2013

Pedogenesis of ant-colonized soils at Doolittle Prairie State Preserve, Iowa

Mary Lee Tiedeman

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Pedogenesis of ant-colonized soils at Doolittle Prairie State Preserve, Iowa

by

Mary Lee Tiedeman

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Co-majors: Soil Science (Soil Morphology and Genesis); Environmental Science

Program of Study Committee:
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Thomas Loynachan
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Iowa State University
Ames, Iowa
2013

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Chapter 1. General Introduction

The breadth, diversity, and population density of ants are tremendous. Because of this, and because they are such dominant ecosystem engineers, ants greatly alter their surrounding environments. The purpose of my research is to document the influence of ant activity on pedogenesis in Doolittle Prairie State Preserve. The land from which my samples were taken has never been cultivated and is one of the few remnant prairies within the state of Iowa.

The hypotheses driving this investigation are:

**H₀**: Pedological properties on and off mounds are identical.

**Hₐ₁**: Pedological properties vary on and off of mounds, and properties within a mound are isotropic.

**Hₐ₂**: Isotropy extends beyond the mound radius.

These hypotheses were tested by sampling and describing 11 ant mound transects within Doolittle Prairie State Preserve. Each transect began at the mound periphery and extended across the mound center into the adjacent soil.

In Chapter 2, I present a review of the literature that has prepared me for this bioturbation study. Chapter 3 details and discusses how *Formica montana* Wheeler colonies have influenced the soils of a remnant prairie in Iowa. Conclusions of this study are presented in Chapter 4.
Chapter 2. Literature Review

Introduction

Classic pedological theory identifies five environmental state factors of soil formation: climate \( (cl) \), time \( (t) \), parent material \( (p) \), relief \( (r) \), and organisms \( (o) \). Vasili Dokuchaev, who is known as the father of soil science, was one of the first scientists to develop a model of soil genesis in which soils were seen as a function of varying environmental state factors (Schaetzl and Anderson, 2005). Hans Jenny (1941) further developed this model of soil formation in his famous book, *Factors of Soil Formation*. Jenny’s work elevated the “state factors” model into the primary pedogenic model worldwide (Schaetzl and Anderson, 2005). This model is of great importance, especially when used for soil mapping or education (Jenny, 1946; Johnson and Hole, 1994; Schaetzl and Anderson, 2005).

A major weakness of the “state factors” model is in the way the “o” factor has been interpreted throughout its history. The majority of those applying the model have viewed the “o” factor almost exclusively as the influence of vegetation on soils. Unfortunately, this has resulted in the neglect of other important biological soil forming mechanisms, such as bioturbation (Johnson, 2000).

Bioturbation is the physical displacement of soil by organisms. It is a concept that was first formally discussed by Charles Darwin in his book entitled “*The Formation of Vegetable Mould through the Action of Worms, with Observations on their Habits*” (1881). Within this work, Darwin touched on many key pedological concepts related to activities of earthworms, including rates of bedrock weathering
(i.e. soil formation), incorporation of organic material into the soil subsurface horizons, mineral transport across landscape gradients, and the burial of coarse materials over time (Darwin, 1881). Unfortunately, classical pedology did not incorporate these early concepts. Luckily, by the mid-20th century, a few influential pedologists began where Darwin left off.

The work of Hole (1961) and Johnson et al. (1987) began to remind soil scientists of two major aspects of soil genesis in relation to soil mixing: isotropy and anisotropy. Soil anisotropy is the movement of soil bodies to a more ordered state. Alternatively, soil isotropy is the movement of soil bodies towards disorder (Schaetzl and Anderson, 2005).

In the context of pedoturbation, Francis Hole (1961) relayed the idea that order and/or soil development can be and are commonly disrupted by physical and biological soil mixing. Though anisotropy and isotropy starkly contrast one another, it is important to recognize that both processes can occur simultaneously within a soil profile (Schaetzl and Anderson, 2005). For example, while pocket gopher bioturbation disrupts and or destroys soil horizonation, it also has been shown to assist in the formation of subsurface stone lines (Johnson, 1989).

**Formica montana Wheeler**

The prairie ants involved in this study (*F. montana* Wheeler) were identified by Stefan Cover, curatorial assistant of Harvard University’s Museum
of Comparative Zoology. This organism was first identified by Carlo Emery (1891). A revision of the species was made by William Wheeler in 1913.

*F. montana* mounds have flat, elevated surfaces covered with fragmented plant material. These ants are predominately found in prairie soils with udic and aquic moisture regimes. Occurrence of mounds within prairies can be over one hundred per hectare with mound diameters ranging from tens of centimeters to over two meters in length (Wheeler, 1902; Talbot, 1934; Curtis, 1955; Baxter and Hole, 1967).

These ants are polydomous, meaning that each colony commonly has multiple queens and is capable of producing more than one mound. Budding mounds are located relatively close to each colony’s older, established mound (Henderson et al., 1989; Henderson and Jeanne, 1992). Tunnels connect the established mound to budding mounds, which may explain why queens are rarely seen flying to new locations (Henderson and Jeanne, 1992). The expansion into new mounds is most likely influenced by the availability and access to food sources, such as aphid honeydew (Henderson and Jeanne, 1992).

Smaller ephemeral mounds are often built to access aphid populations near the central mound. These “food source” mounds are seasonal and are vacated with the onset of winter (Denning et al., 1977). A colony’s central mound can remain active for several decades (Henderson et al., 1989).
Many factors influence the size of ant mounds. Baxter and Hole (1967) studied *F. montana* colonies in both well-drained and poorly drained prairie soils. They noticed larger mounds in poorly drained soils compared to those that were well drained. A possible reason for this could be that ants must expand their nests outward in wet conditions to make up for their inability to dig deep into the soil profile (Baxter and Hole, 1967). A few other factors that could influence size of mounds include mound age and presence or absence of competing colonies. When studying mound longevity in *F. montana* in southwestern Wisconsin, Henderson et al. (1989) noted that mounds of these organisms also occasionally merge together.

**Influence on soil properties**

Bioturbation by ants results in low soil bulk density throughout their mounds (Baxter and Hole, 1967; Rogers, 1972; King, 1977, Lobry de Bruin and Conacher, 1990). Baxter and Hole (1967) also noted nearly 85% of surface material of *F. montana* mounds consisted of material from the B horizon. Illuviation of clay is then disrupted due to the constant displacement and removal of material from the subsurface to the upper profile (Baxter and Hole, 1967).

**Influence on soil chemical properties**

Ants impact soil nutrient availability. Previous studies by Baxter and Hole (1967) showed that *F. montana* activities increased available soil phosphorus, potassium, exchangeable calcium, and magnesium. Lane and BassiRad (2005) have also observed nutrient accumulation within mounds, but showed that this
variability in relation to adjacent soils decreases with mound age. Influence on soil pH is variable. Some studies have shown the activity of ants to increase soil pH (Petal, 1980; Czerwinski et al., 1971; Levan and Stone, 1983), while others found no difference (Baxter and Hole, 1967; Petal, 1980; Culver and Beattie, 1983).

Doolittle Prairie State Preserve

Natural history

Doolittle Prairie State Preserve is located in the southeast quadrant of the Des Moines Lobe in Iowa. The Des Moines Lobe is one of the eight designated landform regions within the state, and is set apart from the others because it was the last region to be touched by glacial ice (Fig. 2.1). This Late Wisconsin glacial ice sheet extended from Canada into the United States and was as far reaching as southern Indiana and Ohio (Fig. 2.2). It advanced south into central Iowa between 12,500 to 14,000 years ago and fully receded by 10,500 years before present (Prior, 1991). The landform patterns of the Des Moines Lobe directly reflect this most recent glacial activity and include morainal ridges, eskers, kames, till and outwash plains, broad valleys formed from glacial melt water, and closed drainage basins (Prior, 1991).

