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THE EFFECT OF ANTS ON THE SOIL OF A SEMI-ARID SALTBUSH HABITAT

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SUMMARY

The estimated annual soil turnover by the ant community of an *Atriplex vesicaria* dominated shrub steppe in south-eastern Australia was 350-420 kg/ha/yr. Plant and animal material was brought to the nests by the ants and mixed with excavated soil, resulting in an increase in carbon, nitrogen and phosphorus in the surface soil about the nest site. These increases were similar to those found to occur as a result of litter deposition under perennial shrubs, and it is suggested that the ant community could contribute to the pattern of nutrient concentrations known in saltbush dominated vegetation.

RESUME

Les effets des Fourmis sur le sol d'un habitat salé semi-aride à végétation buissonnante

La quantité de sol remanié par l'ensemble des espèces de fourmis peuplant une steppe buissonnante dominée par *Atriplex vesicaria* dans le sud-est australien est estimé à 350-420 kg/ha/an. Le matériel animal et végétal rapporté au nid par les insectes est mélangé avec du sol excavé, provoquant ainsi une augmentation locale des teneurs en Carbone, Azote et Phosphore de la surface de celui-ci à l'emplacement du nid. Les augmentations de teneurs ainsi réalisées semblent du même ordre de grandeur que celles résultant du dépôt de litière sous les buissons pérennes. Ceci suggère que les diverses espèces de fourmis peuvent contribuer à distribuer les éléments nutritifs selon le type connu dans ces milieux salés à végétation buissonnante.

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INTRODUCTION

The distribution of shrubs in a perennial saltbush (*Atriplex vesicaria* Hew. ex Benth.) community shows a strong spatial pattern (ANDERSON, 1967). RIXON (1970) found that the vegetation pattern in such a plant community had an overriding effect on the rate of cycling of the major nutrients, there being localized intensities of cycling immediately beneath individual perennial shrubs. The surface soils in these regions had twice the potential capacity to supply mineral nitrogen as the soil from interbush areas.

Recently, it has been shown that another element of the saltbush ecosystem which could be involved in nutrient cycling, the ant community, was also strongly patterned (BRIESE and MACAULEY, 1977). These authors found a total of 195 colonies belonging to 22 species of ant in a 500 m^2 plot of *A. vesicaria* dominated vegetation. All species built nests in the soil, and exhibited two characteristics which could be important in soil relationships: they brought soil to the surface from lower horizons through their nest excavations, and many of the species brought considerable amounts of plant and animal material to the nest sites, where they formed local concentrations (BRIESE, 1974). Several studies have shown that large mound-building ants can influence both physical and chemical properties of the soil (BAXTER and HOLE, 1967; BUCHER and ZUCCARDI, 1967), and while none of the ants considered in the present study built large mounds, the cumulative action of many species that build relatively small nests could also be quite important.

This paper presents data collected to see if there were a *prima facie* case that the ant community in an *A. vesicaria* shrubland could significantly affect soil properties, and perhaps provide an auxilliary path to that described by RIXON (1970) for nutrient cycling.

METHODS

The Site

The site, 51 km north of Deniliquin in south western New South Wales, Australia, has been described in detail by BRIESE and MACAULEY (1977). The vegetation is a shrub-steppe formation dominated by the perennial saltbush, *A. vesicaria*, with a ground flora of numerous forbs and grasses. The main soil type is a heavy grey clay, finely textured, but showing weak development of horizons; the surface soil is a platy lighter clay with some quartz grit, while below this the clay becomes heavier and more blocky with the deeper subsoil containing some gypsum. It has poor physical qualities being relatively impermeable to water, and on drying cracks deeply (STACE *et al.*, 1968).

Physical Effects

To examine the role of ants in soil turnover, collections were made of the total soil brought to the surface by various ant species after periods of heavy rain during 1972. In addition, the mean nest density was calculated from the colony census of the 500 m^2

saltbush plot (BRIESE and MACAULEY, 1977). The amount of rain sufficient to stimulate extensive nest excavation was found to be approximately 15 mm or more, and the frequency of such rainfalls was estimated from meteorological records to be five to six times per year. From this information an estimate of annual soil turnover by the ants was made.

