Are Texas Forest Soils Being Re-Engineered By An Invasive Earthworm Species?

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Abstract: Earthworms are usually considered beneficent soil engineers. However research in the Great Lakes Region of the USA has demonstrated that exotic invasive species of earthworms have altered hardwood forest ecosystems. *Amynthas diffringens* (Baird 1869), an exotic invasive earthworm from Southeast Asia, is in high numerical densities in hardwood bottomland forests soils throughout East Texas. Also present in these same soils are numerous native earthworm species, all which have a markedly different behavior from *A. diffringens.* A microcosm study investigated changes in four physical soil variables by the activity of *A. diffringens*. The influence of *A. diffringens* on saturated hydraulic conductivity, formation of water stable aggregates, bulk density, and incorporation of the O horizon were compared with values determined for soil influenced by the native earthworm species *Diplocardia eiseni* and *D. komareki*.

Keywords: earthworms, invasive species, soil, *Amynthas*, *Diplocardia*

Introduction

Earthworms are important in forest soils. It is well documented for a relatively small group of earthworm species that they strongly influence, for example, soil organic matter dynamics, nutrient cycles, terrestrial food webs, and functional interactions with microbes and plants. At the same time it is widely agreed among those who study soil invertebrates, that there is a lack of research on some of the most fundamental questions related to earthworms in the forests of North America. In the forests of the Southeastern United States, and especially Texas, there is even less known. This is true for native earthworm species, and even more so concerning non-native species. Of the more than 3500 described species of earthworms worldwide, there are more than 150 described earthworm species in North America north of Mexico, and, among these, approximately one third are non-native invasive species, mainly from Europe and Asia.

The concept of ecosystem engineers is fairly new in the ecological literature. Termites, ants and earthworms are examples of terrestrial soil ecosystem engineers, with earthworms generally considered the most influential in temperate forests of North America. Some researchers do not like the term for its implied anthropomorphism. Regardless, in the 13th edition of a highly popular college text on fundamental concepts of soils (Brady and Weil 2002) the concept of ecosystem engineer is explored in detail, especially related to earthworms. An ecosystem engineer is distinguished from other photosynthetic or heterotrophic species by the extent of its temporal and spatial influence on ecosystem processes. Ecosystem engineer species directly or indirectly control the availability of resources to other organisms by causing physical state changes in living or nonliving materials, and whose influence often persists long after the engineer is no longer present in the environment.

Biogeographers of earthworms commonly agree that glaciation in Canada and the northern tier states of the US obliterated native earthworm species, except in a narrow strip of land along the Pacific coast. The south and west regions of the United States has been a refugium for many species of earthworms indigenous to North America. In the last 300 to 400 years, only non-native European earthworms have been introduced into these soils devoid of native species. This invasion was inadvertent when Europeans brought plants from the home country into the New World, as well as other modes of introduction documented for other terrestrial invasive species. Two recent studies in east and central New York investigated the impact of European and Asian non-native invasive species of earthworms on forest soils (Burtelow, et al. 1998; Bohlen, et al. 2004.) In Minnesota and the Great Lakes Region numerous European invasive earthworm species are impacting forest soils (Hale 2004.) Prior to an invasion of a suite of European earthworm species in a Minnesota forest, a well-developed O horizon rests on top of a distinct A and E horizon. After an invasive wave of non-native earthworms, the litter layer is practically obliterated, and the mineral soil horizons are all mixed. Tree roots and surface mineral soil have been exposed, and understory plant communities dramatically altered. Other than distribution records, occasionally accompanied by scant ecological observations, there is little known about non-native species of earthworms and their impact on native earthworm communities and the forest soils of the Southeastern United States refugium.

