



ELSEVIER

Soil Biology & Biochemistry 36 (2004) 797–804

Soil Biology &
Biochemistry

www.elsevier.com/locate/soilbio

Development of harvester ant colonies alters soil chemistry

Diane Wagner^{a,*}, Jeremy B. Jones^a, Deborah M. Gordon^b

^aDepartment of Biology and Wildlife, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-7000, USA

^bDepartment of Biological Sciences, Stanford University, Stanford, CA 94305, USA

Received 5 June 2003; received in revised form 20 November 2003; accepted 13 January 2004

Abstract

Nests of the harvester ant *Pogonomyrmex barbatus* typically contain higher concentrations of organic matter, nitrogen and phosphorus than surrounding soils. The difference between nest soils and surrounding soils is due, at least in part, to ant foraging behavior. Ants retrieve seeds from the environment and concentrate seed nutrients in the vicinity of the nest. But elevated nutrient concentrations in nests may also reflect initial conditions, if nest-founding queens are more likely to choose or survive in soils with high organic matter and nutrient content. By measuring the soil nutrient content and surface area of *P. barbatus* nests ranging from 1 to 20 years of age over two sampling periods, we (a) investigated the relationship between nest soil characteristics and colony age, and (b) tested the hypothesis that nest soils differ from background soils when nests are established. Nest surface area increased with colony age until age 5–10 years and leveled off thereafter. Relative to surrounding soils, concentrations of total nitrogen and orthophosphate increased, and pH decreased, with increasing colony age. The difference between nest soils and surrounding soils in total nitrogen, nitrate, and ammonium concentrations also increased over a 9-month interval between sampling bouts. Extrapolations from regressions of soil chemical variables against colony age provided no evidence that nest founding and early colony survival is more likely to occur in high-nutrient soils.

© 2004 Elsevier Ltd. All rights reserved.

Keywords: Ant colony age; Arid lands; Formicidae; Heterogeneity; Nitrogen

1. Introduction

When sufficient water is available, nitrogen limits primary productivity in North American deserts (West and Skujins, 1978; Nobel et al., 1987; Fisher et al., 1988; Sharifi et al., 1988; Lathja and Klein, 1988; Lathja and Whitford, 1989; Mun and Whitford, 1989). Total nitrogen storage is relatively low in deserts compared with other life zones (Post et al., 1985). Soil organic matter and mineral nutrients in North American deserts tend to be heterogenous, with high concentrations found under shrubs and near the nesting sites of central-place foraging animals (Garcia-Moya and McKell, 1970; Charley and West, 1975; Santos et al., 1978; Whitford, 1988; Schlesinger et al., 1996). The distribution of nitrogen-containing compounds, as well as other nutrients, can have important implications for plant community composition and dynamics (Schlesinger et al., 1990). Microsites with high-nutrient concentrations can support different species than lower-nutrient interspaces

(Grubb, 1977; Carlson and Whitford, 1991; Dean and Yeaton, 1993; Whitford and DiMarco, 1995; Rissing, 1986; Brown and Human, 1997; Folgarait et al., 2002). In addition, some plant species growing in high-nutrient microsites attain higher growth rates and reproductive success than those growing in interspaces (Rissing, 1986; Anderson, 1988; Whitford, 1988; Brown and Human, 1997).

Ant nests contribute to soil nutrient heterogeneity in many ecosystems. The soils near ant nests often contain higher concentrations of organic matter and mineral forms of nitrogen and phosphorus than soils collected off the nest mound (reviewed by Petal, 1978; Beattie, 1985; Folgarait, 1998; MacMahon et al., 2000). Nutrient cycling rates, as well as standing stocks, can be altered in ant nest soils. For example, nitrogen and carbon mineralization rates are often higher in ant nest soils than surrounding soils (Wagner, 1997; Petal, 1998; Dauber and Wolters, 2000; Dauber et al., 2001). In addition, elements of the soil biota have been reported to be more abundant and functionally diverse in ant nests (Wagner et al., 1997; Dauber and Wolters, 2000).

* Corresponding author. Fax: +1-907-474-7666.

E-mail address: ffdwl1@uaf.edu (D. Wagner).

The difference between ant nest soil and surrounding soil probably results, at least in part, from ant foraging behavior. Food items are collected throughout the foraging range of the colony, but debris and waste products are deposited near the nest entrance, thereby concentrating these materials in space. Harvester ants (*Pogonomyrmex barbatus*) forage from 1 to 20 m from the nest (Gordon, 1992a) but deposit the seed chaff and other debris onto the surface of their nest mound, <2 m from the nest entrance. As young colonies grow, they must collect more food and hence create more waste, so colony effects on both the quantity and the quality of soil should intensify. In areas with low and periodic rainfall, the rate at which even moderately sized colonies deposit debris may exceed rates of decomposition and nutrient dispersion from the nest mound (Strojan et al., 1987).