The landscape of and surrounding Doolittle Prairie State Preserve is characterized by its flat topography dimpled with shallow closed drainage basins. The region is casually referred to as the “Story City Flats.” Between 12 and 13 thousand years ago during the last glacial advance, the Story City Flats region (roughly 900 square kilometers) was covered by glacial Lake Wright (Figure 2.3).
Figure 2.1. Landform regions of Iowa (original map from *Landforms of Iowa* Prior, 1991).

Figure 2.2. Extent of the Late-Wisconsinan glacial advance into Iowa (original map from *Landforms of Iowa* Prior, 1991). The star indicates the location of Doolittle Prairie State Preserve.
In turn, the surficial diamicton blanketing this area is fine textured lacustrine sediment atop glacial till (DeWitt, 1984).

**Soils of Doolittle Prairie**

The soils encompassing Doolittle Prairie State Preserve are poorly to very poorly drained, are of silty clay loam textures, and are members of the Kossuth-Ottosen-Bode soil association (DeWitt, 1984). Soil series of relevance are the Kossuth, Ottosen, Bode, Okoboji, and Harps (Table 2.1). The dominant map units within the preserve are 388 (Kossuth) and 288 (Ottosen) (Figure 2.4) (DeWitt, 1984).
Table 2.1. Soil legend for Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th>Soil map unit</th>
<th>Soil series</th>
<th>USDA soil taxonomic class</th>
</tr>
</thead>
<tbody>
<tr>
<td>288</td>
<td>Ottosen</td>
<td>Aquic Hapludoll</td>
</tr>
<tr>
<td>388</td>
<td>Kossuth</td>
<td>Typic Endoaquoll</td>
</tr>
<tr>
<td>Δ 6</td>
<td>Okoboji</td>
<td>Cumulic Vertic Endoaquoll</td>
</tr>
<tr>
<td>Δ 95</td>
<td>Harps</td>
<td>Typic Calciaquoll</td>
</tr>
</tbody>
</table>

Figure 2.4. Soil map of Doolittle Prairie State Preserve (NRCS, 2010). Stars to the right represent the eleven mounds sampled for this study. The white star represents Mound 10. The darkest star represents Mound 11.
Chapter 3. Pedogenesis of Ant Colonized Soils at Doolittle Prairie State Preserve, Iowa

Mary L. Tiedeman and C. Lee Burras

A paper to be submitted to the Soil Science Society of America Journal

Abstract:

Ants are among the most prolific soil-dwelling organisms in terms of overall biomass, spatial distribution, and diversity. Though the breadth of ant activity within soil is tremendous, little work has been done to show the influence of ants on near-hydric and hydric soils. This study quantified the impact of *Formica montana* Wheeler activities on soil morphology and genesis in an undisturbed Iowa prairie. Soils were sampled to depths of 120 cm or greater along transects to include mound centers, peripheries, and adjacent areas. Results showed soil profiles within mounds had deeper A horizons and thinner B horizons than adjacent soils. Profile differences on and off of mounds also included color, structure, depth to carbonates, calcite and dolomite content, stable aggregate content, and total nitrogen.

Introduction:

Many people have investigated the impact of ants on their soil environments. These studies have shown increased soil nutrient levels, lower bulk densities, alterations in pH, and burial of coarse materials in association with ant colonization (Baxter and Hole, 1967; Petal, 1980; Czerwinski et al., 1971; Rogers, 1972; King, 1977; Levan and Stone, 1983; Lane and BassiRad, 2005; Johnson and Johnson, 2010). In other words, ant bioturbation results in chemical and physical
changes in soil properties. Presumably, they also result in biological and pedological changes.

The ants involved in this study were identified as *Formica montana* Wheeler. This ant species inhabits prairie soils with udic and aquic moisture regimes (Stefan Cover, Personal Communication, July 2nd, 2013). The density of their mounds within prairies can be over one hundred per hectare with mound diameters ranging from tens of centimeters to over two meters in length (Wheeler, 1902; Talbot, 1934; Curtis, 1955; Baxter and Hole, 1967). *F. montana* are polydomous, meaning that each colony commonly has multiple queens and is capable of producing more than one mound (Henderson et al., 1989; Henderson and Jeanne, 1992). Ephemeral mounds are commonly built to serve as a direct access to aphid populations from the central mound. These “food source” mounds are seasonal and are vacated with the onset of winter (Denning et al., 1977). The colony’s central mound can remain active for several decades (Henderson et al., 1989)

**Materials and Methods**

**Study area**

Doolittle Prairie State Preserve, located six km south of Story City, Iowa, encompasses 10.5 hectares of remnant tall grass prairie (Herzberg and Pearson, 2001). The landscape of Doolittle Prairie is dimpled with several prairie potholes, and is one of the few remaining prairie pothole wetland complexes left within the Des Moines Lobe of Iowa (Herzberg and Pearson, 2001).
The land area surrounding this preserve is intensively cultivated, and has been since European settlement in the mid to late 1800's. The majority of the land contiguous to Doolittle Prairie State Preserve is extensively artificially drained. The preserve itself has never been tilled, cultivated, or drained (Wetzel, et al., 1999).

Soils of Doolittle Prairie State Preserve

The soils at Doolittle Prairie are derived from lacustrine sediments over Wisconsin aged glacial till (DeWitt, 1984; NRCS, 2013). This area contains two soil map units: the Kossuth (388) and Ottosen (288) (DeWitt, 1984; NRCS, 2013). Inclusions within these two map units are the Bode, Okoboji, and Harps soil series (DeWitt, 1984; NRCS 2013) as shown in Figure 2.4 and Table 2.1 in Chapter 2 of this thesis.

Mound and soil sampling

Eleven active mounds were selected for investigation. The height and diameter of each mound were determined. The surface volume of each mound was generated with height and diameter data to calculate the volume of a cylinder.

Seventy-eight soil cores were sampled from 11 ant mounds within Doolittle Prairie State Preserve (Figure 2.4). Cores were collected using the sampling scheme presented in Figure 3.1. Sixty-four of these cores were sampled to a depth of 120 cm using a push tube with a diameter of 1.9 cm. The other eight cores were from Mound 11 (Figure 2.4). Cores were sampled using a truck-mounted hydraulic soil
Figure 3.1. Sampling scheme of ant mounds and surrounding areas; center of mound ("bullseye"), mound periphery (on circle), and adjacent soils (two times the diameter's length away from the periphery).

A probe (Giddings's Machine Company, Windsor, CO) fitted with a 150-cm long, 6-cm diameter soil sampling tube. This variation in sampling methods was done to accommodate for the size of Mound 11, which was extensively larger than the other 10 mounds. The number of cores taken from each mound and their sampling geography is shown in Table 3.1.

Table 3.1a. Cores sampled from Doolittle Prairie State Preserve. Underlined cores in red were analyzed for total carbon, total nitrogen, stable aggregate content, pH, and calcite/dolomite content. Those italicized and in blue were analyzed for total carbon, total nitrogen, calcite/dolomite content, bulk density, and percent coarse fragments.

<table>
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<tr>
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<td>1</td>
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<td>2</td>
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<td>4(1)</td>
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<td>6</td>
<td>6</td>
<td>14</td>
<td>8</td>
<td>78</td>
</tr>
</tbody>
</table>

Table 3.1b. Laboratory analyzed samples from Doolittle Prairie State Preserve.
### Soil description and characterization

Each core was described according to the methods outlined in the Field Book for Describing and Sampling Soils (Schoeneberger et al., 2002). Horizon type, depth, boundary, structure, redoximorphic features, mottling, roots, pores, and presence of biological activity were determined for each horizon. Color (Hue, Value, and Chroma) was determined using a Munsell Soil Color Chart. Effervescence was determined by applying 10% hydrochloric acid to each sample to note the severity of the acid’s reaction to soil carbonates. Seventy-two of the 78 profiles were classified to subgroup using US Soil Taxonomy (Soil Survey Staff, 2010). Two periphery soil descriptions from Mounds 1 and 4 and four periphery soil descriptions from Mound 2 were omitted due to a lack of information.