Effects on Soil Nutrient Levels

In August 1972 soil samples were taken from the nest sites of several species of seed-harvester ant (*Chelaner* spp. and *Pheidole* sp.A), the dominant non-harvester ant *Iridomyrmex* sp.A, and a large predatory ant *Odontomachus* sp. The samples consisted of 3 cm diameter cores, taken at two depths, 0-2 cm and 2-4 cm. Control samples were taken at similar depths at a distance of 30 cm away from the nest site in a randomly chosen direction. Deeper samples were not taken. The possible effect of ant modification of soil nutrients on plant composition and growth was the main consideration, and CHARLEY (1971) has pointed out that nutrition of perennial saltbush communities in New South Wales is determined mainly by the chemical status of surface soils. The samples were taken in interbush areas, to avoid any bias due to the accumulation of soil nutrients beneath bushes (RIXON, 1970).

The soil samples were analyzed for pH, carbon, phosphorus and nitrogen. Soil pH was determined from a 5 : 1 aqueous soil suspension. Total carbon was estimated gravimetrically as CO_2 following oxidation in a LECO high frequency induction furnace. Available phosphorus was determined on a Prototype auto-analyser following sodium bicarbonate extraction of the soil (COLWELL, 1965), and total nitrogen was similarly estimated after Kjeldahl digestion of the soil using selenium catalyst, by an automated distillation procedure (KEAY and MENAGE, 1969).

RESULTS

Physical Effects

During nest excavations, many abandoned galleries were found in the soil. They appeared to be structurally stable in these heavy grey clays, and although no measurements were taken, may facilitate the movement of air and water as the clays themselves are relatively impermeable (STACE *et al.*, 1968). Investigations by GREEN and ASKEW (1965) on English clay soils showed that permeability was greater in clays containing such galleries and pores, than in a clay soil without them. It should be noted though, that the soils at the study site are cracking clays, and these cracks might be the main method of aeration and infiltration. However, the ant burrowings extend to deeper levels than the cracking (beyond 60 cm) and provide further passages for air and water movement.

Through their burrowing, the ants bring 350 to 420 kg of soil per hectare to the surface from deeper horizons each year *(table I)*. In the present area soil is deposited in piles around the nest entrance, but these are not stable and are soon spread or compacted by wind and rain. The bulk density of the grey clays at the study site is 1.4 m/cc (STACE *et al.*, 1968) which means that the soil brought to the surface annually would form a uniform layer approximately 0.03 mm thick.

Table I. — Soil turnover by ants in the saltbush area.

Tableau I. — Remaniement du sol par les fourmis dans les aires salées et buissonnantes.

Species	Average soil excavated per colony per rainfall event (gm)	Colony density (No/m²)	Soil excavated per species (gm/m²)	Estimated † annual soil turnover (kg/ha)
Chelaner sp. A (*whitei* group)	49.5	0.018	0.9	45-54
Chelaner sp. B (*rothsteini* group)	30.0	0.004	0.1	5-6
Pheidole sp. A	17.5	0.084	1.5	75-90
Iridomyrmex sp. A	30.8	0.096	3.0	150-180
Large non-harvesters * (8 species)	18.3	0.070	1.3	65-78
Small ant species ** (10 species)	1.6	0.118	0.2	10-12
Total		0.39	7.0	350-420 kg/ha/yr

* Worker body length ⩾ 4 mm.
** Worker body length < 4 mm.
† Based on 5-6 periods of extensive excavation (see text for details).

