Biol Fertil Soils (1995) 20:169–173

ORIGINAL PAPER

Walter G. Whitford · Rudolfo DiMarco

Variability in soils and vegetation associated with harvester ant (*Pogonomyrmex rugosus*) nests on a Chihuahuan Desert watershed

Received: 4 January 1994

Abstract The effects of harvester ant (*Pogonomyrmex rugosus*) nests on the density and cover of spring annual plants and on soil characteristics were measured at three locations characterized by different soils and dominant vegetation on a desert watershed. There were few differences in vegetation and soils associated with harvester ant nests at locations at the base of the watershed where brief periods of flooding and sediment deposition occur at periodic intervals. At mid-slope locations, there were significant increases in total nitrogen, inorganic phosphorus, and cover (biomass) of four species of spring annuals at the edges of nest disks when compared with reference sites. The spring annuals that exhibited increased cover were species that increase biomass as a function of available nitrogen. At a clay-loam, *Scleropogon-Hilaria*, grassland site, there were significant reductions in the concentrations of Ca^{2+} and Mg^{2+}, significant increases in nitrate and total nitrogen, but a significant increase in cover in only one species of annual plant. The data demonstrate that the effects of ants on soil properties and vegetation vary with site location and soil type.

Key words Annual plants · Desert · Harvester ants · Soil nutrients · Spatial variability · *Pogonomyrmex rugosus*

Introduction

In the process of building and maintaining nests, storing food and eliminating nonusable materials, ants frequently modify the soil and consequently the vegetation in the vicinity of their colonies (Malozemova 1970; Wiken et al. 1976; Beattie and Culver 1983; Culver and Beattie 1983; Cowan et al. 1985; Lockaby and Adams 1985; Lobry de Bruyn and Conacher 1990; Carlson and Whitford 1991). The activities of ants frequently reduce bulk density and available nutrients such as potassium, phosphorus and calcium (Lockaby and Adams 1985). Ants also tend to increase available cations and organic matter content of the soil (Baxter and Hole 1967; Petal et al. 1967; Czewinsky et al. 1971; Gentry and Stiritz 1972; Levan and Stone 1983). The available data (Lobry de Bruyn and Conacher 1990) demonstrate that certain species of ants affect soil properties in a single location but the data frequently indicate contradictory results. None of the studies reviewed by Lobry de Bruyn and Conacher (1990) examined the effects of a species of ant on soils over a large area where there are several soil types.

Seed-harvesting ants of the genus *Pogonomyrmex* are abundant and widely distributed in the northern Chihuahuan Desert (Schumacher and Whitford 1976; Whitford 1978). Ant nests of the large harvester ant *Pogonomyrmex rugosus* are patchily distributed on Chihuahuan Desert watersheds with densities ranging from 6 to 21 nests ha^{-1} (Whitford and Ettershank 1975; Whitford et al. 1976). *P. rugosus* nests are flat to slightly concave with a gravel surface devoid of vegetation in the center. The nests of *P. rugosus* have abundant interconnected burrows in the upper 20 cm ending in a single main tunnel toward the bottom of the nest (Whitford et al. 1976; MacKay 1981). The average diameter of the nest disks is about 1 m.

Pogonomyrmex rugosus may affect soil properties and vegetation in the vicinity of their nests (Whitford 1988). The abundance and importance of these ants as seed harvesters in the northern Chihuahuan Desert and their distribution over an entire watershed led us to design a study to answer the following questions: (1) are the assemblages of winter annual plants adjacent to *P. rugosus* nests different from assemblages not in the influence zone of ant nests, (2) what soil properties are modified by *P. rugosus* nests and (3) are the patterns of soil properties and vegetation associated with harvester ant nests consistent in the various habitats on a desert watershed?

