MODIFICATIONS OF FINE- AND COARSE-TEXTURED SOIL MATERIAL CAUSED BY
THE ANT *FORMICA SUBSERICEA*

BY

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ABSTRACT

The majority of ant-related bioturbation research has focused on physiochemical properties of the nest mound. However, ants are also known to line subsurface nest components (chambers and galleries) with coarse material, and may expand or backfill areas as colony size expands and contracts. These alterations may contribute to significant redistribution of soil material leading to alterations in soil physical and hydrological properties. The goal of this study was to examine the physical, chemical, and hydrological effects of the subterranean portion of ant nests on the soil profile. We measured soil in the field that was located near (<2 cm) and away (<1 m) from ant nests, and compared them to unaltered soil approximately 2 m away. Two-dimensional tracings of nest architecture were used to predict the nest effect on hydraulic properties of a fine-textured soil. In addition, we took approximately 1600 ant specimens from one of these nests and placed them into two formicaria with coarse-textured soil that approximated horizons in the field. Overall, the mound showed the largest differences from the original soil, having lower bulk density and higher total carbon than the rest of the nest. Ant-altered portions of soil extended laterally well beyond the surface mound in soils with vertic properties, whereas effects of ants on nest carbon were restricted to nest walls in coarse-textured soils. This difference was due to ants utilizing interpedal spaces of vertic soils that were open during dry years. Hydrologic properties calculated from cross-sectional photographs and tracings of the excavated nest showed that ant activity significantly increased the saturated hydraulic conductivity of the soil, and was associated with faster increases and decreases in moisture content. This preferential flow effect was present, but more muted in coarse-textured soils with naturally high saturated conductivity. Regardless of soil type, the effects of ant altered soil diminish with increasing depth, as nest structures decrease in density and the soil becomes harder to excavate, especially during dry years.

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CHAPTER 1. INTRODUCTION

Ants are important bioturbators due to their extensive ranges, large populations, and high density of nests on the landscape (Lobry de Bruyn, 1999). The majority of ant species are soil dwellers, excavating nests that can vary in size by orders of magnitude—from centimeters to meters deep, depending on the species (Tschinkel, 2003). Many ant species pile mounds of excavated earth at nest entrances; these structures are often modified to optimize the thermoregulation of the colony (Bucy and Breed, 2006; Jones and Oldroyd, 2006). As ants move excavated material to the mound, they redistribute soil and alter soil material properties. The rate of soil turnover caused by moving subsurface material to the mound can be as little as 100 years in some environments (Eldridge and Pickard, 1994).

Due to its conspicuousness and ease of access, the nest mound is often used to approximate rates of bioturbation. Many studies describe ant-altered soil by measuring physical and chemical properties and calculating rates of soil turnover only in the mound (Lobry de Bruyn and Conacher, 1990). These studies do not attempt to quantify subsurface mixing, which can happen as ants line subsurface structures or backfill unused nest components (Halfen et al., 2010; Halfen and Hasiotis, 2010). Subsurface nest material is usually sampled by coring directly though the nest mound or sampling anywhere underneath the mound, whereas the proximity of subsurface samples to nearby nest components (chambers or galleries) is not measured or recorded (e.g., Baxter and Hole, 1967; Cowan et al., 1985; Mandel and Sorenson, 1982; Salem and Hole, 1968). This only provides a coarse-resolution picture of how ants modify the soils surrounding their nests, and does not quantify any lateral effect on the surrounding soils. The hydrology of ant-affected soil is often measured by the conductivity of the soil near nest

entrances, and varies widely depending on the species and environment under consideration (Lobry de Bruyn and Conacher, 1990).

Observing the subsurface portion of ant nests is impeded by several challenges that make sampling and observation difficult. In the field, nests should be cast in order to highlight features for sampling. However, plaster casting does not always capture the full extent of structures due to the formation of bubbles in the cast or actions of the colony that impede the flow of plaster (Tschinkel, 2003). Excavating an ant nest is also time intensive; the excavation must be started well outside the region of the perceived ant activity, then carefully expanded towards the nest to avoid damaging the cast (Smith and Tschinkel, 2009). Furthermore, in order to capture details associated with individual nest structures, soil analyses are limited to techniques that require only small volumes of soil.

Besides some notable studies (e.g., Greaves and Hughes, 1974; Halfen et al., 2010; Halfen and Hasiotis, 2010; Tschinkel, 2005), few works examine ant nest architecture and how it changes with the life of the colony. Changes in the structure of a single colony are difficult to measure, as the casting of nests in the field is destructive and often results in colony death. It is also difficult to simulate a natural colony excavation in the lab. Aggregates must be destroyed to make a homogenous media, lest the ants take advantage of interpedal pores rather than making their own nest structures. In order to observe ant activity, formicaria must be designed to encourage ant activity near the outside walls of the enclosure. This means that laboratory nests are limited to being long and narrow, which distorts the natural shape of the nest. Although the overall dimensions of the nest are reduced, it is still possible in these studies to make observations of individual nest component growth and changes to the volume of formicarium

media. In addition, measuring the transportation of grains in formicarium is possible by introducing artificially colored media (Halfen et al., 2010; Rink et al., 2013).

This thesis describes the physical, chemical, and hydrological properties of nests of a widely-distributed North American ant, *Formica subsericea,* in both the field and laboratory (Francoeur, 1973). My goals were to determine the physical and chemical properties of soils adjacent to and within 1 m of subsurface nest structures in the field and to determine the hydrological properties of the biopores that constitute the nest (Chapter 2). In the laboratory, I relocated ants from one of the nests excavated in Chapter 2 to laboratory enclosures filled with a sandy soil taken from the field. This was done in order to determine how nests in differing stages of development affect the transportation of water throughout the soil horizon and to compare them to a nest that was excavated in a fine-textured soil (Chapter 3).

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CHAPTER 2. EFFECTS OF ANT (*FORMICA SUBSERICEA*) BIOTURBATION ON PHYSICAL AND HYDROLOGICAL PROPERTIES OF A FINE-TEXTURED SOIL

ABSTRACT

The majority of ant bioturbation research has focused on physiochemical properties of the nest mound. Ants are also known to preferentially line subsurface nest components (chambers and galleries) with coarser or finer material, however, and may expand or backfill areas as colony size expands and contracts. These modifications may contribute to significant redistribution of soil material leading to changes in soil physical and hydrological properties. A total of 102 small-volume (~1 cm^3) soil samples were taken from the mound, near individual subsurface nest components, and in soils surrounding two *Formica subsericea* colonies to determine how ants affect soil bulk density, organic carbon content, and particle-size distributions. Samples were taken at depths corresponding to three morphological horizons (A, Bt, and Btss horizons) at four directions, and at increasing distances from a chamber or gallery near the nest center (5 samples per layer per direction, ≤1 m away). Overall, the mound had higher organic carbon and silt content than the rest of the nest, galleries in the upper horizons had higher bulk density, and chambers in the lower horizons had higher carbon values. Ant-modified soil properties extended beyond the extent of the surface mound, and could be seen up to 1 m away. Cracks exacerbated by the vertic properties of the surrounding soil provided higher surface area for carbon mineralization and spaces for ants to travel through, which could explain the lowered bulk density outside the nest if ants modify interpedal pore spaces during dry periods. Hydrologic properties of the ant-modified soils were used as inputs into a 1-D variably saturated flow model (HYDRUS-1D) and, even under conservative assumptions, were predicted to

significantly impact the vadose zone transmission of water. Modeling results from the soils in this study showed that ant nests can increase the infiltration of water following simulated precipitation events largely because of their effect on increasing saturated hydraulic conductivity. Soils with ant-modified properties were associated with more rapid increases and decreases in moisture content than the control soil (i.e., unmodified by ants). Physical and chemical alterations of ant-modified soil appear to diminish with increasing depth, as nest structures decrease in density.

INTRODUCTION

Ants are diverse, ubiquitous, and abundant. Well over 12,000 species of ants reside almost everywhere on Earth except for subarctic to arctic climates and some islands (e.g., Hölldobler and Wilson, 1990). Most ant species are soil excavators whose nests may occupy a substantial portion of a landscape—density can be up to 17,000 nests per hectare in certain parts of the world (Lobry de Bruyn, 1999). The life of a colony can be as little as three months to tens of years or more, depending on the species (e.g., Foster and Kettle, 1999; Wagner et al., 2004).

Soil-dwelling ant nests are composed of subsurface chambers that are used to house brood, food, and queen(s) (e.g., Hasiotis, 2003). These chambers are connected to the surface and to each other by branching vertical and/or horizontal tunnels, called galleries (e.g., Hölldobler and Wilson, 1990; Hasiotis, 2003). The density of these subsurface structures is highest near the soil surface and decreases with depth (e.g., Denning et al., 1978; Hasiotis, 2003). The deepest chambers in a nest can be from several centimeters to several meters deep, depending on the species (e.g., Hasiotis, 2003; Tschinkel, 2003).

In addition to subsurface structures, many species of ants also construct mounds of earth at the nest entrance, which are usually conical or dome shaped (e.g., Wheeler, 1910a, 1910b). Ant mounds range in diameter from several centimeters to over 10 m (e.g., Wang et al., 1995; Wheeler, 1910a). The construction and presence of the mound is important to soil hydrology and ecology as this material often has physical, chemical, and biological properties that are distinct from the surrounding topsoil. Nest mounds generally contain a higher concentration of base cations, nitrogen, phosphorous, and potassium (e.g., Lockaby and Adams, 1985; Lobry de Bruyn and Conacher, 1990; Wagner et al., 2004; Kilpelainen et al., 2007). The relative abundance of nutrients in the nest mound combined with the propensity of some ant species to disperse seeds provides an environment surrounding the nest mound where plants may thrive after seed disposal or colony abandonment of the nest (e.g., Culver and Beattie, 1983; Hölldobler and Wilson, 1990).

Although the mound is often the most physically and chemically modified portion of the nest, soil modifications of ants extend well below the surface mound (e.g., Frouz and Jilková, 2008; Halfen and Hasiotis, 2010a, 2010b). Specific physical and chemical changes compared with the surrounding soil are dependent on such factors as the species of ant, the surrounding habitat, and the soil environment in which the nest was excavated (e.g., Frouz and Jilková, 2008; Lobry de Bruyn and Conacher, 1990; Whitford and Eldridge, 2013). In general, subterranean portions of ant nests are often associated with a shift towards a neutral pH and an increase in concentrations of base cations, nitrogen, potassium, $CaCO_3$, and the coarse fraction of particle sizes (e.g., Baxter and Hole, 1967; Salem and Hole, 1968; Denning et al., 1978; Mandel and Sorenson, 1982; Levan and Stone, 1983). In these studies, ant-modified soil samples are only associated with depth and not distance from individual nest structures.

Ant-modified soil is generally considered to be directly underneath the nest mound. During a soil survey of Romney Marsh on the south coast of England, however, researchers noticed that subsurface nest structures extended laterally well beyond the nest mound, even in parts of the soil that were predicted to be well outside the boundaries of the nest, though it was unclear whether these structures were recent or abandoned (Green and Askew, 1965). There are other observations on the lateral extent of ants (e.g., Hasiotis, 2003; Moreira et al. 2004), however little work has been done on its effects on soil modification aside from surface foraging tunnels and tracks (e.g., Markin et al. 1975; Nkem et al., 2000).

The amount of ant activity on the landscape is typically measured by the amount of material moved to the nest mound. These estimates can vary widely depending on the environment, from tens to thousands of kilograms of soil per hectare per year (e.g., Lobry de Bruyn, 1999;   Frouz and Jilková, 2008; Halfen and Hasiotis, 2010a). Ant activity varies with soil texture, as well as the species targeted for research. Whitford and DiMarco (1995) reported that ants in a grassland of the Chihuahuan desert were estimated to move 21–86 kg ha^{-1} yr^{-1} to their mounds in sandy and sandy loams compared to 0.1–3.4 kg ha^{-1} yr^{-1} in clay and clay loams. In a sandy Wisconsin cornfield, *Lasius neoniger* is estimated to turn the soil over in 1000–2800 years (Wang et al., 1995), whereas *Aphaenogaster barbigula* may turn over 92% of the volume of a sandy eolian soil in Australia in only 100 years (Eldridge and Pickard, 1994).

In addition to carrying particles to the surface and depositing them on the mound during nest excavation, ants also continually modify the subsurface environment by expanding, lining, or backfilling nest components (e.g., Halfen and Hasiotis, 2010b; Rink et al., 2013). Ants also display a preference for building materials of certain sizes. When presented with a variety of particle sizes for nest construction, the wall-building ant *Temnothorax albipennis* always collects

some smaller particles for building materials during nest construction, even though it would be more efficient to carry only larger grains to the nest construction site (Aleksiev et al., 2007b). Similarly, Wang et al. (1995) observed coarse material infilled with finer particles lining galleries in thin sections of subsurface *Lasius neoniger* nests, which can be speculated to be a result of this preferential selection. Other studies have observed clay cements and infillings of finer materials added for stability; these infillings have been observed in in thin sections of subsurface structures and mounds of several species (e.g., Humphreys, 1993; Cosarinsky, 2006; Cosarinsky and Roces, 2007). Similarly, Ettershank (1968) observed a saliva-silt mixture lining galleries of *Iridomyrmex pupureus* nests. Halfen and Hasiotis (2010b) documented western harvester ant (*Pogonomyrmex occidentalis*) gallery linings composed of large aggregates in laboratory enclosures, though thin section analysis was not used to observe infillings in that study. The long-term result of this particle-size preference is the modification of pore-size distributions at the surface of ant galleries, which contributes to the physical and hydrological properties of subsurface soils near their nests.

While modification of bulk density and particle size can change the hydraulic conductivity of the soil, macropores created by the construction of ant nests likely make the most significant modification to hydraulic properties in a soil containing ants. Pore networks beneath *Formica cinera* mounds were wide enough to conduct water 200–700 times faster than the rainfall rate of an intense precipitation event, such as a rainstorm (e.g., Denning et al., 1978). The extent of the effect on hydraulic properties from ant excavation of soil material, however, is dependent on the existence and concentration of open nest tunnels that reach the land surface, though even burrows with closed entrances or buried portions of abandoned or tilled-over macropores may contribute significantly to flow (Logsdon, 1995). Eldridge and Pickard (1994)

report that *Aphaenogaster barbigula* nests with open nest entrances on average had steady state

infiltration rates ~4 times larger than those without open nest entrances (Eldridge and Pickard,

1994). A similar study performed on the same species found that soils with nest entrances

averaged 1026 mm hr^{-1} compared to 120 mm hr^{-1} from soil without nest entrances (Eldridge,

1993). Not all studies, however, found a significant increase of hydraulic conductivity in ant-

modified soils. Wang et al. (1996) measured the effects of *Lasius neoniger* nests on hydraulic

conductivity in a sandy soil and found no significant difference between the hydraulic

conductivity of ant-modified material and the same unmodified material. This lack of difference

was thought to be due to the naturally high hydraulic conductivity of the Sparta sand used in that

study; however, the study also noted that 80% of nest entrances were closed after a heavy

saturation event (Wang et al., 1996).