We have conducted earthworm species distribution surveys in north and central East Texas since 2001. From these surveys we have discovered that *Amynthas diffringens* (Baird, 1869) appears to be common in bottomland hardwood forest soils of East Texas. In the

bottomland hardwood forest soils of the Stephen F. Austin Experimental Forest (SFAEF) in Nacogdoches County, there is a reproducing population of *A. diffringens* among a diverse community of native earthworm species. The bottomland hardwood forests soils of the Little Sandy National Wildlife Refuge (LSNWR) in Wood County, Texas were also found to have *A. diffringens* coexisting in a community of native earthworm species, even though it was anticipated that this site would be free of invasive earthworms because of the site history of this wildlife refuge. In Caddo Lake National Wildlife Refuge (CLNWR) located in Harrison County, a portion of the watershed of Harrison Bayou, including the bottomland hardwood forests, the soils are free of invasive species of earthworms, including *A. diffringens*. Many native species of earthworms have been identified in this watershed. The CLNWR recently has been designated as a RAMSAR site, a wetland of international significance. Consequently, we wondered if *A. diffringens* were to find its way into this bottomland soil associated with Harrison Bayou, how might it impact the soil ecosystem? Also, how, possibly, has *A. diffringens* impacted the forest soils of SFAEF and LSNWR of Nacogdoches and Wood Counties, respectively?

Methods

Collection and Description of Earthworms

Earthworms used in this microcosm study were collected from two locations in Nacogdoches County, Texas in May 2005. Within two days prior to the assembly of the microcosms, adult and preclitellate specimens of *Diplocardia eiseni* (Michaelsen, 1894) and *Amynthas diffringens* (Baird, 1869) were collected from the soils of a constructed wetland that parallels La Nana Creek on the campus of Stephen F. Austin State University. Also, within two days prior to the assembly of the microcosms, adult and preclitellate specimens of *Diplocardia komareki* Gates, 1977 and *Amynthas diffringens* were collected from soil of a bottomland hardwood forest within the Stephen F. Austin Experimental Forest. All specimens were briefly stored in large volumes of native soil at ambient laboratory temperatures. Representative adult earthworm specimens of all three species from both collecting locations were preserved according to James (1990) to verify microscopically taxonomic classification for both genus and species epithet (Reynolds 1977; Schwert 1990; and James 1990.)

Diplocardia eiseni (De) is a small native species of earthworm commonly found in the same hardwood bottomland soils of East Texas as *A. diffringens*. The mean fresh biomass for the 56 specimens used in this study was 0.18 ± 0.04 g. Percent mortality after 70 d was less than one percent.

Diplocardia komareki (Dk) is a medium-sized native earthworm species that is commonly found in the same bottomland hardwood forest soils of East Texas as *A. diffringens*. The mean fresh biomass for the 56 specimens used in this study was 1.20 ± 0.49 g. Percent mortality after 70 d was less than one percent. *D. komareki* for this study has a biomass 6.7 times greater than *D. eiseni*.

Amynthas diffringens (Ad) is easily collected throughout the Southeast United States, including East Texas, anytime of the year from various soils, provided there is adequate moisture. *A. diffringens* is indigenous to Southeast Asia and is considered a non-native (exotic) invasive earthworm species in North America (Hendrix, 1995; Edwards and Bohlen 1996). Distribution records indicate that it has been in the United States for over one hundred years. *A.*

diffringens appears to have a particular affinity for bottomland hardwood forests in East Texas where periodic flooding occurs. The mean fresh biomass for the 56 specimens used in this study was 0.88 ± 0.36 g. Percent mortality after 70 d was less than one percent. The *A. diffringens* specimens used in this study had a mean wet biomass 4.9 times greater than the *D. eiseni* specimens and a mean wet biomass 0.7 times less than *D. komareki* specimens.

Microcosm Set-up and Experimental Design

Microcosms were contained in clear plastic tubes 30.5 cm in length and 49.5 mm in diameter with a wall thickness of 0.3 mm. A plastic cap was placed on the outside diameter of one end the tube. The cap was then punctured with five narrow evenly spaced slits approximately 2 mm in length; the two edges of the slit touched together after the initial puncture. These punctures allowed water to drain from the microcosm during incubation.

