Ant-mound Effects on Two Adjacent Prairies: Virgin and Plowed

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Abstract

Mound-building *Formica* ants may be important biotic factors within prairie restorations because mounds found in virgin prairies can exist for decades, with densities up to 1,148 mounds/ha (465 mounds/acre). Research on the effects of *Formica* ant mounds on a virgin and an adjacent restored prairie (treatments) was established in 2003 near Olathe, Kansas; and it was expected that percent soil moisture, soil bulk density, plant species' distributions, and percent plant cover would be significantly affected. Data were collected from active mounds (28 in virgin prairie, 21 in restored prairie), and from paired off-mound sites 1 m (3.3 ft) north of each mound. On-mound soils were significantly drier and less dense when both treatments were combined, and within each treatment ($P < 0.05$, respectively). Goldenrod (*Solidago* spp.) and sleeping plant (*Chamaecrista fasiculata*) occurred significantly less often, and with lower cover, on mounds when both treatments were combined ($P < 0.01$). Within the virgin prairie, goldenrod differences were significant ($P < 0.03$), and within the restored prairie, sleeping plant differences were significant ($P < 0.01$). The cover of big bluestem (*Andropogon gerardii*) was significantly higher on mounds when both treatments were combined ($P < 0.03$), and when compared within the restored prairie ($P < 0.02$). This paper demonstrated that mound-building ants significantly affected the virgin and restored prairies' soils and plants, but with variable intensities. These variable effects may have been caused by soil structure and plowing history interactions because mound surfaces were different colors between treatments. These possible interactions should be studied. Also, effects may not be the same at other locations because some prairie restorations have many mound-building ants while others have few. It may be determined, with more study, that mound-building ants should be included in restoration plans.

Keywords: Ant-mound effects, prairies, restoration, *Formica* spp., mound-building ants, soil quality.

Introduction

In many documented cases, virgin prairies often contain mound-building *Formica* ants yet restored prairies contain few or none (Curtis 1959, Baxter and Hole 1967, Kline and Howell 1987, Foster and Kettle 1999). On the occasions when mound-building ants are observed in restored prairies and disturbed grasslands, their colony densities are lower compared to virgin prairies; and colonization takes several years (Curtis 1959, Kline and Howell 1987, Trager 1990, Curry 1994). This trend may not be universal, though, because prairie restorations at Fermi Lab in northern Illinois and The Nature Conservancy's Dunn Ranch in northwest Missouri appear to have mound densities comparable to virgin prairies. However, ant colonies and their effects have not been measured at these sites. Why there are often fewer mound-builders in restored prairies is still uncertain, but their presence may be an important issue in prairie restoration due to their interactions with soils and plants.

Mound-building *Formica* ants are important biotic factors with their soil and herbivorous interactions in several ecosystems, including prairies (Baxter and Hole 1967, Wali and Kannowski 1975, Beattie and Culver 1977, Umbanhowar 1992), forests (Wiken and others 1976), fens (Carpenter and DeWitt 1993, Lesica and Kannowski 1998), and meadows (Levan and Stone 1983, McCahon and Lockwood 1990). Soil interactions include a re-engineered soil environment (sensu Jones and others 1997) with altered moisture, chemistry, and structure (Thorp 1949, Baxter and Hole 1967, Levan and Stone 1983, Laundrè 1990, McCahon and Lockwood 1990, Carlson and Whitford 1991, Curry 1994). These re-engineered soils affect plant community diversity, succession rates, and seed viability (Beattie and Culver 1977, King 1977a and 1977b, Lesica and Kannowski 1998). *Formica*'s effects in prairies, specifically, include changes in soil texture within horizons (Baxter and Hole 1967), added soil fertility in mounds (Wali and Kannowski 1975), and plant species distribution differences between mound and off-mound locations (Beattie and Culver 1977, Umbanhowar 1992). Additionally, these effects may be long-term and large because *Formica* spp. colonies can exist up to 30 years (Henderson and others 1989) with densities as high as 1,148 active mounds/ha (465 mounds/acre) (Baxter and Hole 1967).

Formica's importance in virgin prairies compared to restored prairies is unknown, so a project to study the effects of *Formica* mounds on both a virgin and an adjacent restored prairie was established in 2003 near Olathe, Kansas. Ant mounds were expected to have significant effects on soil traits and plant responses within and between each prairie. Soil trait data included percent soil moisture, and soil bulk density; plant response data included plant species' distributions, and percent plant cover.

