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Impact of Imported Fire Ants on Mississippi Soils

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Abstract

Imported fire ants and their large mounds are notorious throughout the Southeast, and they may be changing the soil. A study was conducted to examine their effects on Mississippi soils by comparing the structure, composition, and function (temperature and hydrology) of formicarious pedons (mound-bearing soil units) and undisturbed soils on 11 soil types and then inferring the long-term implications. The formicarious pedons have a very porous structure consisting of a large mound over a buried soil, both of which are riddled with channels. The mound is constructed of soil (excavated from various depths) and plant debris, mixed by the ants, and is typically higher in clay, phosphorus, and potassium, and lower in organic matter, sand, and silt, than the undisturbed topsoil. It heats up quickly in the spring and summer, reaching higher temperatures than the surrounding soil. It also gets drier than the adjacent soil, but seems to allow more infiltration and leaching through the fragile crust and porous channel network. As old colonies die and new ones build mounds or as existing colonies relocate, it may take less than 100 years for the ants to affect 100% of a given landscape. Long-term effects will include the homogenization of the upper part of the soil, which could change the nutrient and water retention in the soil. Nitrogen, phosphorus, and potassium may be lost from the soil by concentration in and leaching from the mounds. Greater macroporosity and increased drainage could also result. These effects will be felt by farmers, homeowners, land developers, and all of society.

Introduction

What happens if we add a new ingredient, imported fire ants, to the tried and true recipe for Mississippi soil? The recipe calls for marine, alluvial, or wind-blown geological materials, various topographies, a generous amount of heat and rain, a long aging period, and a balanced mixture of Mississippi flora and fauna. Then suddenly, a small winged insect drops from the sky, and our soil will never be the same. It is the mated queen of the ant *Solenopsis richteri* Forel (Figure 1), seeking shelter in the ground. If we could view this plot of ground over the next 3 years with time-lapse photography, it would look as if the soil were being turned inside-out, squirted out of the ground in a foaming mass. When we stopped the film, we would see a foot-and-a-half high spongy mound of soil burying the former soil surface and drastically changing the form of the soil (Figure 2).

This striking process is not an isolated phenomenon. We do not see one queen dropping into a pasture. Instead we see thousands, falling like rain onto the soil surface. There may be 40 large mounds per acre (Figure 3), and instead of each mound staying in the same location for 3 years, a single colony may abandon old mounds to build new ones every 3 months. Over time, colonies move their mounds, old colonies die, and new colonies form new mounds. If we could watch this pasture over a period of decades with time-lapse photography, the landscape might appear as the surface of a pond in the rain, and the mounds as the bubbles briefly formed by the impacts of giant, unseen raindrops. There is no doubt that such a force would play a profound role in determining the characteristics of the soil, or changing them.

No one knows exactly how the two species of imported fire ants, *S. richteri* and *S. invicta* Buren, came here from southern Brazil about 50 years ago. They may have come as stowaways on a ship as both were first sited at Mobile, Alabama. *Solenopsis invicta* has since spread throughout the southeastern United States, whereas *S. richteri* has become restricted to northern Mississippi and Alabama. The fire ant ingredient has been added to soils that never saw such populations of mound-building ants. The native fire ants were never as prolific as the intruders (Wilson 1959), whose mounds can number hundreds per acre.

The imported fire ants have the potential to change this precious natural resource drastically, with serious implications for agriculture and other land uses. Wise stewardship calls for understanding the effects and potential future changes. Detrimental effects may be preventable. Understanding them may enable us to better manage the ants now. With these goals in mind, a project was undertaken to study the effects of imported fire ants on the soils of Mississippi.

Background

From our human perspective, the soil is practically constant, like the hills and the sky. If we could view the soil from the perspective of an amoeba, we would see that the soil is anything but constant. The soil is alive with organisms. Parts of the soil are dissolving as other parts are newly forming. Some parts of the soil are passing through or out, while others are just entering. However, the overall characteristics of the soil are relatively constant at human time scales, barring accelerated erosion or other catastrophes. The form of the soil represents the balance of five environmental factors: parent material (the sediment or rock in which the soil formed), climate, topography, time, and organisms (which include plants, microorganisms, mammals, earthworms, and insects).

It is reasonable to ask, then, what role a given organism, such as the imported fire ant, plays in maintaining, or changing, the balance of factors and the characteristics of a given soil. As members of the Formicidae (the ant family), imported fire ants are part of a group that can have considerable impact on the soil. Fire ants can move more soil than earthworms in Australia (Humphreys 1981). They can deposit 1 inch (2.5 cm) of soil on the surface in 250 years in Connecticut (Lyford 1963). They can transform forest soil into timber soil or deposit 6 inches of soil on the surface in 106 years in Wisconsin (Baxter and Hole 1967; Salem and Hole 1968). Furthermore, they can move more soil than any other animal in parts of the semiarid western United States (Scott 1951).

These last three examples pertain to the mound-building ants, which include imported fire ants. Rather than dumping excavated soil around the entrance to their formicary (nest), thus forming a simple crater, these ants use the excavated soil to build a mound that contains channels (Wheeler 1910). The mound provides extra living space and may also provide more favorable temperature and moisture conditions for the ants. It also creates a three-dimensional soil unit (a pedon) that is distinctly different from the undisturbed soil that surrounds it. This unit of soil has a very different balance of factors than the surrounding, undisturbed soil. We have called these new soil units "formicarious pedons" (Figure 4). The formicarious pedon represents the first stage of the effects of the mound-building ants on the soil. It is the initial stage of the process of "formicopedogenesis," the term we have given to the soil changes caused by mound-building ants. The long-term stage is the cumulative effect over time on the entire soil landscape of the formation of mounds, presence of the mounds with their distinct balance of factors, and collapse of the mounds. As colonies relocate through time, the effects of the ants can be applied to entire landscapes.

The initial effects determine the long-term effects. With this in mind, let's explore the initial effects, the formicarious pedons, of mound-building ants in general (excluding the imported fire ants). In doing so, we can focus on three different aspects: the structure, the composition, and the function or behavior of the pedon.

Formicarious pedons are part of a very different pedogenic regime that begins with the process of mound construction. From the perspective of an individual ant, the process can be broken down into four steps. The ant must first select a site at which to dig, whether it is on the ground surface or deep within an existing channel. Differences in grab site selection among different species may be the reason that different species produce different kinds of channel networks in their nests (Sudd 1970a). The geometry of the channel network can also be influenced by soil properties (Sudd 1975), and the soil properties may exert their influence by changing the selection of grab sites.

The next step for the ant is to dig. The act of digging includes three steps: grabbing a grain, making a pile with the forelegs, and carrying the whole pile away in the mandibles to the ground surface (Sudd 1969). Once at the surface, some species may simply deposit excavated soil particles in a loose pile and then later dig tunnels in the pile. The channels in the mounds of these species are excavated channels, just like those below the ground surface. In other species, however, the channels in the mound are not excavated, but constructed. McCook (1877) described this process of channel construction by *Formica rufa*. The ants first constructed parallel vertical walls, then soil particles were added to the upper, inner edges of the walls and pressed into place until the two sides met in the middle, forming a roofed arch -- a covered channel.

The strength of an arch is not available until it is completed, so external support is required during construction (Hansell 1984). The ants may simply employ the natural cohesive properties of soil particles for this purpose. Ants can carry water from other locations to moisten dry soil, and they do not like to work with dry soil (Wheeler 1910). In coarse soils, it is possible that the ants use some other material to seal the walls, as may have been the case with the channel wall linings observed by Cowan et al. (1985). The walls of the channels of *Lasius neoniger* Emery (a crater-building ant) in sandy Wisconsin soil had dark infillings (spherical particles as small as 0.0004 inch) between sand grains (Wang et al. 1995). For species such as McCook's *F. Rufa*, mound construction entails the assembling of a complex structure by the ants. Courtois and Heymans (1991) produced a computer model of the construction of termite nests that accounts for the construction of pillars. In their model, the termites are attracted by pheromones on previously deposited particles and deposit their loads near them. An ordered structure arises out of an initially random distribution of particles.

Whatever the construction method, the large nest mounds of ants such as the western harvester ant (*Pogonomyrmex occidentalis* Cresson) and the Allegheny mound-building ant (*Formica exsectoides* Forel) are highly visible manifestations of the interaction between organisms and soil. The mounds of formicarious pedons can be as tall as 14 inches (36 cm) (Scott 1951) and can have basal dimensions as great as 6 feet (180 cm) (Denning et al. 1977), but these dimensions vary with species and with soil characteristics (Table 1).