The A horizon of an Entisol was collected from the Harrison Bayou bottomland hardwood forest in the CLNWR of Harrison County, Texas. In the Forestry Soils Laboratory of the Arthur Temple College of Forestry and Agriculture the A horizon soil was air-dried, then coarsely ground, and passed through a 2 mm sieve. 300 grams of this soil were placed in each microcosm tube. Weathered overcup oak leaf litter collected from the same location as the A horizon soil was rinsed, oven-dried to a constant weight at 60º C, ground, and passed through 1.5 cm mesh hardware cloth. Five grams of this leaf litter were added to each tube on top of the mineral soil column.

There were six earthworm treatments, with four individual earthworms placed in each experimental tube: *Amynthas* only, *D. komareki* only, *D. eiseni* only and then combinations of *Amynthas* and *D. komareki*, *Amynthas* and *D. eiseni*, and *D. komareki* and *D. eiseni*. An earthworm free control was also set up. There were 7 replicates for each earthworm treatment and the control. On the day earthworm specimens were placed in the microcosms, each individual was inspected for general robustness (free of wounds and loss of vigor) after collection, transport, and short-term storage in the laboratory. Wet biomass determinations for each specimen, to the nearest tenth of a gram, were made after rinsing in distilled water and blotting on a paper towel.

All experimental and control microcosm tubes were randomly assigned to a 7 X 7 grid on the floor of a growth chamber maintained at spring-like conditions determined for Harrison Bayou bottomlands: 22º C, with a 10/14 h light/dark cycle, at 50% humidity. Tubes were maintained at 45-50% volumetric water content (VWC) for 70 days before observations and measurements were made.

Microcosm Processing

All microcosm tubes were processed randomly within 48 hours. Four soil variables for each microcosm were determined in succession on the same day.

Unincorporated leaf litter was the first step in processing the microcosm tubes. Water was poured in the empty space above the soil column of the microcosm tube, which floated any leaf litter that did not adhere to mineral soil particles. Leaf litter material carried by the water was decanted from the microcosm tube into a preweighed standard coffee filter supported by a bowl-shaped sieve. The leaf litter and coffee filter were placed in a soil bag, oven-dried at 60º C to a constant weight, and then weighed to the nearest tenth of a gram.

Bulk density (Db) determinations were made on all microcosm tubes since the mass of all microcosm tubes were 300 g and the volume, in cm^3, occupied at the end of the 70 d incubation

could be determined by measuring the length of the soil column within the tube multiplied by the area (πr^2), with the radius (r) determined by dividing the inside diameter of the tube by one half. Thus, bulk density was calculated by dividing the weight of the soil particles by the volume of the entire soil column. The units were converted by standard convention from g cm^{-3} to Mg m^{-3}.

Determination of saturated hydraulic conductivity (SHC) was by the Constant-Head Method because preliminary studies indicated conductivities for earthworm-inoculated soils would be greater than 0.01 cm min^{-1} (Klute 1965). The plastic cap was removed from the lower end of microcosm tube and replaced with 1.25 mm wire mesh fastened by a large rubber band. The length of the soil core (L) was measured to the nearest millimeter. Since the soil was maintained at 50% VWC during incubation, it was not necessary to soak samples overnight. The top of the microcosm tube was lowered below the top of the water supply cylinder. A siphon tube from the water supply cylinder was used to slowly fill the upper part of microcosm tube, while simultaneously raising the microcosm tube to the predetermined mark to maintain a constant hydraulic head. Water was not allowed to drain from the top of the microcosm tube. A constant hydraulic head was maintained on the soil column for ten minutes. Water was allowed to drain through the microcosm tube for ten minutes before collecting three successive percolate samples in beakers. Percolate water volume (Q) was collected for a predetermined time (t) based on the estimated rate of flow for any given microcosm tube. The water volume was measured using graduated cylinders to the nearest tenth of a millimeter. A metric tape was used to measure the hydraulic head difference (ΔH) to the nearest millimeter and the water temperature was recorded in degrees Celsius. Hydraulic conductivity (K) was determined using the following equation: $K = (QL)/(A\, t\Delta H)$ or $(Q/A\, t)/(L/\Delta H)$, where: K is the hydraulic conductivity, Q is the volumetric flow over a period of time t, L is the length of the sample (cm), t is the time in hours (h), A is the cross sectional area of core (cm^2), and ΔH is the hydraulic head difference in cm. Thus, values reported are expressed as saturated hydraulic conductivity of water in cm h^{-1}.