Actual measurements of flow through ant nests may vary widely due to effects of the nest

mound. In particular, nest mounds can develop a crust shortly after the beginning of a rainfall

event and can greatly reduce infiltration. Mandel and Sorenson (1982) observed this

phenomenon on *Pogonomyrmex occidentalis* mounds, which are lined with a mulch composed of

coarse soil particles and plant fragments. After a rainfall event, the ants burrowed through the

crusted mound to reform the nest entrance. Denning (1978) measured the hydraulic conductivity

of *Formica cinera* mounds in a fine-textured soil, and found that the saturated hydraulic

conductivity of the uncrusted mound was reduced 300–600 fold after a crusting event. The

mound, however, is short-lived compared to subterranean portions of the nest. After the nest has

been abandoned, the materials making up a mound can be eroded away in a few years to a few

decades if not replaced by other excavation materials (e.g., Cowan et al., 1985; Lane and

BassiriRad, 2005; Whitford, 2005). Subterranean macropores have much longer effects on

hydrological flow patterns with soils, as they have the potential to remain in the soil for 50–100 years or more once preferential flow paths of water have been established (e.g, Beven and Germann, 1982; Hagedorn and Bundt, 2002).

In this study, the extent of surface and subsurface soil modification caused by ant nest construction, maintenance, and function was measured by using small volume samples focused near and away (≤1 m) from individual nest components—subsurface chambers and galleries, as well as the mound. The geometry and density of subsurface nest components was measured to determine and document the potential hydraulic conductivity of subsurface nest structures. By focusing on structures and near-structure properties, the goal was to create a conceptual model for how a common and widely distributed local ant, *Formica subsericea*, modifies physical and hydrological properties of fine-textured soil.

MATERIALS AND METHODS

Study Area and Ant Nest Sampling

Field studies were conducted during July and August 2012 at the Fitch Natural History Reservation of the University of Kansas Field Station (KUFS) (Fig. 1). This area commonly contains nests of *Formica subsericea,* a species of large-bodied ants (≤1 cm). *Formica subsericea* is typically found in temperate deciduous forests or forest-edge habitats, but also resides in fields, pastures, and lawns (Francoeur, 1973; Foster and Kettle, 1999). This species was chosen because of its large nests and local abundance at the field station, as well as its wide distribution across the eastern United States (Francoeur, 1973). *Formica subsericea* constructs low mounds up to 1 m in diameter, though nests can also be found under rocks and leaf litter (Francoeur, 1973). Soils in this study are from an area mapped as the Rosendale-Bendena

complex (Rosendale series—fine, mixed, superactive, mesic Typic Eutrudepts; Bendena series—clayey, smectitic, mesic Lithic Hapludolls), with textures ranging from silty clay to silty clay loam (Soil Survey Staff, 2010; United States Department of Agriculture, 2013).

Two *F. subsericea* nests with mounds approximately 40 cm in diameter were chosen for sampling. Specimens were collected and identified using keys from Francoeur (1973) as *Formica subsericea* before the nest was cast with dental plaster (Castone™, Patterson Dental, St. Paul, Minnesota). The plaster was allowed at least 24 hours to set, then excavation was started approximately 1 m from the center of the nest mound to prevent accidental damage to the cast or disruption of adjacent soils (Tschinkel, 2003, 2010). Excavation of the initial pits was done with a small, trailer-mounted backhoe (Dirt Master 55-32710, Sioux Falls, SD).

After the initial pit was dug, vertical slices were carefully hand carved from the pit wall facing the nest to expose the sampling area. Using this technique, two diagonally positioned square pits were excavated at opposite ends of the nest area to form four sampling faces (A–D), which intersected at the center of the nest mound (Fig. 2). While expanding one of these two pits, nest structures were documented by photographing and by placing transparencies over the exposed face and tracing the visible nest structures. Transparencies were only taken where a relative abundance of nest structures were observed. Each transparency was labeled as a distance from the center of the nest mound, and only galleries and chambers that visually were determined to be interconnected were documented.

From each pit face, 5 samples were taken in each of three sampling depth layers (upper, middle, and lower) corresponding to three major horizon breaks—upper layer (A and BAt horizons), middle layer (Bt horizons), and lower layer (Btss horizons) (Fig. 2; Table 1). Within each face and layer, at least one sample was collected within 2 cm of an open gallery or chamber

(when present) near the center of the nest and four additional samples were taken at increasing distances from the nest center. These samples were taken to compare ant-modified soils with soils not normally considered to be modified by ants.

A total of 100 1-cm^3 soil samples were collected from both nests. Since open nests galleries were not visible in some areas of the lower depth, only two of the four faces were sampled from each nest. Thus, 40 samples were taken from the upper and middle depths, and 10 samples were taken from the lower depth of each nest (Fig. 2). Three samples were unusable due to insufficient material, bringing the total number of subsurface samples to 97. Each mound was also sampled depending on the stability of the material (1 sample from Nest 1, and 4 from Nest 2); in addition, soils were described following Schoeneberger (2002) and sampled by horizon an undisturbed (control) profile approximately 2 m from the nest center.

Samples were collected by carefully removing approximately 1 cm^3 of material within 2 cm of the chamber or gallery using dental tools and placing them in pre-weighed sampling bags. Using the compliant cavity method, the resulting void was filled with plaster for bulk density analysis using a procedure similar to Frisbie et al. (2014), except that a reference ring was not used; the ring was neglected in order to minimize any errors associated with the insertion of the ring on the boundary of the small (1 cm^3) excavation, and also because the top of the excavation could be easily defined and identified in the fine-textured material in this study. Samples were then analyzed to determine bulk density, organic carbon (OC) content, and particle-size distribution.

Laboratory Analysis

Plaster casts of the cavities were scanned with a three-dimensional scanner (Desktop 3D Scanner, NextEngine, Santa Monica, CA) to determine the volume of the soil removed following Rossi et al (2008) and Platt et al. (2010). Scans were exported to RapidWorks (v. 3.5.0, NextEngine, Santa Monica, CA) to determine the plaster cast volumes. The excavated soil material was weighed and an aliquot was dried in an oven at 105°C, then reweighed to determine and correct for gravimetric water content. The remainder of the sample was used to determine OC content and particle-size distribution.

Aliquots of 10–30 mg of sample were analyzed by coulometry following Jackson and Roof (1992). Samples were combusted at 930°C for 7.5 min using a CO_2 coulometer (UIC CM5015, Joliet, IL) and furnace apparatus (UIC CM1620, Joliet, IL). Samples were visually tested for inorganic carbon content by observing the reaction of a subsample with 10% HCl; no reaction was observed in any of the samples.

After bulk density and OC analyses, the remainder of the sample was used for determining particle-size distribution following a procedure similar to Hirmas et al. (2013). Representative 0.5 g aliquots were pre-treated with 2 ml of 30% H_2O_2 in 20 mL of DI water. Samples were heated to 90°C on a hot plate until cessation of reaction. DI water was continually added during this process to prevent the sample from drying out. Suspensions were rinsed into 50 mL centrifuge tubes and volumes reduced by centrifugation at 4000 RPM for 5 min. Pellets were re-suspended in 20 mL DI water and sonicated with an ultrasonic dismembrator for 30 seconds (Fisher Scientific, Model 500, Waltham, MA).

The particle-size suspension was analyzed within four hours of sonication using a laser diffractometer (Malvern Mastersizer 2000, Malvern Instruments, Worcestershire, UK). Samples

were added to the Malvern by pipette from stirred suspensions to ensure a representative aliquot of the suspension was taken. A vortex was used to resuspend the samples before they were placed into 100 mL of DI water in a 250 mL beaker and stirred them with a stir bar at ~800 rpm. The stirred suspension was sampled using a pipette, then gradually added to the laser diffractometer (pump speed: 2500 rpm, ultrasonic displacement: 10.0, ultrasonic timer: 3 min) until the sample obscuration value was ~7.0%. The diffractometer was rinsed twice with DI water between each sample to prevent contamination between samples.

Hydrological Analyses

Nest architecture photographs and transparencies obtained in the field were used to determine the area of the nest and sample buffer, which was defined as the area within 2 cm of each nest structure. Photographs were aligned and lens-corrected in Adobe Photoshop 6.5, then exported to Adobe Illustrator 6.5 where they were digitally traced over using the transparencies as a guide. Buffer areas were created around the nest structures by adjusting the stroke width to 2 cm using the photo scale for reference. Layer boundaries were delineated digitally using the ruler tool and photo scale along with the soil description. The resulting nest diagram was exported to ImageJ 1.48e for analysis. The desired feature (buffer or nest area) was isolated using the 'Adjust Threshold' option and the rectangular area and perimeter of each feature was measured using the 'Analyze Particles' command.

Averge bulk density and particle-size distributions were used for samples within the same layers to predict hydraulic properties of the samples taken in the buffer areas, outside the buffer areas, and in the control profiles using the pedotransfer function ROSETTA (Schaap et al., 2001; Šimůnek et al., 2005). These predictions were used to produce an estimate of the hydraulic

properties near the nest using an equation similar to the one used in Amer et al. (2009). The

saturated hydraulic conductivity (K_s) of soils with open ant-created macropores was estimated

using Eq. [1]:

$$K_s = K_s^{\text{matrix}}(f_p - 1) + \frac{\rho g w^2 \zeta f_p}{32\eta} \qquad [1]$$

where K_s^{matrix} is saturated hydraulic conductivity of the soil matrix estimated with a pedotransfer

function using bulk density and particle-size distribution, f_p is the fractional area of the pores, ρ

and η is the density and viscosity of water, respectively, w is the average width of the nest

macropore, and ζ is the tortuosity of the pore estimated as the ratio of the projected length

(rectangular area) to actual length of the pore (half the pore perimeter). Saturated conductivities

were calculated for all pores in each image; the images each represent a distance from the center

of the nest mound. Using the distances represented by each image, then the average

conductivities for each cross section were interpolated to a 7.5-cm distance from the mound

center (the midpoint between the mound center and edge) assuming a linear trend. The resulting

7.5-cm K_s values for the pores were combined with the K_s values calculated from the

surrounding nest features. Pore flux and soil K_s components were transformed according to

proportion of cross-sectional area and added the components to produce an estimate of the

hydrologic properties of an ant-modified pedon in the field following Eq. [1].

The variably saturated flow model, HYDRUS-1D (Šimůnek et al., 2005), and the van

Genuchten (1980) description of water retention was used to simulate water flow through a soil

with the aggregated K_s values described above. Meteorological data was taken from the Natural

Resource Conservation Service (NRCS) Soil Climate Analysis Network (SCAN)

(http://www.wcc.nrcs.usda.gov/scan/); 92 days representing the growing season from (June–August 2013) were used for the meteorological input values (Schaefer et al., 2007). Three soil layers were defined that corresponded with the sample layers (upper, middle, and lower), with a maximum soil depth of 70 cm (the vertical extent of the cross section drawings). The Penman-Monteith evapotranspiration formula (Monteith, 1965), 'Atmospheric Boundary Conditions with Surface Run Off', and 'Free Drainage' settings were used in the simulation. In order to determine realistic initial moisture values for the soil, the model was run with two iterations of the 92-day meteorological data period that were used through the growing season (184 total running days). The first iteration of the model was begun from field capacity and used to spin up the model for the remaining 92-day period. Only the second 92-day period with normalized moisture values was used in the analysis.

RESULTS

Nest Soil Properties

Texture of nest soils ranged from a silt loam to silty clay loam (Table 1, Fig. 1). These soils showed very little range of color (10YR 2/1–10YR 3/1), making the identification of bioturbated areas by visible color alone difficult. The soils displayed vertic properties (i.e., slickensides and wedge-shaped peds), and large cracks were open during the excavation likely exacerbated by the dry conditions prior to sampling in July 2012. Ants were observed to be moving through interpedal pores and root cavities as well as permanent subsurface nest structures during the excavation, a phenomenon similar to the one observed by Green and Askew (1965). Granular and subangular blocky structures were observed in the A horizon and angular to subangular blocks were observed in the BAt horizons (Table 1). The Bt1 and Bt2 horizons were

composed of angular and subangular blocks; the Btss1 and Btss2 horizons were composed of subangular blocks and prismatic structures except for the Btss2 horizon of nest 1, which contained moderate fine wedges and coarse angular blocks. Dry rupture resistance classes for most of the soil ranged from hard to rigid (Table 1). Upon moistening, however, rupture resistance ranged from very friable to very firm.

The particle-size distribution of the unmodified soil increased in the sand and clay fraction with depth, whereas the silt fraction decreased with depth (Table 2). Overall, ant-modified soils from nearly all depths displayed an increase in the sand fraction and a decrease in the clay fraction when compared with the unmodified soil (Fig. 3). Tukey's HSD analysis of the residuals (nest minus control) for all nest samples in each layer revealed no significant difference in particle-size distribution among individual nest components except the mound, which had higher silt content than samples not directly associated with a nest feature.

All average bulk densities near nest features in the middle and lower layers were lower than the undisturbed soil (Table 2, Fig. 4). In the upper layer, however, galleries were significantly higher in bulk density compared to undisturbed soil (Table 2, Fig. 4). Average organic carbon content of the soil mound was significantly higher than any of the subsurface nest feature samples (Table 2).

Nest Hydrology

The aggregated results of the ROSETTA pedotransfer function used to calculate hydraulic properties from soil bulk density and particle size are presented in Table 3. In general, K_s values were closer to the control values in the upper and lower layers, while the middle layer showed the highest increase compared to the control. Most of the upper and lower layer K_s values for the ant-modified soils were 1.4 and 1.8 times higher than the control values. The

middle layer value was ~8 and 3 times the control values for Nests 1 and 2. The total cross

sectional area for Nests 1 and 2 were 244 cm^2 vs. 167 cm^2 total cross sectional area, respectively.