If we break through the exterior of the mound, which is often crusted or mulched with pebbles or plant fragments (Scott 1951; Mandel and Sorenson 1982; Cowan et al. 1985), we find a network of channels, the geometry and size of which depend on the ant species and local conditions. The channels can vary from 1/16 to 1 inch (0.16 to 2.54 cm) in diameter and can occupy 20% of the volume of the mound (Salem and Hole 1968). The channel walls can appear "mammillary in contour," or they may be characterized by "anastomosing microridges" and "pitted furrows" (Baxter and Hole 1967). They may also be characterized by a glaze of soil material mixed with fine organic material (Cowan et al. 1985). Channels typically are concentrated in the mound and the upper part of the soil, with some extending as deep as 20 to 65 inches (50 to 165 cm) into the underlying soil (Baxter and Hole 1967; Wiken et al. 1976; Levan and Stone 1983; Cowan et al. 1985). Subsurface channeling can affect as much as 50 cubic feet (1.4 cubic meters) of soil volume (Scott 1951). All this channeling disrupts soil horizons and changes soil structure (Wiken et al. 1976). The result is a soil unit structurally distinct from the undisturbed soil.

The formicarious pedon is also compositionally distinct from the surrounding soil. The color of the mounds can reflect the source of the mound materials in the A, the B, and sometimes the C horizons that lie below them (Baxter and Hole 1967; Wiken et al. 1976; Cowan et al. 1985). Alternatively, it may reflect a darkening of the initial soil materials (melanization) caused by the ants' activity (Mandel and Sorenson 1982).

The mixing of soil from various depths below the surface causes mounds to be typically higher in clay than the adjacent surface soils (Baxter and Hole 1967; Salem and Hole 1968; Levan and Stone 1983; Cowan et al. 1985), although in some cases ants may transport sand or clay preferentially to the mound (Wiken et al. 1976; Mandel and Sorenson 1982; Carlson and Whitford 1991). The mixing of source materials also can result in organic matter differences between the mound and adjacent soil. Lower organic matter in some mounds compared with the undisturbed soil is the result of dilution of the organic-rich topsoil with organic-poor subsoil (Baxter and Hole 1967; Salem and Hole 1968; Denning et al. 1977). On the other hand, higher organic matter in some mounds indicates enrichment in organic materials from other sources (Carlson and Whitford 1991). The ants can also increase the organic matter content in the soil below the mound (Baxter and Hole 1967).

The addition to the mound of materials that do not come from the underlying soil is indicated in the chemistries of the formicarious pedons. The pH of the formicarious pedon is typically higher than that of the uninhabited pedon, perhaps because of accumulation of basic plant and animal remains within the mound (Baxter and Hole 1967; Denning et al. 1977; Wiken et al. 1976). The mounds can be enriched in nitrogen (N), phosphorus (P), and potassium (K) contents, which can be up to 10 times higher than those of adjacent soils (Baxter and Hole 1967; Carlson and Whitford 1991). The P content of the sub-mound portions of the formicarious pedons also can be enriched (Salem and Hole 1968; Levan and Stone 1983).

Higher calcium (Ca) in the mounds than the undisturbed soil can be due to enrichment or mixing (Wiken et al. 1976; Levan and Stone 1983), and mounds can also be lower in Ca or have the same Ca concentration as surrounding soil (Mandel and Sorenson 1982). Similar variability in relationships has been observed for magnesium (Wiken et al. 1976; Denning et al. 1977) and sodium (Wiken et al. 1976; Denning et al. 1977; Mandel and Sorenson 1982).

The mixed and enriched materials in the formicarious pedons are subjected to very different moisture and temperature conditions from those of uninhabited pedons because the formicarious and undisturbed pedons differ in behavior. Although the highly porous mounds have high hydraulic conductivities, crust formation during rainfall and protective gravel mulches may limit infiltration. Higher cation contents in mounds may reflect this limited infiltration (Mandel and Sorenson 1982; Wiken et al. 1976; Denning et al. 1977; Cowan et al. 1985). Mounds can allow less infiltration than undisturbed soil (Blom et al. 1994).

Mounds can tend to be drier than the undisturbed soil in the upper part and wetter in the lower part (Scherba 1959), but the creation of vegetation-free areas (discs) around mounds of the western harvester ants may help to conserve moisture (Carlson and Whitford 1991).

Compared with undisturbed adjacent soil, mound temperatures can be generally higher, fluctuate seasonally over a wider range, and have a wider variation between 2- and 12-inch (5- and 30-cm) depths because of solar heating and rapid cooling caused by the high porosity (Scherba 1962).

Environmental conditions of the formicarious pedon affect the plant and microbial communities they support. Mounds in the western United States can support fewer species and different dominant species than non-mound areas (Culver and Beattie 1983; Carlson and Whitford 1991). Mounds can show increased development of bacteria and fungi but decreased actinomycetes relative to the adjacent soil because of the intensification of the primary stages of organic matter decomposition (Czerwinski et al. 1971).

The sum of the distinct structural, compositional, and behavioral characteristics of the formicarious pedons amount to a balance of factors that is very different from that of undisturbed soil units, and the collective force of these factors over time will amount to a changed balance of factors for entire landscapes.

If colonies at a given site regularly relocate their nests, which several species have been shown to do (Smallwood 1982), they eventually will affect the entire landscape. The effects inherited by the landscape will depend on the effects seen in the formicarious pedons and on the changes in those effects that take place after the mound collapses. As an abandoned mound collapses, some constituents may leach downward in the profile, others may simply revert to normal levels, and structural changes in the soil may deteriorate or persist (Czerwinski et al. 1971; Wiken et al. 1976). The rate at which the effects will be transmitted to entire landscapes will depend on the density of the nests (how many nests per unit area) and the rate of nest relocation.

The density of mounds reported in the literature ranges from 2 to 800 mounds per acre, affecting from 0.01% to 7% of the land surface (Table 1). Twenty-five percent of the 620 mounds per acre counted by Baxter and Hole (1967) were abandoned, as were 30% of the 466 per acre counted by Wiken et al. (1976). Mound relocation rates must be fairly high. Some species can relocate their nests twice or more per season (Czerwinski et al. 1971).

The drastically different characteristics and behavior of the formicarious pedons combined with high densities of frequently relocated mounds on the landscape mean that the ants are playing a significant role in maintaining or changing the characteristics of the soil in their given regions. It is important to understand these processes.

In the Southeast, imported fire ants may be playing such a role, and it behooves us to find out its exact nature. At the very least, it is an important process in maintaining the present characteristics of our soil, and it may be a process that is drastically changing our soil. The former would be true if the imported fire ants were playing the same role as the native fire ants they have displaced. However, considering that the imported fire ants are introduced, it is more likely that they are changing the soil.

Solenopsis richteri was first discovered in Mobile, Alabama, shortly after World War I. "It is typical of introduced pests," wrote E.O. Wilson (1959, p. 278), "that at first the ants seemed relatively harmless -- indeed, they were limited to a precarious 'beachhead' within the city itself..." But in 1928, when entomologist W.S. Creighton visited Mobile, he found that the ants had spread to the suburbs and warned that they might eventually become a pest; in the early 1930s, the Mobile population exploded (Wilson 1959, p. 280).

The explosion of the range of the ants corresponded with the appearance of a red form of fire ant, differing from the black ants that were first discovered. We understand now the red form is actually a different species. The first species was the black imported fire ant, *Solenopsis richteri*, which today is restricted to parts of northeastern Mississippi and northwestern Alabama. The second species, *Solenopsis invicta* (the red imported fire ant), has spread throughout the Southeast. Today their aggressive stinging and large nest-mounds are a nuisance to the human inhabitants from central Texas to North Carolina and north into Tennessee (Vinson 1997).

"It is an interesting fact," wrote Wilson of the imported fire ants, "that in its South American homeland, the ant is not abundant enough to be a serious pest, and no special efforts are expended to control it. Exactly the same situation holds for the three fire ant species that are native to the southern United States (*S. aurea, S. geminata*, and *S. xyloni*), which can occasionally become minor pests but at present time are completely overshadowed by the invaders (1959, p. 280)."

The range of the fire ants expands in waves several times a year. Beginning in the spring, the colonies produce young with the potential to be sexual. These winged male and female ants wait in the darkness of the nest until the right time, a few days after a warm rain, when they will emerge from the nest. They will fly hundreds of feet into the air, meet with hordes of winged ants from other colonies, and copulate in midair. Hundreds of thousands of winged ants emerge from each acre of infested land. The male drones fulfill their purpose upon mating, but the queen's work has only begun. The mated queen may travel some distance before settling to the ground, and in one wave the fire ants may extend their range 12 miles. Their spread is further eased by humans when mated queens or colonies are carried long distances in the backs of trucks or in containerized plants (Lofgren et al. 1975; Vinson 1997).

After landing, the queen immediately digs a small burrow into which she retreats to begin laying eggs. Vulnerable, like a seed in the ground, the queen begins to produce sterile female offspring that will enlarge the nest and provide for her every need. Her success in establishing a colony depends on her escaping predation and on soil moisture conditions (Green 1962). It is apparently this need for moist soil conditions that drives the ants to mate shortly after a rainfall event. Summer rainfall patterns are apparently important in producing outbreaks (Green 1962). If the colony survives this initial precarious stage, it will soon become invulnerable to all but the harshest circumstances, and it will exert a tremendous force on its environment as its population and the dimensions of the nest explode.

