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MICROHABITAT-SPECIFIC CONTROLS ON SOIL RESPIRATION AND DENITRIFICATION IN THE MOJAVE DESERT: THE ROLE OF HARVESTER ANT NESTS AND VEGETATION

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ABSTRACT.—Seed harvesting ants (*Pogonomyrmex rugosus*) concentrate organic matter and nutrients near their nests and create biogeochemical hotspots in desert soil. We examined factors regulating denitrification and soil respiration in a Mojave Desert ecosystem to determine the role harvester ant colonies play in nitrogen loss and carbon mineralization. Organic matter and nutrient storage were significantly greater in colonies than under the dominant vegetation (i.e., *Pleuraphis rigida,* a bunch grass) and in bare soil, with standing stocks of inorganic nitrogen in colonies nearly 4-fold greater than in the other microhabitats. Soil respiration, measured with laboratory incubations, was below detection limits under ambient soil conditions. Respiration rate in soil from bare patches and under grass was limited by water and labile organic carbon, with secondary nitrate limitation evident only once carbon limitation was alleviated. Soil respiration in ant nest soil was limited by water and labile organic carbon only. Denitrification, measured by the acetylene block technique, was elevated in bare soil and under grass with the addition of nitrate. Ant nest soil also responded to a nitrate addition; however, denitrification rate was greatest with addition of glucose. Ordinarily desert soil has low rates of respiration and denitrification due to dry ambient conditions. However, ant colonies likely function as important sites for nitrogen loss and carbon mineralization following rain storms, especially if storms coincide with seed set and the temporally pulsed input of organic matter into colonies.

Key words: ant nests, Mojave Desert, nitrogen, soil respiration, soil denitrification, spatial heterogeneity.

In desert soil of the southwestern United States, nitrogen limits primary production following the alleviation of water stress (West and Skujiņš 1978, Nobel et al. 1987, Lajtha and Klein 1988, Sharifi et al. 1988, Lajtha and Whitford 1989, Mun and Whitford 1989). Nitrogen storage in deserts is low relative to other biomes (Post et al. 1985), and factors regulating the storage and transformation of nitrogen can have large impacts on plant productivity. The typically dry, nutrient-poor condition of desert soil is unfavorable for anaerobic metabolism; however, when soil is wetted, denitrification rate can be comparable to more mesic ecosystems and may be an important loss mechanism in desert soil, further exacerbating nitrogen limitation (Westerman and Tucker 1978, Virginia et al. 1982, Peterjohn and Schlesinger 1991).

The distribution of soil nitrogen is heterogeneous in deserts, with elevated standing stocks under shrubs and in soil affected by nesting activities of animals such as seed-harvesting ants (Garcia-Moya and McKell 1970, Charley and West 1975, Santos et al. 1978, Whitford 1988, Schlesinger et al. 1996). Harvester ants in the genus *Pogonomyrmex* are present at high density in many arid ecosystems in North America (MacMahon et al. 2000). Nest mounds of *Pogonomyrmex* can reach 4 m^2 in area (Wagner and Jones 2004) and can last for more than 15 years (Keeler 1988, Porter and Jorgensen 1988, Gordon 1991). Over the life of the colony, harvester ants collect seeds and deposit seed chaff and other debris on the mound, redistributing organic matter and nutrients within the landscape. By concentrating organic matter and nutrients, the inorganic nitrogen standing stock in harvester ant mounds can be an order of magnitude greater than in surrounding soil and 2–5-fold higher than in soil under vegetation (Wagner et al. 2004, Wagner and Jones 2004). As well as having elevated nutrient standing stocks, ant nest soil can harbor high microbial populations and have rapid increase in microbial biomass when water is available (Boulton et al. 2003, Wagner and Jones 2004).

Whereas the role of ant nests in nutrient storage is well established, little is known regarding the role of colonies in soil nitrogen

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transformations. The combination of high microbial growth potential and availability of organic and inorganic nutrients in harvester ant nests suggests that nests may constitute hotspots for biogeochemical transformations in arid ecosystems. For example, previous studies of other ant genera have documented higher rates of carbon and nitrogen mineralization in ant nests than in surrounding soil (Wagner 1997, Petal 1998, Dauber et al. 2001).

