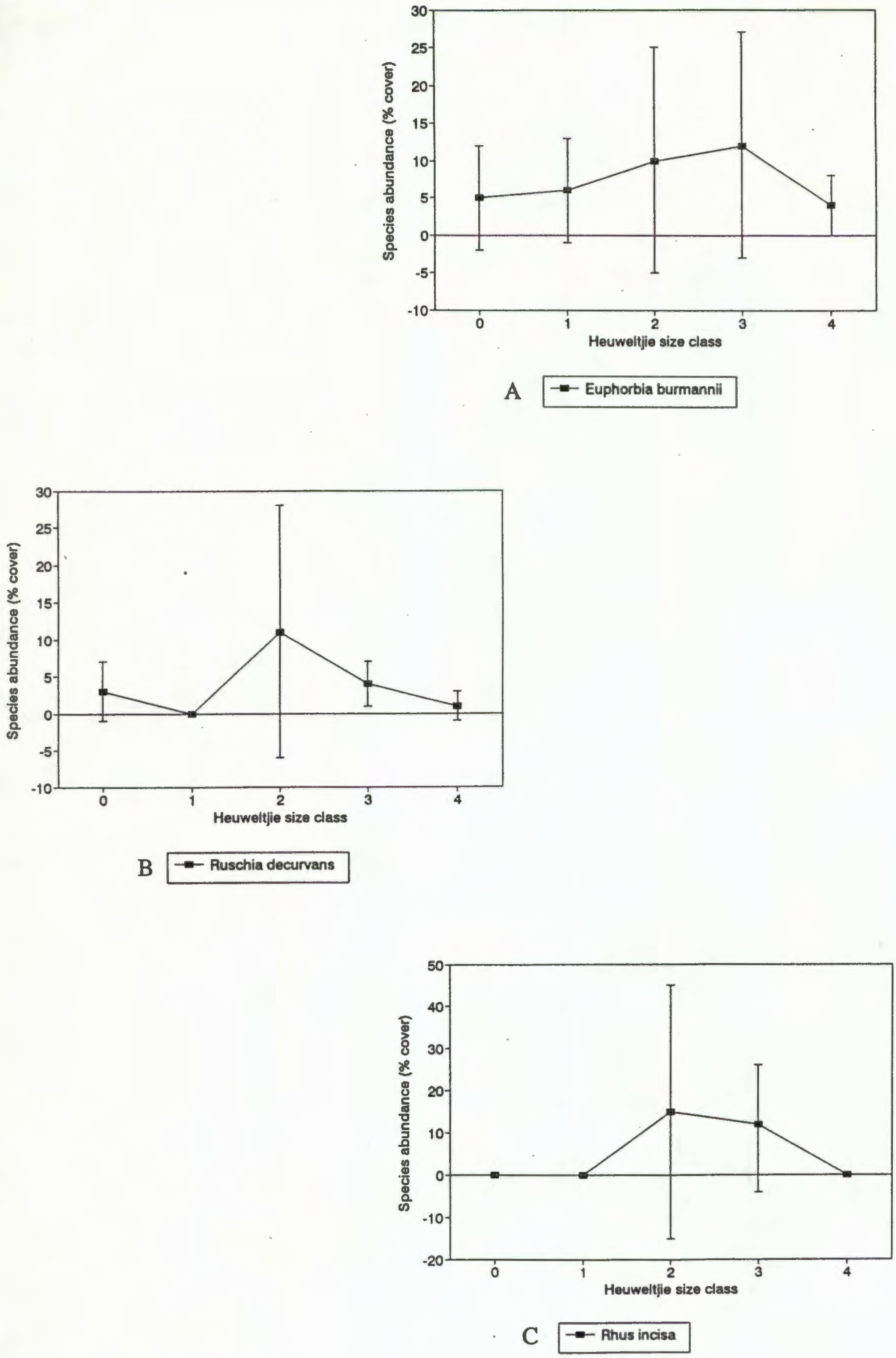

Fig. 10. Abundance values (percentage cover) verses an off-mound plot and a range of mound sizes, for plant species showing peak values at intermediate size classes. A = *Euphorbia burmannii*, B = *Ruschia decurvans*, C = *Rhus incisa*.

[X-axis size-class categories: as above]

to *heuweltjie* size.