W.G. Whitford[1] (✉) · R. DiMarco
Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA

Current address:
[1] US-EPA, Environmental Monitoring Systems Laboratory, PO Box 93478, Las Vegas, NV 89193-3478, USA

Materials and methods

Site description

This study was conducted on one of the Jornada Long-Term Ecological Research Program sites on the New Mexico State University Ranch, 45 km NNE of Las Cruces, Dona Ana County, New Mexico. This site is a small watershed of approximately 3 km length from the base of a small mountain to a dry lake (playa). The watershed has a 1–5% slope with typical desert vegetation (creosote bush, *Larrea tridentata*, shrublands) on the upper slopes and mixed grassland-shrubland on the lower slopes and is dissected by channels (arroyos) that drain into the playa lake. The watershed varies in elevation from 1300 m (4000 ft) to 2000 m (6000 ft). The 100-year annual rainfall is 211 mm with a standard deviation of 77 mm (Houghton 1972). More than half of the annual rainfall occurs between July and early October as intense convectional storms. Potential evapotranspiration exceeds precipitation every month of the year. Summer maxima regularly reach 40 °C, and winter minima range between 0 °C and −10 °C.

This study was conducted at sites in three vegetation zones of the watershed: (1) a burrograss (*Scleropogon brevofolia*)-tabosa grass (*Hilaria mutica*) grassland at the lowest slope of the watershed, (2) a mixed shrubland at the edge of the dry lake characterized by scattered mesquite (*Prosopis glandulosa*) mixed with *Yucca elata*, creosote bush (*Larrea tridentata*) and perennial grasses and (3) a subshrub-grass forb area dominated by snakeweed (*Gutierrezia sarothrae*) and a high diversity of annual and perennial forbs and grasses which is located on the mid-slope of the watershed. The soils of these sites are: (1) Dalby series – Typic Torrents, fine, and Headquarter series – Ustollic Haplargid, fine-loamy, (2) Bucklebar series – Typic Haplargid, fine-loamy and (3) Dona Ana series – Typic Haplargid, coarse loamy.

Vegetation

We selected eight *P. rugosus* nests at site 1, five at site 2 and seven at site 3 for study. Because it was necessary to study the nests at a site on the same soil, it was not possible to sample eight nests at each site. Annual plants were censused and measured in 0.16-m^2 quadrats. At each ant nest, a quadrat frame was randomly placed at the edge of the nest disk, then a second quadrat was placed at the edge of the disk directly opposite the first quadrat. Two quadrat frames were placed at 5 m distance from the nest edge quadrats in the same cardinal direction as the nest edge quadrats from the nest center.

The density and cover of all winter annual plants were measured at approximately 30-day intervals from the end of January to mid-May by recording the numbers of plants in each permanent quadrat and estimating the canopy as a perpendicular projection of a grid on the plant canopy. Overlap of canopies was measured with the result that, on occasion, cover exceeded 100%. In June after all the winter annuals had senesced, a 400-cm^3 soil core (upper 15 cm of soil) was collected from each quadrat.

Soil characteristics

Soil samples were collected from the nest disk and at 5 m distance (at a randomly selected cardinal direction) from five nests in each site. Soil samples were collected in open areas away from shrub canopies because *P. rugosus* nests are located in open areas. In January, 35-cm^3 cores, 15 cm deep, were collected for organic matter content. Organic matter content was measured as mass loss by combustion at 600 °C for 8 h. At 600 °C, the calcium carbonate in the soil remains stable. Prior to combustion the soil was air dried to a constant mass for determination of soil water content. Additional soil cores were collected in February, March, and May for measurement of soil water contents.

Chemical analyses

In June 400-cm^3 soil samples were collected for chemical analyses. All chemical analyses were made on the <2-mm soil fraction. Total nitrogen was measured by micro Kjeldahl digestion as described by Bremner and Mulvaney (1982). Ammonium (NH_4-N), nitrite (NO_2-N) and nitrate (NO_3-N) were extracted with 100 ml 2 *N* KCl on 10-g soil samples and were measured by the methods of Keeney and Nelson (1982). Inorganic phosphorus was extracted with 100 ml 0.5 *M* $NaHCO_3$ in 10-g soil samples and was measured with an autoanalyzer (Olsen and Sommers 1982). Exchangeable cations were extracted with 1 *N* ammonium acetate (pH 7.0) and were analyzed with an atomic absorption spectrophotometer (Thomas 1982). Cation exchange capacity (CEC) was determined by the NaOAc method and the concentration of sodium in solution was measured by atomic absorption spectrophotometry (Rhoades 1982).