Although infrequent rains limit the importance of denitrification in deserts, denitrification rates can approach those of more mesic sites after rainstorms (Peterjohn and Schlesinger 1991). The rate of denitrification is positively related to the concentration of organic matter, nitrate, and water (reviewed by Broadbent and Clark 1965, Payne 1973), all of which can be present at higher standing stocks in harvester ant nests than elsewhere on the desert landscape (MacMahon et al. 2000). This elevated nitrogen suggests that ant nest soil may contribute disproportionately to nitrogen losses through denitrification. More generally, soils of harvester ant nests may respire at a greater rate than soils from other microhabitats. Moreover, since the chemical characteristics of ant nest soil differ greatly from those of other microhabitats, the factors that limit rates of denitrification and respiration may differ as well.

We examined the factors regulating denitrification and soil respiration in a Mojave Desert ecosystem to determine if ant nests are important microhabitats for denitrification loss of soil nitrogen and carbon mineralization. Denitrification and respiration in the soil of ant nests were compared to the same processes in soil under the dominant vegetation and soil devoid of vegetation. We also tested 3 potential factors limiting denitrification and respiration rates: water, nitrate, and carbon.

METHODS

Study Site

The study was conducted in Kane Springs Valley, located ~130 km northeast of Las Vegas, Nevada, on a 2.0-ha plot (37°11′15″N, 114°6′34″W, elevation ~1250 m). The site was located at the edge of the Mojave Desert and had a mean annual precipitation of 162 mm · yr^{-1}. The site had burned prior to this study and was dominated by the perennial bunch grass *Pleuraphis rigida.* The site had a history of sporadic grazing by cattle.

The study plot supported a population of the seed-harvesting ant *Pogonomyrmex rugosus.* Nests of this species are large and conspicuous gravel-covered discs. At the study site, *P. rugosus* nests ranged in size from 0.06–1.8 m^2 (Wagner and Jones 2004). Mature colonies of *P. rugosus* contain 10,000–12,000 workers (MacKay 1981). Foragers collect seeds from the surrounding habitat and carry them to the nest. Ants consume the nutrient-rich seed kernel and discard the seed coating on the surface of the nest. We located all colonies of *P. rugosus* on the study plot in 1999 by walking a grid. Each nest was permanently tagged and mapped using a theodolite. Ant nests covered 0.5%, and *Pleuraphis rigida* covered 25.3% of the study plot. The remaining 73.1% of the plot was bare soil or areas that intermittently supported small annual plants (Wagner and Jones 2004).

Respiration and Denitrification Incubations

Soil respiration was measured as production of CO_2 and denitrification as production of N_2O using the acetylene block technique. Soil for respiration assays (collected on 15 July 2002) and for denitrification assays (collected on 19 March 2002) was obtained from the 3 dominant microhabitat types on the study plot (ant mounds, under grass, and soil devoid of vegetation). Twenty-five soil cores (20 cm depth) were randomly collected from each microhabitat type (75 cores total) in plastic cores constructed of ABS pipe (4.0 cm diameter) by driving the pipe into the ground with a sledge hammer. Cores were perforated with about one hundred 3-mm holes that were uniformly drilled along the pipe to allow gas exchange between soil interstitial space and chamber head space. Soil cores were immediately capped on the 2 open ends with aluminum foil held by rubber bands and then placed in a nylon stocking to prevent loss of soil (Peterjohn and Schlesinger 1991). The foil caps and stockings remained in place throughout the experiment. Cores were then placed in a cooler above ice for transport to the laboratory.

To identify factors limiting respiration and denitrification, we assigned soil cores from each microhabitat type (for both respiration

and denitrification assays) randomly to 5 treatments: no additions (controls) or addition of water, nitrate, labile organic carbon, or nitrate + carbon (n = 5 cores per treatment and microhabitat type). For all wetting treatments, 25 mL of solution was added to cores, which equates to 2.0 cm of precipitation or a storm frequency of ~1.3 events per year. The amendment solutions consisted of reverse osmosis water only for the water treatment; 1.26 g N · L^{-1} of $NaNO_3$ for the nitrate solution (~100 μg NO_3–N · g^{-1} Soil); 27 g C · L^{-1} as dextrose for the carbon treatment (~2.5 mg C · g^{-1} Soil); and 1.26 g N · L^{-1} of $NaNO_3$ and 27 g C · L^{-1} of dextrose for the nitrate + carbon treatment. Amendment solutions were added 24 hours prior to initiation of incubation to allow soil microbes time to respond to the additions.