### Laboratory analyses

Bulk density was determined on eight profiles (Table 3.1). The volume of each horizon was calculated as horizon length times the cross-sectional area of the soil core. The mass of each sample was determined after oven drying at 105°C for

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<td>33</td>
<td>73</td>
<td>58</td>
<td>256</td>
</tr>
</tbody>
</table>
24 hours. Bulk density was calculated by dividing the mass of each horizon by its volume.

After soil samples (Table 3.1) were oven-dried, weighed, and ground, they were passed through a 2-mm sieve. All fragments greater than 2 mm were rinsed with de-ionized water to remove any residual fine material. The coarse fragments were then oven dried and weighed. Coarse fragment percentage per sample was determined as percent of the total sample weight.

Stable aggregate content (Table 3.1) was determined using dried soil aggregates following the method of Patton et al. (2001).

Forty-one profiles (Table 3.1) were analyzed for pH, total carbon, total nitrogen, calcite and dolomite content, and calcium carbonate equivalency.

Soil pH was measured in water with a battery operated pH pen using a two-to-one water:soil suspension. This method was chosen due to the minimal amount of soil available for all analyses. Total carbon and total nitrogen were measured using the dry combustion method on a Leco elemental analyzer (St. Joseph, MI, USA).

Calcite and dolomite contents were determined gravimetrically using a modified version of the gas evolution method published by the USDA-NRCS (Soil Survey Field and Laboratory Methods Manual, 2009). A known weight of 6M HCl was added to a known weight of ground soil, in a weighing boat on a top-loading balance. The weight losses due to emissions of CO₂ after 30 seconds and 30 minutes were recorded and assigned to calcite and dolomite decomposition, respectively.
The calculations for deriving percent calcite and percent dolomite are outlined below:

**CaCO₃:**

\[
\text{\%} = \frac{g \text{ CO}_2 \text{ lost @ 30 sec}}{g \text{ soil}} \times \frac{g \text{ CaCO}_3 \text{ mol}^{-1}}{g \text{ CO}_2 \text{ mol}^{-1}} \times 100 \\
= \frac{g \text{ CO}_2 \text{ lost @ 30 sec} \times (2.273)}{g \text{ soil}} \times (100)
\]

**CaMg(CO₃)₂:**

\[
\text{\%} = \frac{g \text{ CO}_2 \text{ lost @ 30 min.} - g \text{ CO}_2 \text{ lost @ 30 sec}}{g \text{ soil}} \times \frac{g \text{ CaMg(CO}_3)_2 \text{ mol}^{-1}}{g \text{ 2CO}_2 \text{ mol}^{-1}} \times 100 \\
= \frac{g \text{ CO}_2 \text{ lost @ 30 min.} - g \text{ CO}_2 \text{ lost @ 30 sec} \times (2.095)}{g \text{ soil}} \times (100)
\]

**Statistical analyses**

The data from mound centers, peripheries, and adjacent soils were analyzed statistically using Microsoft Excel 14.3.6 (Santa Rosa, 2011). The following were determined: mean, standard deviation, t value, linear regression, skewness, and kurtosis. T values were generated using a two-tailed t-test assuming equal variance. Regression analyses were executed through the chart function within Excel. Significance was obtained using the linear regression model within STATPLUS 2009 (2010).

**Conventions and abbreviations**

The rest of this manuscript contain these conventions and abbreviations:

1. All averages within the following tables are paired with their associated standard deviations.
2. Many tables contain kurtosis and skewness values alongside calculated averages and standard deviations. Though there is no further discussion of these values, it is important to highlight how they should be interpreted. Kurtosis measures the height and sharpness of a distribution's peak. High values represent high, sharp peaks. Low values represent low, less defined peaks. Skewness measures the symmetry of a distribution. A distribution is symmetrical if it has a skewness of zero, weighted left if it has a negative skewness value, and weighted to the right if it has a positive skewness value.

3. Abbreviations:
   - * - 5% level of significance
   - ** - 1% level of significance
   - *** - \( \leq 0.1\% \)
   - Bulk Density - BD
   - Calcium Carbonate Equivalency - CCE
   - Carbon Nitrogen Ratio - C:N
   - Coarse Fragments - CF
   - Organic Carbon - OC
   - Stable Aggregate Content - SAC
   - Total Nitrogen - TN
Results and Discussion:

Mound characteristics

The 11 mounds were all flat, saucer-shaped, had minimal vegetative cover, and were covered with fine fragments of dried plant material (Figure 3.2). The mineral surface of the mounds consisted of very fine calcareous material atop a rigid crust. Multiple entryways into each mound were observed. Over the two years of this study, all mounds were active, and were not abandoned by ants.

Figure 3.2. Mound 5: an example of an *F. montana* mound at Doolittle Prairie State Preserve.

Mound volumes varied considerably, ranging from 0.01 to 0.97 m$^3$. The average height, diameter, and surface volumes were 0.19 m, 0.89 m, and 0.17 m$^3$, respectively (Table 3.2). Unpublished research by Bolender, Burras, and Ricks (1996) estimated that there are roughly 100 mounds per hectare within Doolittle Prairie State Preserve. When incorporating the information from this study with
Table 3.2. Aboveground dimensions of *F. montana* mounds at Doolittle Prairie State Preserve. (n=11)

<table>
<thead>
<tr>
<th></th>
<th>Minimum</th>
<th>Maximum</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (m)</td>
<td>0.11</td>
<td>0.30</td>
<td>0.19 ± 0.07</td>
</tr>
<tr>
<td>Diameter (m)</td>
<td>0.40</td>
<td>2.03</td>
<td>0.89 ± 0.45</td>
</tr>
<tr>
<td>Surface Volume (m³)</td>
<td>0.01</td>
<td>0.97</td>
<td>0.17 ± 0.27</td>
</tr>
</tbody>
</table>

that from Bolender, Burras, and Ricks (1996), it could be estimated that the surfaces of these mounds cover nearly 650 m² of the 10.5-hectare preserve, or 0.6% of the total land area. Baxter and Hole (1967) estimated that *F. montana* covered 1.7% of the surface area of a prairie remnant in Wisconsin.

Depth of ant bioturbation was determined using presence of channels and backfill containing color, structure, or mineralogy different from the soil matrix. The average depth of bioturbation for mound centers was 90 cm and the average depth for the mound periphery was 83 cm. It is important to note that of the 16 center soils, 75% of them showed channeling and/or backfilling at the base of the profile. Thirty-one percent of the periphery cores showed signs of bioturbation at the base of their profiles (Table 3.3).

Bioturbation extended deeper than was sampled in many cases. This is one reason why Mound 11 was sampled at a greater depth. The two cores taken from the center of Mound 11 had an average ant bioturbation depth of 158 cm. The four periphery profiles showed bioturbation reaching an average depth of 153 cm.
Table 3.3. Profiles with observed ant bioturbation (BT) at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>n=cores sampled</th>
<th>n= cores w/BT</th>
<th>Avg. BT depth (cm)</th>
<th>Percent of cores w/ BT to base</th>
<th>Max depth of BT (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Center</td>
<td>16</td>
<td>16</td>
<td>90±29</td>
<td>75%</td>
<td>162</td>
</tr>
<tr>
<td>All Periphery</td>
<td>48</td>
<td>43</td>
<td>83±29</td>
<td>31%</td>
<td>175</td>
</tr>
<tr>
<td>All Adjacent</td>
<td>14</td>
<td>2</td>
<td>79±22</td>
<td>14%</td>
<td>93*</td>
</tr>
<tr>
<td>M11 Center</td>
<td>2</td>
<td>2</td>
<td>158</td>
<td>100%</td>
<td>162</td>
</tr>
<tr>
<td>M11 Periphery</td>
<td>4</td>
<td>4</td>
<td>153</td>
<td>50%</td>
<td>175</td>
</tr>
<tr>
<td>M11 Adjacent</td>
<td>2</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* It is interpreted that the two adjacent cores with observed ant bioturbation were previously occupied and now abandoned.
(Table 3.3). When accounting for total above and belowground bioturbation, the volume of Mound 11 was 5 m$^3$.