3.5 Termite herbivory effects on *P.ciliata*.

Table 3. Kruskal-Wallis analysis of condition of *P.ciliata* plants close to mounds (1m) by condition of plants far from mounds (5m).

Level	Sample size	Average rank
Pteronia near	50	36.64
Pteronia far	50	64.36

Test statistic = 23.3431 Significance level = 1.35529E-6.

The condition of adult *Pteronia ciliata* bushes occurring within a one metre radius of *heuweltjie* edges was found to be significantly poorer compared to *P.ciliata* bushes further from the *heuweltjie* perimeter (Plate 7), in that a greater percentage of the canopy consisted of dead branches.

Plate 7. Dead *Pteronia ciliata* bushes on the perimeter of a large *heuweltjie*, indicating the effects of termite herbivory.

3.6 Termite interactions.

Aggressive interactions were recorded between two different pairs of class 4 mounds, while non-aggressive interactions were recorded between termites captured from opposite sides of the same mound. Interaction studies were also performed between large earth mounds and "intermound" areas where small, incipient colonies were found to occur. Aggressive interactions were recorded in all cases (n = 3), when termites from "intermound" colonies where brought into contact with termites occupying class 4 mounds. Aggressive interactions were recorded between pairs of intermound colonies (n = 3). However, non-aggressive interactions were also recorded between pairs of intermound colonies (n = 2).

4. DISCUSSION

4.1 Carbon-isotope values.

Carbon isotope values show that *M.viator* has a diet composed largely of C3 plants (Table 1). Termites were, however, observed to graze grass species intensively when available. Carbon isotope values may indicate the predominance of C3 plants in the region of the study site, rather than a particular preference for this plant guild. However, this does provide an initial hypothesis for future studies into the feeding behaviour of *M.viator*. The distribution of *heuweltjies*, which covers several different vegetation types, seems to be a further indication that the feeding preference of *M.viator* may not be limited to a particular plant guild (Burgers, 1975).

The isotope values also indicate that there has been no significant change in vegetation composition in terms of photosynthetic pathways, for at least the period in which the upper metre of mound material was laid down (i.e. the lowest level at which carbon isotope values were obtained). Soil layers making up a *heuweltjie* appear to be stable once laid down by termite activity. Tunnelling activity below the sand capping (± 30cm) appears to be minimal. The integrity of alternate soil layers would be maintained once laid down, as a result of negligible particle movement between layers. This means that a particular soil layer should provide an accurate and reliable measure of what vegetation was harvested at that particular time.

Carbon-14 dating of calcrete material suggests that the *heuweltjies* at Clanwilliam are in the order of 4000 years old (Moore and Picker, 1991). Thus results from this study suggest that there has been no substantial change in vegetation, and therefore climate, over the last 4 000 years in the Clanwilliam region. This is supported by studies on pollen-core samples in the Cedarberg (Meadows and Sudgen, 1991), ostrich egg-shell isotopes (Lee-Thorp, unpublished data) and pollen data from hyrax middens (L.Scott, pers. comm.), which suggest no climate change in the area, from 4 000 years ago to the present .

Using the isotope value obtained from inorganic material, we can estimate the ^{13}C isotope value for calcrete, which forms layers at the base of *heuweltjies* (Moore and Picker, 1991). This gives some idea as to the composition of vegetation present when this calcrete was laid down. Interestingly, the value obtained is intermediate to those characteristic of C3 and C4 plants respectively, and is less negative than the values recorded in higher soil strata of the *heuweltjies* sampled. It is possible that this reflects part of the boundary between alternate xeric and mesic climatic periods that are hypothesized to have taken place in this region (Burgers, 1975; Merryweather, 1965), which could have supported an intermediate plant community of C3 and C4/CAM plants. This transitional period could have initiated the invasion of *M.viator* into the region, displacing the non-mound building harvester termite *Hodotermes mossambicus*, which is known to predominate in grassy environments (Coaton, 1958; Midgley and Hoffmann, 1991). Fossil nests, resembling those of *H.mossambicus* have been recorded in the region, evidence of their possible previous presence in the landscape (Moore and Picker, 1991). At some point in time, changing conditions in climate or vegetation must have been significant enough to initiate the migration of *M.viator* into the region. Conditions would have favoured the establishment of *M.viator* colonies, while negatively impacting *H.mossambicus*.

