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Patch creation by fossorial rodents: a key process in the revegetation of phytotoxic arid soils

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The recolonization by plants of overburden dumps created more than 20 years ago by opencast diamond-mining activities on the west coast of South Africa is very slow to non-existent. Only on dumps where the fossorial rodent *Parotomys brantsii* has created burrow networks has some natural revegetation occurred. We tested the hypothesis that this plant colonization is facilitated by rodent burrowing activities which create soil patches containing organic matter and soil microbial propagules. Nearest-neighbour analysis of burrow–plant and random point–plant pairs showed that rodent burrows are associated with the occurrence of plants. There was a significantly higher pH, significantly lower electrical conductivity, and a five-fold increase in microbial activity between control and burrow mound soils on dumps. These fossorial rodents create small patches (*c.* $0{\cdot}5 \times 0{\cdot}5$ m) of increased 'fertility' that encourage plant colonization in an otherwise edaphically hostile environment.

Keywords: arid rangeland; Brant's whistling rat; *Parotomys brantsii*; patch creation; phytotoxic soil; restoration; soil microbial activity; winter rainfall desert

Introduction

Since 1929, opencast mining for diamonds along the arid west coast of southern Africa has created large overburden dumps and other disturbed areas. Generally, these mining activities result in an inversion of the soil profile to bedrock (up to 30 m), which for the most part are left in an unamended state. These overburden dumps comprise mounds of ancient aeolean dune soils and marine deposits, which have characteristically high pH values and are saline sodic (Scott & Johnson, 1995). Although these exposed subsoils appear to contain adequate levels of most plant nutrients (Scott *et al.*, 1994), factors such as soil salinity, clay and sodium content and dump architecture in terms of steep slopes, best explain the lack of natural plant recolonization (Scott *et al.*, 1994; Scott & Johnson, 1995; le Roux & Odendaal, unpublished). In addition to these physical and chemical factors, dump subsoils lack a microbial component. Undoubtedly this also contributes to the lack of plant colonization as the presence of a functional soil microbial community is directly related to the establishment and maintenance of plant communities in arid systems (Allen, 1988; Whitford, 1988).

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Some natural recovery of vegetation on overburden dumps does occur (le Roux & Odendaal, unpublished). There is a gradient of increasing rate and extent of plant recolonization that runs perpendicular to the coast. As one moves away from the coast, the amount of aeolean sand movement decreases. Aeolean deposition of sand on overburden dumps is important in revegetation since wind-deposited sand does not possess the chemical and physical properties of overburden dump soils and, therefore, facilitates plant colonization. A parallel gradient of increasing soil depth occurs from the coast to inland where depth to bedrock and degree of phytotoxicity of subsoil are highest. Subsoils closest to the coast are least phytotoxic. In one case, a series of overburden dumps created in the 1970s are still totally bare today (pers. obs.). The dumps, 8 km from the coast, occur at the inland limit of marine-terrace prospecting (*c.* 100 m altitude) and are thus the oldest colluvial soils disturbed by diamond mining along the coast. These overburden dumps represent the most extreme case in terms of dump phytotoxicity and adverse physical properties.

The Namaqualand Sandveld is also home to a burrowing rodent, Brant’s whistling rat, *Parotomys brantsii*. These fossorial rodents occur in high densities throughout the area. They create and occupy a warren comprising an intricate and extensive tunnel network with up to 200 burrow entrances (De Graaff, 1981; Dean & Milton, 1991; Jackson, 1998). Diurnal foraging is conducted strictly within the bounds of the burrow network of the individual’s warren. The rats are strict vegetarians and will drag large twigs below ground to feed on at night (De Graaff, 1981; Jackson, 1998). A small mound develops (<1 m diameter) at each burrow entrance consisting of soil, faeces and organic matter ejected from the burrow network.

Ecologists have long recognized the keystone role of fossorial animals in the structure of the edaphic environment and resultant effect on the structure and dynamics of plant communities (e.g. Steinberger & Whitford, 1983; Jeffrey, 1987; Allen, 1988; Stolp, 1988; Whitford, 1988, Chew & Whitford, 1992). A well known example of this is the termite-created ‘heuweltjies’ or Mima-like mounds in the winter rainfall in Succulent Karoo (Lovegrove & Siegfried, 1986; Yeaton & Esler, 1990; Dean & Yeaton, 1993). Termites have also been associated with the creation of nutrient-rich patches in nutrient-poor tropical forests (Salick *et al.*, 1983). The burrowing scarabid beetle, *Peltotrupes youngi*, has a significant patch-creating impact in Florida long-leaf pine communities (Kalisz & Stone, 1984). Amongst arachnids, Danin (1994) has demonstrated the association between the establishment of *Salsola inermis* and scorpion burrows.