Soil cores were incubated in gas-tight chambers constructed from ABS plastic pipe. Laboratory chambers were 5.0 cm in diameter, 20.0 cm long, and sealed with a glued-on slip cap on one end, and with a male-threaded plug on the other end (Peterjohn and Schlesinger 1991). In the top of the threaded plug, a luer lock fitting was installed with epoxy glue and a syringe stopcock valve was attached.

Soil cores were incubated in batches of 30 with batches initiated on consecutive days. For each batch, equal numbers of cores from each microhabitat and treatment were incubated to avoid confounding temporal changes with treatment effects. Laboratory incubations were completed within 4 days of field collection.

Incubations were conducted by carefully placing each wetted and control core into an incubation chamber and closing the chamber with the threaded plugs wrapped in Teflon tape to assure a gas-tight seal. Twenty milliliters of air was injected via syringe into the chamber for respiration incubations, and 20 mL of acetylene was injected for denitrification incubations. The gas within chambers was then pumped 5 times with the syringe to aid with diffusion and mixing of gas throughout the soil cores. An initial gas sample of 20 mL was withdrawn and injected into a serum vial for later gas analysis. After 22 hours a final gas sample was collected by mixing the chamber headspace (i.e., pumping the collection syringe 5 times), withdrawing 20 mL, and injecting the gas sample into a serum vial.

At the completion of incubations, the headspace volume of each chamber-sample combination was calculated by measuring the change in pressure with a known volume addition of gas (Parkin et al. 1984). Chamber valves were first opened to allow the internal pressure to equilibrate with the laboratory. Second, 50 mL of air was injected into each chamber and the increase in chamber internal pressure measured using a Druck DPI 705 pressure gauge. Chamber headspace volume was calculated as

$$V_{chamber} = \frac{V_{syringe}}{\frac{P_{chamber}}{P_{laboratory}} - 1}$$

where $V_{chamber}$ is the chamber headspace volume, $V_{syringe}$ is the volume of air injected into the chamber, $P_{laboratory}$ is the lab atmospheric pressure, and $P_{chamber}$ is the gas pressure in the chamber following the over-pressurization with air. Carbon dioxide and nitrous oxide were measured on a Varian 3800 gas chromatograph equipped with a flame ionization detector with a methanizer and an electron capture detector.

Soil Nutrient Stocks

Following incubations, we characterized soil moisture and organic matter content of the soil. Soil cores were dried at 105°C for 48 hours. Field moisture was estimated from the mass loss in control cores (Jarrell et al. 1999). Following drying, organic matter was measured as ash-free dry mass (AFDM) by combusting 10-g subsamples at 400°C for 16 hours (Nelson and Sommers 1996).

Salt extractable nutrients in the 3 microhabitat types were measured on soil cores (10 cm depth) randomly collected from each microhabitat type (n = 25 random points sampled per microhabitat type with 3 cores per sample point) in November 2000. After cores were dried and sieved, we extracted nutrients using 2 M KC1 to extract ammonium and nitrate and using a solution of 0.03 M NH_4F and 0.025 M HC1 to extract phosphorus. Concentrations of ammonium, nitrate, and phosphorus 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 and are reported as μg · g^{-1} dry mass of soil.

TABLE 1. Mean ($\pm s_{\bar{x}}$) chemical composition of soil from 3 microhabitats. Values annotated with different letters are significantly different ($P < 0.05$).

	Organic matter (mg AFDM · g Soil^{-1})	NH_4 (μg N · g Soil^{-1})	NO_3 (μg N · g Soil^{-1})	PO_4 (μg P · g Soil^{-1})
Bare soil	15.2 ± 0.5 a	3.5 ± 0.2 a	4.1 ± 0.2 a	10.4 ± 0.5 a
Grass	17.7 ± 0.6 b	7.4 ± 2.5 a	5.5 ± 0.6 a	8.5 ± 0.3 a
Ant nest	21.6 ± 0.8 c	31.4 ± 3.0 b	23.7 ± 2.9 b	48.5 ± 4.1 b

Statistical Analyses

The effects of microhabitat type on organic matter and nutrient standing stocks were assessed with 1-way ANOVA. The effects of microhabitat and water/nutrient treatment on respiration and denitrification were assessed with 2-way ANOVA. Data were log-transformed prior to analysis. Following a significant ANOVA result, comparisons among microhabitat means were tested using Tukey-Kramer HSD tests.