In 3 years the colony can go from 16 tiny workers in a burrow 0.1 inch in diameter and 3 inches deep to 120,000 minor and major workers in a mound 16-24 inches (41-60 cm) in diameter and 10-12 inches (25-30 cm) high. The colony may one day number 230,000 strong (Markin et al. 1973) in a mound 3 feet (90 cm) tall (Green 1952).

All of the ants typically come from a single queen (although multiple queen "polygyne" colonies are common in some areas) that can produce her own weight in eggs every day (Tschinkel 1986). The workers consist entirely of sterile females whose only purpose is to give their lives for the good of the colony. The worker ants live and die for the success of the colony, constantly moving the larvae to the most comfortable part of the nest and doting over the queen and the young, all to maximize the growth and health of the colony. Because their fathers come from unfertilized eggs, the female worker ants are more closely related to each other than they are to their own parents or than they would be to their own children if they could reproduce. By pouring their lives into their sisters, they ensure greater success of their own genes (Hˆlldobler and Wilson 1990, p. 183).

As the colony matures, it will begin to produce the fertile male and female winged ants that take part in the mating flights, but the sterile females do all the work. They are responsible for foraging for food, feeding and caring for the queen and the brood, defending the colony, and constructing the nest. This writhing ant-producing machine can triple its biomass in a single month (Tschinkel 1986) and can have extensive impacts on its environment.

While the eggs and brood are incubating in the mound, the arms of the colony sweep the surrounding land for food, mostly from animal sources but from some plant sources as well. Worker ants retrieve food through underground foraging channels, which radiate out as far as 80 feet (24 meters) from the mound, just below the surface (Green 1952). These omnivorous feeders are aggressive competitors and dominant predators and can displace native ant species and lower the overall insect species diversity of ecosystems (Porter and Savignano 1990). Fire ants have also been reported to cause crop damage and injury to livestock and wildlife. Not only are their painful stings a tremendous annoyance, but some people can have severe allergic reactions to stings inflicted after a mound or a foraging trail is accidentally stepped on (Adams 1986).

Beyond these direct interactions with other animals and humans, fire ants indirectly cause problems because of their large mounds, which can damage farm equipment and are an unsightly nuisance to grounds keepers and homeowners.

Mounds are constructed by the ants largely of excavated soil and are filled with a sponge-like network of channels and chambers (Figure 5), which can extend below the mound to a depth of about 2 feet (60 cm). Additional vertical channels can extend as much as an additional 3.3 feet (1 meter) to the water table. The volume of voids in the entire structure can be 1.4 cubic feet (0.04 cubic meters) (Markin et al. 1973). Mounds can be as tall as 3 feet (90 cm) (Green 1952), but a more common height for a mature mound is about 1 foot (30 cm) (Markin et al 1973; Vinson 1997). Mounds may be taller on clayey soil (Lofgren et al. 1975) and in wetter weather (Green 1952), and their size is most dependent on the age and size of the colony.

These mounds can be very numerous, which enhances their negative impact. Their density on the landscape depends on environmental conditions and on the maturity of the colonies (and subsequently the size of the mounds). Mounds measuring 10-12 inches (25-30 cm) in diameter typically number 20-40 per acre (50-99 per hectare), but they later grow to 18-36 inches (46-91 cm) in diameter with reductions in density to 20-30 per acre (50-74 per hectare) (Green 1962). These large colonies are spaced about 30-40 feet (9-12 meters) apart (Green 1952).

Fire ant mounds are absent or rare in forested areas (Tschinkel 1986), although they can be present after timber harvesting. Mound densities are low the first season after timber harvest, peak the third season, and are rare by the fifth season, apparently because of canopy closure (Lockaby and Adams 1985). Very few colonies are found in hardwood forest and johnsongrass meadows, but heavy infestations are found in row crops (cotton, corn, sorghum), and the heaviest infestations are found in pastures (Green 1952).

Mounds probably are relocated often. H.B. Green (1952) stated that "every colony in a locality may change the location of their mounds in a single day, and then, as suddenly, reoccupy the old sites." He once observed a single colony to change the location of its mound three times in one 24-hour period. The black imported fire ants in their native land move their mounds an average of every 3 months, and they move them an average of 10 feet (3 m) away (Briano et al. 1995).

Considering the large size, high density, and potentially frequent relocations on the landscape, it is clear that these ants are affecting the soil rapidly. The nature of their effects on the soil will depend on the initial and long-term effects. What do they do to the soil as they build and maintain the mound, and how are these effects passed on to entire landscapes as mounds collapse and colonies relocate?

Blust et al. (1982) found that *Solenopsis invicta* mounds in a Sharkey clay soil pasture in Louisiana contained greater concentrations of clay, extractable P and K, and lower pH than surrounding surface soil. No difference in extractable magnesium (Mg) or organic matter was observed. These results are similar to those of Herzog et al. (1976), who found that *S. invicta* mounds on Commerce loam and Sharkey clay soils of Louisiana pastures were higher in P, K, and pH than the adjacent surface soil. Blust et al. (1982) also found that the amounts of P and K in killed mounds did not decrease after 1 year, suggesting that the decrease occurs slowly and overall fertility of the pasture may be affected with time.

Lockaby and Adams (1985) studied the effect of fire ants (*S. invicta*) on forest soils (Typic Hapludults and Vertic Paleudalfs) in north central Louisiana. They found the surface 2 inches (5 cm) of the ant mounds were lower in bulk density and higher in organic matter, P, K, Ca, and Mg than in the surface of the surrounding soil. In the 6-8 inch (15-20 cm) depth the mounds were higher only in organic matter and K. There were no significant differences in the pH values between the mounds and undisturbed soils.

As with other mound-building ant species, the composition of the imported fire ant mounds can be different from the surrounding topsoil, and these effects may persist after the collapse of the mound (Blust et al. 1982). All three of these studies found similar effects on P and K but varied in their results for other constituents tested. This is similar to reports in literature for other ant species. There seems to be variability in the ants' effects that depends on the soil type or other environmental factors.

Long-term effects on compositional soil properties like plant nutrient concentration and clay or organic matter could have profound impacts on agriculture and other land uses. It is important to determine these compositional effects on the wide variety of soil types in Mississippi.

It is also clear from the literature for other ant species that the ants can have other types of effects on the soil, namely structural and behavioral effects. What is the nature of these effects of the imported fire ants, and how do these effects interact with the compositional effects? The effects must be viewed holistically, because it is the whole soil composition, structure, and behavior that are being affected. They may be having broad impacts on every aspect of our precious soil resource.

The objectives of this study were to evaluate the long-term impacts of the imported fire ants on Mississippi soils by exploring the composition, structure, and behavior of formicarious pedons on many soil types.

Materials and Methods

The objectives required a holistic approach, and this research employed diverse methods applied to an equally diverse array of sites/soils. Studies were conducted on 12 sites/soils throughout the state of Mississippi (Figure 6, Table 2).

Because the structural properties of the mounds were expected to depend on the texture of the soil, the structural study was carried out on three soils (Sites A, B, and C; Figure 6, Table 2), each belonging to a broad textural class (Table 3). The texture, organic matter content, and pH of these mounds and control topsoils are given in the Appendix, Tables A1 and A2. The ants at sites A, B, and C were red imported fire ants, and voucher specimens were deposited in the Mississippi Entomological Museum. The structural study included exploration of the channel network geometry, microstructure, aggregate stability, bulk density, capillary contact angles, and droplet absorption properties of the mounds.

The channel network geometries were compared among single mounds from each site. A cylindrical, intact sample (about 5 inches diameter and as tall as the mound) was taken from the center of each mound, and the channels were filled with a fast-hardening resin (Buehler SAMPLE-KWICK Fast Cure Acrylic). The hardened casts were sectioned horizontally and vertically, and two horizontal cross-sectional surfaces, from about midway down each cast, were chosen for the analysis. Three transects, which each passed through the center of the circular section, were randomly selected on each surface. Along each transect, the cumulative distance to each intersection with a wall or channel was recorded and four indices were generated: (1) number of channels per inch of transect; (2) average channel width; (3) average wall width; and (4) the ratio of the average channel width to the average wall width. To determine the percentage of the cross-sectional area occupied by channels, the channel network was first traced onto a transparency. Three circular sampling regions within the cross-section were selected and overlaid with graph paper. The areal percentage of the channels was determined from the ratio of the number of grid squares occupied by channel space to the number occupied by wall space.

Two methods were employed for the microstructural analysis. Intact, air-dried, and sputter-coated samples (Lynn and Grossman 1970) were examined with a scanning electron microscope (JEOL JSM-35CF). Specimens examined included samples from sub-mound channels on a Malbis sandy loam (Site D), mound samples from a Vaiden silt loam (Site E), and samples from a mound on an Alligator clay (Site F). Thin sections were prepared (Brewer 1964) from samples taken as intact cores from single mounds on Sites A, B, and C. Replicate samples were taken from the crust of each mound, the interior of each mound, and the crust of the undisturbed topsoil about 3.3 feet (1 m) from the center of the mound. After vacuum impregnation, the blocks were cut, and at least one specimen of each mound and control material for each site was prepared for microscopic examination.