Probably the most studied fossorial creatures are North American gophers, *Geomys* sp. There has been much discussion on the impacts of the spatial, temporal and intensity effects of gopher-mediated disturbance regimes on the dynamics of various plant communities (e.g. Kalisz & Stone, 1984; Spencer *et al.*, 1985; Hobbs & Mooney, 1985, 1995; Andersen, 1987; Koide *et al.*, 1987). Although a non-fossorial mammal, nest building and foraging by kangaroo rats have similar impacts on their environments to pocket gophers (Mun & Whitford, 1990; Chew & Whitford, 1992; Heske *et al.*, 1993; Guo, 1996). The Indian crested porcupine, *Hystrix indica*, is also an important patch creator in the arid systems of Israel (Alkon & Olsvig-Whittaker, 1989; Gutterman *et al.*, 1990; Shachak *et al.*, 1991; Boeken *et al.*, 1995, 1998). One general conclusion that we can draw from these studies is that soil mixing by burrowing animals creates patches of soil in the landscape that differ both in their physical and chemical properties from those of the surrounding landscape. Also, patches created by animal digging provide microsites for plant colonization in an otherwise ‘homogeneous’ vegetation matrix and consequently have a profound effect on plant community structure and dynamics (Steinberger & Whitford, 1983; Contreras & Gutierrez, 1991; Chew & Whitford, 1992; Guo, 1996; Gutierrez *et al.*, 1997; Boeken *et al.*, 1998).

Not only are gopher activities instrumental in creating patches in existing vegetation matrices, but they can also play a key role in facilitating the return of vegetation by creating patches that favour plant establishment and growth (e.g. Steinberger

& Whitford, 1983; Hawkins, 1996). Anderson & MacMahon (1985) have shown that the burrowing activities of northern pocket gophers facilitated plant recolonization on ash-covered landscapes after the eruption of Mount St Helens in 1980. In their study it was shown that gopher mounds enhance seedling establishment and growth due to more favorable soil moisture, temperature, nutrients and organic matter. Gopher burrowing activities are also instrumental in the dispersal of mycorrhizal spores (MacMahon & Warner, 1984; Hawkins 1996). The soil associated with dung middens produced by rabbits, *Oryctolagus cuniculus*, on limestone quarry-spoil are areas of enhanced biological activity, increased soil moisture, higher nutrients, lower pH, and are more humic than surrounding spoil (Dixon & Hambler, 1993). These sites are also the focus of enhanced pioneer plant colonization.

An active soil microbial community is necessary for the biogeochemical cycling of nutrients and is a direct indicator of general soil fertility (Rowell 1994). The soil microbial community is involved with the sequestering of soil nutrients and the breakdown of organic matter and release of nutrients, and it plays an integral part in determining soil fertility (Nedler & Steinberger, 1993). In a landscape characterized by poor soils for plant growth, the activities of fossorial animals can condition soil such that when animal activity ceases, the mounds become foci for plant establishment.

In the study area used here the overburden dumps colonized by Brant's whistling rats are also colonized by plants. Where there is no apparent rodent activity there appears to be no plant colonization. Thus, given the above discussion and this apparent association between patch creation and plant recolonization of overburden dumps, the aims of this study were two-fold: (1) to show that there is an association between rodent burrowing and plant recolonization of, and distribution on, overburden dumps; and (2) to show that this association is due to the amelioration of soil conditions on burrow mounds that create sites suitable for plant establishment and growth.

Materials and methods

Study site

The study site is located on the farm Swartbank approximately 35 km south of Alexander Bay on the west coast of South Africa. Prospecting occurred at the site in the early 1970s, but mining the diamond deposits proved to be uneconomical. Since then the site has remained relatively undisturbed except for occasional sheep and antelope grazing.

The site receives < 60 mm of rainfall annually and is located within the winter rainfall and fog zone of the southern Namib Desert. The vegetation of the site is classified as Strandveld Succulent Karoo (Low & Rebelo, 1996). For a more detailed description of the vegetation of the area see Desmet & Cowling (1998) and Milton *et al.* (1997). The soils are aeolean sands being derived principally from reworked marine deposits. The soil profile to bedrock (10–20 m) consists entirely of aeolean deposits over marine gravels that lie on the bedrock surface or between layers of aeolean deposits. There is extensive dorbank (siliceous hard-pan) and calcrete development below the surface horizons throughout the whole area.