The above results are also consistent with those of Bond *et al.* (1994), which suggest a stable shrub-dominated vegetation type in the south and south-western areas of the Karoo (encompassing the Clanwilliam study site), during contemporary time (i.e. 1 000 years before present).

The isotope results are also important for our understanding of the dynamics of *heuweltjie* formation. Because no significant change in vegetation composition has occurred in the region over at least the last 4 000 years, one can assume that inter-colony and resource dynamics that shaped the spatial pattern of large mounds in the past, are the same today. We can therefore study dynamics of the current landscape to understand processes which lead to spatial patterns that were formed in the past.

4.2 Characterising Mound Development

The grids of mound distribution provide a good starting point to explain the dispersion of colonies. Size class 4 mounds dominate the landscape physically, being highly visible and conspicuous features (Hoffmann and Midgley, 1991, Moore and Picker, 1991). In the past, investigations into heuweltjies and the mound-building termite *M. viator,* have considered only this size class (Cox *et al.*, 1987; Lovegrove and Siegfried, 1986, 1989). However, as can be seen from fig. 5(a) and (b), the area between class 4 mounds includes mounds of various sizes, including representatives from size classes 1 - 3. This part of the landscape has been referred to in past research papers as "intermound" areas (Lovegrove and Siegfried, 1986, 1989). Although technically incorrect, I will still refer to these areas as intermound areas.

4.2.1 Termite interaction tests.

Results suggest that large mounds constitute a single colony. This is consistent with results of Coaton (1958), who recorded a single hive per colony, with a single colony occupying each mound. Other results were consistent in indicating that colonies occurring in "intermound" areas are in fact separate from colonies occupying large mounds, and are distinct from each other. The results are inconsistent, however, in revealing how to accurately delimit the physical area occupied by a founder colony. In particular, it is still uncertain as to what physical features can repeatedly and accurately be used as an indicator of founder colonies.

4.2.2 The structure and physical development of mounds.

Class 1 mounds are the most difficult to identify and delimit spatially, in terms of the physical area occupied by young *M.viator* colonies. Founder colonies apparently require some form of protection against predation (see below), and are usually found at the base of perennial shrubs or underneath rocks (Plate 2). Once the colony has established itself, the construction of a hard clay surface capping (the result of tunnel construction beneath the surface) provides a distinctive feature indicating the construction of an incipient mound. The establishment and expansion of a colony will usually result in the destruction of cover vegetation, leaving a bare, hard-capped shallow dome, up to approximately 0.5m in diameter. As the colony, and therefore the mound, continues to expand, the activities of *M.viator* change the chemical and physical structure of the surrounding soil. These changes in soil structure could determine sites of establishment for species such as *R.incisa*, a species restricted to intermediate sized mounds (see later). The presence of this distinct vegetation results in class 2 and 3 mounds being readily visible in the environment. Characteristic features of intermediate sized mounds are a diameter of approximately 6m, a height of up to 0.5m and cover vegetation consisting of perennial bushes of medium height. The soil texture of class 2 and 3 mounds is fine and fairly unconsolidated. Continued termite activity, including frass expulsion and accumulation, results in an increase in mound diameter and height. The shape of class 1, 2 and 3 mounds is irregular in comparison to class 4 mound which are generally a more regular, circular shape. Class 4 mounds, well described in earlier literature (see Lovegrove and Siegfried, 1986, 1989; Moore and Picker, 1991), have darker soil which is more consolidated, although equally fine. Areas of hard capping may be present on large mounds, where recent superficial tunnel construction has taken place.

4.2.3 Rate of growth of termitaria.

Two study sites were investigated, using aerial photographs, to investigate change in size of class 4 mounds over time. The first study site produced a mean change in area of 1.4% per annum [fig. 2 (a)]. However, it appeared that an increase in the density of cover vegetation over the study period had resulted in inflated values (as vegetation had been used to delimit the boundaries of mounds) [Plate 1 (a) and (b)]. The change in vegetation could be attributed to factors including increased precipitation over the study period or a change in management practices (evidence included the construction of new fence lines and dams). The second study site, including a period of 43 years, showed an average change in area of 0.39% per annum. As vegetation cover had remained constant, it is suggested that this represents a more accurate estimate of the rate of change of *heuweltjie* size than study site 1. Note that although the mean shows a positive increase in area, some mounds were shown to decrease in size over 43 years. The point to note is that *heuweltjies* are dynamic, and not static features of the landscape. Class 4 *heuweltjies* are, on average not senescent, but are increasing in size as a result of active and expanding colonies. Termite activity on class 4 mounds has also been observed to be intensive, covering a large proportion of the mound surface, indicating that these colonies are still active. The 12% of mounds that showed a decrease in size could represent those that are senescent.