Effect on Soil Nutrient Levels

The results of the soil analyses *(table II)*, show that there were only small variations in soil pH between samples, and no trend was found in the changes between ant nest and control sites. Gentry and Stiritz (1972) and Breckle (1971) also found that ants did not alter soil pH at their nest sites, though studies on Polish meadow ants suggested that changes in pH observed there were probably dependent on local physical and chemical properties of the soil (Petal, 1978). In the three harvester species samples, when comparisons were made with the paired controls, carbon concentrations in the surface layer increased by 1.3 to 2.3 times, phosphorus by 3.3 to 12.7 times and nitrogen by 1.4 to 1.9 times. The amount of these minerals generally declined at the sub-surface layers of the ant nest area. The accumulation of such nutrients in the surface layer is most likely due to presence of the waste plant material such as seed husks and leaf and twig fragments which are discarded about the nest entrance, and perhaps to some extent to metabolic waste products af the ants themselves. The non-harvesting ant *Iridomyrmex* sp.A which does not deposit waste material about the nest, did not show nutrient concentrations, and in fact levels of all three minerals decreased, possibly due to the deposition of soil from lower horizons during nest excavation. The predatory ant *Odontomachus* sp. however does discard fragments of arthropod prey about its nest, as well as using leaf and twig matter to decorate the site. Its nest-sites showed a twofold increase in carbon, phosphorus increased by 3.3 times and nitrogen by 1.5 times, though only at the surface layer.

Table II. — Soil nutrient analyses of single ant nest and control sites compared with that of soil under *Atriplex vesicaria* shrubs (see text for details).

Tableau II. — Analyses des éléments nutritifs du sol de sites avec 1 seul nid et de sites témoins comparés aux éléments nutritifs du sol sous des buissons d'*Atriplex vesicaria.*

Species		pH		Total C (%)		Total N (%)		Available P (ppm)	
		0-2 cm	2-4 cm	0-2 cm	2-4 cm	0-2 cm	2-4 cm	0-2 cm	2-4 cm
Chelaner sp. A	Nest	7.23	6.65	1.53	1.12	0.17	0.14	40.1	12.9
(*whitei* group)	Control	6.85	7.04	0.82	0.95	0.11	0.11	12.0	6.0
Chelaner sp. A *	Nest	6.84	6.69	2.81	1.59	0.26	0.17	103.4	30.6
(*whitei* group)	Control	6.74	6.91	1.20	1.01	0.14	0.13	16.8	10.6
Chelaner sp. B	Nest	5.92	6.78	1.44	1.53	0.18	0.17	209.0	118.3
(*rothsteini* group)	Control	6.15	7.16	1.12	0.61	0.13	0.08	16.5	4.8
Pheidole sp. A	Nest	6.60	6.51	1.81	1.54	0.20	0.16	39.7	16.9
	Control	6.49	7.15	1.19	1.15	0.13	0.12	7.4	4.6
Iridomyrmex sp. A	Nest	6.57	6.71	0.52	0.52	0.08	0.09	10.3	6.0
	Control	6.80	6.90	0.94	0.92	0.13	0.11	10.8	7.3
Odontomachus sp.	Nest	7.16	7.32	2.47	1.38	0.20	0.15	20.8	10.0
	Control	7.39	6.99	1.06	1.44	0.13	0.16	6.2	13.9
Atriplex **	Under bush	7.49		1.230		0.126		No data	
vesicaria	Between bush	7.48		0.713		0.086			

* Nest in grassland site, where *A. vesicaria* has been removed due to overgrazing by sheep.
** Data from Rixon (1970), for top 8 cm of soil.