Pattern analysis

To test whether there was an association between plant occurrence and rodent burrows, nine quadrats of 5×5 m, three each on three separate dumps, where placed over areas of noticeable whistling rat activity. All perennial plants present in each plot were identified and their mean diameter and height recorded. These data were compared to nine randomly chosen quadrats, three on each of the three dumps sampled, and each placed over areas where there was no evidence of any rodent activity. The mean number of plants per plot in the rodent plots was compared to that in rodent-free plots using a non-parametric Mann-Whitney test.

To examine the relationship between the occurrence of plants and burrow mounds at a finer scale, nearest-neighbour distances between all burrow entrances (active and old) and their nearest plant neighbour were measured in each of the plots. The cumulative distribution of these nearest-neighbour distances was compared to that of point–plant distances in each plot. Points were stratified in each plot on a regular 1×1 m grid (16 points in total per plot). A Kolmogorov–Smirnov test was used to test whether the cumulative frequency distribution of point–plant and burrow–plant distances were significantly different. If the two samples are distributed independently of one another then this test is applicable irrespective of the type of distribution of the data and the size of the two data sets (Upton & Fingleton, 1985).

Soil analyses

To test whether the edaphic properties of burrow mounds were different from matrix soil, six soil samples, two each from the three separate dumps, were collected from: (1) control sites on overburden dumps away from any rodent influence (rodent-free plots); (2) uncolonized burrow mounds; (3) under established plants on burrow mounds; and (4) topsoil from undisturbed areas in the surrounding dunes. We only collected topsoil to a depth of 5 cm. For each sample we measured the pH and electrical conductivity (EC), and analysed the soil microbial activity. The methods outlined in Rowell (1994) were followed for all analyses. pH was measured in both distilled water and a strong ionic solution (0.01 M $CaCl_2$). EC was measured in deciseimens per metre (dSm^{-1}). Both pH and EC measurements were made in 1 : 5 soil to solution

Table 1. *Occurrence of perennial plants in rodent plots*

Species	Family	Occurrence
Psilocaulon subnudosum	Mesembryanthemaceae	7
Ruschia cyathiformis	Mesembryanthemaceae	6
Lycium cinereum	Solanaceae	4
Zygophyllum cordifolium	Zygophyllaceae	4
Stoeberia beetzii	Mesembryanthemaceae	3
Hypertelis salsoloides	Aizoaceae	2
Pteronia glabrata	Asteraceae	2
Euphorbia mauritanica	Euphorbiaceae	2
Lebeckia multiflora	Fabaceae	2
Cladoraphis cyperoides	Poaceae	2
Galenia crystallina	Aizoaceae	1
Tetragonia fruiticosa	Aizoaceae	1
Ornithogalum sp.	Asphodelaceae	1
Othonna sedifolia	Asteraceae	1
Salsola zeyheri	Chenopodiaceae	1
Phyllobolus scintilans	Mesembryanthemaceae	1
Drosanthemum ramosissimum	Mesembryanthemaceae	1
Zygophyllum clavatum	Zygophyllaceae	1

Nomenclature follows Arnold & De Wet (1993).

extracts. A laboratory-based method was used to assess microbial activity by measuring respiration of incubated soil, and activity expressed in terms of grams carbon dioxide respired per gram air dried soil per second (g CO_2 g^{-1} dry weight $soils^{-1}$). A one-way ANOVA was used to compare the results of the four sites for each analysis. A matched *t*-test was used to test for significant changes in pH at each site between the water and calcium chloride solutions. The colour of each dry soil sample was determined using standard soil colour charts and qualitative colour record of the 1 : 5 soil-to-water extract was also made.

Results

The association between rodent burrows and plant occurrence is significant. No plants were found in any of the rodent-free plots compared to 8 ± 3 in the rodent plots. Rodents avoid constructing warrens on steep slopes and the maximum average slope angle measured in any of the rodent plots was 15° (M ± S.D. $8 \pm 5{\cdot}0°$) compared with a maximum of 22° ($12{\cdot}4 \pm 5{\cdot}8°$) for the comparison plots. Members of Mesembryanthemaceae and Aizoaceae were the most common plants encountered on the dumps (Table 1).