For the aggregate stability analysis, three mounds (Table 3) were selected at each site. For each mound, samples were first taken from the crust of the mound. Samples from the center of the mound interior and from the undisturbed soil 3.3 feet (1 m) away from the center of the mound were taken to a depth of 6 inches, and samples were treated with chloroform to kill the ants. The stability of air-dried aggregates in the size range 0.25-0.08 inch (0.64-0.2 cm) was determined by oscillation in water (Russell and Feng 1947). The means of the weights of aggregates remaining after each oscillation period were compared among the crust, interior, and control for each of the three soils using t-tests.

For the bulk density analysis, intact peds were taken from the crust and interior (about 3 inches deep) of each of the three mounds sampled for aggregate stability (Table 3). Samples were also taken from the adjacent undisturbed topsoils (about 3 inches deep). Bulk density was determined on air-dried peds using the clod method (Blake 1965). The means were compared within each soil type using t-tests.

Capillary contact angles were determined by a variation of the procedure of Letey et al. (1962) in samples from the same mounds and adjacent surface soils used for the aggregate stability study. Equal amounts of soil were added to two glass tubes [0.3 inch (0.8 cm) inner diameter, 2 feet (60 cm) long] plugged at the bottom with cotton gauze. One tube was set in ethanol so the level of ethanol was equal to the bottom of the soil column, while the other tube was set similarly in water. The height of rise in each column was recorded every 5 minutes for 1 hour, and the slope of the height-time line was determined. The capillary contact angle was determined by the following formula:

$$\mathbf{Cos\ q = (M_w/M_a)^2\ (S_aN_w/S_2N_a)}$$

where N=density of liquid, S=surface tension, M=slope of line, a=alcohol, w=water, and Q=contact angle.

Samples taken from these mounds and adjacent soils for the bulk density study were used for the droplet disappearance study, in which water droplets were applied to peds from the crust, mound interior, and topsoil. The time for disappearance of the droplets was recorded (Scholl 1971). Means were compared using t-tests.

The compositional study included four groups of sites representing four different approaches. The texture, organic matter, pH, and plant nutrients of formicarious and undisturbed pedons were compared on Sites C-L. Studies of compositional effects on Sites D and E included replication, while studies on Sites F-K were part of a survey-type study and did not include replication. Studies of nitrogen content that included replication were conducted on Sites A, B, and C. Site L involved a comparison of an active and a collapsing mound and represented a first step in extending into the long-term effects.

Two contrasting soils were chosen for replicated studies (Sites D and E) based on their high density of undisturbed, large mounds. The first site was located in Pearl River County on a well-drained Malbis soil (Site D), an acid, highly leached, and weathered soil. The slope was about 5% with a northern aspect. Vegetation at the site was 25- to 30-foot-tall (8 to 9 m) loblolly pine trees spaced at 3 to 10 feet (1 to 3 m) in double rows about 50 feet (15 m) apart with grass pasture between the rows. The second site was located at the MAFES Prairie Research Unit in Monroe County on a soil of the somewhat poorly drained Vaiden series (Site E) with a 0-3% slope. This site consisted of a low-management pasture with annual weeds, dallisgrass, fescue, hop clover, bermudagrass, bloodweed, blackberry, cedar, and broomsedge vegetation.

At Site D, active and inactive mounds were counted within four 40-by-40-foot (12-by-12 m) plots located between rows of trees. There were 225 mounds per acre (556 per hectare), 70% of which were located on the downslope position, where exposure to sunlight was greatest. Based on randomly selected active and inactive mounds, those at the site averaged 7 inches (18 cm) tall and 21 inches (53 cm) in basal diameter.

Three mounds at Site D were selected for sampling based on similarity in height, proximity to one another, and conformity to the typical dimensions of mounds on the site. The three mounds selected for study were located in downslope positions and were within the dripline of the pine trees. One active and two inactive mounds were sampled. The inactive mounds showed no evidence of degradation and had intact crusts. The first mound was 9 inches (23 cm) tall with unrecorded basal dimensions. The second was 7.5 inches (19 cm) tall, 23 inches (58 cm) in the long basal dimension, and 22 inches (56 cm) in the short basal dimension. The third was 9.5 inches (24 cm) tall, 31 inches (79 cm) in the long basal dimension, and 27 inches (69 cm) in the short basal dimension.

At Site E, there were 37 mounds per acre (91 per hectare). Ten mounds, located along a transect across the plot, averaged 12 inches (30 cm) tall, 26 inches (66 cm) in the long basal dimension, and 24 inches (61 cm) in the short basal dimension. Three active mounds of similar size were selected for sampling. The first was 13 inches (33 cm) tall and 20 inches (51 cm) in basal diameter. The second was 11 inches (28 cm) tall, 27 inches (69 cm) in the long basal dimension, and 24 inches (61 cm) in the short basal dimension. The third mound measured 12 inches (30 cm) tall, 30 inches (76 cm) in the long basal dimension, and 25 inches (64 cm) in the short basal dimension.

At the Malbis and Vaiden sites (D and E), undisturbed pedons about 3.3 feet (1 m) from the center of each selected mound were sampled to 3.3 feet (1 m), with depth increments determined by changes in soil characteristics. After sampling the crust of the mounds, the remaining portions of the mounds were sampled by thirds with a posthole digger or spade from the center of the mound. The sub-mound portion of each formicarious pedon was sampled according to the depth increments used for the adjacent undisturbed pedon. At the Vaiden site, the active colonies were killed with about 2 ounces (60 ml) of chloroform before sampling.

Soil, site, and sampled mound characteristics for the unreplicated studies conducted on Sites F-L are given in Table 4. On Sites F-K and Site C, each formicarious pedon was sampled by spade or soil auger from the crust of the mound to 3.3 feet (1 m) below the buried soil surface. Within the mound, samples were taken by arbitrarily defined increments. Below the mound, samples were taken incrementally according to horizons determined by changes in texture or color. Undisturbed pedons 3.3 feet (1 m) away from the center of the mound were sampled using similar increments.

At Sites A, B, and C, samples taken from the crust, mound interior, and control topsoil for the aggregate stability analysis were also used for nitrogen analysis.

All compositional samples were air-dried, crushed, and passed through a 0.079-inch (2 mm) sieve to remove coarse fragments. The hydrometer method with sieving was used to determine the particle size distribution (Day 1965). Organic matter content was determined by wet combustion (Allison 1935). The pH of a 1:1

(soil:water) suspension was measured after 30 minutes equilibration. Concentrations of phosphorus, zinc, and sulfur were determined by the Mississippi Soil Testing Procedure described by Raspberry and Lancaster (1977). Concentrations of potassium, calcium, and magnesium were determined by ammonium acetate extraction (Schollenberger and Simon 1945) and inductively coupled plasma detection. The nitrogen content, which was performed on samples from Sites A, B, and C, was determined by the Kjeldahl method (Bremner and Mulvaney 1982).

The data from the studies involving replication were compared using t-tests. For the texture, organic matter, pH, and plant nutrient studies, means from within the mound were compared with means from the uppermost increment of the undisturbed, adjacent pedon, and means from below the mound were compared with equivalent depths in the undisturbed pedon. The nitrogen means were compared among the crust, mound interior, and adjacent, undisturbed topsoil at each site.

The behavioral study included explorations of the temperature and moisture relationships and the hydrological properties of the formicarious pedons. The temperature study was conducted on a Kipling soil in grass pasture (Site M). Two approaches were taken to explore these relationships -- a study involving replication and a detailed study of a single mound. For the first study, three mounds along the fence row were selected, and thermocouple probes were implanted at 2 and 12 inches (5 and 30 cm) deep (Scherba 1962). Probes were implanted in the undisturbed soil about 3.3 feet (1 m) from the center of each mound at the same depths. Temperatures were measured at 6 a.m., noon, and 6 p.m. every day for four consecutive days in February, April, and August 1997.

In the second approach, thermocouple probes were installed at 12 positions in one mound-adjacent soil pair, forming a three-dimensional grid (Coenen-Stas 1980). Probes were also installed in the undisturbed soil at three depths. The arrangement of the probes within the mound is shown in Figure 19. The temperature was monitored for four consecutive days in May 1997.

To explore the moisture relationships of the formicarious pedons, soil and mound samples were taken from formicarious and undisturbed pedons while sampling for compositional analysis. Moisture content was determined gravimetrically (Scherba 1959). Data from replicated pedons were available from Sites D and E, and means from these data were compared using t-tests.

Infiltration properties of the formicarious pedons were assessed by determining the moisture content at various depths in the formicarious and undisturbed pedons before and after a rainfall event (Blom et al. 1994). This approach was taken at four different sites: the Falkner site (Site H), an area adjacent to the Vaiden site (Site E), the Grenada site (Site A), and the Sharkey site (Site C). At the Falkner site, one formicarious and one undisturbed pedon were sampled July 18, 1997, 4 days after 0.5 inches (1.3 cm) of rainfall, and another pair were sampled August 13 after 0.4 inches (1 cm) of rainfall. The first mound was 8.3 inches (21 cm) tall, 28 inches (70 cm) in the long basal dimension, and 19 inches (48 cm) in the short basal dimension. The second was 9 inches (23 cm) tall and 19 inches (48 cm) in basal diameter. Two other small mounds and adjacent topsoils were sampled the same day, one immediately after a brief shower.