Statistical analyses

Density and cover were analyzed by ANOVA using a hierarchical or nested classification. Two observations (subsamples) were made within each experimental unit (two quadrats at the ant-nest edge and two quadrats at sites 5 m from the nest edge). The resulting variance was used to determine sampling error. All other data were analyzed by ANOVA without subsamples (except for exchangeable cations). Unless otherwise indicated in the text, differences reported were significant at $P<0.05$. Means of all data were compared by Scheffe's test, which is conservative in the election of the critical value for any contrast (Steel and Torrie 1980).

Results

Vegetation

The effects of *P. rugosus* nests on the density and cover of winter annual plants varied during the spring, primarily as a result of the direct effects of the ants on the nest corona vegetation in late spring. There were significant differences in annual plant densities on and off mounds only in the sub-shrub grassland site in mid-May (Table 1). Species that were common on the nest disks of the harvester ants on all parts of the watershed exhibited growth (increase in cover) through March followed by a decrease in cover. This change in cover was due to the clearing of vegetation from the nest disk at the beginning of the foraging season (Wheeler and Wheeler 1963).

The differences in cover and density of annual plants associated with *P. rugosus* nests were reflected in the species composition of annual plants associated with the nest disks. Four species of annual plants had higher cover on nest disks in the sub-shrub grassland area than on soils not modified by ant activity (Table 2). On the other sites the low densities and differences in species composition reduced the number of species that occurred at higher cover on the perimeters of the nest disks (Table 2).

Table 1 Effect of harvester ant (*Pogonomyrmex rugosus*) nests on density and cover of spring annual plants on three sites on a Chihuahuan Desert watershed (*AN* data for edge of nest disk, *OAN* data for a reference site 5 m from the edge of the nest)

Date	*Scleropogon-Hilaria* (grass) basin		Mixed shrubland basin		Sub-shrub grassland mid-slope	
	AN	OAN	AN	OAN	AN	OAN
Density (No. m^{-2})						
January	151	113	111	75	332	225
February	131	136	119	106	430	333
March	70	130	89	117	405	392
May	43	88	46	64	190	358*
Cover (%)						
January	4.5	1.6	1.7	0.8	4.2	1.9*
February	14.4	5.1	7.2	2.9	24.3	5.5*
March	36.6	11.2	20.3	10.9	70.5	21.2*
May	23.4	22.2	30.9	44.1	55.7	26.3*

$*P<0.05$

Table 2 Effects of *Pogonomyrmex rugosus* nests on spring annual plant assemblages at three sites on a Chihuahuan Desert watershed. Data are expressed as an index of affinity for nest sites. Calculation of percentage affinity = (mean cover percentage on nest perimeter/mean cover percentage on perimeter + mean cover percentage in reference sites) × 100 (0 indicates species not found at a site, – indicates a species with < 1% cover)

	Scleropogon-Hilaria (grass) basin	Mixed shrub basin	Sub-shrub grassland mid-slope
Crypthantha angustifolia	0	74.2	35.9
Descurainia pinnata	–	72.4	95.1
Eschscholzia mexicana	0	–	66.6
Eriastrum diffusum	0	–	63.3
Eriogonum abertianum	–	–	73.2
Eriogonum rotundifolium	–	17.7	–
Erodium texanum	24.6	0	0
Lesquerella gordonii	79.4	–	62.8
Malacothrix fendleri	–	–	73.8

Soil chemical properties

The concentrations of sodium, potassium and ammonium were essentially the same at the edges of nest disks and in unaffected soils. The soils at the edges of ant nests had lower concentrations of calcium and magnesium and higher concentrations of nitrate at the *Scleropogon-Hilaria* site (Table 3). Concentrations of inorganic phosphorus and total soil nitrogen were significantly higher at the mid-slope site. Concentrations of total nitrogen were significantly higher at the edges of nests in the *Scleropogon-Hilaria* grassland (Table 3).