Mound construction (i.e. size) is therefore in a constant state of flux, albeit on a macro-time scale not readily visible in contemporary time. This is presumably dependant on the condition of the resident colony. For example, mounds decreasing in size could represent colonies severely affected by aardvark predation. Erosion of material off mounds would result in a decrease in heuweltjie size if colony activity had been reduced by the effects of predation, resulting in a decrease of material deposited through termite activity.

The dynamic nature of mound construction also implies that nutrient cycling is also in a state of flux in the environment. This has particular significance for plant community structure. Vegetation change in the Karoo has been partly linked to the movement of nutrients associated with *heuweltjie* construction and degradation [see below] (Yeaton and Esler, 1991). This suggests that plant establishment can be partly influenced by the status of a *M.viator* colony. If a colony is senescing (i.e. mound size decreasing [see above]) then soil nutrients are moving off mound, initiating the establishment of a particular guild of species. The opposite would be true for a mound concentrating nutrients on-mound.

4.3 Spatio-temporal patterns in mound establishment.

Size class frequency data showed that there is a sharp decrease in the number of large mounds present (fig. 3). No mounds with a diameter of between 6 and 11m metres were recorded from the field transects. This suggests that only a small proportion of founder colonies are progressing to form mounds greater than 6m in diameter. The resolution of earlier aerial photographs (see above) was not great enough to provide empirical evidence regarding the recruitment and development of new mounds. However, the above size-class data suggest that recruitment of mounds greater than 6m in size could be extremely limited. In that case, one would expect minimal evidence of new recruitment from aerial photographs, as mounds are being eliminated before they reach a size that is detectable at a scale of 1: 3000. Taking the poor quality of earlier photographs into account, however, only a single possible recruitment event was identified in the areas studied for mound area changes [see above]. Some pressure is therefore responsible for eliminating founder colonies and so maintaining a fairly constant number of large mounds in the landscape. The variable numbers of mounds recorded for each diameter-class greater than 6m, suggest a lack of size-class specific pressures above this diameter. In other words, once a colony survives past a certain "threshold" limit, then its relative chances of persisting increases considerably. Survival rates would thus also be equal across the range of mound sizes greater than 6m in diameter. Furthermore, evidence from aerial photographs suggests that no mounds were eliminated from the landscape over a time period of approximately 50 years (pers. obs.). This supports the idea that a mound is difficult to eliminate once it has developed past a certain size. This could be a function of either of colony size (whose survival probability appears to increase with increasing size), or the actual physical size of the mound itself.

Two possible processes responsible for the elimination of founder colonies are predation and intraspecific competition between colonies for resources. Founder populations appear to be highly susceptible to predation, which may be intense. *Crematogaster peringneyi*, a carnivorous ant, had recently invaded and occupied the nests of a number of class 1 mounds in the study area and could be responsible for a high proportion of extinctions of founder colonies. A range of other species were observed to prey on *M.viator* including carnivorous ants and a Scarab beetle. The foraging ports which open up on the soil surface are fiercely defended by soldier termites, preventing entry of any intruders. Another indication that *M.viator* colonies are sensitive to predation is the remarkable speed at which these foraging ports are closed. By cementing together soil fragments, worker termites were able to close a foraging port in less than 5 minutes (pers. obs.). This indicates that *M.viator* colonies are extremely sensitive to the effects of predation. Predation may therefore be a major factor causing the elimination of incipient colonies, maintaining a relatively constant number of class 4 mounds in the landscape. Another major predator of *M.viator* is the aardvark (*Orycteropus afer*), although minimal signs of this mammals activity was seen on class 1 - 3 mounds. Aardvark activity was recorded on mounds that were devoid of vegetation cover, suggesting that founder colonies establish below bushes and rocks that would provide protection against predation. Although a large percentage of class 4 mounds showed evidence of Aardvark activity, they are more resilient to the effects of predation as a factor of their larger colony size (ability of workers to produce new queens), making them difficult to eliminate entirely.