At the Vaiden site (Site E), the first mound was 14 inches (35 cm) tall and 35 and 28 inches (90 and 70 cm) along its basal axes. It was sampled on July 15, after 1 week without rainfall. The second mound was 13 inches tall (33 cm), 25 inches (64 cm) in the long basal dimension, and 24 inches (61 cm) in the short basal dimension. It was sampled on July 18 after 10 consecutive rainless days. The third mound was sampled July 23 after 0.7 inches (2 cm) of rainfall. It was 15 inches (38 cm) tall and measured 30 inches (75 cm) and 27 inches (68 cm) along its basal axes. The last mound sampled in the infiltration study at the Vaiden site was 17 inches tall (43 cm), 24 inches (60 cm) in the long basal dimension, and 20 inches (50 cm) in the short basal dimension. It was sampled August 14 after 1 week of frequent rainfall totaling 1.6 inches (4 cm). A single, small mound was sampled on the Grenada site August 12, less than one day after 0.6 inches (1.5 cm) of rainfall. Auger samples were taken from formicarious pedons and undisturbed pedons about 6.5 feet (2 m) away from the mound. Undisturbed soil was sampled at various increments: 2-inch (5-cm) increments to 12 inches (30 cm); 4-inch (10-cm) increments to 40 inches (100 cm); and 8-inch (20-cm) increments to 55 inches (140 cm).

The hydrology of the formicarious pedons also was examined using a bromide tracer (Afyuni et al. 1994). The tracers were applied in solution (500 ml of 1 M KBr) to 2-inch-deep (5 cm) holes created in the crust of the mound and the undisturbed soil before the final sampling at the Vaiden and Falkner sites. At the Sharkey and Grenada sites, the tracers were applied to the open channels after removal of the mound and to the undisturbed soil. Bromide concentration was determined using a bromide-sensitive electrode.

Results and Discussion

Structure

Exploration of the formicarious pedon revealed that the nest-building activities of imported fire ants produce a body of soil that is profoundly different from the undisturbed soil. The differences in structure and composition interact to produce different behaviors concerning temperature, moisture, and overall pedologic and agronomic function. Perhaps the most obvious distinction between the formicarious and undisturbed pedons is their structure. The ants open up the structure of the soil. The formicarious pedon is characterized by a large, channel-filled mound of soil overlying a perforated soil profile.

The channel network can occupy more than half the cross-sectional area of the mound, and the exact percentage and geometry depends on the texture of the soil. In textures finer than sandy loam, the walls are thinner, and there are more channels per inch of transect. A mound in these finer soils also has a higher percentage of its cross-sectional area occupied by channels. In clayey textures, the walls are about the same width, but the channels become wider, increasing the ratio of the channel-to-wall width (Figures 7 and 8, Table 5).

These relationships hint at the process and principles of mound construction as discussed in the Background section of this publication. Our field observations indicate that the imported fire ants construct their mounds in much the same manner as the *F. rufa* of McCook (1877). After a rainfall event in warm weather, the ants can often be seen active on the surface of the mound constructing what appear to be the channel walls out of pellets of excavated soil and plant debris (Figure 9).

Some insights on mound construction are gained through the knowledge that building activity is associated with moist soil conditions and that channel network geometry depends on soil texture. These factors indicate the natural cohesive properties of the soil stabilize the structure, rather than some organic material excreted or added by the ants. Sand has little cohesiveness and little structural strength as a channel wall, and the ants need to make the walls wide to support the structure. Clay has high strength and cohesiveness, and very thin walls will do the same job.

The interaction of the ants with the soil is a self-organizing process. A distinct pattern in the channel network cross sections is not evident horizontally (Figure 7) or vertically (Figure 8). Instead, the geometry appears to result from a random aggregation process as described by Courtois and Heymans (1991) for termite nests. The intricate structure of the mound "crystallizes" out of the interaction of the colony and the soil.

This type of process in the case of the imported fire ants produces a very "dense" network of channels. Channels seem to occupy a greater percentage of the cross-sectional area in fire ant mounds than in the mounds of other species reported in the literature (*Formica exsectoides*, Salem and Hole 1968; and *Formica cinerea*, Baxter and Hole 1967), and this may be the result of the construction behavior of the imported fire ants versus what may simply be digging into a pile of soil by some other species.

The microscopic structure of the imported fire ant mounds also reflects the construction process (Figure 10). Pellet by pellet, the ants construct walls to create corridors, and then they build arched roofs over the corridors to create tunnels. This process is repeated on top of the completed tunnels. The ants may then smooth the surface of the walls to create a semi-coherent lining, which makes the channel more distinct from the porous pellet framework that comprises the wall matrix (Figure 11). The bridged pellet framework of the wall matrix has a lower bulk density than the undisturbed topsoil (Table 6). The wall matrix and lining may be rendered less porous by wetter conditions at the time of construction (Figure 12).

The channel wall linings on two of the three soils of the structural study absorbed water droplets more slowly than the wall matrix. It took from 7 to 253 seconds for a water droplet to be absorbed by the wall lining and from 1 to 75 seconds to be absorbed by the wall matrix on the Grenada soil. On the Sharkey soil, it took from 174 to 443 second for absorption by the lining and 2 to 357 seconds for absorption by the matrix. Thus, the wall linings serve to restrict the movement of water between the matrix and the channels. Water moving in the channels will tend to stay in the channels, and water moving in the matrix will tend to stay in the matrix.

It is not clear whether the ants add some stabilizing material to the walls during construction, but our research seems to indicate that they do not. Although we observed what appeared to be a possible binding material (Figure 13), its presence in undisturbed samples casts doubt on this interpretation (Figure 14). The material on the channel walls may have been organic waste material from the ants' activity. A distinct wall lining in the subsoil B horizon below a mound (Figure 15) was reminiscent of that described by Cowan et al. (1985), but it may have been illuviated materials, deposited by water running through the channels.

The absence of an ant-based stabilizing material agrees with the findings of our channel network geometry study, indicating a strong dependence of the structural stability on the natural soil cohesion. Further evidence for soil-based stabilization was provided by our aggregate stability study. Materials from the interior of the mounds were similar in stability to the undisturbed topsoil (Table 7).

An interesting twist came from our determinations of the capillary contact angles of the materials, which is a measure of their water repellencies. The ants seem to increase the water repellency of the soil, and the capillary contact angles of the materials from the mound interiors were similar (Table 8). This is notable considering the diversity of the soil types involved and the differences in organic matter and clay content among them (Table A1). It appears that something other than the natural soil properties is determining the contact angle. It is unknown whether the ants are adding material to the soil during construction that affects wetting. None of the materials would be considered hydrophobic in that none of the angles were greater than 90 degrees (Emerson and Bond 1963).

Despite these interesting observations, the evidence seems in favor of a soil-based stability. This soil-based stability extends also to the "crust" of the mound, which is less stable than the control topsoil and the mound interior (Table 7). The crust is really more of a roof of the mound (Figure 16). It originates when, at some point after the ants have constructed new tunnels on top of the mound, the ants cease construction and cover the last tier of tunnels with a thin mulch of debris.

What is called the "crust" of the mound is actually a mulch of debris lying on the thin roofs of the outermost tier of tunnels. In this way, the crust is much different from that formed by some other species. The outer layer of *F. ulkei* mounds studied by Scherba (1959) was compact, laminated, and up to 2 inches (5 cm) thick. In contrast, the thickness of the crust of imported fire ant mounds is measured in millimeters and can be highly porous depending on conditions of soil moisture and weather.

The crust was most pervious in the Grenada soil, where the porous crust contrasted with the raindrop-induced crust of the adjacent undisturbed soil (Figure 10). The mound crust was most coherent in the Sharkey soil (Figure 16), and this may be because of wetter conditions at the time of construction. The feature that limits the perviousness of the crust is the channel wall lining, which is continuous with that of the channels below the crust. To the extent that this lining provides a separation between the channels and the wall matrix, it could also provide separation between the channel network and the atmosphere. It does provide some restriction of air and moisture exchange between the network and the atmosphere, although the network is open to the atmosphere through the pores in the crust.

The openness of the network to the atmosphere might be further restricted if a surface seal were to form on the crust of the mound during rainfall, as suggested for *F. cinerea* mounds by Denning et al. (1977). The low aggregate stability of the crusts suggests that an infiltration-inhibiting surface seal could form during rainfall, and the crust of the Malbis mound appeared to have been degraded by raindrop impact (Figure 17). However, under heavy rainfall, we have observed that the crust can erode away and leave channels open to the atmosphere at the surface of the mound (Figure 18). Thus, environmental conditions may affect the movement of air and moisture into the open structure created by the ants within the pedon. The crust is not water repellent (Table 8), and this would further encourage the absorption and infiltration of water through the crust.

Any moisture or air that enters through the crust can move freely within the mound and into and through the channels that penetrate the underlying soil.