Table 3 Selected chemical properties of soil from the edge of *Pogonomyrmex rugosus* nests and soils 5 m from the edge of the nests at three locations on a Chihuahuan Desert watershed. Na^+, K^+, Ca^{2+}, and Mg^{2+} concentrations in meq 100 g^{-1} soil; NO_3-N, NH_4-N, total N, and inorganic P concentrations in mg kg^{-1} soil (*WC* water content (%), *OM* organic matter content (%), *AN* nest edge, *OAN* reference, *a* indicates significant site by treatment interaction)

	Scleropogon-Hilaria (grass) basin		Mixed shrub basin		Sub-shrub grassland mid-slope	
	AN	OAN	AN	OAN	AN	OAN
Na^+	0.04	0.04	0.01	0.02	0.02	0.02
K^+	2.1	2.0	1.0	1.1	0.9	0.8
Ca^{2+}	21.8	24.8a*	13.8	15.1	5.9	7.4
Mg^{2+}	2.5	3.0a*	1.6	1.6	2.0	2.0
NO_3-N	8.2	2.6a**	1.8	0.9	2.5	0.8
NH_4-N	1.0	1.3	3.6	1.0	1.7	0.7*
Total N	692.0	657.0**	479.0	465.0	433.0	389.0**
P (inorg.)	12.4	7.4	4.7	4.6	20.0	48.0**
WC	8.3	8.4	6.6	6.8	4.8	4.9
OM	0.8	1.0	0.6	0.7	0.6	0.5

$*P<0.05$, $**P<0.01$

Discussion

This study demonstrates that the effects of harvester ant nests on soil properties and subsequently on vegetation vary with location (topographic position) and soil type. In this study there were no effects of *P. rugosus* nests on the soil characteristics that we measured in the mixed shrub habitat at the base of the watershed. However, two species of annuals developed higher cover on the edges of nests in this location than that recorded in reference sites. These cover differences may be the result of competition among the species of annuals for soil resources that we did not measure.

The presence of *P. rugosus* nests had the largest effects on vegetation and soil in the sub-shrub grassland habitat at the mid-slope position on the watershed. In their review, Lobry de Bruyn and Conacher (1990) point out that some of the results of studies of the effects of ants on soils have been contradictory. Of the 17 studies of the effects of ants on soils that they reviewed, none examined the effects of a species in more than one habitat. The contradictory results of the effects of ants on soils is undoubtedly due in part to the characteristics of soils of various habitats and to differences in behavior of different species of ants.

In our study the differences in the effects of ant colonies on the soils cannot be attributed to differences in behaviors of the ant species because we examined the effects of a single species that had been shown to have an effect on soils and vegetation at one location in the region (Whitford 1988). The differences in effects of harvester ants on soils among locations on the watershed in this study may be in part due to disturbance frequencies. The shrubland at the base of the watershed is a depositional area. During intense rains, that area is inundated by sheet flow water which contains high concentrations of suspended sediments. This recurrent disturbance probably affects the accumulation of nutrients and modification of soil physical properties that result from the long-term activities of the ants. In order for ants to significantly modify the chemical characteristics of the soil, nests must remain in place for a relatively long time without surface disturbance. This criterion is met by the *P. rugosus* nests at the mid-slope site and in the *Scleropogon-Hilaria* grassland site.

The lack of differences in soil water contents and soil organic matter contents between nests and reference areas may be attributable to soil characteristics or characteristics of the nests. Ants may impede or facilitate the flow of water through the soil by their channels that open to the surface and by their effects on the soil surface (Thorp 1967; Majer et al. 1987). Our study was conducted during the dormant season for *P. rugosus*. In winter, nest entrances are closed and ants do not maintain the gravel layer on the surface of the nest. These factors may partially account for the lack of water content differences with respect to the soils of the reference areas. The organic matter content of the ant nest soils was higher than the reference soils in some other studies (Lobry de Bruyn and Conacher 1990). Levan and Stone (1983) argued that the organic matter content of nest soils should be a function of the soil's origin as surface soil/subsoil composites. Since *P. rugosus* transports virtually no subsoil to the surface after a nest is established and does not produce distinct refuse piles at the perimeter of the nest disk, the conditions for producing an organic matter rich surface soil are not met.