The impact of competitive interactions are difficult to quantify. Nearest-neighbour analysis (of size class 4 mounds) suggests that competitive effects between class 4 mounds are minimal (fig. 4), although this technique could be misleading in that it ignores the effect of colonies in the intermound areas. An assumption of nearest neighbour analysis was that mound sizes are the result of competitive interactions between class 4 mounds. However, mounds from size classes 1, 2 and 3, which are found in the "intermound" area could also affect the sizes of class 4 mounds through competitive interactions for resources. It is interesting that class 2 and 3 mounds establish in a zone equidistant from the closest class 4 mounds. This possibly represents the only zone where founder colonies are able to establish and survive. This would suggest that inter-colony competition does play a role in shaping the spatial pattern of mounds in the environment. Competitive interactions are likely to be of greater importance in extinction of class 3 mounds, as at that size colony numbers are great enough to withstand impact of predation by insects.

4.4 Plant community dynamics.

4.4.1 Termite-herbivory driven dynamics.

It appears that community dynamics can in part be understood by invoking termite herbivory and soil-chemical/structural changes (through mound construction), as the mechanisms driving species replacement in an arid, *heuweltjie*-dominated landscape.

Yeaton and Esler (1990) invoke a model of erosion of nutrient-rich soil off *heuweltjies* and interspecific plant competition to explain patterns of plant establishment and succession in the arid and semi-arid environment of the Karoo. Yeaton and Esler (1990) identified a predictable pattern of species replacement in space and time, based on a process of succulent species providing sites of establishment for woody shrubs. Through competitive interactions, woody species replace the succulent guild over time. This study provided further evidence that predictable patterns of species replacement do occur in semi-arid and arid environments, a process previously identified in similar environments across the globe (Cody, 1986; Yeaton and Cody, 1979; Yeaton, 1978; Yeaton, 1988). Central to the pattern of replacement described by Yeaton and Esler (1990), was the tenet that erosion of nutrient-rich soil off *heuweltjies* resulted in the differential establishment of various species of Mesembryanthemaceae on the fringes of mounds. The mechanism which drives the system is thus a predictable interaction between plants and the physical environment. This process does not seem to be the overriding mechanism shaping the succulent fynbos of the Clanwilliam region however, due to the alternative explanation of termite herbivory.

The abundance of *P.ciliata* was found to decrease with increasing *heuweltjie* size, being entirely absent from class 4 mounds (fig. 9, Table. 3, Plate 7). If one accepts that termite herbivory intensifies with increasing colony size (reflected by an increase in mound size), then a pattern emerges of the gradual exclusion of *P.ciliata* on-mound through increasing herbivory. The significantly poorer condition of plants occurring closer to mounds suggests that *P.ciliata* is negatively effected close to mounds, possibly through termite herbivory. The other possibility is that *P.ciliata* plants are negatively affected by altered soil nutrient conditions of class 4 mounds. However, senescence of *P.ciliata* near-mound is unlikely to result from possible allelopathic effects of altered nutrient conditions "poisoning" plants, as seedling establishment and growth to maturity had already occurred. This indicates that *P.ciliata* is able to establish and grow in the soil of class 4 mounds. Observations were also recorded on the up-slope perimeter of mounds, to control for possible nutrient effects. This suggests that changes in abundance of *P.ciliata* are the result of termite induced herbivory. *P.ciliata* was the only species that *M.viator* was observed to harvest live material from. In contrast, perennial shrubs such as *Galenia africana,* which increase in abundance with increasing *heuweltjie* size are largely unpalatable to *M.viator* and can thus establish on large mounds. Live material of *E.burmannii, G.africana* and *R.decurvans* is not grazed by *M.viator*, possibly explaining their presence on classes 2, 3 and 4 mounds respectively. The spatial distribution of perennial shrubs in the landscape thus follows a predictable pattern in relation to mound size. This appears to be partly driven by termite herbivory, a process not previously suggested to play a role in vegetation dynamics on *heuweltjies* in previous research.