Differences between ant nests and surrounding soils might also stem, in part, from initial conditions. Harvester ant colonies reproduce each summer, when winged reproductive males and females meet in a mating swarm. Newly mated females fly some distance from the mating site, then search along the ground for a place to dig a nest. Soils in which queens choose to nest may have different soil characteristics than areas not so chosen. Once a site is chosen, soil properties may contribute to patterns of early survivorship. Studies of the microdistribution of sympatric populations of the harvester ant species *P. barbatus* and *P. rugosus* support segregation based on soil particle size, with *P. barbatus* occupying soils higher in clay and moisture holding-capacity (Johnson, 1998; 2000a,b). An association between successful colony founding and soil nutrient concentration might arise indirectly, from a correlation between nutrient content and soil texture, or directly, if soils high in organic matter are easier to excavate or contain more water.

Although ant behavior likely enhances soil nutrient concentrations, the dynamics of this process have never been quantified. Ant species associated with high soil nutrient concentrations typically have long residence times (Hughes, 1990), complicating studies of soil change over time. Harvester ant colonies, for example, can occupy the same nest for 20 years (Gordon, 1991, 1992a,b). In addition, the relative contributions of nutrient accumulation and initial conditions to soil nutrient enrichment in ant nests have never previous been examined. In this study, we analyze nest soils from a harvester ant population in which the ages of all colonies are known. We compare the soil of ant nests ranging in age from 1 to 20 years, collected over two sampling years, to investigate changes in soil chemistry as harvester ant colonies age and grow. Specifically, we address two questions. (1) Does the degree to which ant nest soils are enriched relative to surrounding soils increase as colonies age? (2) Are the areas where ants found successful nests enriched relative to surrounding soils prior to ant colonization?

2. Materials and methods

2.1. Study site and species

P. barbatus is a large, seed-eating ant species that occurs throughout south-central North America (Cole, 1968; Johnson, 2000a,b). Each colony is founded by a single queen that may live 15–20 years (Gordon, 1991). Worker number increases until about 5–6 years of age, leveling off at approximately 10,000–12,000 workers (MacKay, 1981; Gordon, 1992a,b). When colonies mature, they begin to produce reproductive males and females. In general, the number of reproductive individuals produced increases as a colony ages, but the numbers of reproductives a colony produces each year (≤ 300 , Wagner and Gordon, 1999) is small relative to worker numbers. Workers live about a year (Gordon and Hölldobler, 1987), so on average a mature colony must gather enough seeds to produce $\geq 10,000$ new workers, plus reproductives, annually.

Nests appear as large disks (≤ 2 m diameter) or shallow mounds surrounding the nest entrance. Workers kill existing plants and clip seedlings on the mound, preventing plants from growing on nest sites while the colony is alive. Onto the surface of the mound, workers place debris, excavated soil, and gravel retrieved from surrounding areas. Ants deposit seed husks and other organic debris onto the surface of the nest mound in small piles, or middens, that shift in position throughout the active season. The edge of the mound is typically clearly delineated by the edge of the gravel coating. Only about 10% of colonies 2 years or older relocate their nests per year, and the same colonies tend to move year after year (Gordon, 1992b).

We studied a population of *P. barbatus* in an arid grassland habitat near Rodeo, New Mexico (elevation ~ 1200 m). Lying at the intersection of the Chihuahuan and Sonoran deserts, the area receives much of its precipitation in monsoon rains that typically fall in July and August. At the time we conducted the study, cattle grazed the site. Vegetation is described in Gordon (1993). The density of *P. barbatus* on the study site was approximately 30 colonies/ha (Gordon and Kulig, 1996).

2.2. Sampling design

P. barbatus colonies on the study site have been individually labeled, mapped, and tracked in annual censuses since 1985 (techniques described in Gordon, 1991, 1992a). The ages and relocation histories of all colonies were established from the census data. From the set of all colonies that had never moved from their natal site, we sampled 3 colonies each from two-year age groups ranging from 2–3 to 18–19 years (total $n = 27$ colonies). One of the colonies was later determined to have died in 1998, and was discarded from the data set. We sampled colonies in October, 1999, and July, 2000. At each colony, we collected three replicate soil cores (7 cm wide \times 10 cm deep) from within the nest mound

and from a paired, control site 3 m away. On ant nests, all cores were taken within the periphery of the gravel-covered disc, and areas on and off midden piles were sampled in a stratified random fashion. Control site soils were taken from the appointed site regardless of whether there was vegetation growing on the sampling site or not, although most of the time the control sites were bare. Soil samples were placed in plastic bags and transported on ice to the laboratory. Nest surface area was estimated from the maximum and minimum width of each nest. Between the two sampling dates, four of the original colonies died or moved.

2.3. Soil chemical and physical measurements

Replicate soil cores from each sampling site were mixed and sieved (2 mm mesh). Ammonium and nitrate were extracted from 2 subsamples per sample in 2-M KCl (Black et al., 1969) and phosphorus extracted in 0.03-M NH_4F and 0.025-M HCl solution (Bray and Kurtz, 1945). To estimate total nitrogen, 2 subsamples per sample were digested using a standard Kjeldahl procedure (Bremner, 1996). Concentrations of total Kjeldahl nitrogen, $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and $\text{PO}_4\text{-P}$ were determined colorimetrically using an Alpkem FS3000 automated ion analyzer (OI Analytical, College Station, TX). All soil chemistry measurements were adjusted for soil moisture content. We measured water content as the proportion of mass lost after drying at 105 °C for 48 h (Jarrell et al., 1999), and organic matter as the mass lost after combustion at 400 °C for 16 h (Nelson and Sommers, 1996). We measured pH in a one-to-one solution of soil and water using a digital pH meter.