The lack of differences in densities of annual plants adjacent to and at 5 m distance from nests is similar to the result reported by Whitford (1988) for *Erodium texanum* and harvester ant colonies at a *Scleropogon-Hilaria* site near the watershed used in this study. Whitford (1988) found that the biomass differences were attributable to differences in soil water content. However, the data in this study show no differences in water content. The species of spring annual plants that dominated the edges of the ant nests were species that Gutierrez and Whitford (1987) found to respond to available nitrogen. The differences in cover of annuals adjacent to nest disks in comparison to soils not modified by ants are most probably due to the differences in nitrogen content and nitrogen availability. Nitrogen mineralization rates are generally directly related to total soil nitrogen in these desert ecosystems (Whitford et al. 1987).

The focus of this study and that of most studies reviewed by Lobry de Bruyn and Conacher (1990) has been on ant species that build large, conspicuous nests that are characterized by colony longevity of decades and that collect seed plus other plant and animal materials that are stored in the nests. These characteristics provide the time necessary for soil turnover and accumulation of nutrients from decomposing organic matter to account for the differences in the physical and chemical properties of soils associated with the nests. While *P. rugosus* meets these criteria, the colonies located in the area of sediment deposition probably have shorter life spans than colonies on more stable soils. While we have no quantitative data, there are no noticeable differences in spring and summer annual plant assemblages associated with *P. desertorum*, another seed-harvesting ant that is abundant on the watershed used in this study. The colonies of *P. desertorum* are smaller and have shorter life spans than those of *P. rugosus* (Whitford and Ettershank 1975; personal observation).

The studies done to date suggest that ants are important agents in the development of heterogeneity of soils, thereby affecting the patchiness of landscapes, especially in arid regions (Lobry de Bruyn and Conacher 1990). Our study demonstrates that the effects of ant nests on soil properties and vegetation are site specific and vary greatly depending upon landscape position and topography. However, comprehensive studies of entire ant faunas in a wide variety of habitats and measurements that include rainfall infiltration and quantities of subsoil moved to the surface as well as soil physical and chemical properties are required before conclusive generalizations can be made.

Acknowledgements This study is a contribution of the Jornada Long-Term Ecological Research Program supported in part by Grant No. 881160 from the National Science Foundation and cofunded by the U.S. Environmental Protection Agency, Environmental Monitoring Systems Laboratory, Las Vegas. The research described herein has not been subjected to the Agency's peer and administrative review. Therefore the conclusions and opinions drawn are solely those of the authors and should not be construed to reflect the views of the Agency.

References

Baxter FP, Hole FD (1967) Ant (Formica cinerea) perturbation in a Prairie soil. Soil Sci Soc Am Proc 31:425–428

Beattie AJ, Culver DC (1983) The nest chemistry of two seed-dispersing ant species. Oecologia 52:99–103

Bremner JM, Mulvaney CS (1982) Total nitrogen. In: Page AL, Miller RH, Keeney DR (ed) Methods of soil analysis. Part 2. Chemical and microbiological properties, 2nd edn. American Society of Agronomy, Soil Science Society of America, Madison, Wis, pp 595–624

Carlson SR, Whitford WG (1991) Ant mound influence on vegetation and soils in a semiarid mountain ecosystem. Am Midl Nat 26:125–139

Cowan JA, Humphreys PB, Murphy CL (1985) An assessment of pedoturbation by two species of mound building ants, *Camponotus intrepidus* (Kirby) and *Iridomyrmex purpureus* (F. Smith). Aust J Soil Res 22:95–107

Culver DC, Beattie AJ (1983) Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. Ecology 64:485–492

Czewinsky Z, Jakubczyk H, Petal J (1971) Influence of ant hills on the meadow soils. Pedobiologia 11:277–285

Gentry JB, Stiritz KL (1972) The role of the Florida Harvester Ant, *Pogonomyrmex badius*, in old field mineral nutrient relationships. Environ Entomol 1:39–41