4.4.2 Vegetation dynamics driven by mound building-induced changes to soil nutrient status.

Results show an overriding pattern of decreasing perennial cover with increasing *heuweltjie* size, coupled with an increase in annual cover on the same gradient (fig. 7). It is possible that a thinning out of perennial vegetation, driven by termite herbivory, has lead to this increase in annual cover. Cunliffe et al. (1990) illustrated the competitive effects of perennial vegetation on annual cover. Plant size and fecundity of the annual under study (*Gorteria diffusa*) was decreased when plants established in close proximity to a perennial shrub. A removal of this negative competitive effect through the exclusion of perennial shrubs on-mound could lead, in part, to an increase in annual cover.

The reproductive strategy of annuals could also favour their establishment on-mound, relative to perennial species. The life-cycle of annual vegetation is initiated and completed during the period of winter rainfall (June - September), which coincides with a period of minimal termite activity. Termite herbivory of annuals is therefore limited to the dried remains of adult plants. The harvesting of dried annual material, which is intensive, does not effect annual recruitment in any way as the life cycle has already been completed (i.e. seed has largely been set). However, the removal of a perennial shrub through grazing will lead to a decrease in reproductive output as seed set of future years is reduced.

Another factor affecting increasing annual cover could be the continuum of changing soil characteristics that is linked to increasing *heuweltjie* age and size. The fine, nutrient rich soil of large earth mounds (i.e. class 4) could provide an ideal "disturbed" environment for fugitive annual species to colonize. The distribution of annual species on-mound is clearly delimited, ending abruptly at the edge of *heuweltjies* (pers. obs.). This indicates the effects of altered soil conditions on the establishment of annual species, and suggests that it may be the overriding factor limiting annual species abundance.

4.4.3 Plant succession

Altered soil conditions could also be invoked to explain the successional pattern of species replacement that occurs with increasing mound size, a mechanism separate from herbivory-driven dynamics. This succession is illustrated by the changing cover abundance of various individual species, which peak at different mound size classes (Table 2). *E.burmannii* and *R.incisa*, for example have a peak in cover abundance at intermediate size classes 2 and 3 (fig. 10). *R.incisa* is actually restricted entirely to classes 2 and 3, being absent from the remaining classes (fig. 10). *E.burmannii* on the other hand, is present on all size classes, but shows increased abundance for classes 2 and 3. Another example is *Lycium ferocissimum*, which occurs only on class 4 mounds.

It appears that there is a continuum in the degree to which the distribution and abundance of individual species is affected by increasing mound size (or changing nutrient status). At the one extreme are species such as *R.incisa* and *L.ferocissimum*, which are obligately restricted to a particular size class. At the other extreme are species such as *Hermannia cuneifolia*, which are entirely unaffected by changing mound size. Intermediate to these extremes are species which are affected to various degrees by changes in mound size. The mechanism driving these changes could be the continuum of changing soil nutrients and structure, resulting from increasing mound age (and therefore size). Presumably, the age of a mound should reflect the degree to which soil structure and nutrient status has been affected by termite activity. This continuum in altered soil conditions could therefore favour particular specialist species, adapted to establishing in a certain soil type. Generalist species, on the other hand, capable of establishing across the entire continuum would be largely unaffected by changing nutrient status.

The key question, is, whether certain species show differential establishment in the soils from mounds of separate size classes, or if mounds reach an intermediate size as a result of the greater protection against predation provided by species such as *R.incisa* (see above). This question could be answered conclusively through *ex situ* germination experiments, which were not possible in this study due to time constraints. For example, if changes in soil structure are driving the succession, we would expect the germination and growth rates of *R.incisa* to be greater in soil from size class 3 mounds than germination in soil from size class 4 mounds. On the other hand, if differential levels of predation were driving change, then one would expect no significant difference in germination and establishment of different species in various soils.

Patterns of abundance for individual species do suggest that there is a succession in species replacement, along the continuum of mound sizes, with particular species establishing on particular mound sizes. As discussed above, the only possible mechanism to account for this pattern is changing soil conditions, with unique nutrient and other physical properties of the soil of each mound size facilitating the establishment of a unique guild of species. A model of species adapting to a narrow, yet constant set of physical conditions provided by a particular size class, could account for this pattern.