Increases in the conductivity of the middle layer were higher than the upper layer when

compared to the control due to the lower saturated conductivity of the soil matrix in that area.

The lower layer was 1.4 and 1.1 times the control values for Nests 1 and 2, respectively.

HYDRUS-1D was used to simulate the hydrological response of ant activity in the three

sampling layers of both nests using the aggregated hydraulic properties displayed in Table 3. The

mound was excluded from the simulation because of its unique physical properties (e.g., very

low bulk density and strength) and the inability to track ant galleries or chambers due to

sampling difficulties. This eliminated the need to quantify a crusting effect, though it limits the

application of our results to mounds without crusting effects or abandoned nests where the crust

or entire mound has eroded away. Results show that, for the same record of precipitation, ant-

modified soil is predicted to have a lower moisture content when compared to unaffected soil

due to the enhanced drainage of the ant-modified soils as reflected in higher K_s values (Fig. 6).

The lower layers of the soil responded to precipitation events in a manner more similar to the

control soil. Only during or immediately after a heavy precipitation event were $\Delta\theta$ (i.e.,

$\theta_{nest} - \theta_{control}$) values closer to zero for the upper and middle layers.

DISCUSSION

Evidence from both Wang et al. (1995) and Halfen and Hasiotis (2010a, 2010b) strongly

suggests that ants modify the particle size of the subsurface environment by lining their tunnels

with materials of coarser size, but these studies were either done in sandy soil and a formicarium

media of pure sand, respectively. Thin section analysis of a leafcutter ant (*Atta vollenweideri*)

nest in an Alfisol revealed that clay cements were used between patches of coarser material in fungus chambers, and a spongy structure composed of aggregates of finer grained particles was used in the mound (Cosarinsky and Roces, 2007). Though the effects of preferential particle sorting were not observed in subsurface structures of *Formica subsericea*, there was a significant increase of silt content in the mound. Whether micromorphological modifications as the spongy structure or a saliva-silt mixture are responsible for this change in texture is uncertain (e.g., Ettershank, 1968; Humphreys, 1993). Future work should include methods for scraping the surfaces of chambers and galleries for samples to determine nest lining particle-size and aggregate-size distribution, as well as methods for taking thin sections for further analysis of nest wall micromorphology for nests excavated in both coarse and fine soil.

The high OC concentrations in the mound were typical, as ants deposit colony refuse on top of their mounds; some species such as *Pogonomyrmex occidentalis* even have dedicated middens, or circular refuse piles restricted to certain areas of the mound (e.g., Hölldobler and Wilson, 1990; Lobry de Bruyn and Conacher, 1990). Subterranean nest samples in upper layers showed a decrease in OC content compared to the surrounding soil (as seen by the red dots indicating depleted soil values in Fig. 4). In the middle and lower layers of the nest, however, nest samples showed an increase in carbon content compared to the control. OC concentration was significantly higher in soil sampled near the lower chambers. The raw OC values for these features were ~1% higher than the average values of the other samples in their respective layer.

The surface depletions of OC content suggest that ants may be excluding root growth in ant-affected soil near the surface. Ohashi et al. (2007), however, found that root biomass directly beneath the mound in ant-affected soil was not significantly different from control plots. Instead, differences in carbon concentration may be due to an increase in surface area and air flow for

organic matter mineralization (Nkem et al., 2000) combined with the mound conduction of heat to the upper areas of the soil (Coenen-Staß et al., 1980) rather than a change in the abundance of root biomass. The subsurface nest structures provide an environment ideal for carbon respiration, at least in the upper layers of soil where nest temperatures and pore densities are highest. This may be confirmed by the higher OC concentrations found in the lower chambers (Table 2), as these areas of the nest are located away from the thermally conductive effects of the mound and have less air flow due to lower pore density.

Changes in bulk density that extended laterally beyond the visible boundaries of the mound may be due to ants utilizing the shrink swell properties of the soil for transport. During dry years, ants may utilize these enlarged pores for transport, and may even modify them to their increase size or interconnectivity. Whether intentionally, by backfilling, or inadvertently, through clearing material in upper horizons and connecting interpedal pores, ants may be contributing to decreased bulk density, even in areas which they do not appear to normally inhabit. Another possibility is that *F. subsericea* may be constructing foraging tunnels, however foraging tunnels were not observed during this excavation.

Bulk density changes as a function of depth may be due to the interaction between ant behavior and soil horizon properties—for example, bulk density and soil structure. The materials in the upper sampling layer (A and BAt horizons) are not as consolidated as the lower layers, and may tend to become loose during ant excavation or disturbance at the nest surface. For middle and lower layers, the soil is more consolidated as evidenced by the larger aggregate size. The cavities left during soil sampling, for instance, were very stable, whereas samples in upper layers were very crumbly and porous, making them much more difficult to cast and sample accurately.

Little to no stability enhancing modifications are necessary in the middle and lower horizons as they would be in the uppermost horizons.

Increased bulk density around galleries in upper layers may be due to packing or lining material of nest walls in order to decrease tunnel failure in these areas. Sorting of loose materials was demonstrated in laboratory studies of the wall-building ant, *Temnothorax albipennis*, which concluded that ants may preferentially select particles in order to infill walls with smaller size grains for higher stability (Aleksiev et al., 2007a; Aleksiev et al., 2007b). Nest linings of coarse grains infilled with finer material were also observed in thin sections of nests of soil excavating species (e.g., Wang et al., 1995; Cosarinsky and Roces, 2007). Another possibility is that ants are packing soil materials as they reinforce nest walls; this behavior was observed in galleries within *Camponotus punctulatus* mounds (Gorosito et al., 2006), and in formicaria containing *Pogonomyrmex occidentalis* (Halfen and Hasiotis, 2010b). The low bulk density and higher stability of the middle and lower layers may not facilitate the need packing or sorting to increase nest stability, but the effects of continued maintenance on lower-stability soil near the surface may lead to increased bulk density in these areas through time.

Due to the high conductive nature of pores, the hydraulic conductivities of ant-modified soil were greatly influenced by pore density; pore density was highest in the upper horizons of the soil and tapered with increasing depth. In general, the ant nests appeared to channel water through the horizon before it could diffuse into the soil matrix. This channeling effect was highest near the surface, but still present to a lesser degree in the middle and lower horizon. The spikes in precipitation during a heavy rain event were associated with a brief spike in residual moisture content values of the soil, where nest moisture values approached the control. These spikes were much less pronounced in the lower layer, where nest pores were the least

concentrated, and moisture values raised and lowered gradually after heavy precipitation. Higher concentrations of nest pores are associated with a faster response soil moisture values, as is evidenced by the difference between the upper and lower horizons, as well as the differences between Nest 1 and Nest 2.

The simulation results (Fig. 6) suggest that the increased hydraulic conductivity of the ant-modified soil increases the rate of deep drainage (below 75 cm), as water is quickly conducted to lower horizons. The enhanced infiltration and drainage may have a significant effect in reducing surface water erosion and in maintaining lower antecedent moisture conditions throughout the growing season preventing saturation excess overland flow. After the colony dies, abandoned nests still contribute significantly to groundwater flow through buried soils and sedimentary rocks (Logsdon, 1995; Hasiotis, 2003) Though the mound was not included in this particular analysis, the very low bulk density and coarser texture of the mound would likely not limit the increased percolation by a large degree especially given the absence of a crust in the mounds of this species.

Patterns of soil characteristics exist outside the boundaries of the excavated nest structures that are consistently different from soil where ant-nest modification is limited, based on the proportional circle maps in Figure 4. The pattern of depleted concentrations of OC and lowered bulk density was consistent across both nests, implying that ant modification extends beyond the visible and/or active nest structures. No foraging tracks or other structures were observed that extended laterally past the nest mound, therefore these differences may be due to the difficulty of ant excavation of the fine-textured soil at this site in combination with the shrink-swell properties of the soil. During wet years, chambers and galleries are easier to construct in the soil, as the resistance to rupture decreases when the soil is moistened. Layers that

are unworkable during dry years (particularly the middle and lower layers) become easier for ants to excavate and utilize during these moist periods. During times of decreased precipitation, however, ants may be restricted to the upper layer of soil, and may utilize interconnected interpedal pores as a result of soil shrinkage and open macropores, which provide a network of cavities in which ants can transport themselves underground.

The polygynous nature of *F. subsericea* means that a colony can still persist after the death of a queen, and, therefore, a nest may be capable of surviving a decade or more (Francoeur, 1973; Foster and Kettle, 1999). The longevity of this species allows them to last through multiple wet-dry periods with the size of the colony and nest expanding or contracting through these cycles. Colonies can improve their nests through normal excavation in wetter years, and during dry years may utilize and modify interpedal cracks and macropores connected and/or extended through the nest subterraneously.

CONCLUSIONS

This study increases the resolution of ant-soil property observations by measuring soil near individual nest structures, and expands our view on ant-modified soil by measuring properties not directly underneath the nest mound. Local effects of ant nest structures on the soil are dependent on the stability of the soil excavated as well as structure proximity to the warmer area of the nestcreated by the mound. These modifications are likely species-specific as well as soil-specific, as different behaviors such as lining nest structures with fine materials versus compacting loose soil to stabilize nest structures would produce different effects on the soil near nest features. Furthermore, temperature conductivity enhancements of the mound would also affect the rates of carbon respiration, especially in areas of the nest that are closest to the surface.

More work is needed to determine both the lateral extent of ant activity during wet and dry years, and the extent of ant activity outside of traditional nest boundaries. The conceptual model presented in this paper, however, appears to be supported by the data collected from soil in small volumes throughout the nest and observations made in the field during the excavation of the sampling pits. The major implication of this work is that the physical and hydrological effects of ant activity are not only restricted to the mound, but also extend into the subsurface and even beyond typical ant nest structures. The effects of subsurface ant activity appear to correlate with the density of nest structures, though the lateral boundary of ant activity extends well beyond these structures (i.e., at least 1 m from the center of the nest). Thus, *Formica subericea* does not merely carry up materials and deposit them on the surface mound. Rather, this species has a dynamic relationship with the soil that depends on the physical characteristics and heterogeneity of the soil material, and local and regional moisture conditions.

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Table 1. Detailed morphological descriptions for unaltered soil pedons near Nests 1 and 2 at the Fitch Natural History Reservation of the University of Kansas Field Station.

Horizon	Depth	Moist Color	Text†	Structure‡	Rupt Resist§		Ped/void¶	Roots#	Pores††	Other
	cm				Dry	Moist				
Nest 1 Pedon: N 39.03843°, W 95.20188°; 4% toeslope; 164°SE aspect; linear vertical/convex horizontal slope shape										
A	0–8	10YR 3/1	sil	3vf, f, m gr, 3m, co sbk	eh	vfr		2 vf, f, m, 1 co T	1 vf, f dt	
BAt	8–18	10YR 3/1	sil	2m, co sbk 2f abk	ha	fi	pCLF	2 vf, 1f, m, co, vc T	1 vf, f, m dt	
Bt1	18–34	10YR 3/1	sil	3m, co pr, 2m, co sbk	r	fi	dCLF	1 vf, f, m T	1f, vf, f, m, vc, dt	
Bt2	34–58	10YR 2/1	sil	2m, co pr 2m, co sbk	vh	fr	cCLF; few, fine F3M	1 vf, f, m T	1f, m, co, vc dt	3 RTH cracks
Btss1	58–74	10YR 3/1	sil	2m, 3co pr, 2m, co sbk	vh	vfr	cCLF; few, fine F3M; SS	1 vf, f, m T	1f, m, co, vc dt	2 RTH cracks
Btss2	74–85+	10YR 2/1	sicl	2f weg, 2co abk	eh	vfr	cCLF; SS	1 vf, f, m t	1f, m, co dt	
Nest 2 Pedon: N 39.03868°, W 95.20303°; 3% toeslope; 164°SE aspect; linear vertical/convex horizontal slope shape										
A	0–4	10YR 2/1	sil	3vf, f gr, 3vf, f abk, 2vf, f sbk	sh	fi		2 vf, f, 2 m, 1 co T	1 vf, f dt	
BAt	4–21	10YR 2/1	sil	3vf, f, m abk, 2vf, f, m sbk	ha	fi	pCLF	1vf, f, m, c T	1 vf, f, m dt	
Bt1	21–30	10YR 3/1	sil	3vf, f, m, co sbk, 2 vf, f, m abk	vh	fi	cCLF	1vf, f, m T	1f, vf, f, m, vc, dt	
Bt2	30–48	10YR 2/1	sil	2f, m, co sbk, 2m pr	vh	fr	cCLF	1 vf, f, m, c T	1 vf, f, m dt	
Btss1	48–56	10YR 2/1	sil	2vf, f, m, co sbk, 2m pr	vh	vfr	cCLF; SS	1 vf, f T	1 vf, f dt	
Btss2	56–81+	10YR 2/1	sil	2f, m, co sbk, 2m pr	eh	fi	cCLF; SS	1 vf, f T	1 vf, f, m dt	

† Text, Texture; sil, silt loam; sicl, silty clay loam.

‡ Structure; 1, weak; 2, moderate; 3, strong; vf, very fine; f, fine; m, medium; co, coarse; gr, granular; abk, angular blocky; sbk,

§ Rupt resist, Rupture resistance; sh, slightly hard; ha, hard; vh, very hard; eh, extremely hard; r, rigid; vfr, very friable; fr, friable; fi, firm; vfr, very firm.

¶ Ped/void; p, patchy; d, discontinuous; c, continuous; CLF, clay films; F3M, oxidized iron nodules; SS, slickensides.

1, few; 2, common; 3, many; vf, very fine; f, fine; m, medium; co, coarse; T, throughout.

†† 1, few; 2, common; vf, very fine; f, fine; m, medium; vc, very coarse; tu, tubular; dt, dendritic tubular.