RESULTS

Ant nest soil stored significantly greater organic matter and nutrients than soils under the dominant bunch grass or bare soils. Organic matter storage in ant nests was 22% higher than under grasses and 42% higher than in bare soil ($P < 0.05$; Table 1). Even more striking was that nutrient storage in ant nests was many times greater than in bare soil or under grass (Table 1). Salt extractable nitrate and ammonium storage in nests averaged 23.7 μg N · g Soil^{-1} and 31.4 μg N · g Soil^{-1}, respectively, whereas nitrate and ammonium storage in the other 2 microhabitats was <8 μg N · g Soil^{-1}. Phosphorus storage in ant nest soil was 3–4 times higher than in the other microhabitats (Table 1).

Soil respiration and denitrification responded to water and nutrient amendments, and the response varied among microhabitats (Figs. 1, 2). Microhabitat and treatment explained a significant amount of variation in both soil respiration and denitrification rates (microhabitat: $F_{2, 60} > 37$, $P < 0.001$; treatment $F_{4, 60} > 55$, $P < 0.001$), with significant interactions among the main effects ($F_{8, 60} > 4$, $P < 0.001$).

In all soil microhabitats, the ambient respiration rate measured in the control cores was below detection limits. Addition of water significantly increased respiration in soils under grass and in ant nest soil, but not in bare soil; means of water-amended soil respiration ranged from 0.9 μg C · g Soil^{-1}d^{-1} to 4.0 μg C · g Soil^{-1}d^{-1} (Fig. 1). Addition of nitrate had no further effect on respiration rate above water alone, but addition of glucose caused a significant increase of respiration rate in all microhabitats (Fig. 1). In bare soil and soil under grass, the combination of glucose and nitrate significantly elevated respiration rate over all other treatments, including glucose alone. In contrast, respiration of ant nest soil amended with glucose + nitrate was not significantly different from those amended with glucose alone (Fig. 1).

The denitrification rate of bare soil and soil under grass increased only in response to nitrate amendment, whereas the denitrification rate of ant nest soil responded to both carbon and nitrate additions. In bare soil and soil under grass, denitrification rate did not vary significantly among the control, water, and carbon treatments, with the rate ranging from 0.6 ng N · g Soil^{-1}d^{-1} to 3.1 ng N · g Soil^{-1}d^{-1} (Fig. 2). Amendment of these soils with nitrate caused a significant increase in denitrification. The combination of glucose and nitrate did not significantly increase denitrification rate over addition of nitrate alone in bare soil and under grass. In ant nest soil, denitrification rate was similar to the other soil types in the control and water treatments (1.6–2.0 ng N · g Soil^{-1}d^{-1}; Fig. 2). As in the other microhabitat types, denitrification rate in ant nest soil increased significantly with the addition of nitrate. Unlike the other microhabitats, denitrification in ant nest soil increased over 37-fold in response to glucose addition relative to the water-only treatment. In ant nest soil, amendment with a combination of glucose and nitrate did not increase denitrification rate significantly over glucose alone (Fig. 2).

DISCUSSION

Respiration and denitrification rates were quite low in unamended soil and did not vary

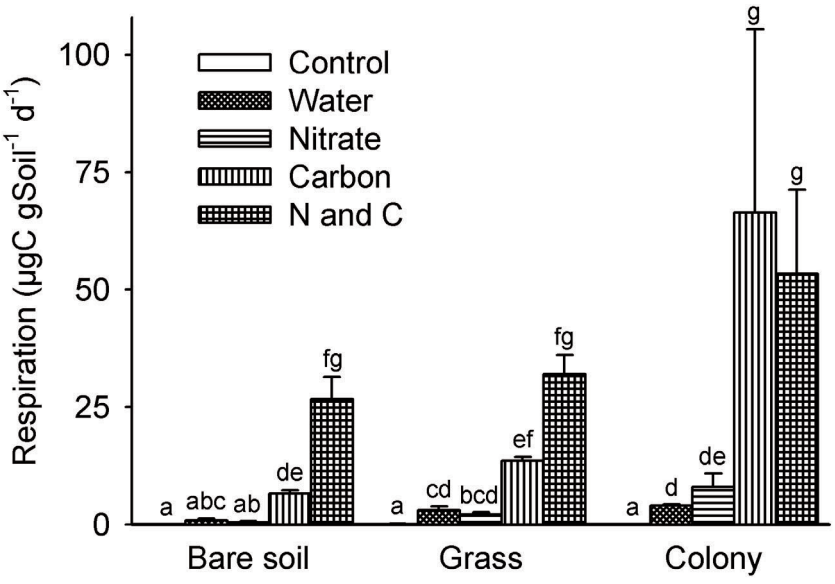

Fig. 1. The effects of water, nitrogen, and organic carbon amendments on respiration rate in the soil of harvester ant colonies, under the bunch grass *Pleuraphis rigida,* and in bare interspace (± *s*). Letters above bars denote significant differences among microhabitat–treatment combinations ($P < 0.05$).