At a finer scale, within rodent plots there was no significant association between all burrow entrances (i.e. active and non-active) and the occurrence of plants (Fig. 1). There was however, a strong positive association ($p < 0{\cdot}01$) between active burrow entrances and plants, and a weaker negative association between non-active burrow entrances and plants. A positive association is inferred when the slope of the curve is

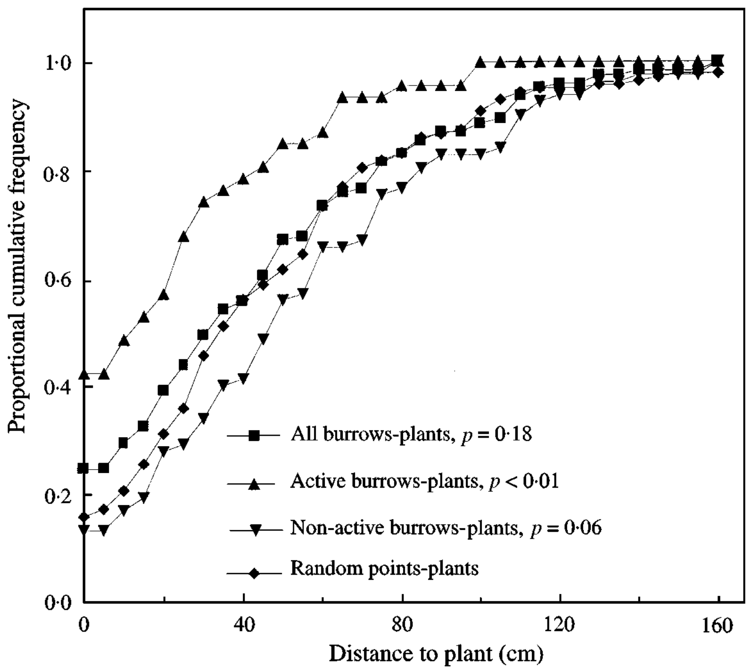

Figure 1. The cumulative frequency distribution of nearest-neighbour distances between all burrows, active burrows, non-active burrows and plants, respectively, compared to between random points and plants. *p* values show whether each curve is significantly different to the random point plant curve.

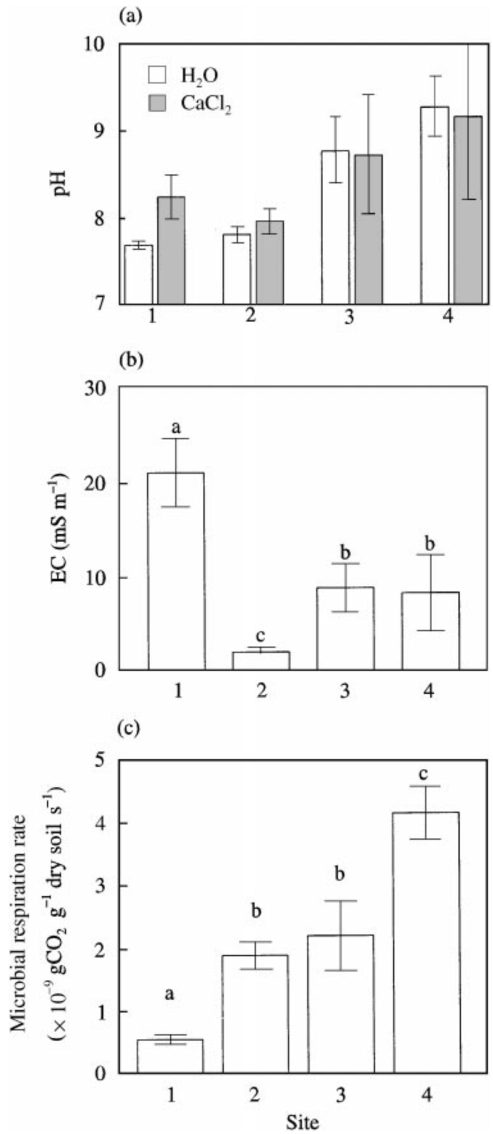

Figure 2. Characteristics of soils sampled in different sites in the study area. (a) pH in water and a strong ionic solution (0·01 M $CaCl_2$); (b) conductivity; (c) microbial respiration. The sites are: (1) control soils from overburden dumps; (2) normal dune soils from the surrounding landscape; (3) uncolonized rodent burrow mounds; and (4) soil from under the canopy of plants growing on overburden dumps. Different letters indicate treatments that are significantly different ($p < 0{\cdot}05$) from one another.

above that of the random point–plant curve in Fig. 1. Conversely, a negative association is inferred when the curve is below.