Table 2. Averages of residual† sample values from Nests 1 and 2, with Tukey's HSD‡. Values with the same letter are not significantly different (α=0.05)

Sample	Bulk Density	Organic Carbon	Clay	Silt	Sand
	g cm^{-3}		%		
Upper Layer					
Mound§	-0.40b	0.95a	4.68a	-6.07a	1.39a
No Feature¶	-0.19b	-2.06b	2.32a	0.24b	-2.56a
Galleries	0.29a	-1.99ab	3.31a	-1.19ab	-2.12a
Chambers	--	-1.76ab	1.68a	-4.14ab	2.46a
Middle Layer					
No Feature¶	-0.34a	-0.03a	4.63a	3.05a	-7.67a
Galleries	-0.51a	0.00a	4.28a	3.26a	-7.54a
Chambers	-0.81a	0.44a	0.00a	-2.09a	-9.19a
Lower Layer					
No Feature¶	-0.06a	0.35b	1.58a	1.45a	-3.03a
Galleries	-0.07a	0.25b	1.72a	0.90a	-2.62a
Chambers	0.01a	1.26a	-0.25a	5.85a	-5.59a

† Residuals are nest values minus control values.

‡ Tukey's HSD analyses performed separately on each layer and property.

§ Mound control was the sum of each control layer value multiplied by the proportion of nest pores in each layer.

¶ Samples taken >2 cm from any nest feature, up to 1 m from the mound

Table 3. Initial soil moisture values obtained from the ROSETTA pedotransfer function and used in the HYDRUS-1D simulation.

Layer†	θ_r‡	θ_s§	α¶	n#	K_s††	θ_r‡	θ_s§	α¶	n#	K_s††
			Control Samples					**Nest Samples**		
			cm⁻¹		cm d⁻¹			cm⁻¹		cm d⁻¹
					Nest 1.					
Upper	0.0725	0.4633	0.0051	1.6631	39.3447	0.0727	0.4631	0.0051	1.6625	72.1745
Middle	0.0707	0.3950	0.0066	1.5685	6.7384	0.0723	0.4066	0.0067	1.5660	54.4675
Lower	0.0681	0.3594	0.0091	1.4235	2.3186	0.0682	0.3600	0.0091	1.4243	3.3183
					Nest 2.					
Upper	0.0733	0.4684	0.0047	1.6899	54.1123	0.0727	0.5114	0.0049	1.6792	75.7520
Middle	0.0582	0.3395	0.0091	1.4338	2.8699	0.0592	0.3454	0.0090	1.4408	8.4073
Lower	0.0728	0.4026	0.0077	1.5141	6.5804	0.0728	0.4026	0.0077	1.5142	6.9695

† Sampling layer.

‡ Saturated water content.

§ Residual water content.

¶ Inverse of the air entry value.

Pore size distribution.
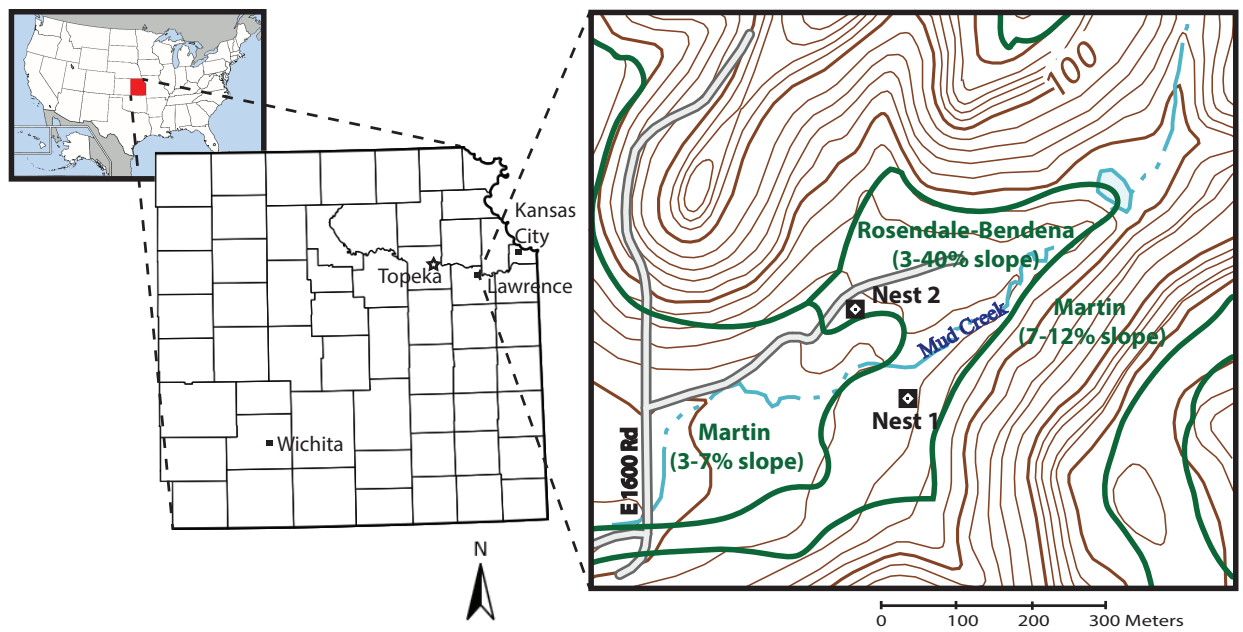
†† Saturated hydraulic conductivity.

Figure 1. Map of sampling locations at the Fitch Natural History Reservation of the University of Kansas Field Station, Douglas County, Kansas, USA.
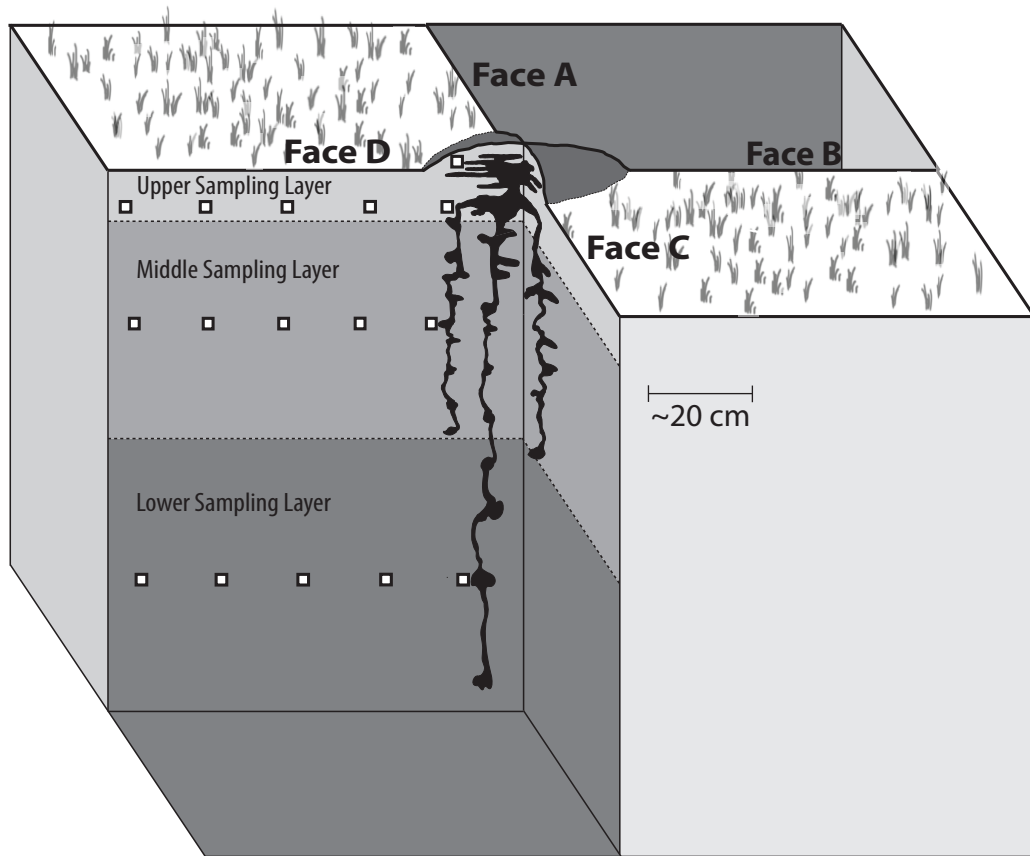
Figure 2. An example of the nest excavation pit used for this study, with relevant nest structures labeled. Face D displays locations of sampling depths and sample points.
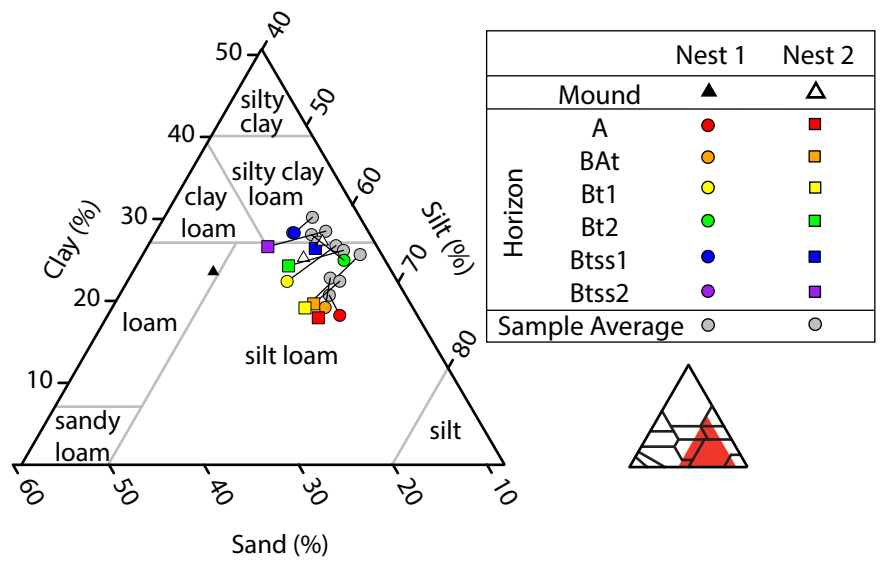
Figure 3. Particle-size distribution of control samples compared to averages of samples taken from the same layer depth within the nest. Particle-size distributions of the mound are also displayed for reference.
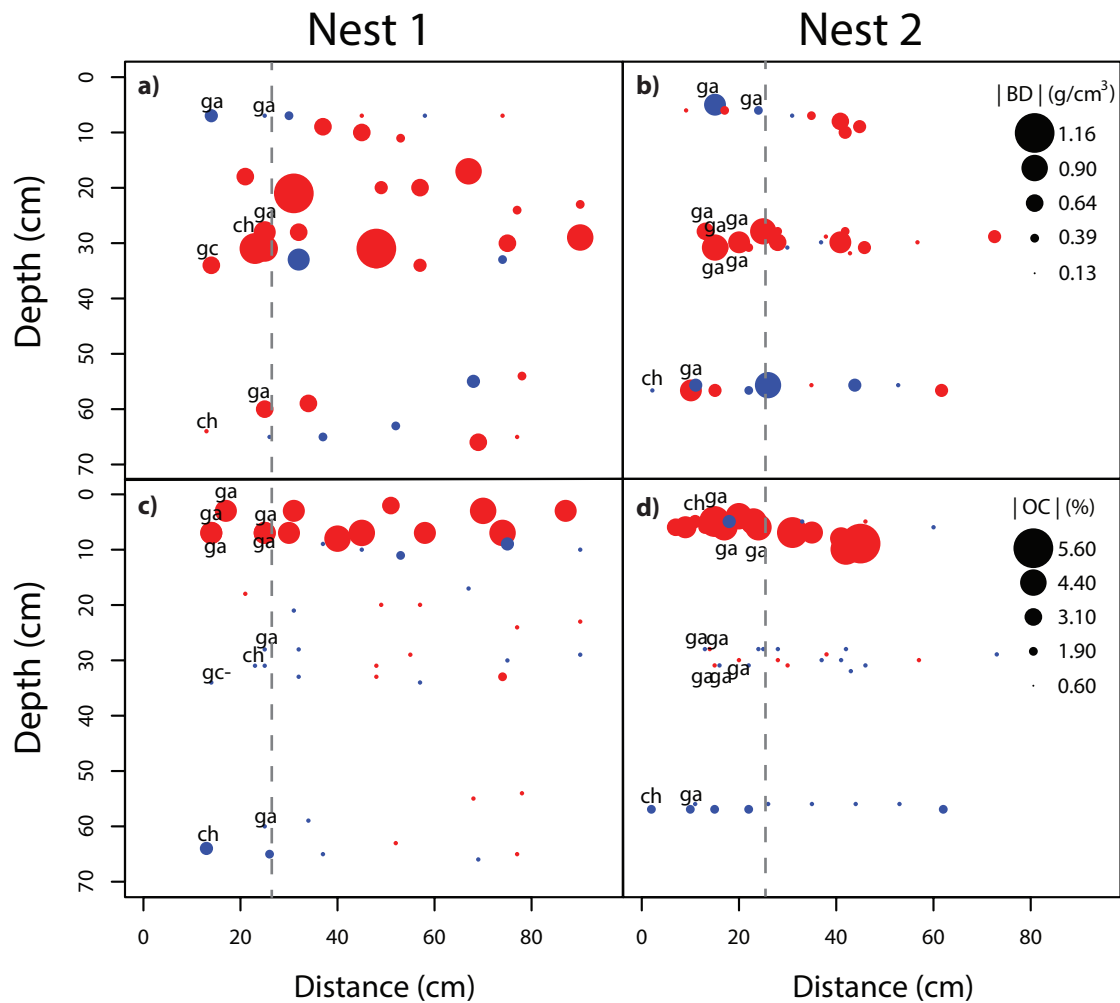
Figure 4. Locations of bulk density (a-b) and organic carbon samples for each of the four faces projected on each other (c-d) for Nest 1 and 2. Values higher than the surrounding soil are indicated in blue, and values lower than the surrounding soil are indicated in red. Letters next to spots indicate sample's proximity to a nest feature (ga=gallery, ch=chamber, gc=gallery and chamber). Horizontal distance is measured from the center of the nest mound, and dashed lines indicate the edge of the nest mound.
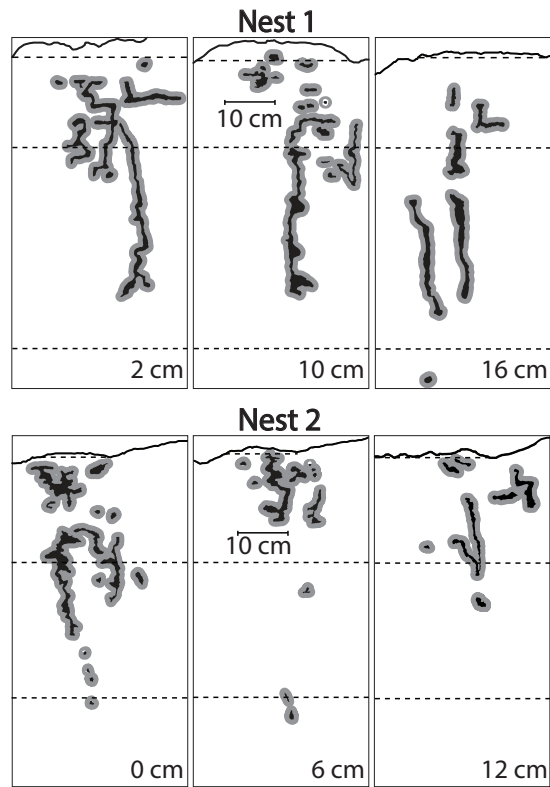
Figure 5. Digitization of vertical cross sections of each ant nest, with upper, middle, and lower sampling layers delineated (dashed lines). Distances on the bottom right-hand corner of each cross section are taken from the center of the nest mound.
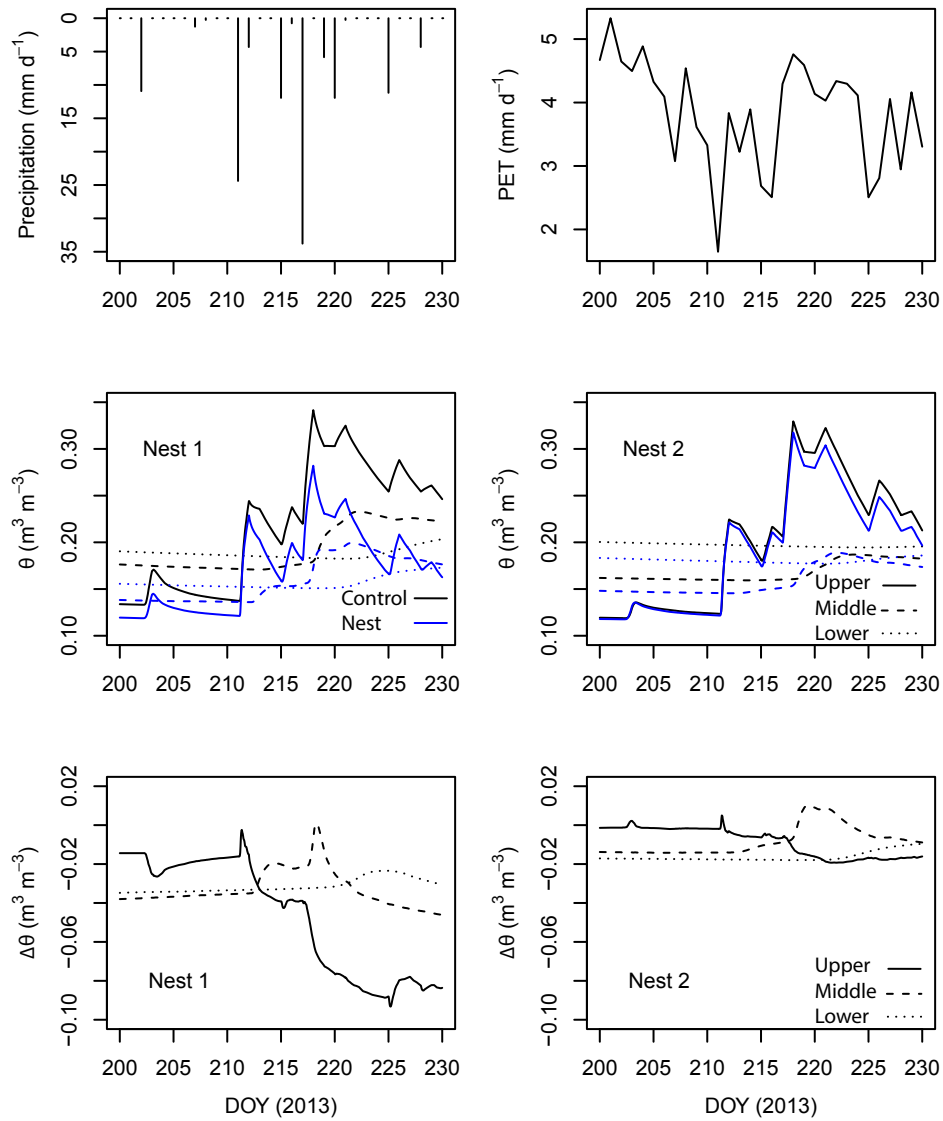
Figure 6. Input values for precipitation and potential evapotranspiration (top row) after several rain events, along with the resulting volumetric water content (θ, middle row) and change in water content from the control soil (Δθ, bottom row) for both nests.
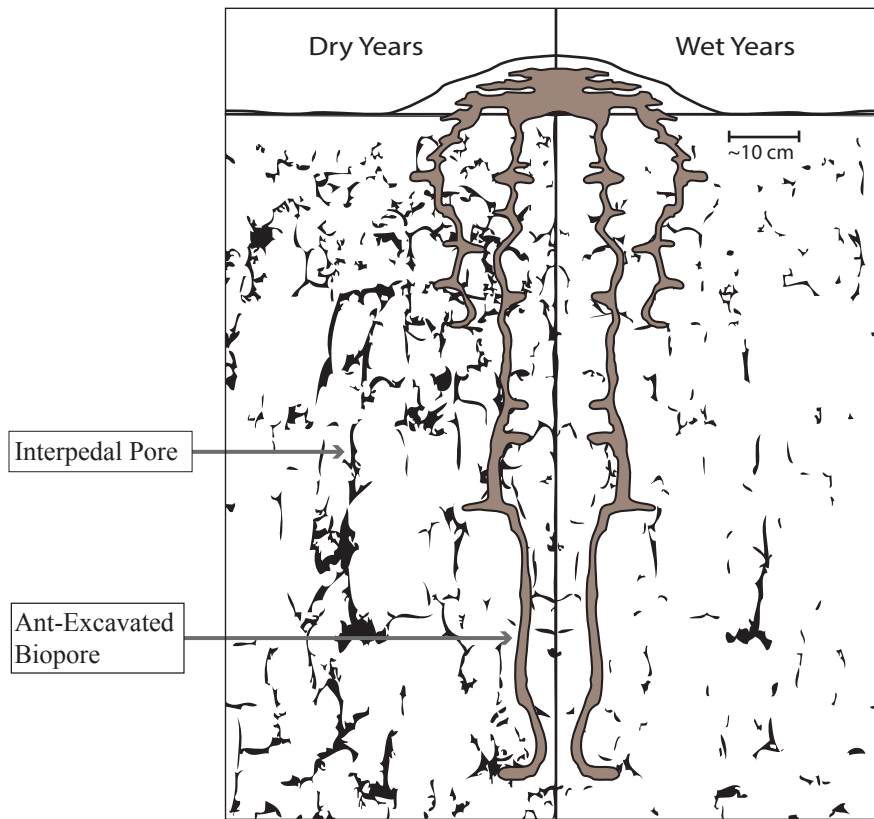
Figure 7. Conceptual model of an ant nest and surrounding soil in wet years and dry years. During wet years (left), structural pores are opened or exaggerated by soil shrinkage due to dry conditions. Ants may utilize and modify these pores, increasing their potential as possible conduits for preferential flow.