It was assumed that ant bioturbation was limited to the depth of the water table. However, it was observed that ant activities went well beyond the depth of gleying, which occurred at an average depth of 75 cm for soil adjacent to ant mounds. Our interpretation from this is ants are opportunists who take advantage of the subsurface horizons during the months when the seasonally high water table has receded.

**Soil classification**

All 72 profiles classified were Mollisols. Fifty-seven of these were udolls and 15 were aquolls. When comparing the 16 center profiles with their associated adjacent soils, 31% were of a different suborder, 88% were of a different great group, and 100% were of a different subgroup. Twelve percent of the periphery soils were of a different suborder, 90% of a different great group, and 98% of a different subgroup (Table 3.4).

Table 3.4. Percent of mound profiles varying taxonomically from adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Order</th>
<th>Suborder</th>
<th>Great Group</th>
<th>Subgroup</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Center</td>
<td>0 %</td>
<td>31%</td>
<td>88%</td>
<td>100%</td>
<td>16</td>
</tr>
<tr>
<td>Periphery</td>
<td>0%</td>
<td>12%</td>
<td>90%</td>
<td>98%</td>
<td>42</td>
</tr>
</tbody>
</table>
Of the 14 adjacent profiles classified, nine were Aquic Hapludolls, three were Typic Hapludolls, and two were Cumulic Endoaquolls. The centers soils were identified as Typic Vermudolls, Haplic Vermudolls, and Typic Endoaquolls. Forty of the 42 periphery soils shared the same three classifications with the center soils (Table 3.5).

The other two profiles (both from Mound 10) were classified as a Vermic Hapludoll and a Typic Hapludoll. These profiles show that bioturbation does not extend radially in a symmetrical manner. In this case, one periphery soil mirrored its adjacent soil (Typic Hapludoll), one showed slight signs of bioturbation (Vermic Hapludoll), and the others mirrored the intensively mixed center soils (Typic and Haplic Vermudolls) (Table 3.5).

Five center and periphery profiles were characterized as Typic Endoaquolls compared to their adjacent soils (which were all classified as Aquic Hapludolls) (Table 3.5). One may assume this classification variation is due to changes in soil hydrology. We would argue instead that ants are influencing soil morphology by moving redoximorphic and gleyed materials from the B horizon to shallower depths. Baxter and Hole (1967) determined that 85% of soil within the mounds of *F. montana* consisted of material from the B horizon. We then suggest that these soils should more appropriately be classified as Vermudolls and not Endoaquolls.

*Soil classification in relation to mound size*

Baxter and Hole (1967) observed *F. montana* mounds in naturally well-drained uplands as well as in wetland soils. They observed that ants inhabiting
Table 3.5. U.S. Taxonomic classification of center, periphery, and adjacent profiles at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>n</th>
<th>Periphery</th>
<th>n</th>
<th>Adjacent</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Typic Endoaquoll</td>
<td>2</td>
<td>Typic Endoaquoll</td>
<td>2</td>
<td>Cumulic Endoaquoll</td>
<td>1</td>
</tr>
<tr>
<td>M2</td>
<td>Typic Vermudoll</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>Cumulic Endoaquoll</td>
<td>1</td>
</tr>
<tr>
<td>M3</td>
<td>Haplic Vermudoll</td>
<td>2</td>
<td>Haplic Vermudoll</td>
<td>4</td>
<td>Aquic Hapludoll</td>
<td>1</td>
</tr>
<tr>
<td>M4</td>
<td>Haplic Vermudoll</td>
<td>1</td>
<td>Typic Vermudoll Haplic Vermudoll</td>
<td>2</td>
<td>Aquic Hapludoll</td>
<td>1</td>
</tr>
<tr>
<td>M5</td>
<td>Typic Endoaquoll</td>
<td>1</td>
<td>Haplic Vermudoll Typic Endoaquoll</td>
<td>3</td>
<td>Aquic Hapludoll</td>
<td>1</td>
</tr>
<tr>
<td>M6</td>
<td>Typic Endoaquoll</td>
<td>1</td>
<td>Typic Endoaquoll Haplic Vermudoll</td>
<td>2</td>
<td>Aquic Hapludoll</td>
<td>1</td>
</tr>
<tr>
<td>M7</td>
<td>Haplic Vermudoll</td>
<td>1</td>
<td>Haplic Vermudoll Typic Endoaquoll</td>
<td>3</td>
<td>Aquic Hapludoll</td>
<td>1</td>
</tr>
<tr>
<td>M8</td>
<td>Typic Endoaquoll</td>
<td>1</td>
<td>Haplic Vermudoll Typic Vermudoll</td>
<td>3</td>
<td>Aquic Hapludoll</td>
<td>1</td>
</tr>
<tr>
<td>M9</td>
<td>Typic Endoaquoll</td>
<td>1</td>
<td>Haplic Vermudoll Typic Endoaquoll</td>
<td>3</td>
<td>Aquic Hapludoll</td>
<td>1</td>
</tr>
<tr>
<td>M10</td>
<td>Typic Vermudoll Haplic Vermudoll</td>
<td>2</td>
<td>Typic Vermudoll Typic Hapludoll Vermic Hapludoll Haplic Vermudoll</td>
<td>5</td>
<td>Typic Hapludoll</td>
<td>3</td>
</tr>
<tr>
<td>M11</td>
<td>Typic Vermudoll</td>
<td>2</td>
<td>Haplic Vermudoll Typic Vermudoll</td>
<td>3</td>
<td>Aquic Hapludoll</td>
<td>2</td>
</tr>
</tbody>
</table>
well-drained upland soils were likely to build mounds with smaller dimensions than ants living in poorly drained soils (25-cm tall, 40-cm wide; 40-cm tall, and 2-m wide respectively) (Baxter and Hole, 1967). Table 3.6 below displays aboveground volumes of mounds in association with their taxonomic classifications.

Table 3.6a. *F. montana* mound volumes in relation to their soil taxonomic classifications.

<table>
<thead>
<tr>
<th>Volume</th>
<th>Adjacent Soil Classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>M2</td>
<td>0.01 m³ Cumulic Endoaquoll</td>
</tr>
<tr>
<td>M9</td>
<td>0.03 m³ Aquic Hapludoll</td>
</tr>
<tr>
<td>M1</td>
<td>0.04 m³ Cumulic Endoaquoll</td>
</tr>
<tr>
<td>M8</td>
<td>0.06 m³ Aquic Hapludoll</td>
</tr>
<tr>
<td>M3</td>
<td>0.07 m³ Aquic Hapludoll</td>
</tr>
<tr>
<td>M7</td>
<td>0.11 m³ Aquic Hapludoll</td>
</tr>
<tr>
<td>M10</td>
<td>0.12 m³ Typic Hapludoll</td>
</tr>
<tr>
<td>M4</td>
<td>0.14 m³ Aquic Hapludoll</td>
</tr>
<tr>
<td>M6</td>
<td>0.15 m³ Aquic Hapludoll</td>
</tr>
<tr>
<td>M5</td>
<td>0.20 m³ Aquic Hapludoll</td>
</tr>
<tr>
<td>M11</td>
<td>0.97 m³ Aquic Hapludoll</td>
</tr>
</tbody>
</table>

Table 3.6b. Average *F. montana* mound volumes in relation to their soil taxonomic classifications.