Methods

The Kansas Department of Wildlife and Parks burned the virgin (never plowed) and adjacent restored (plowed) prairies in early spring 2003. Forty-nine active ant mounds were marked with rebar and identified with metal tags: 28 in the virgin prairie and 21 in the restored. Mound lengths (north/south axis) and widths (east/west axis) were recorded, and each mound was paired with an equally-sized off-mound area located 1 m north (3.3 ft). For example, if a mound's area equaled 0.80 m^2 (8.61 ft^2), then the matching area was also 0.80 m^2. Data collected from comparable paired on- and off-mound areas insured that field-effect errors were reduced. Mound heights were also recorded in order to compare total mound sizes between prairie treatments, but it was not possible to replicate height in the off-mound areas. While it was not possible to replicate mound height, the off-mound areas were more similar to their paired mounds than if only one constant off-mound area was used. Other on- and off-mound data included percent soil moisture, soil bulk density, plant species' frequencies, and percent plant cover.

Soil data were collected August 10–12, 2003 with a corer to depths of 7.5 cm (3 in) for all on- and off-mound samples (corer volume was 14.4 cm^3 (0.9 in^3). This depth ensured that the ant mounds were preserved for future studies. Two soil cores per mound and two per off-mound were collected. Both on-mound samples were combined before analyses, and likewise for both off-mound samples. This created one paired on- and off-mound sample set. Each core's data set included percent soil moisture and bulk density. Percent soil moisture was obtained by weighing each core, drying at 60° C (140° F) for 48 hours, and then weighing again, making the final value for percent soil moisture: % soil moisture = (wet weight-dry weight/wet weight) x 100. Soil bulk density was obtained by the following: bulk density = dry weight/14.4 cm^3.

Plant data were collected during September 7– 20, 2003 by recording species occurrences and assigning cover value categories. Plants species were identified using nomenclature from the PLANTS Database (USDA, NRCS 2005). Cover categories were a modified Daubenmire scale (Daubenmire 1968), and included a trace cover category. During analyses, all plant species were assigned zero if not present, and all field-recorded 0 classes were transformed to 0.5% cover. Percent cover classes, and ranges, were thus: absent = 0, trace = 0.5, 1 = 0.5–5, 2 = 5.0–25, 3 = 25–50, 4 = 50–75, 5 = 75–95, and 6 > 95.

Wilcoxon signed-rank tests were used when soil and plant results were simultaneously compared across both treatments (ant mound and prairie), and Kruskal-Wallis one-way analysis of variance tests were used when results were compared within only one treatment. Statistix (Analytical Software 2000) was used for all statistical tests.

Results

All mounds on the virgin prairie contained one ant species, *Formica subsericea* (Say), with average mound axes just less than 0.5 m (1.6 ft) (Table 1). The restored prairie contained two mound-building species—*F. subsericea* and *F. schaufussi* (Mayr)—but there were too few mounds of each species in the restored prairie to separate them for statistical analyses. Average mound heights and axes for both species combined were significantly less than mounds on the virgin prairie (Table 1, $P < 0.001$).

Percent soil moisture and bulk density were always significantly lower on the mounds within each prairie (Table 2, $P < 0.05$, Table 3, $P < 0.001$), and when all mounds were compared. Percent soil moisture values between off-mound data of virgin and restored prairies were also significantly different (Table 2, $P < 0.03$), but on-mound soil moisture was not significantly different between prairie treatments ($P < 0.33$). Soil bulk densities on mounds were not significantly different between prairie treatments, nor were they for off-mounds (Table 3, $P < 0.13$ and $P < 0.31$, respectively).

Table 1. Average mound sizes (mean + se) in virgin and restored prairies.

	Virgin (n=28)	Restored (n=21)
Height (cm)	15.3 (1.0)	9.1 (0.7)[a]
North/south axis (cm)	47.5 (3.2)	29.2 (9.2)[a]
East/west axis (cm)	44.6 (2.5)	24.3 (1.5)[a]

[a] Significantly different between virgin and restored ($P < 0.001$) using Kruskal-Wallis one-way analysis of variance.

Table 2. Percent soil moisture averages (mean + se) between on and off mounds for combined, virgin, and restored prairies.