CHAPTER 3. EFFECTS OF ANT (*FORMICA SUBSERICEA)* NEST DEVELOPMENT ON PHYSICAL AND HYDROLOGICAL PROPERTIES OF A COARSE-TEXTURED SOIL

ABSTRACT

Ants may compose a large portion of the total biomass in an ecosystem and can play a significant role in soil turnover and nutrient cycling. Monitoring ant nest architecture and growth in the field can be difficult, however, due to the destructive nature of casting ant nests. In order to examine nest effects on soil hydrology during different stages of development, 828 *Formica subericea* workers were placed in each of two large (1.0 m x 1.0 m x 0.1 m) formicaria and allowed to excavate for 82 days in a coarse-textured soil collected from the field. Photographs and transparencies were used to record nest structure for 5 different time steps during development. After the fifth time step on day 82, the nest was cast with dental plaster and the formicarium media was sampled. Overall, ants organic carbon was significantly different near nest structures (0.08%) when compared to the control soil (0.22%, $P < 0.05$). The development of the nest was associated with an increase in saturated conductivity of the soil. Backfilled entrances and vertical galleries contributed to decreasing saturated conductivity as worker numbers declined towards the end of the experiment. The presence of nests was associated with an increase in water flux through the soil material, although the effect was not as dramatic as in soils with a naturally lower saturated hydraulic conductivity.

INTRODUCTION

Soil-dwelling and mound-building ants are important bioturbators that are distributed nearly worldwide in tropical to subarctic climates (e.g., Hölldobler and Wilson, 1990). Ant populations can compose a significant amount of the total biomass in a given area: up to 22% in the tropics (Hölldobler and Wilson, 1990). The behavior of soil-dwelling ants results in significant transport and modification of soil material, though estimates of ant-modified soil vary widely with the species or study area targeted for research (e.g., Denning et al., 1978; Lobry de Bruyn and Conacher, 1990; Lobry de Bruyn, 1999).

Ant nests may have an important effect on the hydrology of the surrounding soil because their nests are macropores in the subsurface (e.g., Whitford and Eldridge, 2013). Although active colonies may impede the flow of water through pores by mound crusting, mound decoration, or tunnel blocking (e.g., Denning et al., 1978; Cowan et al., 1985; Wang et al., 1996), these effects are not present in macropores of abandoned ant nests. Macropores may persist for over a century after preferential flowpaths are established (Hagedorn and Bundt, 2002), and even buried macropores can contribute significantly to subsurface flow (Logsdon, 1995).

Ant nests undergo a predictable ontogeny as the colony matures and colony size increases (Gray, 1974; Hasiotis, 2003; Tschinkel, 2005; Halfen and Hasiotis, 2010b). Nests typically begin with a single, large tunnel (gallery) and one or two chambers (e.g., Greaves and Hughes, 1974; Hölldobler and Wilson, 1990). As the colony grows, chambers and galleries increase in both number and diameter (e.g., Tschinkel, 2005; Halfen and Hasiotis, 2010b). Chamber and gallery density in a developed nest is often highest near the surface and decreases with depth. Nest size is generally related to the population of the colony and not just age (Tschinkel, 2005); unused, unmaintainable nest structures are backfilled by ants if the population of a colony declines

(Halfen and Hasiotis, 2010b). Studies that examine changes in nest subsurface architecture, soil redistribution, and/or physiochemical properties of the subsurface during nest development are rare due to the destructive nature of ant nest sampling in the field, though some examples do exist (e.g., Halley et al., 2005; Tschinkel, 2005; Halfen and Hasiotis, 2010a; 2010b; Rink et al., 2013).

The objective of this study is to relate changes in ant nest architecture to hydrological processes in a coarse-textured soil and compare the values to a nest developed in a fine-textured soil under natural conditions (Chapter 2). Characteristics of the final nest were examined through both nest architecture and organic carbon content. These methods provide a picture of how nests of different developmental stages contribute to alterations in soil hydrology in contrasting soil environments.

MATERIALS AND METHODS

Formica subsericea description

Formica subsericea is a large-bodied (~1cm), polygynous ant that has an extensive range in the eastern US (Fig. 1) (Francoeur, 1973). The authoritative text for this species is the French work by Francoeur (1973), which includes a key to the *Formica* species written in English. *Formica subsericea* prefers boreal and forest-edge habitats, but can also be found in lawns and agricultural fields. Workers construct low mounds up to 1 m in diameter, though nests without mounds can also be found under rocks and plant litter (Francoeur, 1973). Due to the large size of individuals and the high populations of colonies, nests can be quite deep and extensive (e.g.,Wheeler, 1910; Tschinkel, 2003). The study in Chapter 2 found that most of the nest extended to 0.7 m, with a few tunnels extending to >1 m deep. The polygynous nature of this

species allows the colony to persist for tens of years, as the death of a queen does not precipitate the death of a colony (Hölldobler and Wilson, 1990; Foster and Kettle, 1999).

Study Area

Approximately 1656 *Formica subsericea* workers were collected in October 2012 from a vegetated sand dune crest at the Fitch Natural History Reservation of the University of Kansas Field Station (Fig. 1). This is a wooded area that contains a large number of easily accessible nests. After locating several potential nests and identifying workers as the appropriate species, one nest was selected for sampling specimens. A pit was dug with a portable backhoe (Dirt Master 55-32710, Sioux Falls, SD) following methods outlined in Smith and Tschinkel (2009) to expose the nest. A manual aspirator with HEPA filtration was used to collect specimens. For future research on this genus, collection by forceps or with a battery-powered vacuum aspirator is recommended to prevent inhalation of the formic acid excreted by these ants as a defense.

Formicaria Layout and Sampling

About 828 ants were placed in each of the two 1.0 m x 0.1 m x 1.0 m formicaria for observation. Ants were counted by emptying specimen vials into a bucket, then aspirating them and tallying them individually. The formicaria media was designed to approximate soil at the Robinson Tract of the University of Kansas field station, a coarse-textured Grinter soil (Mixed, mesic Lamellic Udipsamments) (NRCS 2013) (Fig. 1). Soil from the A, E, and Bt horizons were collected separately (Table 1). The samples were air-dried at 60°C and ground to homogenize the soil and break up aggregates. The formicaria was layered with samples to mimic the upper 60 cm

of soil at the Robinson tract, with 20 cm layers of the A, E, and Bt horizon material, respectively (Fig. 2).

After the formicaria were filled, the ants were introduced and allowed to burrow for 82 days (Oct 31 2012–Jan 20 2013). Nest architecture was documented by photograph and hand tracing approximately every three days; from this data we chose 5 representative photographs as time steps that demonstrate the nests during periods of growth and decline. One side of each formicarium was fitted with a heating pad set to 25°C. Ant nest construction was excluded by the heat, leaving some of the media unmodified for comparison to unmodified soil adjacent to the nest. After the ants had been allowed to excavate for 82 days, dental plaster was poured into the nest to cast nest structures and prevent their collapse during sampling. After the plaster was allowed to cure for 24 hours, the formicaria were opened and carefully sampled at three locations: adjacent to the nest cast (0 cm), in the center of the formicaria (5 cm), and at the far edge formicaria next to the heating pad (10 cm; Fig. 2).