Composition

As the ants create this open structure, they mix and enrich the soil. Ants form the framework of channels in the mound using soil material previously excavated from the channels below the mound. Thus, the composition of the mound represents a mixture of soil from various depths below the mound. The ants also incorporate plant debris into the framework, and this enriches the mounds in certain elements.

First, mixing occurs within the mound. The mound is a three-dimensional mosaic of soil materials from different depths -- topsoil and subsoil. In soils that increase in clay content with depth, this mixing typically results in higher clay content (and lower sand and/or silt) in and immediately below the mound than in the adjacent soil. This finding was statistically significant in the replicated studies on the Malbis (Site D) and the Vaiden (Site E) soils (Tables 9 and Table10). It was also widespread among Sites F through K, occurring on Falkner (Site H, Table 11), Loring Mounds A and B (Site I, Tables 12 and 13), Oktibbeha (Site J, Table 14), and Sumter soils (Site K, Table 15). These effects are also common for other ant species, including *F. fusca* (Levan and Stone 1983), *F. cinerea* (Baxter and Hole 1967), and *F. exsectoides* (Salem and Hole 1968).

The relative proportions of topsoil and subsoil may change with time as the channel network becomes deeper. The clay content of mounds on the Malbis and Vaiden soils increased with height in the mound, and this indicates that as the mounds grew larger, the ants were using a greater proportion of subsoil materials.

While most of the mounds were higher in clay than the adjacent topsoil, mounds on the two clayey soils, Alligator (Site F, Table 16) and Sharkey (Site C, Table 17), were similar in clay content to the upper 2 inches (5 cm) of the undisturbed pedon. This is also contrary to the study of Blust et al. (1982) on a Sharkey soil. The absence of higher clay content in the mound suggests that in our study the sub-mound channels were concentrated in the upper part of the underlying soil, and/or there was enrichment in coarse particles from the surrounding soil surface.

The mound on the Atwood soil (Site G, Table 18) was another exception. Lower clay and sand contents in the mound than the undisturbed topsoil indicated possible preferential transport of silt to the mound from below or from the surrounding surface. Preferential transport of coarser particles to the mound has been indicated in the case of *P. occidentalis* (Mandel and Sorenson 1982; Carlson and Whitford 1991).

Notwithstanding these exceptions, it is typically the subsoil component that makes the texture of the mound very different from that of the undisturbed topsoil. The subsoil component also makes the organic matter content of the mound very different. Because soils typically decrease in organic matter content with depth, the organic matter content was lower in the mounds than in the adjacent upper 2 inches (5 cm) of most of the soils of this study. This effect proved significant (a=0.05) on the Malbis and Vaiden soils, where it extended 2 inches (5 cm) into the sub-mound soil (Tables 9 and 10). Similar relationships were observed on the Alligator (Site F, Table 16), Falkner (Site H, Table 11), Oktibbeha (Site J, Table 14), and Sharkey (Site C, Table 17) soils. Lower organic matter in the mound than adjacent soil is also typical of other ant species (*F. cinerea*, Baxter and Hole 1967; and *F. exsectoides*, Salem and Hole 1968) and is due to mixing. Blust et al. (1982) and Herzog et al. (1976) found no effects on organic matter, but this may reflect their greater depths of sampling for the control [6 and 8 inches (15 and 20 cm)].

Lower organic matter in the mound was the rule in this study, but the two Loring (Site I) mounds were slightly higher than the adjacent 0 to 2 inches (0 to 5 cm) (Tables 12 and 13). The Atwood soil was in its own class, with variable relationships in the mound (Table 18). These diverging cases may be explained by the lower organic matter content in the upper 2 inches (5 cm) of the undisturbed soils at these sites. This type of habitat dependence also has been reported in the literature for *P. occidentalis* (Carlson and Whitford 1991).

The effect of the mounds on the Ca content also showed habitat dependence. Exchangeable Ca was lower in the Malbis mounds than in the 0- to 2-inch (0- to 5-cm) depth of the adjacent pedons, while there were no significant effects in the Vaiden pedons (Tables 9 and 10). The decreased Ca content in the Malbis mounds is expected because of low subsoil Ca content. The Vaiden soil has a high Ca content in the subsoil, and no similar effect was observed.

The effects on sites F through K were more variable, and simple mixing did not always apply (Tables 11-18). This discrepancy rules out a simple mixing mechanism in these cases and suggests a mechanism of enrichment. Enrichment refers to an increase in the concentration of a constituent to levels above those found in the undisturbed pedon. Enrichment requires either the preferential concentration of constituents from within the soil or the addition of materials from outside the soil. Enrichment mechanisms are needed to explain the Ca content of mounds on Falkner (Table 11) and Loring B (Table 13). Sharkey showed a general loss of Ca (Table 17).

A different type of enrichment was indicated by the Atwood (Site G, Table 18), Loring Mound A (Site I, Table 12), and Sumter (Site K, Table 15) sites of the non-replicated study. These mounds demonstrated enrichment in acidic constituents. However, the effect on pH displayed habitat dependence. The lower pH on Alligator (Site F, Table 16) and Falkner (Site H, Table 11) is attributable to simple mixing. This lowering of pH within and/or below the mound contrasts with studies of other ant species (Baxter and Hole 1967; Salem and Hole 1968; Czerwinski et al. 1971; Wiken et al. 1976; Levan and Stone 1983) and the Herzog et al. (1976) study of fire ants, but it agrees with Blust et al. (1982).

In Sharkey (Site C, Table 17) and Oktibbeha (Site J, Table 14) soils, which have calcareous materials at depth, the mound pH was greater than the adjacent 0 to 2 inches (0 to 5 cm). The pH of mounds on the Malbis and Vaiden soils was not significantly (a = 0.05) different from the adjacent surface soil. The only significant difference was at 2 to 4 inches (5 to 10 cm) below the Malbis mounds (Tables 9 and 10).

The most striking enrichment effect was seen in the P and K concentrations of the mounds. The P and K contents of all mounds indicated enrichment in these elements (Tables 9-18). Most often, P and K contents were higher throughout the formicarious pedons than the adjacent pedons. This effect was significant (a = 0.05) in the replicated studies in and below the Vaiden mounds. The Malbis mounds showed the same trend, but it was not significant (Tables 9 and 10). The Vaiden (Site E, Table 10), Loring Mound B (Site I, Table 13), and Oktibbeha (Site J, Table 14) mounds showed increasing P with height in the mounds, while the P maximum occurred in the lower part of the mounds on the remaining sites. The source of increased P and K may be plant material used in the construction and maintenance of the mound by the ants. The ants often apply plant fragments to the mound surface.

Enrichment in P and K has been observed by Blust et al. (1982) and Herzog et al. (1976) in their studies of imported fire ant mounds. This phenomenon is also typical of other species (*P. occidentalis*, Carlson and Whitford 1991; and *F. cinerea*, Baxter and Hole 1967).

There were no significant differences in N contents of mound interiors, crusts, and adjacent topsoils on Sites A, B, and C (Table 19) of our study, despite the diluting influence of the nitrogen-poor subsoil in the mound. This finding indicates that the ants add nitrogen to the mound. Nitrogen enrichment can occur in mounds of *P. occidentalis* (Mandel and Sorenson 1982; Carlson and Whitford 1991).

Our study found increased levels of P and K below the mounds. This increase in P and K indicates the downward movement of these elements, either by the ants or by water. Our study of N content did not extend below the mounds.

Formicarious pedons of sites F-K, D, and E showed lower clay and higher sand and silt contents below the mound near the clay maximum (Tables 9-18). This finding suggests downward transport of coarser materials by eluviation. Downward transport of constituents was also indicated by the organic matter contents. All of the formicarious pedons, except those on the Atwood (Site G, Table 18) and Oktibbeha (Site J, Table 14) soils, had some increments below the mound that were higher in organic matter than the undisturbed pedon.

Below the mound, pH levels of Oktibbeha and Sharkey soils were higher than or equal to the adjacent pedons, probably due to the influence of more calcareous materials brought up from greater depths by the ants. Sub-mound effects on Ca were variable but did indicate downward movement in some cases. The trend displayed by the formicarious pedons on the Sharkey and Atwood soils is best characterized as a general loss of Ca, perhaps due to leaching.

Movement of constituents down the channels also occurs after the collapse of the mound, as would be expected. A comparison of the active and collapsing formicarious pedons on the Loring soil at Site L provides insight into possible changes that may occur after the collapse of the mound. As the mound collapses, there appears to be some downward movement of clay, organic matter, P, K, and Ca, but there were no clear trends in pH (Tables 20 and 21). These results are similar to the *F. fusca* study of Wiken et al. (1976).

After the abandonment and collapse of a mound, the constituents are washed back down the channels, and this process also seems to occur to some extent in active formicarious pedons, as indicated by the studies of active mounds.

Hydrology

The subsoil compositional effects suggest leaching of constituents down the channels. The open structure of the formicarious pedon would allow such leaching, and our hydrological studies confirmed that the formicarious pedon is an environment of increased leaching and rapid drying in the upper part and water storage in the lower part.