<table>
<thead>
<tr>
<th>Volume</th>
<th>Adjacent Soil Classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1 &amp; 2</td>
<td>0.03 m³ Cumulic Endoaquoll</td>
</tr>
<tr>
<td>M10</td>
<td>0.12 m³ Typic Hapludoll</td>
</tr>
<tr>
<td>M3-9, M11</td>
<td>0.22 m³ Aquic Hapludoll</td>
</tr>
</tbody>
</table>

Mound 11 was five times larger than the second largest mound (Mound 5) (0.97 m³ vs. 0.20 m³). When Mound 11 was considered an outlier, the average volume of the mounds associated with Aquic Hapludolls was slightly smaller (0.11
m$^3$) than that of Mound 10. The mounds associated with the most poorly drained soils (Cumulic Endoaquolls) were the smallest on average.

From the work of Baxter and Hole (1967), we expected the largest mounds to be Cumulic Endoaquolls. With our data, it is difficult to make a strong argument for or against their observations. It is also important to note that many other environmental factors influence mound size. A few examples include mound age, and presence or absence of competing colonies. When studying mound longevity of prairie ants in southwestern Wisconsin, Henderson et al. (1989) noted that mounds occasionally merge, which highlights the fact that this species (*F. montana* Wheeler) is polydomous. Lastly, it is interpreted here that ants may be channeling deeper during the months when the fluctuating water table has receded.

* Soil morphology

Center and periphery soils had slightly thicker A horizons (65 cm and 63 cm, respectively) than their adjacent soils (58 cm). Mollic epipedon depths were similar for center, periphery, and adjacent soils (71 cm, 71 cm, and 66 cm, respectively). Center profiles had the shallowest depth of effervescence (23 cm), periphery soils second shallowest (35 cm), and then adjacent with average effervescence depth of 66 cm. Center soils had the shallowest depth to redoximorphic features at 54 cm, while periphery and adjacent soils had an average depth of 64 cm (Table 3.7).

Structurally, profiles within mounds showed a number of unique characteristics from their adjacent soils. Mound interiors displayed various
Table 3.7. Morphological properties of 78 profiles on or near *F. montana* mounds at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th>Property</th>
<th>Center (n)</th>
<th>Periphery (n)</th>
<th>Adjacent (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A Horizon Length (cm)</td>
<td>65 ± 14</td>
<td>63 ± 14</td>
<td>58 ± 8</td>
</tr>
<tr>
<td>Mollic Color Depth (cm)</td>
<td>71 ± 16</td>
<td>71 ± 15</td>
<td>66 ± 15</td>
</tr>
<tr>
<td>Depth to Eff &gt;3</td>
<td>23 ± 34</td>
<td>35 ± 33</td>
<td>66 ± 18</td>
</tr>
<tr>
<td>A Horizon Eff (1-4)</td>
<td>1.5 ± 1.3</td>
<td>1.4 ± 1.2</td>
<td>0.7 ± 1.0</td>
</tr>
<tr>
<td>B Horizon Eff (1-4)</td>
<td>2.5 ± 1.5</td>
<td>3.2 ± 1.1</td>
<td>2.3 ± 1.6</td>
</tr>
<tr>
<td>Hue (A Horizon)</td>
<td>8.9 ± 2.6</td>
<td>9.7 ± 1.5</td>
<td>9.8 ± 1.2</td>
</tr>
<tr>
<td>Value (A Horizon)</td>
<td>2.5 ± 0.7</td>
<td>2.4 ± 0.7</td>
<td>2.4 ± 0.7</td>
</tr>
<tr>
<td>Chroma (A Horizon)</td>
<td>1.1 ± 0.4</td>
<td>1.1 ± 0.3</td>
<td>1.0 ± 0.2</td>
</tr>
<tr>
<td>Hue (B Horizon)</td>
<td>7.0 ± 2.8</td>
<td>6.5 ± 2.9</td>
<td>6.6 ± 3.0</td>
</tr>
<tr>
<td>Value (B Horizon)</td>
<td>4.2 ± 0.8</td>
<td>4.4 ± 0.9</td>
<td>4.4 ± 0.8</td>
</tr>
<tr>
<td>Chroma (B Horizon)</td>
<td>1.5 ± 0.6</td>
<td>1.7 ± 0.7</td>
<td>1.7 ± 0.6</td>
</tr>
<tr>
<td>Depth of gr structure</td>
<td>55 ± 18</td>
<td>57 ± 24</td>
<td>57 ± 13</td>
</tr>
<tr>
<td>Grade</td>
<td>2.7 ± 0.6</td>
<td>2.7 ± 0.6</td>
<td>2.4 ± 0.7</td>
</tr>
<tr>
<td>Size</td>
<td>1.8 ± 0.5</td>
<td>1.7 ± 0.6</td>
<td>1.9 ± 0.4</td>
</tr>
<tr>
<td>Depth to redox features (cm)</td>
<td>54 ± 19</td>
<td>64 ± 20</td>
<td>64 ± 15</td>
</tr>
<tr>
<td>Depth to Fe</td>
<td>53 ± 22</td>
<td>56 ± 18</td>
<td>61 ± 13</td>
</tr>
<tr>
<td>Depth to FeMn</td>
<td>69 ± 21</td>
<td>71 ± 17</td>
<td>80 ± 12</td>
</tr>
<tr>
<td>Upper Bound. sbk structure</td>
<td>57 ± 19</td>
<td>47 ± 17</td>
<td>51 ± 12</td>
</tr>
<tr>
<td>Upper Bound. pris structure</td>
<td>62 ± 23</td>
<td>57 ± 29</td>
<td>67 ± 6</td>
</tr>
<tr>
<td>Upper Boundary of Gleyed horizon</td>
<td>73 ± 13</td>
<td>74 ± 18</td>
<td>75 ± 13</td>
</tr>
</tbody>
</table>

*Eff = effervescence, gr = granular, redox = redoximorphic, sbk = subangular blocky, pris = prismatic
aggregation patterns, though the most common was the presence of very fine granules in conjunction with strong, medium prisms (Figure 3.3).

![Image](image-url)

Figure 3.3. Prismatic soil structure under *F. montana* colonization at Doolittle Prairie State Preserve.

Very fine granules predominated within channels and were seen both tightly packed as backfill as well as very loosely distributed within mound chambers. It was apparent as well that though subangular blocky aggregates were present within center and periphery soils, when subjected to external pressure, they broke into very fine granules.

Many have observed that during mound construction, ants decompose aggregates and sort finer materials to stabilize channel walls (Baxter and Hole, 1967; Holldobler and Wilson, 1991; Halfen and Hasiotis, 2010). Any unwanted
material is then reconfigured into fine aggregates and either moved to the mound surface, or is used as backfill in abandoned chambers (Halfen and Hasiotis, 2010). Baxter and Hole (1967) suggest that internal shrink-swell properties of wetland soils may influence channel closures. To take these interpretations a step further, it is most likely that these same forces are assisting in the compaction of channel backfill, as well as recreating coarser structures from the very fine aggregates produced by ants. It is quite possible then to assume that densely compacted backfilled channels are relatively older than channels filled with loose aggregates.

Color distribution within center and periphery soils was different from adjacent soils. The soils within mounds had displaced B horizon material in the surface horizons, including redoximorphic features and carbonates. Figure 3.4 below shows examples of backfill comprised of B horizon material within the mollic epipedon of a center profile. Krotovinas were also commonly found in the B horizon (Figure 3.5). Two likely scenarios explain black surface material in the lower profile: it fell down due to gravity or ants moved it there.

Bioturbation: intensity gradient from center to adjacent soils

Mound periphery profiles showed varying levels of bioturbation. The majority of these soils shared similar morphological characteristics to their associated mound centers. Four profiles from Mounds 1 and 10, on the other hand, showed little or no classification change from their adjacent counterparts (Table 3.4).
Figure 3.4. Displaced B material in the epipedon of a center profile at Doolittle Prairie State Preserve.