Laboratory Analysis

Samples were tested for effervescence with 10% hydrochloric acid to confirm that the absence of soil carbonates. Aliquots of 10–30 mg were used to determine organic carbon (OC) content via coulometry following Jackson and Roof (1992). Organic carbon content was tested using a CO_2 coulometer (UIC CM5015, Joliet, IL) and furnace apparatus (UIC CM1620, Joliet, IL), which was set to 930°C for 7.5 minutes.

Hydrological Model

Nest architecture photographs in combination with ImageJ 1.48e were used to determine the cross-sectional area of the nests and surrounding horizons (Ferreira and Rasband, 2011). Photographs were aligned and lens-corrected in Adobe Photoshop™ 6.5 and exported to Adobe Illustrator™ 6.5, where they were manually traced over using the photo scale and nest tracings as a guide. The resulting nest diagrams were loaded into ImageJ for analysis. Desired features (pore or horizon) were isolated with the Adjust Threshold option and measured for area of the feature using the Analyze Particles command. Using these commands, the diameter and two-dimensional area of the tunnels created by the ants during different stages of nest development were measured.

The average bulk density, sand, silt, and clay content of samples collected from the field were used to predict the hydrological properties of each layer using the ROSETTA Lite model in HYDRUS-1D 4.16.0090 (Schaap et al., 2001; Šimůnek et al., 2005). The saturated hydraulic conductivity (K_s) of soils with open ant biopores was estimated using Eq. [1]:

$$K_s = K_s^{\text{matrix}}(f_p - 1) + \frac{\rho g w^2 \zeta f_p}{32\eta} \qquad [1]$$

where K_s^{matrix} is saturated hydraulic conductivity of the soil matrix estimated with a pedotransfer function using the bulk density and particle-size distribution, f_p is the fractional area of the pores, ρ and η is the density and viscosity of water, respectively, w is the average width of the open biopore, and ζ is the tortuosity of the pore estimated as the ratio of the projected length (obtained from the rectangular height) to the actual length of the pore (taken as half the pore perimeter).

HYDRUS-1D and the van Genuchten water retention function were used to simulate water flow through a soil with the resulting K_s values (Schaap et al., 2001) (Table 2).

Meteorological data was taken from the NRCS SCAN website; 92 days representing the growing season from June–August 2013 was used for our meteorological input values (Schaefer et al., 2007). Three soil layers that corresponded with the three 20 cm formicaria layers, with a maximum soil depth of 60 cm were defined. In order to determine the initial moisture values for the soil, the model was run with two iterations of the 92-day meteorological data period used through the growing season (184 total running days). The first iteration (spin up) of the model was started from field capacity, and used to predict the moisture content of the soil for beginning of the second 92-day period. The first 92 days of the model were then discarded, leaving only the final 92-day period in the analysis.

RESULTS

Nest Architecture and Development

Nest construction began quickly after the specimens were introduced. By the end of the first day, workers had dug a single tunnel 38° and 56° from the surface and 35 and 46 cm long in each formicarium, respectively (Fig. 3). These tunnels extended most of the way through the A horizon. After the initial tunnel was dug, the ants constructed other tunnel networks branching off this first main tunnel, then proceeded to excavate more entrances and eventually construct small mounds. During the entirety of the experiment, ants did not dig much farther than the top of the Bt horizon, and ants in formicarium 2 never penetrated the Bt horizon. The nest in formicarium 1 was larger and more complex than the nest in formicarium 2. Formicarium 1 had the largest main tunnel diameter and the highest pore density throughout all horizons in the experiment, except horizon A during day 1.

Laboratory nests contained large, conical-to-square subsurface chamberlike structures, referred to as chambers, present at each nest entrance. Though they resembled chambers due to

50

their increased diameter, they were not used for food storage, and brood or queens were not present in the formicaria. These chambers were located below a raised mound or underneath an eavelike structure of overhanging soil, which was held together by the vegetation that started to grow at the surface of the formicaria. The chambers were often formed as ants dug two shallow, diagonal tunnels from the surface that intersected each other to form a v- or y-shape (Fig. 3). As the nest developed, ants continually expanded these intersecting tunnels downwards and outwards to widen these structures. Chambers were approximately 3–5 times wider than the subsurface tunnels to which they were connected.

Pore density was used as a measure of cross-sectional nest size (Fig. 4). Pore density increased rapidly until nests reached a maximum at 42 days, followed by a period of stagnation and decline toward the end of the experiment. As the experiment reached day 50, the outer structures of the nest began to be backfilled (Fig. 4). After day 50, the pore density of formicarium 2 began to increase again, though it never reached the density of day 42. Nest structure densities in the A horizon were higher than the B horizon, with two exceptions: days 8 and and 82 in formicarium 2. Only minimal backfilling was observed in either nest until the pore density began to decline after day 42 (Figs. 3–4). Ants in formicaria 1 mostly backfilled the lower parts of their nest, whereas ants in formicaria 2 mostly backfilled the area underneath the outer two mounds. In both formicaria, nests structures were lined during this stage, decreasing structure diameter.

Architecture of the laboratory nests differed drastically from nests constructed under natural conditions, even though specimens from the same colony excavated both field and laboratory nests. Field-excavated nests were deep: while most structures were found within 0.7 m, a few tunnels could be seen extending below 1 m deep (Chapter 2). In the laboratory, nests

did not extend much beyond 0.4 m. Formicaria nests had two or three entrances at their highest stage of development, which were not always located underneath a prominent nest mound.

Organic Carbon

Values for OC are presented in Tables 2–3, which display values of field-collected soil, and residual values of the formicaria (field soil values – formicaria sample values). Organic carbon content was higher in the upper layers of the soil for both the field soil and formicaria, with an organic matter-poor E horizon between the A and Bt horizons (Table 2). Organic carbon content of nest structures was significantly higher than the control soil ($P < 0.05$), with most of the modifications in the E horizon (Table 3). Organic carbon content in formicaria samples not associated with nest structures (0.22%) was significantly different from samples taken within 2 cm of nest structures (0.08%, $P < 0.05$), though there was no significant difference between samples taken 5 cm and 10 cm away from nest structures.

Hydrology

Figure 5 outlines the saturated conductivity for various horizons, as well as the averages of the major horizons making up the control soil. The control soil had a naturally high K_s of 309 cm d^{-1} in the A horizons, which tapered off to 129 cm d^{-1} in the E horizons and 32 cm d^{-1} in the Bt horizon. After day 1, ants increased the conductivity of the soil by ~32 cm d^{-1} and did not affect the E or Bt horizons due to lack of ant structures in those depths.

Soil K_s increased rapidly until day 42, when nest structures were the densest. The K_s of both nests in the A horizon (1437 and 2565 cm d^{-1}) were 4.6 and 8.3 times higher than the control soil values. The E horizons were also remarkably higher (1354 and 2801 cm d^{-1}), 10.5

and 21.8 times higher than control values, and the B horizon of formicarium 1 (26.4 cm d^{-1}) was 1.3 times higher than control values. The two nests exhibited increased K_s in different horizons; formicarium 1 showed a higher increase in the middle horizon, whereas formicarium 2 showed a higher increase in the upper horizons when compared days prior to 42. After day 42, ants in formicarium 1 backfilled the small area extending into the Bt horizon, lowering the K_s of that horizon back to control values (Table 4).

As the pore area began to decline, K_s values also declined. Day 50 shows a 0.27 and 7.8x K_s decrease in the A horizon from the maximum value. In the E horizon, formicarium 1 shows a 3.8x decrease, while formicarium 2 shows a 1.03x increase. The higher decrease in formicarium 1 may be due to the backfilling of a main vertical tunnel on the right side. A similar backfilling on the left side of the A horizon of formicarium 2 may be responsible for the drop in K_s between days 42 and 50. It appears that backfilling only one entranceway can greatly influence K_s.

Day 82 shows drastic declines in the A horizon of both formicaria, related to the closing off of entrances and main shafts in this area. The final A horizon value of Formicarium 1 (1395 cm d^{-1}) is still about 4.5 times higher than the unmodified soil (309 cm d^{-1}). The final E horizon value of Formicarium 2 (1680 cm d^{-1}) is approximately 13 times higher than the unmodified soil (129 cm d^{-1}). The A horizon would limit flow in the E horizon during these time steps, however, as multiple nest entrances in each formicarium are blocked at this point.

Figure 6 depicts each time step in the formicaria experiment, as well as the control values, during a 92-day period of the growing season between June and August. Overall, the nests were associated with an increase in soil water percolation rate through the horizons, which lowered overall moisture values for the horizon. As pore volume increased due to nest development, simulated rain events were associated with more rapid increases and decreases in

soil moisture values as compared to unmodified soil. The increase in moisture content between the coarse-textured formicaria soil and the unmodified control soil is much lower than in the nest naturally excavated in the field in a fine-textured soil (Figs. 4, 6–7). When compared to the nests excavated in fine-textured soil, ant nests excavated in coarse material have much less of an observable effect on moisture flux throughout the soil profile. For soils with a naturally lower K_s, ant nests more greatly increase the flashiness of the soil, allowing moisture to travel quickly through the horizons and causing faster increases and decreases in soil moisture values compared to the control (Fig. 7). Overall, ant nests apparently have a more dramatic effect on soil with a naturally low K_s than in a soil that is naturally less permeable (Fig. 4, 7).

DISCUSSION

Nest entrances in the field were cryptic; workers were observed emerging from the base of the nest mound rather than through the cone like *Pogonomyrmex occidentalis* (Mandel and Sorenson, 1982; Halfen and Hasiotis, 2010b), though the exact location of entrances was not determined. While casting *F. subsericea* nests in the field, the tops of the mounds were broken in order to pour the plaster into the nest, and plaster flowed out the sides of the mound before filling the subsurface cavity. In the laboratory, *F. subsericea* never burrowed through the nest mound. This behavior may be unique to this species or genus, as they are not described in the *Pogonomyrmex occidentalis* mounds in Halfen and Hasiotis (2010b). In that experiment, *P. occidentalis* made small vertical tunnels through the topmost part of the mound, though a few entrances were also constructed at the base and sides of the mound as nest development progressed.

Formica subsericea nests in the field did not have any large near-surface chambers or widened galleries. Casts of field-excavated mounds revealed horizontal lobe-shaped structures,

however, which may have been chambers. The chambers in formicaria nests were somewhat similar to lobed structures of mounds constructed in the field (Chapter 2). The most similar lobed structure observed in the lab was under the center entrance of the nest in Formicaria 1 during days 42–82 (Fig. 3), though lobes beneath field mounds were flatter and thinner than the near-surface chambers excavated in the lab. These differences in size and shape may be related to the stability of the soil; formicaria media was more loose and prone to collapse than the fine-textured soil in the field. The shape and position of these structures may be related to the development of the mound. Ants may create lobed structures near the surface, and as more material is piled up to create the mound these structures would move from the original subsurface to the mound itself. As the nest developed, lobes could be expanded outwards to form new entrances at the base of the mound, while new material is piled at the top of the mound, sealing old entrances.

Nest development was consistent with the Tschinkel (2005) study of *Camponotus socius* nests, which concluded that ant nest size is correlated with the population of the residing colony. The *F. subsericea* nests in the laboratory grew quickly in size, then tapered off and began to shrink, which may have been correlated with a decrease in worker numbers as they started to die off. Note that growth rates of laboratory nests are much quicker than a new nest would be in the field (e.g., Rasse and Deneubourg, 2001). Growth of a new colony is limited by the biological constraints of the queen. A new ant nest usually begins with a single queen, who only digs a tunnel and chamber for shelter while her first eggs hatch. The first batch of workers created are smaller and weaker than subsequent brood, and would likely concentrate on feeding the queen before building more of the nest (e.g., Wheeler, 1910; Hölldobler and Wilson, 1990). A group of ~800 workers that had no brood to tend or food to store may spend more time digging than a

colony which would need a longer distance to forage. Under natural conditions, time between days 1 and 8 may actually be many weeks or months.

The structure of the gallery networks differed between field and laboratory-excavated nests. Gallery networks of field nests were long, nearly vertical, and helical, with few inter-gallery connections; laboratory nests contained shallow, angular, lattice-like gallery networks with many connections. Helical galleries were present, but not as common as in the field. The difference between the interconnectivity of laboratory and field gallery networks may be due to the absence of the helical chamber-building process outlined by Halfen and Hasiotis (2010b). That study observed *Pogonomyrmex occidentalis* workers building chambers by first excavating a looped tunnel branching off and reconnecting to a gallery. After the loop was excavated, the ants would backfill the outermost part of the loop to create two chambers connected to a gallery. In this experiment, *F. subsericea* kept open triangular or polygonal tunnel networks, and did not backfill to create chambers.

Although dead end chamber areas were present in the formicaria, their arrangement did not appear to be helical. Rather, they looked like exploratory tunnels that would have been expanded to connect to other areas of the nest if excavation had continued, or they may have been results of false branching as mentioned in Halfen and Hasiotis (2010b). The gallery structure of nests in the field more closely resembled the helical layout described in Halfen and Hasiotis (2010b). The cause of the difference in gallery networks between the field and laboratory is unclear, they could be due to restrictions related to the width of the formicaria, differences in the physical and mechanical properties of the soil (the laboratory soil was less stable), differences in the number of workers (e.g., Rasse and Deneubourg, 2001; Tschinkel, 2005), or environmental differences between the field and laboratory (e.g., Scherba, 1959;

Francoeur, 1973; Bucy and Breed, 2006). The higher interconnectivity of the gallery networks in formicaria nests would lead to a higher saturated conductivity of pores when compared to the field-excavated nests, all else being equal.

The study in Chapter 2 showed that *F. subsericea* nests in the field were associated with a depletion of carbon at the surface that extended laterally beyond the boundaries of the nest mound. This was hypothesized to be the effects of ants using interpedal pores outside of the nest area combined with the thermal properties of the nest mound, and the increased air flow and surface area of the nest pores, which would speed up the process of carbon mineralization (e.g., Coenen-Stass et al., 1980; Jones and Oldroyd, 2006). In this experiment, nest structures also have significantly lower carbon content than soils located greater than 2 cm from a nest structure; no difference was found in soils 5 and 10 cm away from nest structures. It appears that lateral effects of ant nests on soil chemical properties are related to the macroporosity of the surrounding soil.

The hydrological predictions of our model assumed no extensive backfilling that would lower bulk density or preferential particle size selection that would modify the particle-size distribution outside of the nest boundaries. Although several studies have observed nest wall modifications by ants, these preferences may be species specific or environment specific and thus may not apply to *F. subsericea* or the soils used for this study (e.g., Wang et al., 1995). The study in Chapter 2 confirmed that the textural properties of soil next to subsurface nest structures were not statistically different from unmodified soil. Though the mound was not included in this particular analysis, the very low bulk density and coarser texture of the mound would likely not limit soil water infiltration by a large degree as long as no crusting effect is observed (e.g., Denning et al., 1978).