We calculated soil nutrient storage on an areal basis by multiplying soil nutrient concentrations by sample depth, bulk density, and the proportion of soil (<2 mm) mass to whole sample mass. Bulk density was measured for 10 ant nests and 10 surrounding sites just outside the perimeter of the study plot, to minimize disturbance to labeled colonies. On ant nests, the location of each sample was chosen haphazardly within the periphery of the gravel-covered disc. Bulk density was measured using the excavation method (Elliot et al., 1999). Briefly, we dug a cylindrical hole approximately 7 cm wide by 10 cm deep, retaining the excavated soil to determine its dry weight. We then refilled the hole with a measured volume of sand.

2.4. Data analysis

We tested for overall differences in soil chemistry between ant nest soils and surrounding soils by averaging the measurement for each chemical component at each sampling site across the two sampling dates and then applying one-tailed paired *t*-tests. We based predictions for the one-tailed tests on a previous study of nest soil chemistry at this site (Wagner et al., 1997). In all subsequent analyses, described below, we tested the effect of ant nests on soil enrichment, which we define as the difference between each

ant nest soil measurement and the paired soil measurement taken 3 m away.

We tested how ant nest size and soil quality change over time using two approaches. First, we regressed the variable of interest (nest surface area or average enrichment of organic matter, total N, mineral N, orthophosphate, pH) against the age of the colony in 1999. Since worker number plateaus when a colony matures, we predicted that a colony's effect on soil might also level off as it ages, perhaps even decreasing at very old age. We therefore inspected the fit of the data to both linear and nonlinear (exponential rise to maximum and 2nd order polynomial) models, and report the results of the model that explained the greatest amount of variation in nest size or soil enrichment. Second, we tested whether the degree of soil enrichment increased over the 9-month interval between repeated samplings, using one-tailed paired *t*-tests.

If queens tend to found nests or survive better in patches containing a high concentration of soil organic matter or mineral nutrients, then at the time of nest founding the difference between nest soil and surrounding soil in the relevant soil concentration(s) should be positive. If, on the other hand, queen site choice and survival is independent of soil chemistry, then the difference between nest and surrounding soils at nest founding should be zero. We tested the hypothesis that queens select or survive better in patches with high-nutrient content by determining whether the *y*-intercept of each linear regression of soil enrichment against colony age was significantly greater than zero.

Previous work at this site revealed that concentrations of nitrate and ammonium are highly correlated. Therefore, we used the sum of nitrate and ammonium concentrations as a single measure of mineral nitrogen storage for statistical comparisons. To control the type-I error rate within each set of related statistical tests, we used a sequential Bonferroni procedure (Rice, 1989).

3. Results

Ant nest soils were enriched in organic matter, total N, nitrate, ammonium, and orthophosphate relative to paired soils collected 3 m away (Table 1). The mineral N concentration was 600–800% higher, and phosphorus 200–300% higher, in ant nests than surrounding soils. Ant nests contained 25–35% higher concentrations of organic matter, and 50–90% higher concentrations of total N, than surrounding soils. Ant nest soils were more acidic than surrounding soils (Table 1). There was no difference in soil water content between ant nest and control soils.

Per unit area, ant nests stored only slightly (6%) more organic matter than surrounding soils, but storage of total N (140%), mineral N (460%), and orthophosphate (215%) was considerably higher in ant nests than in surrounding soils. Because ants tend to place gravel on the nest mound, ant nest soils contained a lower ratio of soil to whole sample

Table 1
Chemical characteristics of soil from 22 *P. barbatus* nest mounds and control sites, sampled in two years

Component	Concentrations ($\mu\text{g g}^{-1}$ unless noted) (mean \pm SE)				<i>P</i> -value	Area estimates (g m^{-2}) (mean \pm $\text{SD}_{\text{pooled}}$)	
	1999		2000			Ant nest	Control
	Ant nest	Control	Ant nest	Control			
Organic matter ^a	22.2 \pm 1.0	17.8 \pm 1.0	20.8 \pm 1.0	15.4 \pm 0.8	***	2290.4 \pm 4.1	2158.8 \pm 3.1
Total nitrogen ^b	585.2 \pm 38.0	388.7 \pm 25.3	693.3 \pm 52.2	355.7 \pm 24.6	***	68.1 \pm 163.1	48.4 \pm 81.6
NO ₃ -N	48.0 \pm 12.6	3.6 \pm 1.0	98.3 \pm 16.5	13.9 \pm 2.8	***	7.8 \pm 40.6	1.2 \pm 5.1
NH ₄ -N	23.0 \pm 5.7	5.2 \pm 2.1	51.7 \pm 6.8	7.9 \pm 1.2	***	4.0 \pm 18.9	0.9 \pm 4.2
NO ₃ -N + NH ₄ -N	71.0 \pm 17.1	8.8 \pm 2.3	150 \pm 20.8	23.4 \pm 3.8	***	11.8 \pm 56.4	2.1 \pm 7.8
PO ₄ -P	25.5 \pm 3.6	10.0 \pm 0.8	39.3 \pm 5.1	12.7 \pm 0.9	***	3.5 \pm 3.2	1.1 \pm 2.4
pH	7.0 \pm 0.2	7.5 \pm 0.2	6.3 \pm 0.2	7.1 \pm 0.2	***		
Water ^c	1.4 \pm 0.1	1.7 \pm .2	2.6 \pm 0.1	2.1 \pm 0.1	n.s.		