DISCUSSION

As neither past changes in the density and composition of the ant community nor the age of the soils at the study site are known, it is difficult to speculate on the pedological significance of the ant fauna. Comparison with results from other studies, however, does provide some insight. The turnover rate of soil (0.03 mm/year) attributed to the ants studied here is similar to that found for various mound building termites and ants. Williams (1968) and Lee and Wood (1971) estimated rates of soil accumulation for termites ranging from 0.0125 to 0.40 mm/year, and Holt *et al.* (1980) have suggested that, based on present day turnover rates of 0.025-0.05 mm/year, the 20 cm thick A horizons of soils at their study sites could have accumulated from the erosional degradation of termite mounds over the past 8000 years. Bucher and Zuccardi (1967) calculated that the ant *Atta vollenweideri* Forel, which builds large mounds, brought up soil at the rate of 0.085 mm/year, and the data of Baxter and Hole (1967) gave a rate of 0.1 mm/year for the mound-building ant *Formica cinerea* Emery. At this rate of soil turnover, Baxter and Hole suggested the ants were a significant factor in the formation of the prairie soil in which they occurred. The only ant that built large mounds in the present study (though not present in the actual sample quadrat) was *Iridomyrmex purpureus* (SMITH), but the density and turnover of nests of this species appear to be too low for it to have any significant effect on pedogenesis (GREENSLADE, 1974). The 22 species of small-nest building ants have a much greater density and a higher colony turnover rate, but, as it stands, their importance in actually renewing the soil surface from lower horizons cannot be accurately assessed. However, the estimated accumulation of 350 to 420 kg of soil per hectare by ants in the present study is comparable to the estimate of 600 kg/ha for a community of ants in North America, which contributed to the development of a podzolic soil profile (LYFORD, 1963).

From a more immediate viewpoint, though, the important finding is that the ants concentrate plant and animal material around the nest site, and this rapidly becomes mixed with the excavated soil. Nutrients such as mineral nitrogen tend to remain within a decomposing particle unless it is incorporated in the soil (RIXON, 1970), so that this mixing of soil and organic matter by the ants contributes to the release of nutrients. This can be seen in the higher levels of nitrogen, phosphorus and carbon found in the nest areas. The most important of these is probably nitrogen, as BEADLE and TCHAN (1955) and CHARLEY (1971) found it to be the most limiting element in the nutrition of arid zone communities, and one which in saltbush systems exercises primary control over soil fertility.

Such concentration of nutrients in the nest area appears to be a widespread phenomenon in ants, as it has also been reported for a range of species by PETAL *et al.* (1970), CZERWINSKI *et al.* (1969), BRECKLE (1971), GENTRY and STIRITZ (1972). These studies have all dealt with mound building ants and in these cases they have been shown to modify vegetation composition and growth on and about the nest site. As none of the ants examined built large nest mounds, no obvious differences in plant composition were observed. However, GENTRY and STIRITZ (1972) showed that plant growth was significantly greater in soil from ant nests than from control areas, so that it is quite likely that the plant community derives benefit from nutrient concentration by the ants. Although the nests occupied only a small proportion of the total surface area (< 1 %), they probably represent favourable microsites for plant establishment. DAVIDSON and MORTON (in press) found that some non-harvester ant species influenced plant dispersion by removing the seeds of myrmecochores to their nest sites, which contained higher nutrient levels. While myrmecochory was not observed in the present study, the collection of seeds by the harvester ants would increase the probability of germination on nest sites, and in several instances young seedlings of *A. vesicaria* were found growing at such locations. The initial growth and survival of these is probably enhanced by the ant-mediated nutrient enrichment of the soil.

The ants therefore seem to play a part in the cycling of nutrients. These are derived from two sources; plant material, which is cycled mainly by the harvester ants; and animal material, which moves mainly through the non-harvesters. As indicated above, non-harvester ants may contribute to the recycling of plant material by activities such as nest decoration and myrmecochory, while harvester ants invariably supplement their diet with animal matter which would form part of the nutrient pool influenced by them. In the present study, the harvester ants, whose forage consisted of over 90 % seeds and their associated fruiting bodies (BRIESE and MACAULEY, 1981), probably affect the horizontal distribution of nutrients by removing plant material from under the saltbush and depositing it elesewhere. The increases in mineral levels around ant nests are of the same order of magnitude as that found under *A. vesicaria* shrubs as a result of litter deposition *(table II)*. RIXON (1970) and CHARLEY (1971) have pointed out that the concentrations of nutrients which occur beneath the shrubs have resulted in a mineral mosaic. By concentrating nutrients at other sites the ants contribute to the pattern of this mineral mosaic and hence may influence overall community nutrition.

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