Thus the development of *heuweltjies* can influence species diversity on a temporal scale. This is different to the species diversity effects of large mounds that has been documented in earlier research (Knight *et al.*, 1989; Milton and Dean, 1990; Midgley and Musil, 1990). This work showed the effects that *heuweltjies* have in increasing beta-diversity.

4.4.4 Extrapolating results to other plant communities.

Results of this study should not be applied casually to areas with different vegetation types, without reciprocal studies in these areas. *Heuweltjies* within 10km of the study site (on the Pakhuis Pass), appeared to have a different on-mound plant community dominated by perennials (pers. obs.). This indicates that various mechanisms may assume differentially important roles in distinct vegetation communities. However, this study does show that termite herbivory is an important factor shaping vegetation structure, and must be considered in tandem with other previously identified processes, such as altered nutrient status (Midgley and Musil, 1990).

5. Conclusion.

5.1 An inclusive model of vegetation dynamics.

The spatial distribution and relative abundance of species of the succulent fynbos community at Clanwilliam is driven, in part, by two *M. viator*-induced effects. Firstly, termite herbivory and secondly, changes in soil nutrient conditions resulting from mound construction. Neither mechanism appears to have an overriding affect on vegetation composition. The abundance of individual species are differentially affected by termite herbivory as opposed to soil nutrient-status. Uncoupling the effects of either mechanism is simple for some species (e.g. herbivory appears to have an overriding effect on the spatial distribution of *P. ciliata*), but more difficult for others (e.g. are changes in the abundance of *E. burmannii* predominantly an effect of being unpalatable or favouring certain size-class soils ?). Future research could explore the effects of these two mechanisms in more detail. It is clear, however, that *M. viator* has an impact on vegetation community dynamics of the region. *M. viator* could certainly be described as a keystone species, affecting numerous ecological interactions and life-cycles in the landscape. *M. viator* is responsible for nutrient cycling and shaping the physical landscape, is prey to a number of predators, has commensal relations with various species and has an extensive impact on plant alpha- and beta-diversity. Although considered an agricultural pest (Coaton, 1962; B. Visser, pers. com.), the species has an important role to play in the dynamics and maintenance of biodiversity within the ecosystems that it occupies. As *M. viator* colonies are largely eliminated through the effects of agricultural activities such as crop spraying and ploughing, it would be pertinent to maintain a watchful eye on the remaining areas of succulent Fynbos and Karoo shrubland where *M. viator* occurs. Noting the wide-ranging biological impacts of this insect, the conservation of a number of plant and animal species could be intimately linked to the future survival of *M. viator*.

APPENDIX 1

Species checklist from Clanwilliam study site.

AIZOACEAE
Tetragonia rosea

ANACARDIACEAE
Rhus incisa var. incisa

ASPARAGACEAE
Protosparagus africana
Protosparagus capensis var. capensis

ASPHODELACEAE
Trachyandra muricata
Chlorophytum undulatum

ASTERACEAE
Athanasea trifurcata
Didelta spinosa
Dimorphotheca sinuata
Pentzia calva
Pteronia divaricata
Pteronia ciliata
Senecio arenarius
Ursinia spp.

CHENOPODIACEAE
Chenopodium olukondae

EBENACEAE
Euclea tomentosa

EUPHORBIACEAE
Euphorbia burmannii

FABACEAE
Indigofera procumbens
Aspalathus spp.

GERANIACEAE
Pelargonium pulchellum

HYACINTHACEAE
Albuca altissima

IRIDACEAE
Lapeirousia arenicola

Moraea spp.