The effect of rodent organic amendment of soils on edaphic properties is significant. The pH of soils in water on uncolonized mounds and under plants increased by approximately pH 1·5 compared to control and normal soils (Fig. 2(a)). For normal soils, and those from uncolonized mounds and under plants, the pH in calcium chloride showed a slight, although not significant, change in pH. The pH of the control soil, however, increased significantly ($p < 0.01$) by approximately pH 1. Conversely, electrical conductivity was approximately half that of control soils in uncolonized mounds and under plant soils (Fig. 2(b)), but was still approximately three times that of normal soils. Microbial activity on uncolonized mounds was comparable to rates in normal dune soils, approximately three times those of control soils on dumps, but only half those of soils from under plants (Fig. 2(c)).

Discussion

There is a very significant association between rodent activity and the occurrence of plants. Within the proximity of a rodent burrow network, the positive association between the occurrence of active burrow entrances and plants may reflect preferences in rodent behavior to use entrances that are close to or under established plants. The turnover of burrow entrances may be at a much faster rate than the establishment and growth of plants, and thus the pattern of association between the two may be obscured. To determine which came first is not possible from these data. Did a plant manage to establish on an overburden dump, which facilitated the expansion of a nearby rodent warren, or did the gradual expansion of a nearby warren and the subsequent demise of the occupant facilitate the colonization of burrow mounds? The soil data suggest that the latter many be the case.

The activities of rodents on overburden dumps have a significant effect on the edaphic properties of those soils that are directly influenced by their burrowing, i.e. the burrow mounds. The addition of organic matter to these dump soils ameliorates the extreme soil chemical properties and enhances the microbial activity. Burrow mounds constitute islands of soil fertility in an otherwise edaphically phytotoxic environment.

A possible scenario for plant colonization of dumps could be as follows. A rat expands its burrow network onto the edge of a dump. This activity creates favorable sites for colonization in the form of burrow mounds and their associated burrow entrance which acts as a trap for wind-dispersed seeds. A local population crash or the predation of the burrow occupant would create a window of opportunity with no rat foraging that would allow plants to establish. There is some evidence for natural cycles in the populations of these rodents over a period of 4–6 years (T. Jackson & A. Spinks, pers. comm.). Subsequent colonization of the area by another rat could expand the burrow network further onto the dump thus repeating the cycle. This would explain the positive association observed between active burrows and plants on dumps.

How can the burrowing activities of fossorial rodents ameliorate the arid, saline-sodic soils on overburden dumps? The rodents amend these soils with organic matter collected from the surrounding vegetation and their own excretions. The end result is an improvement in the soil fertility of the burrow mounds, expressed in terms of enhanced soil microbial respiration. There are, however, a number of important soil chemical processes, which need to be considered. Analysis of soil pH in both water and strong ionic solution is not only indicative of the nature of these soils, but also the resultant changes due to rodent activity. It is interesting that pH in an ionic solution, when compared to pH in water, increased significantly for the dump control soils but not significantly in the other treatments. In the light of the high EC values measured for this treatment, the known sodic nature of the soil, and also the high pH (*c.* 8·3 in $CaCl_2$), one can conclude that this observed increase in pH is a result of a high concentration of positive ions or strong salt effect (Rowell, 1994) The presence of a high concentration of Ca^{2+} and Na^{+} ions in the soil solution will contribute towards increasing the pH, and with the addition of an ionic solution, this effect is enhanced. For normal dune soils, pH in water is similar to that of the dump control soils, but there is no significant change in pH in an ionic solution, indicating that normal dune soils are not sodic. Thus, the addition of organic matter to the burrow mound soils by rodents initiates a soil chemical process that results in the precipitation of ions out of the soil solution. Below pH 8·0, soil, exchangeable Ca^{2+} ion species and calcium carbonate or calcite ($CaCO_3$) are in equilibrium and CO_3^{2-} is inactive (Ross, 1989). At pH above 8·0, CO_3^{2-} becomes very reactive, resulting in the formation of metal carbonates which impose limits on the solubilities of metal ions and consequently their availability to plants (Lindsay, 1979). Among these metal carbonates is calcite (see Appendix for equations of the reactions). In alkaline soils the partial pressure of CO_2 gas is the controlling variable for calcite solubility (Lindsay, 1979). The observed microbial respiration in rodent-affected soils results in an up to five-fold increase of the soil CO_2 concentration. An increase in soil CO_2 concentration results in a decrease in calcite solubility as calcium ions are precipitated out of solution. In addition to the formation of calcite from an increase in CO_2 concentration, calcite can also be formed by the addition of urea, e.g. in the form of rodent excretions (Ross, 1989). Sodium ions reacting with CO_2 and water can form various sodium carbonate anion complexes and sodium hydroxide (Lindsay, 1979). These sodium complexes will raise the pH of the solution which would explain the observed increase in pH in the uncolonized mounds and under-plant soils. The origin of calcrete horizons under heuweltjies has been ascribed to this process of elevated soil CO_2 through enhanced microbial activity leading to precipitation of calcium (Moore & Picker, 1991).