among microhabitats. This lack of variation under ambient field conditions suggests that soil microbial activity is ordinarily low and exhibits little spatial variation. However, these low rates of microbial activity may also reflect the drought conditions that prevailed throughout southern Nevada in 2002 (Western Regional Climate Center, available from: http://www.wrcc.dri.edu). Ambient soil moisture averaged only 2.0% ($s_{\bar{x}}$ 0.1) in the respiration experiment and 2.9% ($s_{\bar{x}}$ 0.1) in the denitrification experiment. In contrast, soil moisture on this site during the year 2000 averaged 4.9% ($s_{\bar{x}}$ 0.6; Wagner and Jones 2004). Microbial biomass carbon and nitrogen in 2000 was significantly higher in ant nest soil than in the other microhabitat types, suggesting that under normal conditions, more spatial structuring of microbial activity should be expected (Wagner and Jones 2004).

The rates of respiration and denitrification appeared to be limited by different factors in the different microhabitats and followed the patterns in organic matter and nutrient storage. Respiration in soils poor in organic matter was limited by both water and carbon availability. In soil under grass, where soil organic matter is elevated relative to bare soil, respiration increased with water, although the rate was further elevated with addition of a carbon source. Respiration in both bare soil and soil under grass was further limited by nitrogen availability once carbon limitation was relieved (as evidenced by the lack of response with nitrate alone; Fig. 1). In ant nest soils, which are comparatively rich in organic matter, respiration was limited first by water and second by labile organic carbon. Unlike bare soil and soil under grass, there was no evidence of nitrogen limitation on respiration in ant nest soil. The standing stocks of nitrogen, however, were over 4-fold greater in ant nests than in the other microhabitats. Denitrification in bare soil and soil under grass was limited by nitrate, whereas denitrification in ant nests was limited by both labile organic carbon and nitrate. For both respiration and denitrification, the increase in rates following alleviation of nutrient limitation was most pronounced in ant nest soil.

Potential Nitrogen Losses via Denitrification

When we compared the potential loss rate of nitrogen via denitrification to other microbial transformations, we found that the rate is

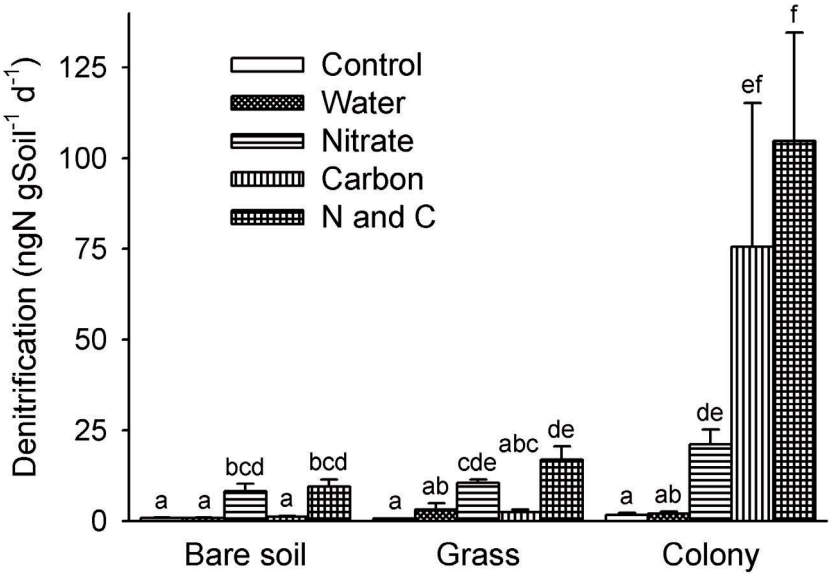

Fig. 2. The effects of water, nitrogen, and organic carbon amendments on denitrification rate in the soil of harvester ant colonies, under the bunch grass *Pleuraphis rigida,* and in bare interspace (± *s*). Letters above bars denote significant differences among microhabitat–treatment combinations ($P < 0.05$).