Hydrological results of the data (Figs. 6–7) show that the increased conductivity of the soil decreases lag time in soil moisture peaks after a precipitation event. The time it takes for water to percolate throughout the horizon is decreased because nest macropores act as conduits for the transmission of soil water. The effects of ant-modfied soils are not as high in deeper horizons because ant tunnel networks decrease in density as soil depth increases (Tschinkel, 2003). Increased percolation rates were observable in all stages of nest development, though the effects of nests with a higher porosity (Day 42) exhibited the greatest effects (Fig. 6). It appears, however, that even less-developed nests can have a large effect on water flux through the soil.

The effects of ant nests are not as high when compared to finer-texture soil with lower K_s (Fig. 7). Infiltration rates are naturally lower in these soils, and thus water is more effectively channeled through the horizons via macropores rather than through the soil fabric. Although macropores increase percolation rates in both coarse- and fine-textured soil, ant-created macropores are more important for hydrologic flow in landscapes that have less permeable soils.

CONCLUSIONS

The nest ontogeny described in this experiment supports previous models of nest development through time; the colony started with a wide main entrance tunnel, which was deepened and to which intricately interwoven tunnels were added (Tschinkel, 2005; Halfen and Hasiotis, 2010b). Towards the end of the experiment as the number of workers began to dwindle, the ants began to backfill unused or unmaintainable areas of the nest, as observed in Halfen and Hasiotis (2010b). Saturated conductivity values were noticeably affected by the backfilling of one or more vertical galleries or nest entrances, which happened during the latter half of the experiment as workers died off.

Soil carbon in nearly all areas of the formicarium nests increased slightly compared to the surrounding soil. In a fine-textured, vertic soil, nests are associated with large areas of depletion that extend well beyond the boundaries of active nest structures. The lateral effects of ant-modified soil seem to be related to the presence of macropores located adjacent to the nest, as lateral effects of carbon were not observed in the formicarium. Further work should be done on *in situ* nests in a coarse-textured soil to confirm the robustness of this assumption.

Differences in nest architecture and soil hydrology caused by *Formica subsericea* in coarse and fine-textured soil reiterates the need for comparative studies of ant nest effects on soils in differing environments. The increased hydrological conductivity of ant nests is significant for nests developed on both coarse and fine-textured soil; even abandoned nests in buried soils and fossilized material can significantly contribute to groundwater flow (Logsdon, 1995; Hasiotis 2003). Though several reviews exist comparing ant nests across different landscapes and soil types, few studies compare nests of the same species in different environments. Such work is needed to predict ant nest effects on the soil in order to provide more accurate estimates of soil turnover, nutrient cycling, and hydrologic effects of ant-modified soils.

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Table 1. Detailed morphological descriptions for a pedon in the Robinson Tract of the University of Kansas Field Station observed from soil pit.

Horizon	Depth	Bndy[†]	Moist Color	Text[‡]	Struc[§]	Rupt Resist[¶]		Stck[#]	Redox[††]	Roots[‡‡]	Pores[§§]
	cm					Dry	Moist				
Pedon: N 39.02118°, W 95.20813°; 13% shoulder; 175°S aspect; convex vertical/convex horizontal slope shape											
A1	0-8	as	10YR 2/2	ls	2f,m sbk/ 2m, co gr	s	fr	so		3vf,f t	3vfir
A2	8-30	vi	10YR 3/2	ls	1m,co sbk	sh	vfr	so		2vft, 2cot	3vfir, 1vfdt
E1	30-42	vi	10YR 4/3	ls	1msbk	mh	vfr	so		1vf,f t	3vfir, 2vfdt
E2	42-69	gw	10YR 5/4	ls	1msbk	mh	vfr	so		1vft, 1fp	3vfir, 1vfdt
Bt1	69-107	as	10YR 5/3, 10YR 4/6 (25%)	scl	2vc,co,m,f pr/ 2f,m abk	eh	fi	ms	f3m, rmx	1f,vf t	2vf,f dt, 1mtu
Bt2	107-122+		10YR 4/2, 7.5YR 4/6 (20%)	cl	2m,co abk	eh	fi	ms		1vft	1vfdt

[†] Bndy, Boundary; v, very abrupt; a, abrupt; g, gradual; s, smooth; w, wavy; i, irregular.

[‡] Text, Texture; ls, loamy sand; scl, sandy clay loam; cl, clay loam.

[§] Struc, Structure; 1, weak; 2, moderate; 3, strong; f, fine; m, medium; co, coarse; sbk, subangular blocky; pr, prismatic; /, parting to.

[¶] Rupt Resist, Rupture Resistance; s, soft; sh, slightly hard; mh, moderately hard; eh, extremely hard; fr, friable; vfr, very friable, fi, firm.

[#] Stck, Stickiness; so, nonsticky; ms, moderately sticky.

[††] Redox, Redoximorphic features; f3m, iron (III) masses; rmx, reduced matrix.

[‡‡] 1, few; 2, common; 3, many; vf, very fine; f, fine; t, throughout.

[§§] 3 many; vf, very fine; f, fine; ir, irregular; d, dendritic; tu, tubular; t, throughout.

Table 2. Soil physical and chemical properties at the Robinson Tract at the University of Kansas Field Station.

Horizon	$K_{s\dagger}$	Bulk Density	Organic Carbon	Sand	Silt	Clay
	cm d^{-1}	g cm^{-3}		%		
A	308.94	1.24	0.48	82.31	16.44	1.46
E	128.66	1.41	0.12	75.57	22.12	2.82
Bt	20.68	1.41	0.19	51.08	28.96	19.96

† Saturated water content.

‡ Residual water content.

§ Inverse of the air entry value.

¶ Pore size distribution.

Saturated hydraulic conductivity.

Table 3. Averages of residual† sample values from Formicarium 1 and 2.

Formicarium	Horizon	Organic Carbon		
		0 cm‡	5 cm‡	10 cm‡
		—————%—————		
1	A	0.06	0.04	0.06
	E	0.00	0.04	0.06
	Bt	0.10	0.14	0.16
2	A	-0.03	0.06	0.03
	E	0.53	0.01	0.31
	Bt	0.09	0.04	0.03

† Residuals are nest sample values minus field sample values.

‡ Horizontal distances of the formicaria. 0 is the nest side of the formicarium.

Table 4. Hydraulic properties of the control soil and formicaria during the experiment, including inputs for HYDRUS 1-D obtained from the ROSETTA Lite pedotransfer function.

	Hydrus Input				
Horizon	θ_r†	θ_s‡	α§	n¶	K_s#
			$1\ cm^{-1}$		$cm\ d^{-1}$
A	0.0378	0.4448	0.0472	1.7272	308.94
E	0.0349	0.3926	0.0432	1.6195	128.66
Bt	0.061	0.4108	0.015	1.4546	20.68

† Saturated water content.

‡ Residual water content.

§ Inverse of the air entry value.

¶ Pore size distribution.

Saturated hydraulic conductivity.
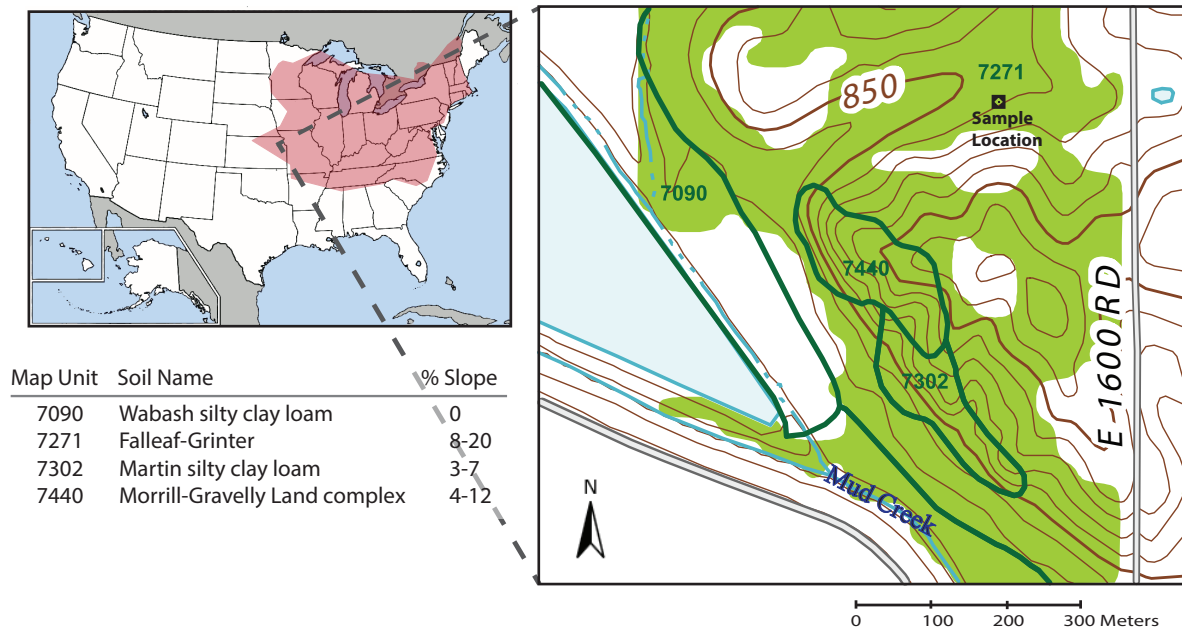
Figure 1. Map of *Formica subsericea* range in the US (left) based on a survey of specimen locations from Francoeur (1973), along with the sample location of formicaria soil (N 39.02118°, W 92.20813°) and soil map of the Robinson Tract at the University of Kansas Field Station (right), Douglas County, Kansas, USA. Specimens were collected from the Fitch Natural History Reservation at the University of Kansas Field Station (N 39.03868°, W 95.20303°).
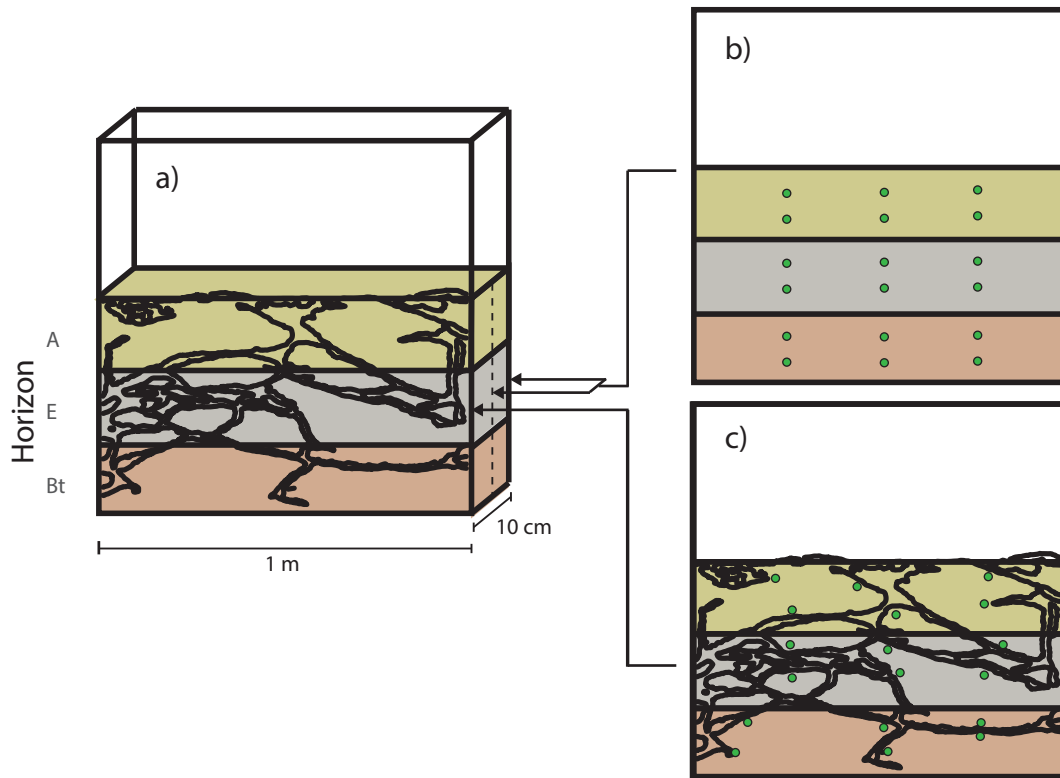
Figure 2. Depiction of the formicaria used to house the *Formica subsericea* workers: a) formicaria depicting a developed nest and layered media, b) samples taken at 5 cm and 10 cm away from the nest, and c) samples taken adjacent to nest structures.
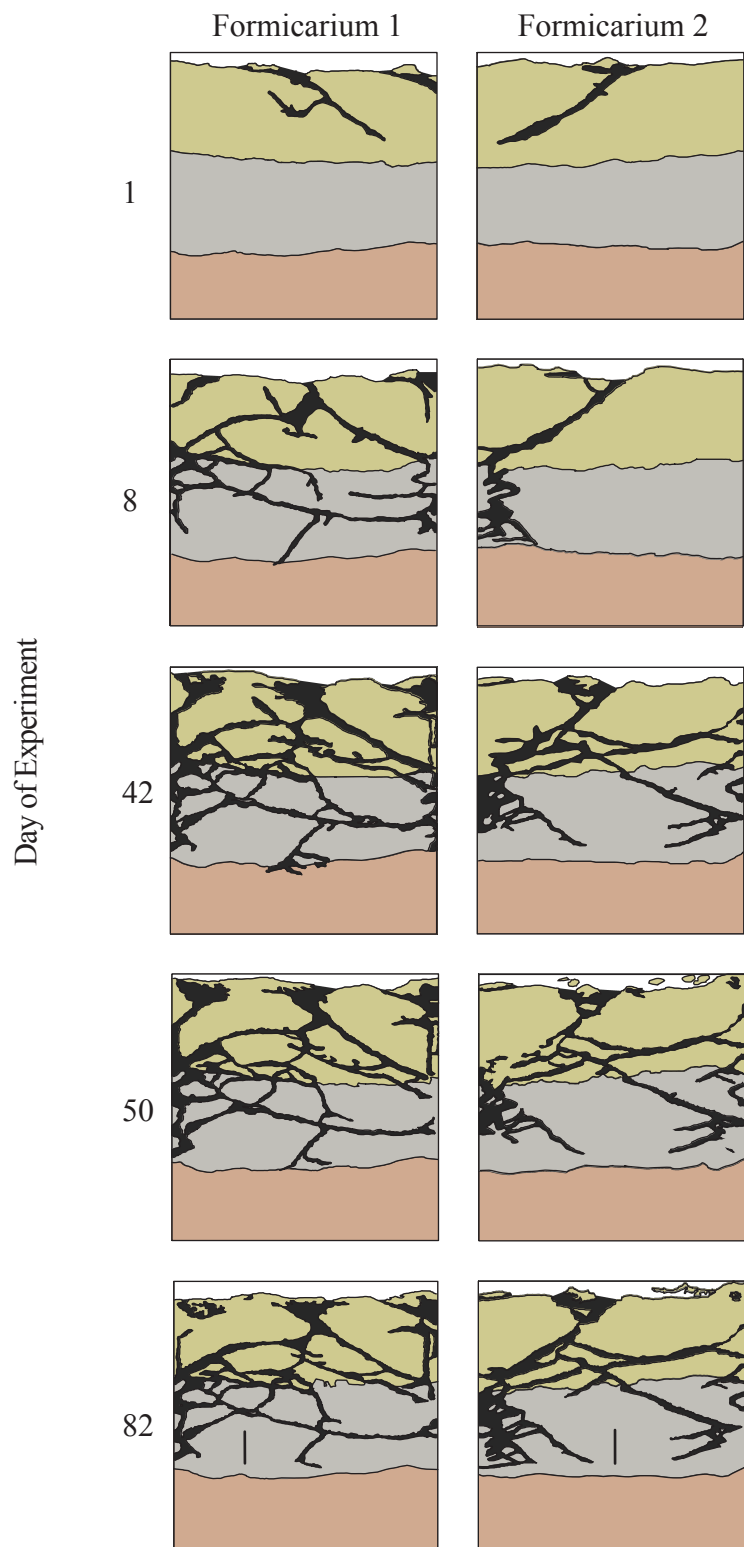
Figure 3. Five time steps of the two formicaria taken over the six weeks of the experiment. Scale bar is 10 cm.
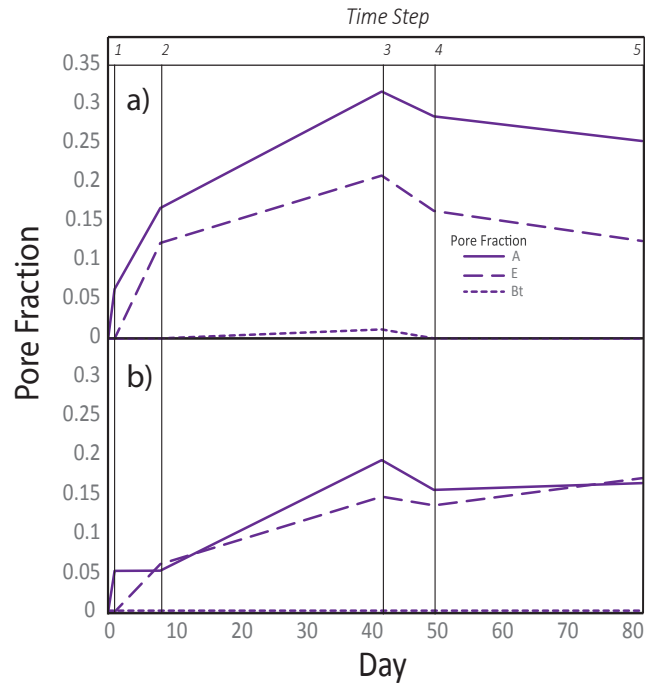
Figure 4. Density of nest pores (pore fraction=area of pores/total horizon area) inside
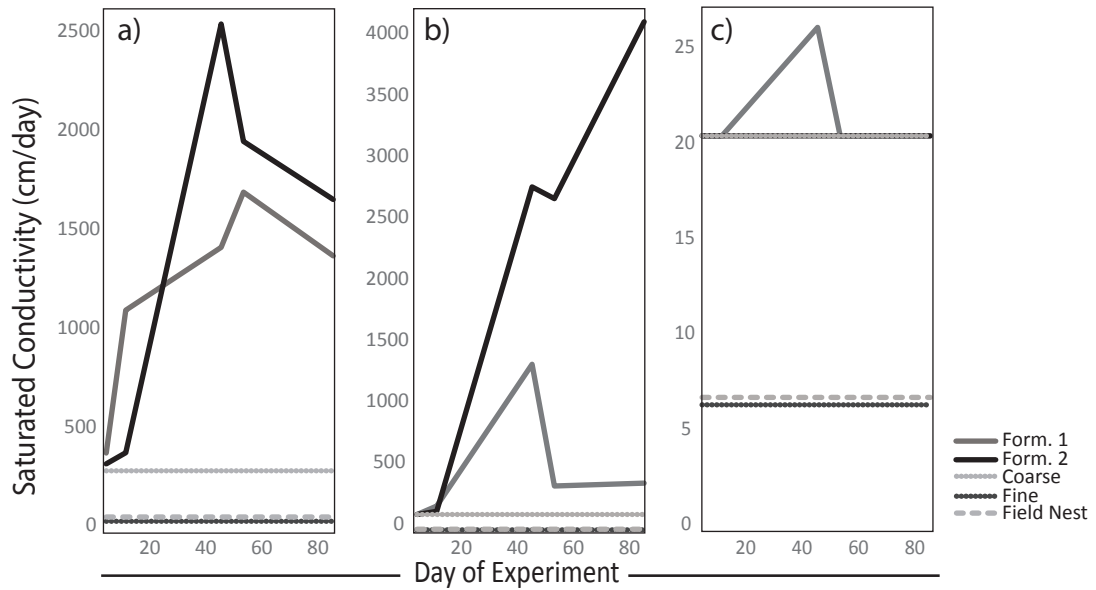each formicarium: a) formicarium 1, b) formicarium 2.