An active soil microbial community is necessary for the biogeochemical cycling of nutrients and is a direct indicator of general soil fertility (Rowell, 1994). The significantly higher microbial respiration rate in soils on uncolonized mounds is direct evidence for an improvement in general soil condition through amendment with organic material ejected from the warren by rodents. The even greater activity of the microbial community under shrubs is expected to be due to the moderated temperatures from shading effects, increased organic matter from both rodent, plant and aeolean inputs, increased water infiltration as a result of rodent digging and deposition of soil, and better moisture retention due to more soil organic matter in these desert microsites. These sites constitute islands of fertility in this desert ecosystem (Garcia-Moya & McKell, 1970; Steinberger & Whitford, 1983; Gutierrez *et al.*, 1993; Hawkins, 1996).

The role that burrowing rodents play is essentially one of a large earthworm. Rodents forage off the overburden dumps and drag organic material back to their burrows for use as food and also as nesting material. At the same time, these rodents are involved in expanding their underground burrow networks, and hence subsoil is brought to the surface. Mixed in this soil are the rodents' faeces and old, decaying, organic nesting materials. Two important processes are being fulfilled by the activities of the rodents. (1) The faeces contain spores/propagules of soil micro-organisms, and thus the soil ejected from burrows is seeded with soil microflora (MacMahon & Warner, 1984; Hawkins, 1996) and possibly plant seeds. (2) Organic matter is being introduced to the soil. This addition of organic biomass to the soil results in an increase in microbial activity (Aoyama & Tomohiro, 1993), and an improvement in the soil physical properties (Mun & Whitford, 1990; Laundre, 1993; Nedler & Steinberger, 1993).

The role that Brant's whistling rat plays in the revegetation of diamond mine overburden dumps highlights two important processes in the functioning of arid systems. The first is that of patch creation. The creation of patches in the landscape that differ in some respect to the surrounding landscape is important in providing microsites for plants to establish. This emphasizes the role of structure in arid system functioning. Second, the structure and functioning of the soil microbial community forms an integral part of the above-ground processes that we observe in these systems. Attempts to restore arid lands to self-sustaining functional ecosystems need to consider the integral role these two processes play in arid systems.

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References

Alkon, P.U. & Olsvig-Whittaker, L. (1989). Crested porcupine digs in the Negev Desert highlands: patterns of density, size and longevity. *Journal of Arid Environments*, **17**: 83–95.

Allen, M.F. (1988). Below ground structure: a key to reconstructing a productive arid ecosystem. In: Allen, E.B. (Ed.), *The Reconstruction of Disturbed Arid Lands. AAAS Selected Symposium 109.* Boulder: Westview Press.

Allsopp, N. & Stock, W.D. (1993). Mycorrhizal status of plants growing in the Cape Floristic Region, South Africa. *Bothalia*, **23**: 91–104.

Andersen, D.C. (1987). *Geomys bursarius* burrowing patterns: influence of season and food patch structure. *Ecology*, **68**: 1306–1318.

Andersen, D.C. & MacMahon, J.A. (1985), Plant succession following the Mount St Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides. The American Midland Naturalist*, **114**: 62–69.

Aoyama, M. & Tomohiro, N. (1993). Microbial biomass nitrogen and mineralisation immobilization processes of nitrogen in soils incubated with various organic materials. *Soil Science and Plant Nutrition*, **39**: 23–32.

Arnold, T.H. & De Wet, B.C. (1993). Plant of southern Africa: names and distribution. *Memoirs of the Botanical Survey of South Africa*, **62**: 1–825.

Boeken, B., Shachak, M., Gutterman, Y. & Brand, S. (1995). Patchiness and disturbance: plant responses to porcupine diggings in the central Negev. *Ecography*, **18**: 410–422.

Boeken, B., Lipchin, C., Gutterman, Y. and van Rooyen, N. (1998). Annual plant community responses to density of small-scale soil disturbances in the Negev Desert of Israel. *Oecologia*, **114**: 106–117.

Chew, R.M. & Whitford, W.G. (1992). A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosotebush (*Larrea tridentata*). *Journal of Arid Environments*, **22**: 375–386.

Contreras, L.C. & Gutierrez, J.R. (1991). Effects of subterranean herbivorous rodent *Spalacopus cyanus* on herbaceous vegetation in arid coastal Chile. *Oecologia*, **87**: 106–109.