The same general pattern occurred in almost all the sampled pedons and mounds -- the upper part of the mound was typically drier than the upper 2 inches (5 cm) of the adjacent soil. Compared with the adjacent pedon, moisture contents in the lower part of the mound or below the mound were either higher [Atwood, Site G (Table 18); Sharkey, Site C (Table 17); Sumter, Site K (Ta ble 15); and Malbis, Site D (Table 9)] or lower [Falkner, Site H (Table 11); Loring Mound A, active, Site L (Table 20); and V aiden, Site E (Table 10)]. The Loring Mound B (Site I) formicarious pedon was wetter in the mound and slightly drier below the mound than the undisturbed pedon (Table 13).

The typical dryness of the mounds was encountered on a variety of sampling dates, and it is the most common condition during the summer months. However, the infiltration study revealed that this was not so immediately after a rainfall event, and this indicates the mound has more rapid infiltration than the adjacent soil.

Under relatively dry summer conditions on the Falkner soil (Site H), the upper part of the formicarious pedon was much drier than the undisturbed pedon. After 0.4 inches (1 cm) of rainfall, however, moisture levels at the top of the formicarious pedon closely approached those of the undisturbed pedon (Table 22).

Formicarious pedons on the Vaiden soil (Site E) exhibited similar patterns. After 1 week of rainless conditions in July 1997, moisture levels in the upper part of a Vaiden formicarious pedon were extremely low, much lower than in the undisturbed pedon. The same held true 3 days later. Then, on day 8, after 0.7 inches (2 cm) of rain, the moisture content of the upper formicarious pedon began to approach the adjacent topsoil. Finally, after a week of frequent rainfall totaling 1.6 inches (4 cm), moisture levels in the upper parts of the formicarious pedon exceeded those in the undisturbed pedon (Table 23).

On two other occasions, higher moisture contents were seen in the mounds than in the adjacent topsoil soon after a rainfall event. On the Grenada soil, after 0.6 inches (1.5 cm) of rain, the crust of the mound was still somewhat drier than the same depth in the adjacent soil; however, below that level, the mound was considerably wetter. The same trend was seen on a mound from the Falkner soil after 0.4 inches (1 cm) of rain and immediately after a brief rain shower (Table 24).

These comparisons of mound and topsoil moisture contents indicate that the mound allows more infiltration than the undisturbed topsoil. Comparisons of formicarious and undisturbed moisture contents at greater depths in the pedons suggest the possible retention of this moisture below the mound.

Under summer conditions, the entire Falkner formicarious pedon was drier than the undisturbed pedon except at two zones below the mound -- two moisture maxima at 8 and 35 or 47 inches (20 and 90 or 120 cm) (Table 22).

After 1 week of rainless conditions in July 1997, moisture levels in a Vaiden formicarious pedon were lower than in the undisturbed pedon above a depth of 35 inches (90 cm), but at greater depths the formicarious pedon was wetter than the undisturbed soil (Table 23). Three days later, the moisture maximum below a Vaiden mound peaked at about 47 inches (120 cm), where the moisture content was considerably higher in the formicarious than undisturbed pedons. After a week of frequent rainfall totaling 1.6 inches (4 cm), moisture levels were higher in lower parts of the formicarious pedon than the undisturbed pedon, and the maximum occurred at 40 inches (100 cm) (Table 23). At the time of sampling, free water was observed at 47 inches (120 cm) below the buried soil surface, while there was no free water in the undisturbed pedon at a depth of 67 inches (170 cm).

A similar effect had been observed twice the previous summer. While sampling a mound on the Alligator soil, water was observed at 18 inches (46 cm), and no water was observed in the undisturbed pedon at 48 inches (122 cm). Free water was observed at 32 inches (81 cm) below a mound on the Loring soil in Marshall County (over a drier fragipan), whereas no free water was observed in the undisturbed pedon at 60 inches (152 cm). We have named this phenomenon the "cistern effect," because it appears the ant nests may act as cisterns to collect and store water.

The greater moisture levels below the mounds may indicate the storage of water that has infiltrated the crust and percolated through the channel network. The percolation/bromide tracer study confirmed that water penetrates more deeply into the formicarious than the undisturbed pedons. In the Bromide tracer studies that involved active mounds, bromide penetrated more deeply into the formicarious than undisturbed pedons. Where the mounds were removed, the same effect was observed (Table 25).

The mound allows more water from rainfall to infiltrate the mound, but this water rapidly drains out of the mound. Water percolates more deeply and rapidly into the formicarious pedons, where it may be stored. By collecting more water and retaining it deeper in the profile, the formicarious pedon may be acting as a cistern for the ants, storing water for use in drier times. Such a mechanism would have profound implications for the spread of these ants into semi-arid regions.

Greater infiltration and percolation cause increased leaching of the soil, especially from the upper pedon, and this may explain the increased levels of P, K, and other soil constituents in the subsoil observed in the composition study. Storage of water below the mound could cause different reduction-oxidation processes in the subsoil.

Temperature

The rapid drying of the mound is due not only to the rapid drainage through the channel network, but also to evaporation caused by higher temperatures in the mounds. The open structure and exposed, conical shape makes the mound function like a greenhouse. Temperatures in the mounds fluctuated more rapidly and over a wider range than undisturbed soils. Mounds reached lower temperatures in the winter and higher temperatures in the spring and summer than the adjacent soils (Tables 26, 27, and 28).

During April and August, the results of our study were similar to those of Scherba: mound temperatures were generally higher than the adjacent soil and fluctuated over a wider range. The mounds reached higher temperatures at both 2 and 12 inches (5 and 30 cm) than the adjacent soil even on cloudy and rainy days, as seen in the last 2 days of the April series. The maximum difference between the mound and adjacent soil at 2 inches (5 cm) was 29.7 ^{o}F (16.5 ^{o}C). In August, the patterns were similar to those of April, but the temperatures were generally higher for the mound and adjacent soil. These results are consistent with the hypothesis that the mound is a solar collector.

Temperature distribution within a single mound in May exhibited horizontal temperature variations in the mound (Figure 18, Table 29). Enhanced heating on the southern and eastern sides of the mound due to solar heating was observed only 1 of 4 days. The highest temperatures were in the upper 6 inches (15 cm) of the mound. In the early morning, mound temperatures were greater in the lower parts of the mound due to the buffering effect of the soil.

Conventional wisdom holds that the primary purpose of the mound of a mound-building ant is to provide higher temperatures for brood production (like an incubator) and to provide a broad range of temperatures so that various stages of the brood can be placed in optimal thermal conditions. However, as Scherba (1962) pointed out, the mound also creates greater fluctuations and extremes of temperature, which may be the price paid for these benefits.

Scherba (1962) reported that thermoregulation did not occur in nests of *Formica ulkei* Emery in Illinois in the coldest winter months. In our February study, the mounds were colder than the adjacent soil for the first 3 days of the February series, which were cloudy.

With the exception of the colder conditions in the winter, the ants heat the soil by building and maintaining the mound. The high temperatures of the spring and summer mounds would encourage rapid decomposition of organic materials, as well as dissolution of minerals and concomitant mineralization of nutrients. This process would increase the availability of these elements for leaching through the pedon. However, the high temperatures may lead to dry conditions, and this could discourage microbial activity and nutrient mineralization, although rapid fluctuations in temperature and moisture could encourage mineral weathering and other chemical processes.

These interrelationships among the structural, compositional, and behavior effects of the ants underscore the need for the holistic approach taken by this research.

The Big Picture

The broad results of this research, combined with information in the literature, allow us to develop a conceptual model of the formicarious pedon of the imported fire ants. This model allows us to make some predictions about the long-term implications.

The formicarious pedon "crystallizes" in a self-organizing manner from the interaction of the ants with the soil. What results is a body of soil very different from the undisturbed soil that surrounds it. It has three basic parts: the porous wall matrix of the mound interior, the less porous matrix of the underlying soil profile, and the void space of the channel network that crosses the boundary between the two. The wall and soil matrices are separated from the channels by a thin layer of reduced porosity, and the channels are separated from the atmosphere by a similar layer. The pores of the wall matrix are basically continuous with the atmosphere.

Although the channels that riddle the buried soil profile are impressive and of profound significance, the most striking feature of this whole unit is the mound. The mound is an intricate structure, more than half of which can be occupied by the channel network. It is basically nothing more than a framework for the channel network, built piece-by-piece out of excavated soil and plant debris.

The mound is a soil-based structure, notwithstanding the considerable input of plant fragments, and its structural stability seems to be a function of the natural soil cohesiveness. Even the channel linings seem to be the result of the simple smearing of soil, rather than the addition of some masticated or excreted material from the ants. The ants work with the soil to produce the structure, and thus they interact with the soil properties. The exact form of the resultant structure -- the shape of the mound and the extent and geometry of the channel network -- is dependent upon the properties of the soil.

The soil-based nature of the mound is reflected in the compositional properties as well. The mound is constructed of excavated soil pellets that are added to the structure in a random fashion, and the mound becomes a three-dimensional mosaic of soil materials from various depths in the soil. The ants also add other materials, which appear to be primarily plant fragments gathered from the surrounding surface, and this results in an enrichment of the mound material in certain nutrient elements. The ants concentrate nutrients from the surrounding landscape into the mounds.