Soil chemistry variables for ant nest and control soils were averaged across years at each sampling site and compared with paired *t*-tests. ****P* < 0.0001; n.s. *P* > 0.05.

^a Concentration units mg g^{-1} .

^b Measured as total Kjeldahl N.

^c %.

mass (ant nest 0.67 ± 0.03 SE; surrounding soil 0.85 ± 0.03 ; $t = -5.4$, d.f. = 9, $P < 0.001$). The bulk density of ant nest and surrounding soils was similar (overall mean 1.56 g/cm^3 , $t = 0.8$, d.f. = 9, $P = 0.4$).

Nest size measurements indicate that nest size increases in early life, slowing and perhaps shrinking thereafter (Fig. 1). The relationship between colony age and average nest surface area was better described by nonlinear models ($R^2 > 0.33$, $F > 6$, $P \leq 0.004$) than by a linear model ($R^2 = 0.22$, $F_{1,21} = 5.9$, $P = 0.02$). A polynomial model, which predicts a slight decrease in nest size at old age, explained slightly more of the variance in nest size than a saturating, exponential model (polynomial $R^2 = 0.38$, exponential $R^2 = 0.33$). The average surface area of the same nests measured 9 months apart increased from 1.57 m^2 (0.2 SE) to 1.77 m^2 (0.2 SE) (paired $t = 3.2$, d.f. = 18, $P = 0.003$).

In contrast to nest surface area, relationships between colony age and soil chemistry variables were not better described by a nonlinear model. For simplicity, we present the results of linear regressions. Relationships between colony age and soil chemistry variables, expressed as the difference between ant nest soils and paired, surrounding soils, are shown in Fig. 2. Inspection of residuals indicated that, for some variables, the variance was larger at old colony ages. In these cases, the dependent variable was log-transformed and the regression analysis repeated. In no case did transformation qualitatively alter the conclusions. Age was significantly, positively related to enrichment of total N and orthophosphate (TKN: Fig. 2A, $F_{1,21} = 12.6$, $P = 0.002$, $R^2 = 0.37$; PO₄-P: Fig. 2D, $F_{1,21} = 12.0$, $P = 0.002$, $R^2 = 0.36$). There was a tendency for soils of older ant nests to contain higher concentrations of mineral N and organic matter as well, but the relationships were not significant (mineral N: Fig. 2B, $F_{1,21} = 3.6$, $P = 0.07$,

$R^2 = 0.14$; organic matter: Fig. 2C $F_{1,21} = 3.2$, $P = 0.08$, $R^2 = 0.13$). Soil pH decreased significantly with colony age (Fig. 2E, $F_{1,21} = 8.1$, $P = 0.01$, $R^2 = 0.29$).

Ant nest soils became significantly more enriched in total N and mineral N during the 9-month intersampling period (Fig. 3A,B; $t \geq 3.0$, d.f. = 22, $P \leq 0.002$). Orthophosphate enrichment also increased over time, but the change was not significant after Bonferroni adjustments (Fig. 3D; $t = 2.22$, d.f. = 22, $P = 0.03$). Changes in organic matter and pH over the interval were not significant ($t \leq 1.3$, d.f. = 22, $P > 0.2$), although trends were qualitatively similar to the regressions on colony age: organic matter increased slightly, while pH decreased (Fig. 3C,E). Concentrations of mineral nutrients in control soils also tended to increase over the 9-month period (Table 1).

We found no evidence that soil chemistry of harvester ant nests differed from surrounding soils at the time of colony

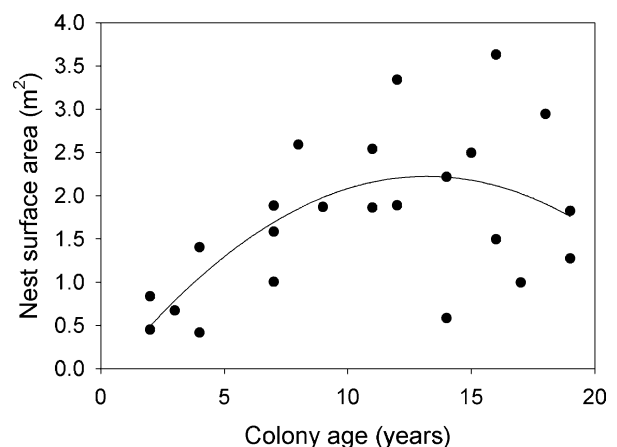


Fig. 1. The relationship between average harvester ant nest surface area (m^2) and years of colony age. The curve illustrates the best fit model ($y = -0.18 + 0.36x - 0.014x^2$, $F_{1,21} = 6.1$, $P = 0.008$, $R^2 = 0.38$).