Figure 3.5. Krotovina within the center profile of an *F. montana* mound at Doolittle Prairie State Preserve (150-cm depth).
Adjacent soil profiles associated with Mounds 8 and 9 showed signs of ant bioturbation, mostly in the form of soil aggregates breaking to very fine, weak granules. Other indices of ant bioturbation included channels filled with very fine granules, and mixing of gleyed colors from the B horizon into the surface matrix. It was interpreted though that in both cases, this soil had been previously inhabited and subsequently abandoned because no ants, larva, or open channels were observed within or around the sampled cores.

Many ant prairie species with similar mound structures to those investigated in this study have been known to be polydomous (Hole, 1981; Henderson et al., 1989; Bristow et al., 1992). *F. montana*, whose diets are comprised of aphid honeydew, have been observed to generate seasonal mounds in association with their stable mounds to serve the purpose of providing direct access to aphid colonies (Hole, 1981; Henderson et al., 1989). Because of this, it is very likely that channeling networks cover a far greater area in the soil subsurface, and in turn, lead to greater soil turnover rates than can be predicted only when considering stable mounds.

*Soil chemical and physical parameters*

The following results (Tables 3.8 through 3.17; Figures 3.6 through 3.17) provide details from a variety of laboratory analyses. Each topic is minimally discussed in itself because the goal of this section is simply to show property-by-property depth trends. The relationships are then discussed as a whole in the next section in order to build a model of soil formation.
Soil organic carbon and total nitrogen

Soil OC and TN decreased with depth in all sampled soils. There was no significant difference in percent OC throughout center, periphery, and adjacent soils (1.4%, 1.4%, and 1.3%, respectively) (Table 3.8, Figure 3.6). A paired T-test showed %TN of the B horizon to be different in center versus adjacent profiles (Table 3.9). Center profiles had a slightly greater %TN in the B horizons at 0.06%, while periphery and adjacent soils shared a %TN of 0.05% (Figure 3.7). Average C:N for center, periphery, and adjacent soils also showed no significant difference on and off of mounds, with entire profile averages being 8:1, 8:1, and 7:1, respectively (Figure 3.8).

A great number of studies have examined the effects of ants on soil nutrients. In the case of *F. montana* mounds in a Wisconsin prairie, higher levels of TN were found within mound boundaries than in adjacent soils (Baxter and Hole, 1967). Research of other soils associated with *Formica spp.* has shown decreased organic matter within mounds (Culver and Beattie, 1983; Levan and Stone, 1983; Beattie and Culver, 1997). Czerwinsky et al., (1971) suggested that poorer soils showcase greater nutrient variability than fertile soils. This is a likely explanation for the minimal difference in soil TN and OC of the center, periphery, and adjacent soils.

Inorganic carbon: calcite, dolomite, and CCE

Calcite and dolomite contents were measured, and it was determined that the A horizons of mound center profiles contained the highest amounts of both
Table 3.8. Percent organic carbon of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>1.4 ± 1.3</td>
<td>-0.37</td>
<td>0.74</td>
</tr>
<tr>
<td>A</td>
<td>2.0 ± 1.2</td>
<td>-0.51</td>
<td>0.29</td>
</tr>
<tr>
<td>B</td>
<td>0.4 ± 0.4</td>
<td>1.17</td>
<td>1.25</td>
</tr>
</tbody>
</table>

Table 3.9a. Percent total nitrogen with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>0.15 ± 0.11</td>
<td>-0.62</td>
<td>0.69</td>
</tr>
<tr>
<td>A</td>
<td>0.21 ± 0.10</td>
<td>-0.74</td>
<td>0.22</td>
</tr>
<tr>
<td>B</td>
<td>0.06 ± 0.03</td>
<td>2.58</td>
<td>1.45</td>
</tr>
</tbody>
</table>

Table 3.9b. Paired t test (assuming equal variance) for total nitrogen of B horizons of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Center</td>
<td>0.18</td>
<td>0.07</td>
<td></td>
</tr>
<tr>
<td>Periphery</td>
<td>0.42</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.6. Percent organic carbon with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center:   \[ % \text{OC} = -0.965 \ln(\text{Depth}) + 4.83, \quad r^2 = 0.71, \quad n=86, *** \]
Periphery: \[ % \text{OC} = -1.803 \ln(\text{Depth}) + 8.02, \quad r^2 = 0.90, \quad n=97, *** \]
Adjacent: \[ % \text{OC} = -1.301 \ln(\text{Depth}) + 6.17, \quad r^2 = 0.86, \quad n=73, *** \]
Figure 3.7. Percent total nitrogen with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center: \[ \%TN = -0.086 \ln(\text{Depth}) + 0.46, \quad r^2 = 0.76, \quad n=86, *** \]

Periphery: \[ \%TN = -0.110 \ln(\text{Depth}) + 0.55, \quad r^2 = 0.84, \quad n=97, *** \]

Adjacent: \[ \%TN = -0.158 \ln(\text{Depth}) + 0.73, \quad r^2 = 0.93, \quad n=73, *** \]
Figure 3.8. Carbon:Nitrogen with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center: \[ \text{C:N} = -0.074 \times \text{Depth} + 11.39, r^2 = 0.52, n=86, \star\star\star \]
Periphery: \[ \text{C:N} = -0.088 \times \text{Depth} + 12.53, r^2 = 0.70, n=97, \star\star\star \]
Adjacent: \[ \text{C:N} = -0.097 \times \text{Depth} + 12.31, r^2 = 0.47, n=73, \star\star\star \]
constituents (0.5% and 5.3%, respectively). Adjacent soil A horizons contained very similar calcite dolomite values (0.2% and 4.5%, respectively). There was no statistical difference between calcite and dolomite values in adjacent and center profiles. Periphery soils did show a significant difference in A horizon calcite and dolomite contents from their adjacent and center counterparts however (0.1% and 3.3%, respectively).

Tables 3.10 and 3.11 and Figures 3.9 and 3.10 provide greater details. Results of a two-tailed t-test showed no significant difference between center, periphery, and adjacent B horizons. Differences in CCE values aligned with calcite and dolomite percentages, where A horizons of periphery soils contained less dolomite and calcite than did center and adjacent soils (Table 3.12, Figure 3.11). The high content of dolomite seem to be the greatest influence on CCE values.

Soil pH

The pH of adjacent soils in Doolittle Prairie State Preserve increases with depth. Surface horizons are acidic (5.5-6.5) and transition to neutral or slightly alkaline (7.5-8.0) within the lower B horizon. Soils within the mound centers, on average, are neutral all the way down (Tables 3.13 and 3.14). When comparing the average A horizon pH, soils from the mound centers are slightly more basic than their adjacent counterparts. Alternatively, when comparing B-horizon data, center soils are slightly more acidic than adjacent soils (Tables 3.13 and 3.14). The pH distribution within periphery soils is more variable (Figures 3.12 and 3.13).
Table 3.10a. Percent calcite with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>1.3 ± 2.7</td>
<td>2.37</td>
<td>0.64</td>
</tr>
<tr>
<td>A</td>
<td>0.5 ± 1.3</td>
<td>6.10</td>
<td>2.60</td>
</tr>
<tr>
<td>B</td>
<td>2.8 ± 3.7</td>
<td>-1.30</td>
<td>0.80</td>
</tr>
</tbody>
</table>