MESEMBRYANTHEMACEAE
Ruschia decurvans

MONTINIACEAE
Montinia caryophyllaceae

OXALIDACEAE
Oxalis palmifrons

POACEAE
Pentachismus spp.
Phalaris tuberosa
Schismus spp.
Stipa capensis

POLYGALACEAE
Nylandtia spinosa var. spinosa

SCROPHULARIACEAE
Nemesia ligulata

SOLANACEAE
Lycium ferocissimum

STERCULIACEAE
Hermannia trifurca
Hermannia cuneifolia var. cuneifolia

TECOPHILAEACEAE
Cyanella hyacinthoides

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CONCLUSIONS

1 Within their distribution, densities of heuweltjies limited by MAR - productivity?

Densities show correlation with current climat

2 MAR does not limit heuweltjie distribution

distribution could be determined by

(i) physiological temperature limit

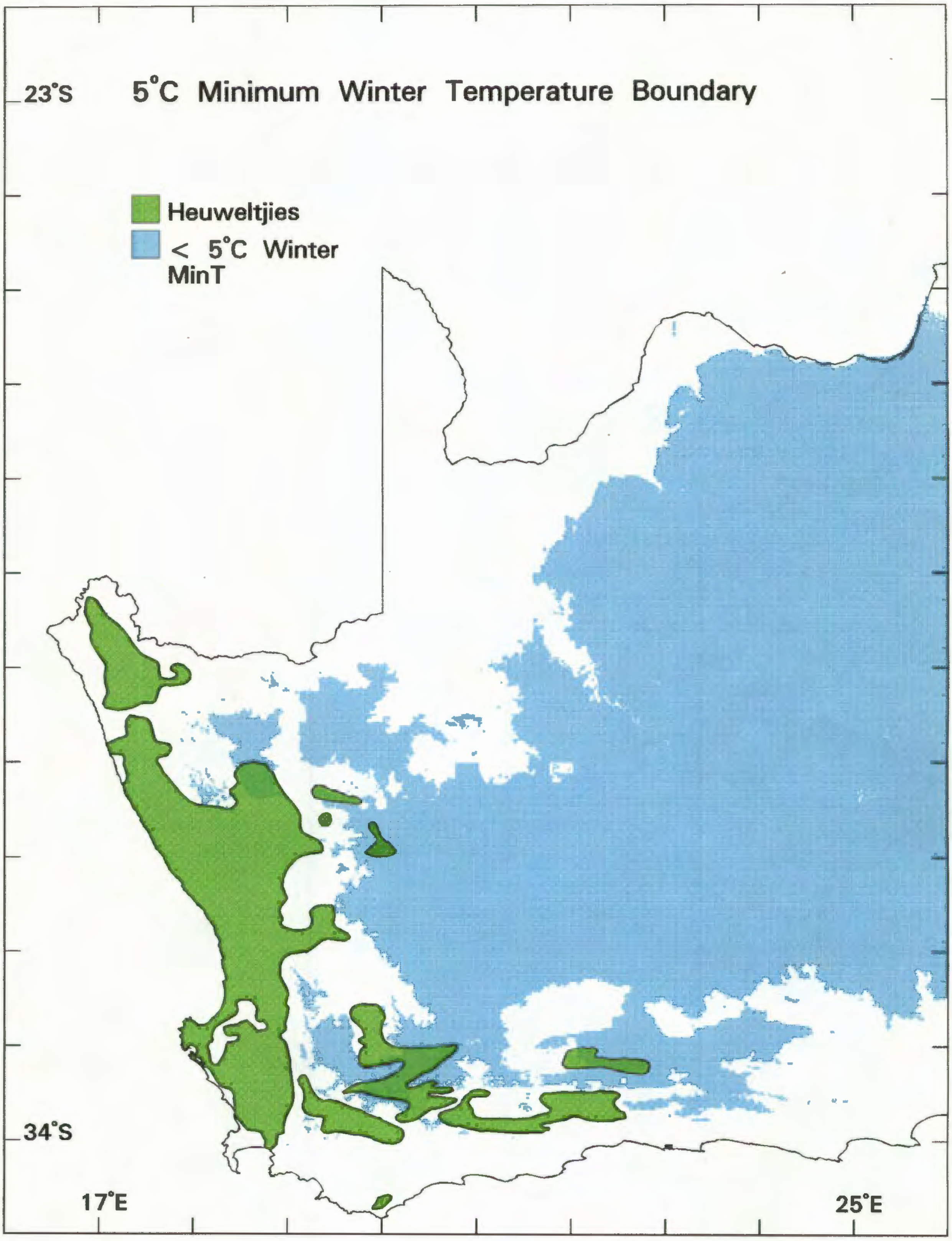
(ii) behavioral temperature limit

(iii) - direct association with vegetation type (grassy)

(iv) - indirect association with vegetation type (competition with other termites/ants)

(v) + direct association with vegetation type (leaf-succulent flora)

#wt.gra


23°S
5°C Minimum Winter Temperature Boundary
🟩 Heuweltjies
🟦 < 5°C Winter MinT
34°S
17°E
25°E

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