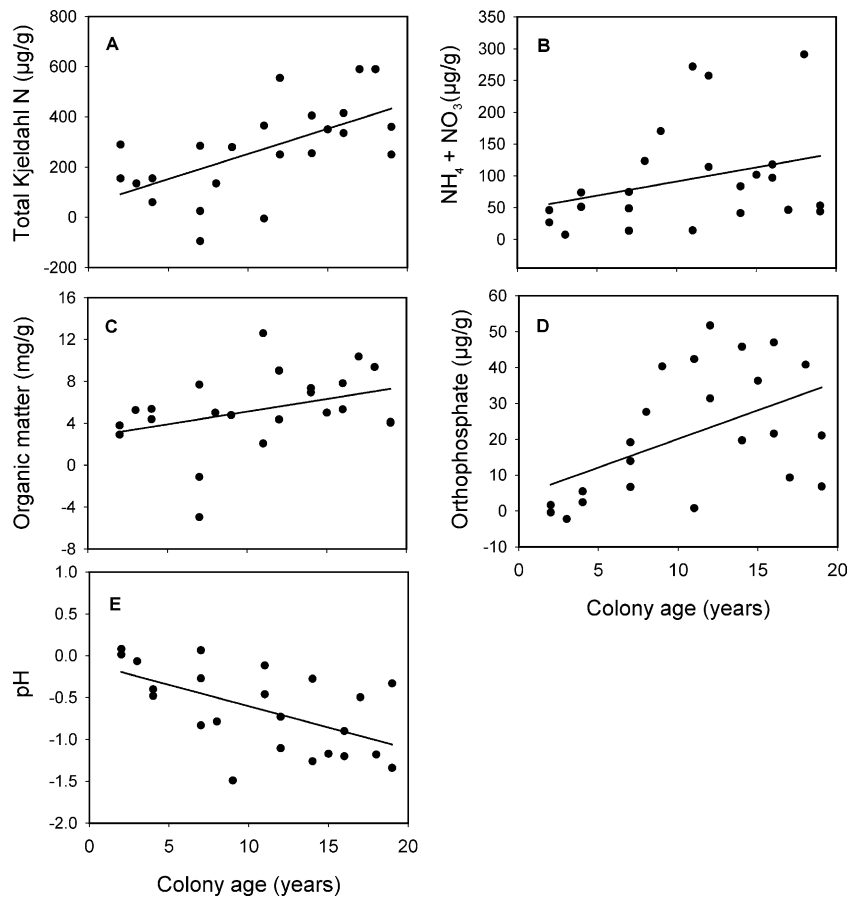


Fig. 2. The relationship between soil enrichment and years of colony age. The y-axis of each graph reports the difference between ant nest soil and paired, surrounding soil.

initiation. The y-intercepts of all linear functions describing changes in soil enrichment with colony age were not significantly different from zero (Fig. 2, $P > 0.05$).

4. Discussion

The effects of harvester ant colonies on soils intensify as colonies age. Relative to soils surrounding the nest, concentrations of soil total N and orthophosphate in ant nest soils were positively related to colony age, while pH was negatively related to age. Repeated sampling of the same sites showed that the difference between ant nest soils and surrounding soils in total N, mineral N, and orthophosphate concentrations (but not organic matter) increased over a 9-month period.

The actual 9-month increase in soil nutrient enrichment we observed was higher by a factor of 6–13 than that predicted by regressions of soil enrichment against colony age. This discrepancy might be explained by seasonal or interannual variability in climate and rainfall. Seasonal variation in rainfall patterns drive changes in food availability and ant foraging behavior. In this case, we think that typical seasonal changes are unlikely to provide a satisfactory explanation for the discrepancy between

observed and predicted changes in nutrient buildup. Harvester ants forage intensively during and after the summer rains. In October, colonies should have accumulated debris throughout the summer monsoon period, yet concentrations of organic matter and other soil nutrients were lower in October than the following July, when the rains were just starting. The seeds collected by harvester ants are a mixture of seeds produced and dispersed in previous seasons, rather than the product of vegetation currently growing on the site (Gordon, 1993). This, in addition to the ants' tendency to store seeds in the nest, probably buffers seasonal changes in the quantity and quality of seed debris entering nest soils. Year-to-year variation in rainfall may offer a better explanation. Severe flooding in the summer of 1999 (Western Regional Climate Center data, www.wrcc.dri.edu, station #026716) may have increased water-borne transport of nest debris and soluble nutrients, leading to abnormally low measurements of soil components in ant nests relative to surrounding soils during that year. In contrast, the area received lower-than-normal rainfall in the summer and early autumn of 2000.