Gutierrez JR, Whitford WG (1987) Chihuahuan desert annuals: importance of water and nitrogen. Ecology 68:2032–2045

Houghton FE (1972) Climate guide, New Mexico State University, Las Cruces, New Mexico 1951–1971. Agricultural Experiment Station, Research Report 230. New Mexico State University, Las Cruces, 20 pp

Keeney DR, Nelson DW (1982) Nitrogen-inorganic forms. In: Page AL, Miller RH, Keeney DR (eds) Methods of analysis, part II. Chemical and Microbiological Properties. Agron 9, Am Soc Agron, Madison, Wis, pp 643–698

Levan MA, Stone EL (1983) Soil modification by colonies of black meadow ants in a New York old field. Soil Sci Soc Am J 47:1192–1195

Lobry de Bruyn LA, Conacher AJ (1990) The role of termites and ants in soil modification: a review. Aust J Soil Res 28:55–93

Lockaby BG, Adams JC (1985) Pedoturbation of a forest soil by fire ants. Soil Sci Soc Am J 49:220–223

MacKay WP (1981) A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Psyche 88:25–74

Majer JD, Walker TC, Berlandier F (1987) The role of ants in degraded soils within Dryandra state forest. Mulga Res Cntr J 9:15–16

Malozemova LA (1970) Interrelations of ants and plants. Ekologiya 2:101–103

Olsen SR, Sommers LE (1982) Phosphorus. In: Page AL, Miller RH, Keeney DR (eds) Methods of soil analysis, part II. Chemical and microbiological properties. Agron 9, Am Soc Agron, Madison, Wis, pp 403–430

Petal J, Jakubczyk H, Wojcik Z (1967) L'influence des fourmis sur la modification des sols et des plants dans le milieu des prairies. Symposium on Methods of Study in Soil Ecology. Paris, pp 235–240

Rhoades JD (1982) Cation exchange capacity. In: Page AL, Miller RH, Keeney DR (ed) Methods of soil analysis, part II. Chemical and microbiological properties. Agron 9, Am Soc Agron, Madison, Wis, pp 149–157

Schumacher A, Whitford WG (1976) Spatial and temporal variation in Chihuahuan Desert ant faunas. Southwestern Nat 21:1–8

Steel RGB, Torrie JH (1980) Principles and procedures of statistics: A biometrical approach. McGraw-Hill, New York

Thomas GW (1982) Exchangeable cations. In: Page AL, Miller RH, Keeney DR (eds) Methods of soil analysis, part II. Chemical and microbiological properties. Agron 9, Am Soc Agron Madison, Wis, pp 159–165

Thorp J (1967) Effects of certain animals that live in soils. In: Drew EV (ed) Selected papers in soil formation and classification. Soil Science Society of America, Madison, Wis, pp 191–208

Wheeler GC, Wheeler J (1963) The ants of North Dakota. University of North Dakota Press, Grand Forks, ND

Whitford WG (1978) Structure and seasonal activity of Chihuahuan Desert ant communities. Insectes Sociaux 25:79–88

Whitford WG (1988) Effects of harvester ant, *Pogonomyrmex rugosus* nests on soils and a spring annual, *Erodium texanum*. Southwestern Nat 33:482–485

Whitford WG, Ettershank G (1975) Factors affecting activity of Chihuahuan Desert ants. Environ Entomol 4:689–696

Whitford WG, Johnson P, Ramirez J (1976) Comparative ecology of the harvester ants, *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). Insectes Sociaux 23:117–132

Whitford WG, Reynolds JF, Cunningham GL (1987) How desertification affects nitrogen limitation of primary production of Chihuahuan Desert watersheds. In: Aldon EF, Gonzales-Vincente CE, Moir WH (ed) Proceedings of the symposium on strategies for classification and management of native vegetation for food production in arid zones. USDA Forest Service, General Technical Report RM 150, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Co., pp 143–153

Wiken EB, Boersma K, Lavkulich LM, Farstad L (1976) Biosynthetic alteration in a British Columbia soil by ants (*Formica fusca* Linne). Soil Sci Soc Am J 40:422–426