In this way, materials from below the soil surface and materials from the surrounding soil surface are exposed to the environment of the mound, which is very different from the environment of the surrounding soil in temperature and hydrology. The open structure of the mound, with its conical shape exposed above the surface of the ground, makes the mound function like a greenhouse, and it heats up quickly in the spring and summer, reaching higher temperatures than the surrounding soil. Higher temperatures increase microbial and chemical reaction rates, leading to more rapid decomposition of plant materials, mineralization of nutrients, and weathering of minerals.

The high temperatures also lead to rapid drying and increased evaporation from the mound, and this might counteract the effect of the temperature on some microbial and chemical reactions. However, rapid temperature and moisture fluctuations may also increase mineral weathering.

The materials of the mound are also exposed to different hydrology. Just as the mound dries more quickly, it also gets wet more quickly during rainfall events. More water moves into and through the mounds more rapidly than the adjacent topsoil. This is facilitated by the hydrophilicity and low aggregate stability of the crust. It leads to more intense leaching in the mound and more rapid removal of particulate constituents and those made available by mineralization and weathering.

The water that percolates through the mound can be collected and stored in the channel network below the mound, which functions as a cistern. Particulate and dissolved constituents, including sand and silt, organic matter, phosphorus, and potassium washed out of the mound also accumulate in the subsoil below the mound. Particulate constituents may end up at the deepest extent of the channel network, which can be 5 feet (1.6 meters) below the ground surface. Dissolved constituents may end up in the ground water and eventually the streams, lakes, and oceans. The mound is an open, aerated environment in which mixed topsoil, subsoil, and plant materials are exposed to rapid moisture and temperature fluctuations, as well as intense heating and leaching. It is a weathering machine and an incubator for microbial activity. The openness of the environment extends deep into the underlying soil, which serves as a sink for materials and water from the mound above. Because the ants concentrate nutrients from the surrounding landscape in the mounds, where they are exposed to increased mobilization and leaching, the formicarious pedons may be acting as funnels, draining plant nutrients from soil landscapes.

These processes are consequences of the ants' activity in building and maintaining their mounds, which they may do for several reasons. It has been suggested that the purpose of the mound is to provide favorable temperature and moisture conditions for the ants and possibly flood protection. While the range of temperature and moisture conditions provided by the mounds may be beneficial to the ants, the rapid fluctuations and extremes of these conditions may not be. In addition, the mound would likely not be stable enough if submersed in floodwaters to provide this kind of protection, although it would certainly provide a refuge from waters that were not as deep as the mound is high.

We suggest an additional explanation for the purpose of the mounds. For an ant with such a large colony as the imported fire ant, living space is at a premium. Just as humans in crowded city environments stop building horizontally and begin building vertically, it would make sense for the ants to use the soil they excavate to build more living space. This seems an efficient alternative to "wasting" the excavated material by simply dumping it on the ground. Thus, the function of the mound is simply that the ants get more living space for their energy dollar.

However, in their efforts to enhance their living conditions, the ants create a distinct soil unit, which serves profound functions in its environment while it is active. Many colonies over time building many mounds will have profound implications for the environment on a landscape scale. As old colonies die and new ones build mounds or as existing colonies relocate, the entire landscape will eventually be exposed to the environment of the mound. The time it will take for the ants to affect an entire landscape will depend largely on the rate of mound relocation by active colonies. In South America, this rate is once every 3 months (Briano et al. 1995). It is reasonable to assume that they move with the same frequency here in the United States.

It is not known why the ants relocate, but it may be because the mound becomes so infested with antagonistic microorganisms that it becomes more efficient for the ants to build a new, clean mound than stay and have to keep suppressing the growing fungi and other organisms. HˆIldobler and Wilson (1990) stated that one reason for the success of ants in general may be their ability to produce antibiotic secretions (p. 30). This ability enables them to exploit the soil environment, which is a haven for fungus, bacteria, and other organisms. But there may be a point when the populations of these organisms, thriving on waste materials too small to be removed from the nest by the ants, become too aggressive.

In any case, the high rate of mound relocation enhances the rate at which the ants will affect a given landscape. The second factor in the equation is the density and size of the mounds on the landscape. Cultural practices, such as pasture improvement, may exert a strong influence on both the density of mounds and the relocation rates. Cursory observations suggest that it may be possible to suppress fire ant populations simply by intensifying fertilization and pasture management. Without control measures, large mature mounds typically number about 40 per acre. Other factors that will affect the rate at which the ants affect the landscape may include agricultural or insect control practices that encourage or discourage periodic re-colonization of areas.

A simplified estimate of such a rate can be obtained by considering our Vaiden site (Site E), which had about 40 mounds per acre, each occupying about 3.14 square feet. If each colony abandons its mound every 3 months and builds a new one in a new, previously uninhabited location, it would take only 87 years for the ants to affect 100% of the surface area of that pasture. A more realistic estimate, assuming that the ants randomly decide where to build the new mound, which may include previously inhabited ground surface, would take them about 350 years to affect 95% of the surface.

It would take them longer to affect the whole soil at greater depths, and if they have any preference for re-inhabiting old mound sites, this would further decrease the rate. However, significant effects would be seen on a landscape scale long before they had affected 100 % of the landscape. Consider the impact, for example, if half the soil were affected.

In any case, the rates will be very fast in terms of soil processes. For example, it is believed that it may take 2,500 years for a strong subsoil B horizon to form. Considering that the ants have been in this country already for more than 50 years, many areas may be well on their way to seeing noticeable changes in their soils and environments.

Perhaps the most obvious long-term effect of the ants will be pedoturbation, the homogenization of the upper part of the soil. The ants bring subsoil to the surface and mix it with topsoil, then as the abandoned mounds collapse, the materials backfill the channels to some extent. The result is subsoil in the topsoil and topsoil in the subsoil. The process may result in increased clay and Ca contents and decreased organic matter in the topsoil, which could change nutrient and water retention in the soil. In the subsoil, there will be increased levels of sand, silt, organic matter, and plant nutrients. These are homogenization effects, and in this way the ants are acting as mixers of the soil on a landscape scale.

Nitrogen, phosphorus, and potassium contents of the topsoil will not be increased, despite the enrichment of the active mounds. The ants simply concentrate existing nutrients from the surrounding environment in the mounds, and there they are exposed to greater mineralization leaching. All materials of the mound will be temporarily exposed to greater weathering and microbial activity and intense leaching. Water, plant nutrients, and weathering products moving down through the pedon may be altogether removed from the soil to end up in surface waters eventually. This process could drastically alter landscape scale hydrological and geochemical cycles.

In this way, the ants serve to chemically excite the soil, and the formico-pedogenic environment is one of increased landscape weathering. Increased erosion rates, which may result from the exposure of the sloping mounds of low aggregate stability, could contribute to changes in denudation and erosion rates.

As colonies relocate through time, these nutrient and chemical funnels sweep the landscape, and this process could result in noticeable increases in the need for agricultural fertilizer and non-point source pollution.

As the mounds are relocated, they also may leave remnants of their structure, namely the subsurface channels. The resultant increase in macroporosity could change soil drainage and alter wetland status in some soils.

All these changes together amount to a change in the character of the soil and the whole environment as well. Soil profiles may need new descriptions and interpretations or classifications. Ecosystems will respond to these changes, as well as changes in nutrient and mineral cycles caused by the ants. These effects will be felt by farmers, homeowners, land developers, and all of society.

Conclusions

The introduction of the imported fire ant to the United States entailed the introduction of a costly, annoying, and dangerous agricultural and urban pest. It also entailed the introduction of a new environmental influence, capable of changing soils and landscapes throughout the Southeast. Some effects could be beneficial, others detrimental, but there will be changes, and they will come quickly if ant populations remain at present levels.

The addition of this new ingredient to our soil recipe has provided an experiment in the role of animals in soil development. It has also provided an example of the impact of human activity on the environment. The environment will adjust to the new changes, and natural processes will go on, but the result may not be as palatable to us as those we were used to.

If efforts are made to understand the interactions of the fire ants with the environment further, it may be possible to manage or control their impact, and lessons will be learned that will benefit science and society as a whole. Meanwhile, our soils are in the mound, being exposed to the formicarious environment. This new recipe is still in the oven, and it already looks a little different from the old one.

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Acknowledgments

This research was supported by the Mississippi Agricultural and Forestry Experiment Station. We also gratefully acknowledge the assistance of several individuals who made this study and the resulting publication possible: Homer Collins and Tim Lockley, USDA-APHIS, Gulfport, Mississippi; Richard L. Brown, Henry N. Pitre, Gerald Baker, and James H. Jarratt, Mississippi State University (MSU) Department of Entomology and Plant Pathology; Darrel W. Schmitz, MSU Department of Geosciences; Harold L. Peterson, MSU Department of Plant and Soil Sciences; and Kay Nevels, Richard Kuklinski, and Bill Monroe, MSU Electron Microscope Center.

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