Danin, A. (1994). Association of *Salsola inermis* and scorpion burrows in leached soils in the Judean Desert, Israel. *Israel Journal of Plant Science*, **42**: 37–40.

De Graaff, G. (1981). *The Rodents of Southern Africa.* Durban: Butterworths.

Dean, W.R.J. & Milton, S.J. (1991). Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *Journal of Arid Environments*, **20**: 231–237.

Dean, W.R.J. & Yeaton, R.I. (1993). The effects of harvester ant *Messor capensis* nest mounds on the physical and chemical properties of soils in the southern Karoo, South Africa. *Journal of Arid Environments*, **25**: 249–260.

Desmet, P.G. & Cowling, R.M. (1999). Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa. *Plant Ecology* (in press).

Dixon, J.M. & Hambler, D.J. (1993). Wildlife and reclamation ecology: rabbit middens on seeded limestone quarry-spoil. *Environmental Conservation*, **20**: 65–73.

Eldridge, D.J. & Greene, R.S.B. (1994). Microbiotic soil crusts: A review of their roles in soil and ecological processes in the rangelands of Australia. *Australian Journal of Soil Research*, **32**: 389–415.

Gallardo, A. & Schlesinger, W.H. (1995). Factors determining soil microbial biomass and nutrient immobilisation in desert soils. *Biogeochemistry*, **28**: 55–68.

Garcia-Moya, E. & McKell, C.M. (1970). Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology*, **51**: 81–88.

Guo, Q. (1996). Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia*, **106**: 247–256.

Gutierrez, J.R., Meserve, P.L., Contreras, L.C., Vasques, H. & Jaksic, F.M. (1993). Spacial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia*, **95**: 347–352.

Gutierrez, J.R., Meserve, P.L, Herrera, S., Contreras, L.C. & Jaksic, F.M. (1997). Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia*, **109**: 398–406.

Gutterman, Y., Golan, T. & Garsani, M. (1990). Porcupine diggings as a unique ecological system in a desert environment. *Oecologia*, **85**: 122–127.

Hawkins, L.K. (1996). Burrows of kangaroo rats are hotspots for desert soil fungi. *Journal of Arid Environments*, **32**: 239–249.

Heske, E.J., Brown, J.H. & Guo, Q. (1993). Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia*, **95**: 520–524.

Hobbs, R.J. & Mooney, H.A. (1985). Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia*, **67**: 342–351.

Hobbs, R.J. & Mooney, H.A. (1995). Spatial and temporal variability in California annual grassland: results from a long-term study. *Journal of Vegetation Science*, **6**: 43–56.

Jackson, T. (1998). Whistlers. A rats tale. *Africa – Environment & Wildlife*, **6**: 38–43.

Jeffrey, D.W. (1987). *Soil–Plant Relationships. An Ecological Approach*. London: Croom Helm.

Kalisz, P.J. & Stone, E.L. (1984). Soil mixing by scarabid beetles and pocket gophers in north-central Florida. *Soil Science Society of America Journal*, **48**: 169–172.

Koide, R.T., Huenneke, L.F. & Mooney, H.A. (1987). Gopher mound soils reduces growth and affects ion uptake of two annual grassland species. *Oecologia*, **72**: 284–290.

Laundre, J.W. (1993). Effects of small mammal burrows on water infiltration in a cool desert environment. *Oecologia*, **94**: 43–48.

Lindsay, W.L. (1979). *Chemical Equilibria in Soils.* New York: John Wiley.

Lovegrove, B.G. & Siegfried, W.R. (1986). Distribution and formation of Mima-like earth mounds in the western Cape Province of South Africa. *South African Journal of Science*, **82**: 432–436.

Low, B.A. & Rebelo, A.G. (1996). *Vegetation of South Africa, Lesotho and Swaziland.* Pretoria: Department of Environmental Affairs and Tourism.

MacMahon, J.A. & Warner, N. (1984). Dispersal of mycorrhizal fungi: processes and agents. In: Williams, S. & Allen, M. (Eds), *VA Mycorrhizae Reclamation of Arid and Semiarid Lands.* Laramie: University of Wyoming, Agricultural Experimental Station.

Milton, S.J., Yeaton, R.I., Dean, W.R.J. & Vlok, J.H.J. (1997). Succulent Karoo. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (Eds), *The Vegetation of Southern Africa.* Cambridge: Cambridge University Press.

Moore, J.M. & Picker, M.D. (1991). Heuweltjies (earth mounds) in the Clansilliam district, Cape Province, South Africa: 4000-year-old termite nests. *Oecologia*, **86**: 424–432.