As colonies age, they also affect a greater quantity of soil. Our data suggest that the surface area of the nest increases for about the first 5–10 years after colony founding, followed by a period of leveling off. This suggests that

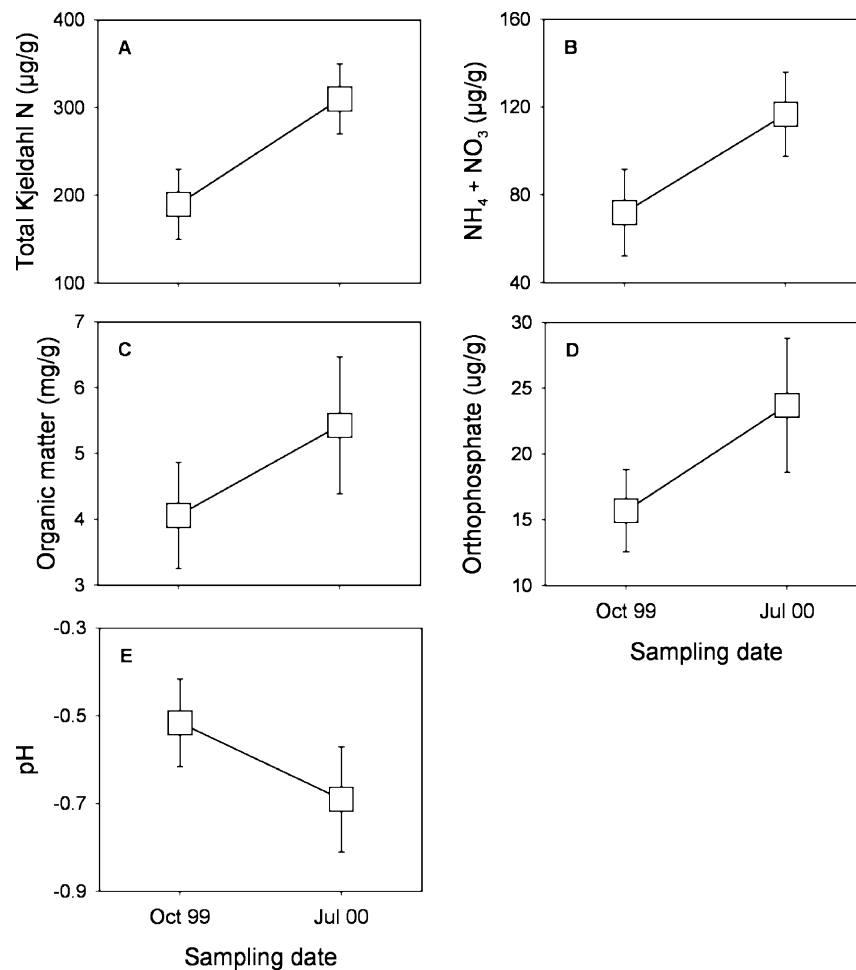


Fig. 3. Change over time in soil enrichment by harvester ant colonies. Enrichment (y-axis) is defined as the difference between ant nest soil and paired, surrounding soil.

the area actively maintained by ants increases in size until, and perhaps beyond, the point at which worker number stabilizes (Gordon, 1992a). The nests of very old colonies may shrink in size, although high variation among old colonies makes this conclusion speculative. A decrease in nest surface area by old colonies might result from decreasing worker numbers, itself a result of a dead or senescent queen, or from a general age-related slowdown in midden work and foraging.

Accumulation of soil nutrients in ant nest soils indicates that the annual rate of nutrient input by ants exceeds the rate of loss from nest soils. Inputs of organic matter to ant nests are a direct result of ant behavior. As central-place foragers, harvester ants sweep organic matter from surrounding areas and concentrate it in and around the nest. As granivores, ants selectively retrieve high-protein plant tissues from the pool of litter present on the landscape (Mattson, 1980), thus disproportionately concentrating N in space. Inside the nest, seed hulls are removed and discarded directly on the surface of the nest mound, while the N- and P-rich seed kernels are consumed by ants. Some portion of this ingested tissue enters the nest soil as feces. An additional portion of

ingested C and N enters the soil as urate. These detrital compounds are then available to other components of the soil food web.

Substances may be lost from ant mounds through several routes. First, organic debris may be lost from the mound by active or passive transport. When ants die, their bodies are typically carried from the nest and placed at the periphery of the mound. Nutrients lost in the form of dead ants may be an important source of nutrient export from the mound, as scavengers often remove carcasses from the vicinity of the nest before they decompose (pers. obs.). Passive transport of materials by wind and water also removes organic debris from the mound. Second, organic materials may be transformed, by ants and other soil organisms, and lost from nest soils in mineral form. C is lost at high rates relative to background soils from the nest soil pool through respiration by ants and decomposers (Dauber and Wolters, 2000; Dauber et al., 2001). While bacteria and fungi are apparently no more abundant in *P. barbatus* nest soils than in surrounding soils (Wagner et al., 1997), ant colony respiration may account for a good deal of carbon loss. Using metabolic rates estimated for

P. rugosus at 25 °C (Lighton and Bartholomew, 1988) and an average fresh mass of 10–12 mg per ant, we estimate that a mature *P. barbatus* colony of 10,000–12,000 ants would be expected to respire roughly 60–90 g of C per year. To our knowledge, rates of organic matter decomposition in ant nest soils have never been reported, but N mineralization in ant nest soils can occur at high rates relative to surrounding soils in this habitat (Wagner, 1997). Regressions of total and mineral N against age, however, suggest that total nitrogen accumulates in nest soils at a higher rate over the span of years than mineral N. It is common to find a resistant layer of calcium carbonate under the surface soil at this site, which probably limits nitrate losses due to leaching, but nitrate may be dispersed into the surrounding area through overland flow during heavy summer rains. Other potential losses of mineral N include ammonia volatilization, denitrification, and uptake by plants. Although ants remove seedlings from the mound, mound soils may be penetrated by the roots of nearby plants. Taken together, these potential loss rates appear to be lower than rates of input by ants.