	Combined (n=49)	Virgin (n=28 pairs)	Restored (n=21 pairs)
On-mound	7.1 (0.0) [a]	6.9 (0.0) [a]	7.4 (0.01) [a]
Off-mound	11.6 (0.0)	11.9 (0.0)	11.0 (0.01)

[a] On- and off-mound data were significantly different ($P < 0.05$) when both prairies were combined, and when data were analyzed within each prairie.

Table 3. Soil bulk density averages (mean + se) between on and off mounds for combined, virgin, and restored prairies.

	Combined	Virgin	Restored
On-mound (g/cm^3)	0.79 (0.04) [a]	0.74 (0.04) [a]	0.86 (0.06) [a]
Off-mound (g/cm^3)	1.37 (0.03)	1.35 (0.03)	1.40 (0.04)

[a] On- and off-mound data were significantly different ($P < 0.001$) when both prairies were combined, and when data were analyzed within each prairie.

Forty plants were identified to genus, but most occurred so infrequently that they were unusable for statistical purposes. Many aster species and goldenrod species were difficult to identify, so they were grouped into their respective genera. The grass species, prairie dropseed (*Sporobolus* spp.), were not blooming at the time of data collection so they were grouped into genus. The final number of plant species usable for analyses was eight: three forbs and six grasses (Table 4). Both sleeping plant (*Chamaecrista fasciculate*, Michx.), and goldenrod (*Solidago* spp.) occurred significantly less often on mounds compared to off mounds (Table 4), but sleeping plant was significantly different within the restored prairie ($P < 0.01$), and goldenrod within the virgin prairie ($P < 0.03$). Frequencies of the other six species were not significantly different between on- and off-mounds, or between prairies.

Plant cover was significantly less on mounds for the two forbs—sleeping plant and goldenrod (Table 5). Sleeping plant was significantly different within the restored prairie ($P < 0.01$), and goldenrod was different within the virgin prairie ($P < 0.03$). For grasses, big bluestem (*Andropogon gerardii*, Vitman) had significantly lower cover off-mounds within the restored prairie ($P < 0.02$), but this difference was great enough to make the combined comparison between all off-mound and on-mound values appear significant ($P < 0.03$). Within the restored prairie, big bluestem had ten cover classes greater than 2 off the mounds, and 14 cover classes greater than 2 on the mounds.

Discussion

Mound-building ants had significant effects on the soils and plants of both the virgin and restored prairies, albeit with inconsistent results. Percent moisture and soil bulk density were both consistently lower on mounds compared to off mounds for both prairies. Even though the ant mounds were significantly smaller on the restored prairie, the effects of mounds on soils were similar. Thus, mound-building ants must have been significant biotic factors affecting soil conditions. Significantly drier and looser (more friable) on-mound soil results have also been observed on another virgin prairie (Foster, unpublished data). Soil moisture trends were not as consistent. Off-mound data trends for soil moisture comparisons between prairie treatments were significant, but bulk density comparisons were not. The plowed prairie's agricultural history may have had a strong influence on the soils' condition, obscuring the ants' mound-building activities. The significantly smaller *Formica* spp. mounds on the restored prairie indicated that these mounds are possibly younger (Henderson and others 1989), and not enough time had passed to produce a prairie-wide change.

Plant frequencies and percent cover were significantly lower on mounds compared to off mounds for a few of the most common species, but not always within the same prairie treatment. There may have been an interaction between the ant mounds and prairie treatment in relation to plant response to moisture and soil bulk density. Nevertheless, the trends were consistent with lower or equal on-mound frequencies and percent cover compared to off-mound data. Lower frequencies and percent cover on mounds were observed in another virgin prairie as well (Foster, unpublished data). The one surprise was the significantly higher on-mound cover for big bluestem within the restored prairie. Higher cover may have resulted from lack of competition for space from other plants. Big bluestem is known to be an aggressive colonizer in restorations such that it has been suggested to introduce this grass species after others have become established (see references in Packard and Mutel 1997). This idea is supported by big bluestem not having significant cover differences within the virgin prairie, and the same trend occurring at the Fermilab restored prairie in Illinois (Sluis 2002).

A reason for lack of significance for most plants may have been sample size. Fifty-eight ant mounds were originally

Table 4. Eight most common plants and their frequencies on and off mounds.