Table 3.10b. Paired t test (assuming equal variance) for percent calcite of A horizons of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Center</td>
<td>0.03</td>
<td>0.29</td>
<td></td>
</tr>
<tr>
<td>Periphery</td>
<td></td>
<td>0.38</td>
<td></td>
</tr>
</tbody>
</table>
Table 3.11a. Percent dolomite in A horizons of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>6.3 ± 4.3</td>
<td>1.53</td>
<td>1.32</td>
</tr>
<tr>
<td>A</td>
<td>5.3 ± 2.9</td>
<td>0.20</td>
<td>1.00</td>
</tr>
<tr>
<td>B</td>
<td>8.1 ± 5.7</td>
<td>-0.50</td>
<td>0.7</td>
</tr>
</tbody>
</table>

Table 3.11b. Paired t test (assuming equal variance) for percent dolomite in A horizons of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Center</td>
<td></td>
<td>0.00</td>
<td>0.24</td>
</tr>
<tr>
<td>Periph</td>
<td></td>
<td></td>
<td>0.05</td>
</tr>
</tbody>
</table>
Figure 3.9. Percent calcite with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center:  \( \%\text{CaCO}_3 = 0.040 \times \text{Depth} - 0.76, \quad r^2 = 0.30, \quad n=86 \)

Periphery:  \( \%\text{CaCO}_3 = 0.051 \times \text{Depth} - 1.53, \quad r^2 = 0.50, \quad n=97, *** \)

Adjacent:  \( \%\text{CaCO}_3 = 0.055 \times \text{Depth} - 1.36, \quad r^2 = 0.29, \quad n=73, * \)
Figure 3.10. Percent dolomite with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center:  \( \%MgCa(CO_3)_2 = 0.047 \times \text{Depth} + 3.85, \quad r^2 = 0.16, \quad n=86, \quad *** \)

Periphery:  \( \%MgCa(CO_3)_2 = 0.077 \times \text{Depth} + 0.76, \quad r^2 = 0.46, \quad n=97 \)

Adjacent:  \( \%MgCa(CO_3)_2 = 0.094 \times \text{Depth} + 1.24, \quad r^2 = 0.30, \quad n=73 \)
Table 3.12a. Calcium Carbonate Equivalency with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>8.2 ± 7.0</td>
<td>1.79</td>
<td>1.57</td>
</tr>
<tr>
<td>A</td>
<td>6.3 ± 4.0</td>
<td>1.10</td>
<td>1.30</td>
</tr>
<tr>
<td>B</td>
<td>11.6 ± 9.6</td>
<td>-1.0</td>
<td>0.70</td>
</tr>
</tbody>
</table>

Table 3.12b. Paired t test (assuming equal variance) for Calcium Carbonate Equivalency in A horizons of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Center</td>
<td></td>
<td>0.00</td>
<td>0.20</td>
</tr>
<tr>
<td>Periphery</td>
<td></td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>Adjacent</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.11. Calcium Carbonate Equivalency with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center: \[ \text{CCE} = 0.092 \times \text{Depth} + 3.44, \quad r^2 = 0.23, \quad n=86, \quad ** \]

Periphery: \[ \text{CCE} = 0.135 \times \text{Depth} - 0.72, \quad r^2 = 0.50, \quad n=97 \]

Adjacent: \[ \text{CCE} = 0.157 \times \text{Depth} - 0.00, \quad r^2 = 0.32, \quad n=73 \]
Table 3.13. Soil pH with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>7.1 ± 0.6</td>
<td>0.47</td>
<td>-0.97</td>
</tr>
<tr>
<td>A</td>
<td>7.1 ± 0.5</td>
<td>0.53</td>
<td>-0.95</td>
</tr>
<tr>
<td>B</td>
<td>7.3 ± 0.7</td>
<td>1.00</td>
<td>-1.26</td>
</tr>
</tbody>
</table>

Table 3.14. Soil pH with depth of center, periphery, and adjacent soils in Mound 10 at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>7.3 ± 0.3</td>
<td>0.26</td>
<td>-0.88</td>
</tr>
<tr>
<td>A</td>
<td>7.3 ± 0.3</td>
<td>-0.33</td>
<td>-0.99</td>
</tr>
<tr>
<td>B</td>
<td>7.4 ± 0.2</td>
<td>-2.58</td>
<td>0.03</td>
</tr>
</tbody>
</table>
Figure 3.12. Soil pH with depth of center, periphery, and adjacent soils for Mound 10 at Doolittle Prairie State Preserve.

Center: $pH = 0.006\text{(depth)} + 7.06$, $r^2 = 0.37$, $n=15$
Periphery: $pH = 0.007\text{(depth)} + 6.98$, $r^2 = 0.65$, $n=41$, ***
Adjacent: $pH = 0.010\text{(depth)} + 6.78$, $r^2 = 0.80$, $n=17$, ***
Figure 3.13. Soil pH with depth of periphery soils for Mound 10 at Doolittle Prairie State Preserve.

Periphery North:  $\text{pH} = 0.0079 \text{ (Depth)} + 6.97$, $r^2 = 0.79$, $n=5$
Periphery South:  $\text{pH} = 0.0078 \text{ (Depth)} + 7.03$, $r^2 = 0.76$, $n=5$
Periphery East:    $\text{pH} = 0.0027 \text{ (Depth)} + 7.12$, $r^2 = 0.65$, $n=5$
Periphery West:   $\text{pH} = 0.0041 \text{ (Depth)} + 7.08$, $r^2 = 0.41$, $n=6$
Petal, 1980; Culver and Beattie, 1983; and Beattie and Culver, 1997 showed no differences in pH between soils on and off of mounds. There is evidence, however, that ants tend to lower the pH of alkaline soils and increase the pH of acidic soils (Dlusskij, 1967; Petal, 1980; Frouz and Jilkova, 2008).

Due to the soil parent material at Doolittle Prairie State Preserve, a carbonate-rich, alkaline glacial till, it is no surprise that the surface horizons of mounds are slightly less acidic than their adjacent counterparts. Because ants could bring calcareous material up from the lower horizons, they are assisting in the neutralization of the acidic surface horizons. Simultaneously, acidic surface material is going downward, either through gravitational movement of sediment or active placement of surface material and organic matter by ants. Other potential explanations for the neutralization of the lower basic horizons could involve the production of organic acids by microorganisms, plant roots, and ants (Folgarait, 1998).

**Stable aggregate content**

In general, SAC decreases with depth in soils at Doolittle Prairie State Preserve (Figure 3.14). Ants have paradoxical impacts on SAC. When simply comparing averages, center and periphery soils have a very similar SAC compared to their adjacent counterparts (54%, 48%, and 48%, respectively) (Table 3.15). B horizon data show alternatively that soils within the mound center have a slightly greater SAC (43%) than both periphery (31%) and adjacent soils (32%) (Table 3.15).
Figure 3.14. Percent stable aggregate content with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center:  \( \% \text{SAC} = -0.329 \text{ (Depth)} + 68.40 \)  \( r^2 = 0.31, \ n=69, \ *** \)

Periphery:  \( \% \text{SAC} = -0.598 \text{ (Depth)} + 77.49 \)  \( r^2 = 0.79, \ n=69, \ *** \)

Adjacent:  \( \% \text{SAC} = -0.602 \text{ (Depth)} + 78.61 \)  \( r^2 = 0.71, \ n=60, \ *** \)
Table 3.15a. Percent stable aggregate content with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>54 ± 16</td>
<td>0.19</td>
<td>-0.67</td>
</tr>
<tr>
<td>A</td>
<td>59 ± 14</td>
<td>-0.16</td>
<td>-0.57</td>
</tr>
<tr>
<td>B</td>
<td>43 ± 15</td>
<td>-1.04</td>
<td>0.47</td>
</tr>
</tbody>
</table>

Table 3.15b. Paired t test (assuming equal variance) for percent stable aggregate content of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th></th>
<th>Center A</th>
<th>Periphery A</th>
<th>Adjacent A</th>
<th>Center B</th>
<th>Periphery B</th>
<th>Adjacent B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Center</td>
<td>0.12</td>
<td>0.08</td>
<td></td>
<td>0.01</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Periphery</td>
<td>0.86</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.75</td>
</tr>
<tr>
<td>Adjacent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
In order to excavate soil, ants deconstruct aggregates with their mandibles (Halfin and Hasiotis, 2010). This allows them to sort out useful materials for nest building and enables them to easily transport soil away from channels. Previous research has shown ants to stabilize channel walls with self-produced waxy exudates (Holldobler and Wilson, 1990), as well as silt and colloidal material (Wang et al., 1995). Increased SAC could also be influenced by an increase in microbiological activity within ant mounds (Friese and Allen, 1993).