Mun, H.T. & Whitford, W.G. (1990). Factors affecting annual plant assemblages on banner-tailed kangaroo rat mounds. *Journal of Arid Environments*, **18**: 165–173.

Nedler, A. & Steinberger, Y. (1993). Trends in structure, plant growth, micro-organism inter-relations in the soil. *Soil Science*, **155**: 114–122.

Ross, S. (1989). *Soil Processes: A Systematic Approach.* London: Routeledge.

Rowell, D.L. (1994). *Soil Science: Methods and Applications.* Harlow, U.K. Longman Scientific and Technical.

Salick, J., Herrera, R. & Jordan, C.F. (1983). Termitaria: Nutrient patchiness in nutrient-deficient rain forests. *Biotropica*, **15**: 1–7.

Scott, D.F. & Johnson, M.A. (1995). *Soil Leaching Trails on Overburden Soil from Kleinzee and Koingnaas. Report number FOR-C 283.* Pretoria: The Division Forest Science and Technology.

Scott, D.F., Du Toit, B., Johnston, M.A. & Burns, M.E.R. (1994). *The Effects of Mining on Soil Properties and the Ability of the Soil to Support Vegetation After Mining at Kleinzee and Koingnaas, on the West Coast of South Africa. Project No. FL 719, Report No. FOR C-*. Pretoria: Division of Forest Science and Technology.

Shachak, M., Brand, S. & Gutterman, Y. (1991). Porcupine disturbances and vegetation pattern along a resource gradient in a desert. *Oecologia*, **88**: 141–147.

Spencer, S.R., Cameron, G.N. Eshelman, B.D., Cooper, L.C. & Williams, L.R. (1985). Influence of pocket gopher mounds on a Texas coastal prairie. *Oecologia*, **66**: 111–115.

Steinberger, Y. & Whitford, W.G. (1983). The contribution of rodents to decomposition processes in a desert ecosystem. *Journal of Arid Environments*, **6**: 177–181.

Stolp, H. (1988). *Microbial Ecology: Organisms, Habitats, Activities.* Cambridge Studies in Ecology. Cambridge: Cambridge University Press.

Upton, G.J.T. & Fingleton, B. (1985). *Spacial Data Analysis by Example. Point Pattern and Quantitative Data. Volume 1. Wiley Series in Probability and Mathematical Statistics.* Chichester: John Wiley.

Whitford, W.G. (1988). Decomposition and nutrient cycling in disturbed arid ecosystems. In: Allen, E.B. (Ed.), *The Reconstruction of Disturbed Arid lands. AAAS Selected Symposium 109.* Boulder: Westview Press.

Yeaton, R.I. & Esler, K.J. (1990). The dynamics of a succulent karoo vegetation. *Vegetatio*, **88**: 103–113.

Appendix

The soil bio-geochemical processes that occur as a result of increased soil carbon dioxide concentration due to increased soil microbial respiration are as follows.

Below pH 8·0, soil exchangeable Ca^{2+}; ion species and calcite ($CaCO_3$) are in equilibrium and CO_3^{2-} is inactive. Above pH 8·0, CO_3^{2-} becomes highly reactive resulting in the formation of metal carbonates imposing limits on the solubilities of metal ions (Lindsay, 1979). Among these metal carbonates is calcite (equations 1 and 2). In alkaline soils the partial pressure of CO_2 gas is the controlling variable for calcite solubility (Lindsay, 1979). An increase in CO_2 results in a decrease in calcite solubility as equation (1) moves to the left.

$$CaCO_3\ (\text{calcite}) + {}^2H^+ \leftrightarrow Ca^{2+} CO_2(g) + 2H_2O \qquad (\text{Eqn } 1)$$

$$CO_2(g) + H_2O \leftrightarrow CO_3^{2-} \qquad (\text{Eqn } 2)$$

In addition to the formation of calcite due to an increase in CO_2 concentration, calcite can also be formed by the addition of urea in the form of rodent excretions (Ross, 1989):

$$CO(NH_2)_2(\text{urea}) + 3H_2O \leftrightarrow (NH_4)2CO_3(\text{ammonium carbonate}) + H_2O \qquad (\text{Eqn } 3)$$

Ammonium carbonate then dissociates in water:

$$(NH_4)2CO_3 + H_2O \leftrightarrow 2NH_{4^+} + HCO_{3^-} + OH^- \leftrightarrow 2NH_3 + CO_2 + 2H_2O \qquad (\text{Eqn } 4)$$

In equation 4 ammonia is volatalized and lost to the atmosphere in a gaseous state, and HCO_3^- and CO_2 will react with calcium ions to form calcite.