nearly 3 orders of magnitude lower than processes such as mineralization. At the same study site, the potential nitrogen mineralization rate of ant nest soil averaged 1.2 μg N · g Soil^{-1}d^{-1} and was twice as high as mineralization potential in bare soil and soil under the bunch grass *Pleuraphis rigida* (unpublished data). In southeastern Arizona, potential mineralization rate in the nests of the ant *Formica perpilosa* also averaged 1.2 μg N · g Soil^{-1}d^{-1} and was 3-fold greater than in soil lacking ant nests (Wagner 1997). In contrast, denitrification in ant nest soil measured in the present study was only 1.6 ng N · g Soil^{-1}d^{-1} under ambient moisture and 2.0 ng N · g Soil^{-1}d^{-1} with water amendment, indicating that, even in ant nests where nitrate and organic matter stocks are high, denitrification is not an important loss mechanism.

The longer-term rate of nitrogen loss via denitrification is likely greater, however, than the rate observed under ambient moisture in this study. In the Mojave Desert, the input of seed chaff to *P. rugosus* ant mounds increases dramatically after the dominant plant species set seed (D. Wagner personal observation). On our study site, low rainfall led to low seed production in 2001. In 2002 annual plants were scarce and *Pleuraphis rigida* produced no seed at all. The influx of organic matter to harvester ant nests in the form of seeds is likely much higher in other years. The episodic input of organic matter and labile carbon to ant nests following seed set may lead to periods with short-lived losses of nitrogen following rain storms that are relatively higher than other microhabitats.

In our study the water amendment alone did not significantly alter denitrification, even in ant colony soil, which is the microhabitat with greatest standing stocks of nutrient and organic matter. This lack of water limitation contrasts with previous studies conducted on desert soil. In both the Chihuahuan and Sonoran Deserts, denitrification rate increased with water additions (Virginia et al. 1982, Peterjohn and Schlesinger 1991). In the Sonoran Desert study, the effect of water addition was pronounced under mesquite (*Prosopis glandulosa;* Virginia et al. 1982), perhaps because denitrification in soil associated with this putative nitrogen fixer was not nitrogen limited. In general, the poor nutrient content of Mojave Desert soil relative to soils of other North American deserts may limit the ability of denitrifying bacteria to respond to adequate moisture (Skujiņš 1981).

Role of Ant Colonies in Soil Microbial Activity

The differential response to nutrient additions of ant nest soil compared with other microhabitats is likely due to harvester ant foraging activities, which redistribute organic matter on the landscape, and ant physiological processes, which further alter composition of organic matter available to soil microbes. Harvester ants selectively transport high quality organic matter to nests in the form of seeds. Ants consume the nutrient-rich seed kernel and retain most of the nitrogen, phosphorus, and labile carbon as biomass. Much of the carbon ingested is respired, although some enters the soil along with nitrogen in the form of uric acid waste. Dead ants are removed from the nest and are typically scavenged from the mound by other insect species. Organic compounds containing nitrogen are mineralized by soil microbes to provide carbon, and, because harvester ants remove plants from the surface of the mound, the resulting ammonium and nitrate tend to accumulate (Table 1). Ant nest soil is elevated in standing stocks of soluble organic carbon and soluble total nitrogen, but the C:N ratio of the soluble compounds is low (12.1) relative to the other 2 microhabitats (17.2 under grass and 18.3 in bare spaces; Wagner and Jones 2004). Assuming the standing stocks of soluble carbon are related to bioavailability of organic matter (Qualls and Haines 1992), the varying response of soil microbes in colony soil versus the other microhabitats may be due, in part, to reduced carbon availability relative to nitrogen (Peterjohn and Schlesinger 1991). In addition, the quality of the carbon that ants return to the soil (e.g., seed hulls) may be poor relative to carbon in leaf litter found under plants.

The connection between harvester ant foraging activities and biogeochemical transformations within the landscape may have an important temporal component, with short, intense periods of high microbial activity. Even though respiration and denitrification in harvester ant nest soils were carbon limited at the time of our study, the standing stock of labile organic carbon may vary in response to temporally pulsed seed production and foraging activity of ants. Following seed set, labile organic carbon may greatly increase in colony soil. Rain storms may trigger episodic pulses of soil respiration and loss of nitrogen via denitrification if readily decomposable stores of carbon are available.

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