On the spatial scale of meters, we found no evidence that successful nest establishment is associated with high soil nutrient concentrations. Extrapolating from the empirical relationship between soil chemistry enrichment and colony age, the chemistry of newly initiated nest soils is indistinguishable from surrounding soils. We emphasize that this is a weak test, given the high variance in soil nutrient concentrations around the regression lines. However, the results suggest that differences between ant nest and surrounding soils result from the combined activity of ant workers, rather than a combination of initial conditions and subsequent worker modification.

Our results indicate that the age structure of the harvester ant population, as well as its density, can have important implications for the spatial distribution of soil nutrients in deserts. The nests of old colonies are particularly rich in N- and P-containing compounds, and contribute heavily to heterogeneity in soil nutrient distribution. When old colonies die, nutrient-rich nest microsites become available for colonization by the plant community.

Acknowledgements

We are grateful to Aimee Classen, Bryan Harper, Won Lee, Chris Starkweather, Amber Steed, Michael Virata, and P. Vongsamphanh, and especially Joshua Hoines, for assistance with data collection. Many thanks to Aimee Classen and Nathan Sanders for comments on the manuscript. The staff of the Southwestern Research Station of the American Museum of Natural History provided support. The study was funded by USDA grant #99-35101-7834 to DW and JBJ.

References

- Andersen, A.N., 1988. Soil of the nest-mound of the seed-dispersing ant *Aphaenogaster longiceps*, enhances seedling growth. *Aust. J. Ecol.* 13, 469–471.
- Beattie, A.J., 1985. *The Evolutionary Ecology of Ant-plant Mutualisms*. Cambridge University Press, Cambridge.
- Black, C.A., Evans, D.D., Ensminger, L.E., White, J.L., Clark, F.E., 1969. *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties*, vol. 9. American Society of Agronomy, Madison.
- Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic and available forms of phosphorus in soils. *Soil Sci.* 59, 39–45.
- Bremner, J.M., 1996. Nitrogen-total. In: Sparks, D.L. (Ed.), *Methods of Soil Analysis. Part 3. Chemical Methods*. Soil Science Society of America, Madison, pp. 1085–1121.
- Brown, M.J.F., Human, K.G., 1997. Effects of harvester ants on plant species distribution and abundance in a serpentine grassland. *Oecologia* 112, 237–243.
- Carlson, S.R., Whitford, W.G., 1991. Ant mound influence on vegetation and soils in a semiarid mountain ecosystem. *Am. Midland Nat.* 126, 125–139.
- Charley, J.L., West, N.E., 1975. Plant-induced soil chemical patterns in some shrub dominated semi-desert ecosystems of Utah. *J. Ecol.* 63, 945–964.
- Cole, A.C. Jr., 1968. *Pogonomyrmex* harvester ants: a study of the genus in North America. The University of Tennessee Press, Knoxville.
- Dauber, J., Wolters, V., 2000. Microbial activity and functional diversity in the mounds of three different ant species. *Soil Biol. Biochem.* 32, 93–99.
- Dauber, J., Schroeter, D., Wolters, V., 2001. Species specific effects of ants on microbial activity and N-availability in the soil of an old-field. *Eur. J. Soil Biol.* 37, 259–261.
- 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. *J. Arid Environ.* 25, 249–260.
- Elliott, E.T., Heil, J.W., Kelly, E.F., Monger, H.C., 1999. Soil structural and other physical properties. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), *Standard Soil Methods for Long-Term Ecological Research*. Oxford University Press, Oxford, pp. 74–85.
- Fisher, F.M., Zak, J.C., Cunningham, G.L., Whitford, W.G., 1988. Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. *J. Range Mgmt* 41, 387–391.
- Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity Conservation* 7, 1221–1244.
- Folgarait, P.J., Perelman, S., Gorosito, N., Pizzio, R., Fernández, J., 2002. Effects of *Camponotus punctulatus* ants on plant community composition and soil properties across land-use histories. *Plant Ecol.* 163, 1–13.
- García-Moya, E., McKell, C.M., 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51, 81–88.
- Gordon, D.M., 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. *Am. Nat.* 138, 379–411.
- Gordon, D.M., 1992a. How colony growth affects forager intrusion between neighboring harvester ant colonies. *Behav. Ecol. Sociobiol.* 31, 417–427.
- Gordon, D.M., 1992b. Nest relocation in harvester ants. *Ann. Entomol. Soc. Am.* 85, 44–47.
- Gordon, D.M., 1993. The spatial scale of seed collection by harvester ants. *Oecologia* 95, 479–487.
- Gordon, D.M., Hölldobler, B., 1987. Worker longevity in harvester ants (*Pogonomyrmex*). *Psyche* 94, 341–346.
- Gordon, D.M., Kulig, A.W., 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology* 77, 2393–2409.