Name	Combined		Virgin		Restored	
	On	Off	On	Off	On	Off
Forbs						
Aster (*Aster* spp)	2	11	1	9	1	2
Sleeping plant *Chamaecrista fasciculata*	3	16[a]	2	4	1	12[a]
Goldenrod *Solidago* spp.	8	24[a]	5	17[b]	3	7
Grasses						
Big bluestem *Andropogon gerardii*	31	38	17	21	14	17
Switchgrass *Panicum virgatum*	5	12	5	10	0	2
Little bluestem *Schizachyrium scoparium*	5	5	4	4	1	1
Indiangrass *Sorghastrum nutans*	9	10	5	6	4	4
Prairie dropseed *Sporobolus* spp.	3	8	1	3	2	5

[a] – Frequencies were significantly different between on and off mounds ($P < 0.01$)
[b] – Frequencies were significantly different between on and off mounds ($P < 0.03$)

Table 5. Percent plant cover listed as minimum to maximum ranges. (See Table 4 for scientific names).*

	Combined		Virgin		Restored	
Name	On	Off	On	Off	On	Off
Forbs						
Aster	15.0 – 15.0	2.3 – 15.0	15.0 – 15.0	2.3 – 15.0	absent	2.3 – 2.3
Sleeping plant	0.5 – 15.0	0.5 – 37.5[a]	2.3 – 2.3	15.0 – 37.5	0.5 – 0.5	0.5 – 37.5[a]
Goldenrod	0.5 – 37.5	0.5 – 85.0[a]	0.5 – 37.5	0.5 – 85.0[b]	2.3 – 15.0	2.3 – 85.0
Grasses						
Big bluestem	0.5 – 97.5	0.5 – 97.5[b]	0.5 – 97.5	0.5 – 97.5	0.5 – 97.5	0.5 – 97.5[c]
Switchgrass	2.3 – 37.5	0.5 – 62.5	2.3 – 37.5	0.5 – 62.5	absent	0.5 – 2.3
Little bluestem	0.5 – 37.5	2.3 – 37.5	0.5 – 37.5	2.3 – 15.0	15.0 – 15.0	37.5 – 37.5
Indiangrass	2.3 – 37.5	2.3 – 37.5	15.0 – 37.5	2.3 – 37.5	2.3 – 15.0	2.3 – 37.5
Prairie dropseed	0.5 – 37.5	0.5 – 37.5	37.5 – 37.5	2.3 – 37.5	0.5 – 2.3	0.5 – 37.5

*Percentages reported as minimum to maximum ranges based on group classifications. Due to pairing, some values may seem equal when they were actually different within pairs.

[a] - Frequencies were significantly different ($P < 0.01$)

[b] - Frequencies were significantly different ($P < 0.03$)

[c] - Frequencies were significantly different ($P < 0.02$)

marked for study but, due to a mowing accident that removed many mounds and vegetation, the number was reduced to 49. Another problem may have been related to which soil horizons the ants were moving. Virgin prairies traditionally have relatively deep A-horizons (Curtis 1959, Weaver 1968), whereas plowed prairies have more shallow A-horizons, due to farming activities, that could take several decades for the disturbed soil to return to pre-disturbance quality (see references in Jastrow 1987). In this study, I found that many mounds on the restored prairie were a lighter color compared to off-mound locations, so it was likely that the ants were moving a different soil horizon to the mounds' surfaces compared to those in the virgin prairie. Additionally, this soil difference may influence ant behavior and cause them to build smaller mounds. These unmeasured interactions should be studied.

Historically, tallgrass prairie restoration managers have assumed that reintroduced plant communities will contain the same levels of plant biodiversity and biotic interactions as those found in extant virgin prairies (Anderson and Cottam 1968, Fitch and Hall 1978, see references in Packard and Mutel 1997). Unfortunately, these restored communities have not reached desired levels (Kline and Howell 1987, Kindscher and Tieszen 1998, Sluis 2002). Planned ant introductions in experimental prairie restorations would be an appropriate next step to document soil changes, including the ants' interactions with soil horizons. Additionally, restored prairies that contain several mound-building ant colonies should be compared to those that lack these insects. If mound-building ants can alter the rate, or quality of restoration, then their inclusion for restoration may become important in prairie management plans (Kline and Howell 1987, Trager 1990).

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