Figure 5. Saturated conductivity of the three major horizons of formicaria 1 and 2 media with time: a) A horizon, b) E horizon, c) Bt horizon. Values from formicaria media source material (coarse), along with the predicted saturated conductivity of the source nest in the field (field nest) and the undisturbed soil from the field collection site (fine) are also included.
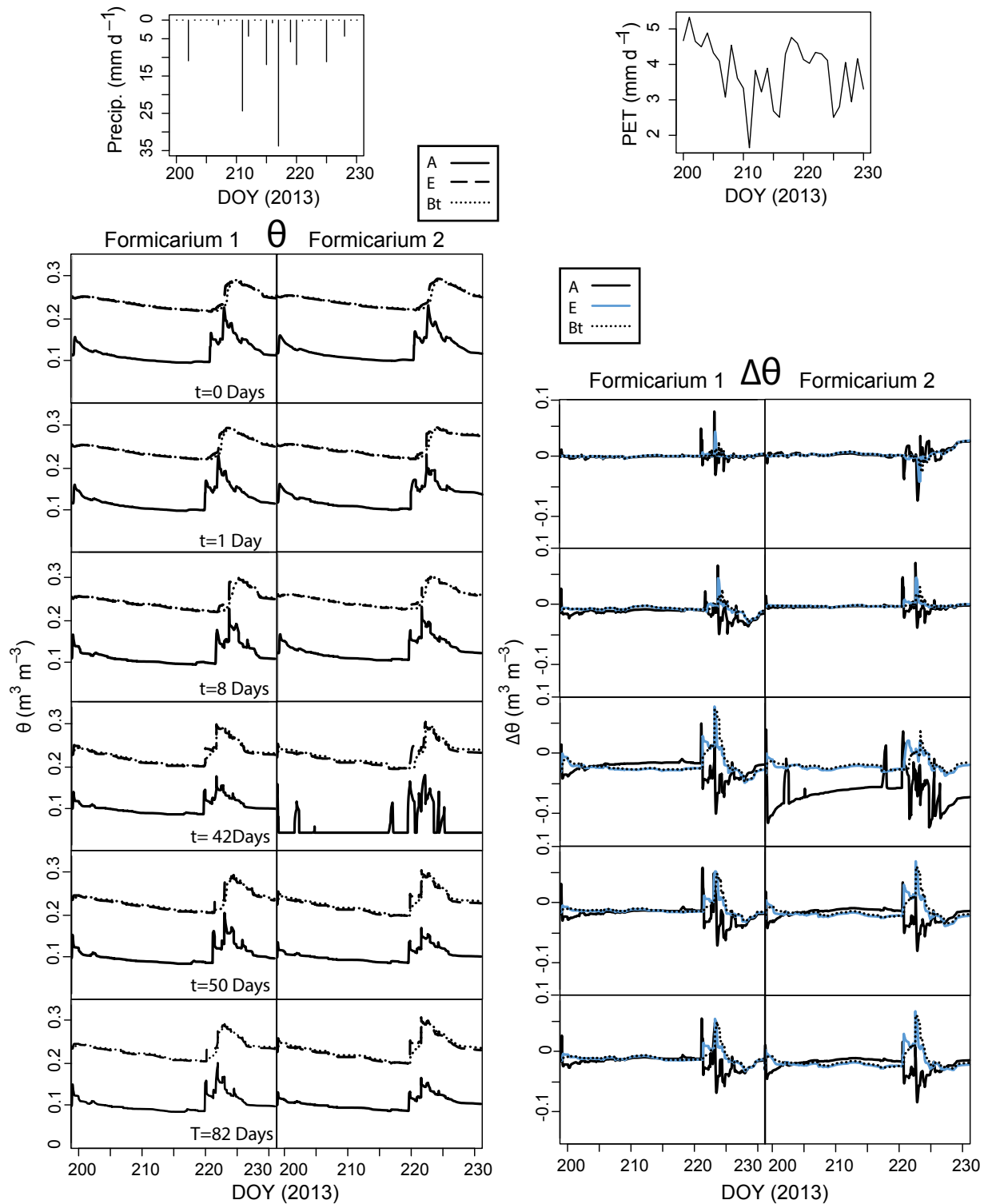
Figure 6. Hydrus 1-D input values for precipitation and potential evapotranspiration (top row) for 92 days during the growing season, along with the resulting volumetric water content (θ), and change in water content (Δθ) from the control soil for both nests. Horizontal rows of graphs depict different time steps in the experiment (Control, 1–5).
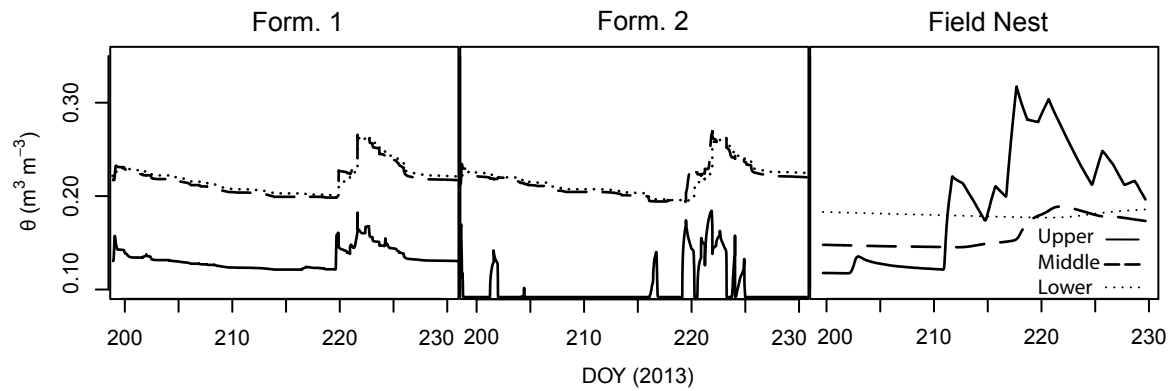
Figure 7. Water content values predicted by HYDRUS 1-D under the simulated climatic scenario illustrated in Figure 5 for the two formicaria during the time of maximum open pore space (Day 42) and for the source nest from which the laboratory ant specimens were collected.

CHAPTER 4. CONCLUSION

Ant nest structure and the physiochemical properties of soil near ant nests components are not often studied in great detail due to difficulty of access as well as the destructive nature of nest casting and excavation. The extent of influence that ants have on the surrounding soil depends of the type of soil studied and may extend laterally well beyond the edge of the nest mound in certain types of soil. Ants appear to decrease organic carbon in carbon-rich areas near the mound and soil surface, perhaps due to increased thermal properties of the mound, the higher surface area of pores near the soil surface, and the effects of increased subsurface airflow through these pores on C-oxidizing soil bacteria. These effects may be exacerbated in soils with vertic properties when fractures open up during dry periods. Ants may increase bulk density near nest structures by packing soil near chambers or tunnels in areas of lower bulk density and stability. Nest mounds were found to have a higher organic carbon content despite increased carbon mineralization, and also a higher silt content in fine-textured soils, perhaps due to preferential particle size collection by workers during nest construction.

The structure of ant nests and their effects on the surrounding soil appears to depend on the type of soil they excavate. Soils with vertic properties extend the boundaries of carbon depletions caused by the ants beyond the boundaries of active nest structures. Ant nests also had different effects on saturated conductivity depending on the surrounding soil—soils with naturally high conductivity were not as influenced by biological macropore networks, whereas soils with naturally lower conductivity were more affected by the open pores of the nest. Nest pores were associated with an increase in soil water flux through horizons following modeled rain events. Ant-modified soils had both a faster increase and more rapid decrease of soil moisture content during simulated rain events than unmodified soils. This effect is less apparent in coarse-textured soils due to the naturally high conductivity of these soils.

Nest ontogeny is associated with an increase of saturated conductivity, and the interconnectedness of pores plays a role in how quickly water is conducted through the soil profile. The effects of ants on a coarse-textured soil have not been studied in field-excavated nests, however, Chapter 3 results imply that nests in coarse-textured soil are shallower and contain subsurface structures in different sizes, shapes, and abundances than in fine-textured soil—at least in the early stages of development. Overall, ant colonies have a dynamic relationship with the soil environment. They influence—and are influenced by—the soil in a number of ways. These studies provide a preliminary description of how nest architecture can vary between soils of varying textures, providing a foundation of research for further studies that may confirm the plasticity of nest architecture and development in different types of soil and more accurately predict ant nest influence on soils of varying properties.