- Grubb, P.J., 1977. The maintenance of species richness in plant communities: the importance of regeneration niche. *Biol. Rev.* 52, 107–145.
- Hughes, L., 1990. The relocation of ant nest entrances: potential consequences for ant-dispersed seeds. *Aust. J. Ecol.* 16, 207–214.
- Jarrell, W.M., Armstrong, D.E., Grigal, D.F., Kelly, E.F., Monger, H.C., Wedin, D.A., 1999. Soil water and temperature status. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), *Standard Soil Methods for Long-Term Ecological Research*. Oxford University Press, New York, pp. 55–73.
- Johnson, R.A., 1998. Foundress survival and brood production in the desert seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus* (Hymenoptera, Formicidae). *Insectes Sociaux* 45, 255–266.
- Johnson, R.A., 2000a. Seed-harvester ants (Hymenoptera: Formicidae) of North America: an overview of ecology and biogeography. *Sociobiology* 36, 83–122.
- Johnson, R.A., 2000b. Water loss in desert ants: caste variation and the effect of cuticle abrasion. *Physiol. Entomol.* 25, 48–53.
- Lajtha, K., Klein, M., 1988. The effect of varying nitrogen and phosphorus availability on nutrient use by *Larrea tridentata*, a desert evergreen scrub. *Oecologia* 75, 348–353.
- Lajtha, K., Whitford, W.G., 1989. The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. *Oecologia* 80, 341–348.
- Lighton, J.R.B., Bartholomew, G.A., 1988. Standard energy metabolism of a desert harvester ant, *Pogonomyrmex rugosus*: effects of temperature, body mass, group size, and humidity. *Proc. Natl Acad. Sci., USA* 85, 4765–4769.
- MacKay, W.P., 1981. A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). *Psyche* 88, 25–74.
- MacMahon, J.A., Mull, J.F., Crist, T.O., 2000. Harvester Ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annu. Rev. Ecol. Syst.* 31, 265–291.
- Mattson, W.J., 1980. Herbivory in relation to plant nitrogen content. *Ann. Rev. Ecol. Syst.* 11, 119–161.
- Mun, H.T., Whitford, W.G., 1989. Effects of nitrogen amendment on annual plants in the Chihuahuan desert. *Plant Soil* 120, 225–232.
- Nelson, D.W., Sommers, L.E., 1996. Total carbon, organic carbon, and organic matter. In: Sparks, D.L., (Ed.), *Methods of Soil Analysis. Part 3. Chemical Methods*. Soil Science Society of America, Madison, WI, pp. 961–1010.
- Nobel, P.S., Russell, C.E., Felker, P., Medina, J.G., Acuña, E., 1987. Nutrient relations and productivity of prickly pear cacti. *Agronomist's J.* 79, 550–555.
- Petal, J., 1978. The role of ants in ecosystems. In: Brian, M.V. (Ed.), *Production Ecology of Ants and Termites (International Biology Programme, no. 13)*. Cambridge University Press, New York, pp. 293–325.
- Petal, J., 1998. The influence of ants on carbon and nitrogen mineralization in drained fen soils. *Appl. Soil Ecol.* 9, 271–275.
- Post, W.M., Pastor, J., Zinke, P.J., Stangenberger, A.G., 1985. Global patterns of soil nitrogen storage. *Nature* 317, 613–616.
- Rice, W.R., 1989. Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Rissing, S.W., 1986. Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. *Oecologia* 68, 231–234.
- Santos, P.F., DePree, E., Whitford, W.G., 1978. Spatial distribution of litter and microarthropods in a Chihuahuan desert ecosystem. *J. Arid Environ.* 1978, 41–48.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huennenke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. *Science* 247, 1043–1048.
- Schlesinger, W.H., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77, 364–374.
- Sharifi, M.R., Meinzer, F.C., Nilsen, E.T., Rundel, P.W., Virginia, R.A., Jarrell, W.M., Herman, D.J., Clark, P.C., 1988. Effect of resource manipulation on the quantitative phenology of *Larrea tridentata* (creosote bush) in the Sonoran Desert of California. *Am. J. Bot.* 75, 1163–1174.
- Strojan, C.L., Randall, D.C., Turner, F.B., 1987. Relationship of leaf litter decomposition rates to rainfall in the Mojave Desert. *Ecology* 68, 741–744.
- Wagner, D., 1997. The influence of ant nests on *Acacia* seed production, herbivory and soil nutrients. *J. Ecol.* 85, 83–93.
- Wagner, D., Gordon, D.M., 1999. Colony age, neighborhood density and reproductive potential in harvester ants. *Oecologia* 119, 175–182.
- Wagner, D., Brown, M.J.F., Gordon, D.M., 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia* 112, 232–236.
- West, N.E., Skujins, J., 1978. Nitrogen in Desert Ecosystems. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- Whitford, W.G., 1988. Effects of harvester ant (*Pogonomyrmex rugosus*) nests on soils and a spring annual, *Erodium texanum*. *Southwestern Nat.* 33, 482–484.
- Whitford, W.G., DiMarco, R., 1995. Variability in soils and vegetation associated with harvester ant (*Pogonomyrmex rugosus*) nests on a Chihuahuan Desert watershed. *Oecologia* 20, 169–173.