**Bulk density**

For Doolittle Prairie soils, BD values increase with depth from 1.4 g/cm$^3$ to 1.7 g/cm$^3$. As would be expected, lower BD values were associated with center and periphery soils (1.2-1.5 g/cm$^3$ vs. 1.3-1.6 g/cm$^3$, respectively). Our statistical analyses show no significant difference in BD when comparing soils on and off of mounds (Table 3.16, Figure 3.15). This suggests that while ants are increasing soil macroporosity through channel building, they also seem to be compacting the soil surrounding their channels. Signs of this phenomenon include increased prismatic structure within mounded soils, as well as channel infilling. In turn, this compaction is cancelling out the heightened level of soil macropores.

**Coarse fragments**

In adjacent soils of Mound 11, CF values increased from 0% at the surface to around 15% at 100-cm depth. CF values then quickly declined at greater depths to around 5%. Percent CF of center soils (starting at 0%) peaked at 7% at a depth of 115 cm and declined thereafter to around 4%. Periphery soils peaked at 9% CF at
Table 3.16. Bulk density (g/cm³) with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th>Horizons</th>
<th>Center</th>
<th>Periphery</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>1.3 ± 0.3</td>
<td>2.26</td>
<td>0.55</td>
</tr>
<tr>
<td>A</td>
<td>1.2 ± 0.2</td>
<td>0.17</td>
<td>-0.70</td>
</tr>
<tr>
<td>B</td>
<td>1.5 ± 0.2</td>
<td>4.17</td>
<td>1.88</td>
</tr>
</tbody>
</table>
Figure 3.15. Bulk density (g/cm³) with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center: $BD = 0.004 \text{ (Depth)} + 0.99$, $r^2 = 0.72$, $n=17$, ***
Periphery: $BD = 0.004 \text{ (Depth)} + 1.08$, $r^2 = 0.51$, $n=28$, ***
Adjacent: $BD = 0.006 \text{ (Depth)} + 1.10$, $r^2 = 0.79$, $n=13$, ***
105-cm depth and declined slightly to 7% at the base of the profiles (Table 3.17 and Figure 3.16).

The variations in depth of CF peaks and percent CF values could be attributed to downward movement of coarse materials in response to biological activity. Previous studies have attributed this occurrence to burrowing animals, where fragments too large for bioturbating organisms to move upwards eventually sink and fall into void spaces (Darwin, 1881; Johnson, 1989, 1990). Simultaneously, burrowing organisms move material above the CF, and bury them further. Another possibility is that bioturbators are fracturing secondary carbonate nodules and redistributing them throughout the profile.

**Model of Soil Formation:**

From the evidence provided herein and through other studies on ant bioturbation, we think soil formation in and near ant mounds occurs in a two-stage system. As ants excavate material to create channels, they destroy soil aggregates. Fine particles are used to reinforce channel walls, while unwanted soil material is moved either to unused/abandoned portions of the mound, or to the soil surface (Figure 3.17a). We speculate here that the decision to move material is based on convenience, which is also path of least resistance.

In this scenario, we suggest that the expansion of the mound is not necessarily symmetrical (Figure 3.17b). It was clearly observed that soil morphological and chemical properties varied amongst periphery soils. Within a single mound, it was quite common to see at least one of the four periphery profiles
Table 3.17a. Percent coarse fragments with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

<table>
<thead>
<tr>
<th>Horizons</th>
<th>Mound 11% Coarse Fragments</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Center</td>
<td>Periphery</td>
</tr>
<tr>
<td>All</td>
<td>2.5 ± 2.2</td>
<td>-0.69</td>
</tr>
<tr>
<td>A</td>
<td>1.1 ± 1.0</td>
<td>0.32</td>
</tr>
<tr>
<td>B</td>
<td>4.5 ± 1.8</td>
<td>-0.07</td>
</tr>
</tbody>
</table>

Table 3.17b. Paired t test (assuming equal variance) for percent coarse fragments of center, periphery, and adjacent soils at Doolittle Prairie State Preserve. A and B horizons.

<table>
<thead>
<tr>
<th></th>
<th>Center A</th>
<th>Periphery A</th>
<th>Adjacent A</th>
<th>Center B</th>
<th>Periphery B</th>
<th>Adjacent B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Center</td>
<td>0.82</td>
<td>0.17</td>
<td>Center</td>
<td>0.15</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>Periphery</td>
<td></td>
<td>0.07</td>
<td>Periphery</td>
<td></td>
<td>0.29</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.16. Percent coarse fragments with depth of center, periphery, and adjacent soils at Doolittle Prairie State Preserve.

Center: \( \%\text{CF} = 0.029 \times \text{Depth} - 0.24 \), \( r^2 = 0.38 \), \( n=17 \)

Periphery: \( \%\text{CF} = 0.057 \times \text{Depth} - 1.15 \), \( r^2 = 0.70 \), \( n=28 \)

Adjacent: \( \%\text{CF} = 0.074 \times \text{Depth} - 0.05 \), \( r^2 = 0.42 \), \( n=13 \)
Figure 3.17a. Deposition patterns within an *F. montana* mound at Doolittle Prairie State Preserve. Blue arrows show direction from excavation to deposition. Dark pockets are infill of surface soil; gray pockets are infill of subsurface soil. The original figure was created using soil from this figure as paint.
Figure 3.17b. Proposed expansion of an *F. montana* mound at Doolittle Prairie State Preserve. As the mound migrates, abandoned channels and voids are filled with excavated soil.
showing minimal pedoturbation, or conversely, very intensive bioturbation. For this reason, Figure 3.17b expresses expansion of the mound in only one direction. This two-dimensional model is simplifying the fact that ants are most likely expanding in several directions, but that growth is not necessarily symmetrical along the periphery.

**Conclusions:**

Ant bioturbation has and is constantly affecting morphological and chemical characteristics of the soils at Doolittle Prairie State Preserve. Soil structure, presence of effervescence, pH, and stable aggregate contents are all characteristics especially influenced by these organisms. Our model to explain these impacts begins with burrowing, soil excavation, and deposition. These processes drive the transformation of soil properties within ant mounds. The model of mound expansion expresses the idea that though the mounds at Doolittle Prairie are symmetrical from the surface, the ants within these structures do not follow the same pattern underground.
Chapter 4: Conclusion

The previous chapter of this thesis details a few of the many ways that ants alter their soil environments. Individual mounds showed changes in horizon depths, soil structure, bulk density, depths of carbonates and redoximorphic features, stable aggregates, pH, nutrient levels, and taxonomy. From the information given above, I reject the null hypothesis and accept that soil properties change with ant activity. I also accept that ants induce soil anisotropy within and beyond the radius of their mounds.

On a larger scale, activities of ants are influencing the downward movement of coarse fragments, and the mixing of subsurface and surface horizons. Channeling by these organisms was observed to depths greater than 150 cm, which was well beyond the depth of the seasonal water table. From this, we can assume that ants utilize the deeper part of the soil profile when the opportunity arises. It is safe to say though that the majority of the active bioturbation of Doolittle Prairie is occurring in the surface 75 cm.

In conclusion, ants are incredible organisms. Their breadth and density around the world is awe-inspiring. If not for their influence, our planet would be a much less habitable place.
References


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