While microcosm soil columns were still saturated, each tube was immediately processed for the determination of water stable aggregates (WSA). The tubes were cut in half to release the soil with minimal disturbance into a stack of four sieves manufactured to ASTM specifications for the U.S. standard sieve series. Sieve mesh sizes were 4.75 mm, 2.00 mm, 1.00 mm, and 0.50 mm. These four sieves established four aggregate size classes: aggregates greater that 4.75 mm, aggregates between 4.75 and 2.01 mm, aggregates between 2.00 and 1.01 mm, and aggregates between 1.00 and 0.51 mm. The stacked sieves, from largest at the top to smallest at the bottom, were immersed in a large bucket. The top sieve was covered by a 420 micron sieve to establish comparable conditions to the other three sieves. This setup was placed on an Eberbach Corporation shaker set at a 3.5 cm stroke length and 60 cycles min^{-1} for ten minutes. The stack of sieves was immediately lifted out of the water bucket and aggregates for each size class were scraped and rinsed onto a preweighed standard coffee filter supported by a bowl-shaped sieve. The aggregates and coffee filter were placed in soil bags and oven-dried at 60º C to a constant weight and then weighed to the nearest tenth of a gram.

Statistical Analysis

All data were analyzed using SAS 9.1 on an XP PRO platform. An analysis of variance (ANOVA) or a general linear model (GLM) of sample means were determined for each soil variable measured on microcosm tubes with a concurrent Ryan-Einot-Gabriel-Welsch Multiple Range Test used to identify significant differences between sample means for the six earthworm treatments and the control.

Results and Discussion

Saturated hydraulic conductivity data show that there was much variance among all the treatments, thus valid statistical inferences could not be made (Table 1, Fig. 1). However, it is apparent from these data that the presence of earthworms, whether native or non-native, increases hydraulic conductivity in soil. Furthermore, hydraulic conductivity appears to vary by species, but is not necessarily proportional to earthworm size, nor are synergistic interactions in the combined earthworm species treatments intuitive. For example, *Diplocardia eiseni* appears to greatly reduce the saturated hydraulic conductivity of *D. komareki*. Also, when *Amynthas diffringens* coexists with either native *Diplocardia* species there seems to be a potential increase in saturated hydraulic conductivity over *A. diffringens* alone (Fig.1). These observations alone encourage refinement of the design and measurement of earthworm-treated microcosms in the determination of saturated hydraulic conductivity. Parsing these interactions could reveal significant ecological consequences for native and non-native earthworm species.

There are two possible aspects of the microcosm design that facilitated the large variance within each earthworm treatment. The inclusion of leaf litter in the microcosm tubes likely confounded the results of this experiment by introducing bias based on the extent in which an earthworm species incorporates O horizon material. Saturated hydraulic conductivity values for the *A. diffringens* microcosms may have been impacted more greatly by the presence of leaf litter in the mineral soil column. Among the three earthworm species used in this study, *A. diffringens* has the greatest propensity to incorporate great volumes of leaf litter to greater depths in the soil profile. It is reasonable to suspect that some of this leaf litter blocked macropores engineered by *A. diffringens*. Yet leaf litter incorporation would not account for the high degree of variance among treatments associated with the two *Diplocardia* species. The mere presence of living earthworms in the microcosm soil column likely influenced the measured rate of saturated hydraulic conductivity by both the extent that macropores were blocked and the degree of activity of individual earthworms during the collection of water samples. Extraction of earthworms from the microcosms was considered during the design of this experiment. In order to maintain the integrity of the earthworm-engineered soil column, options were limited to electrical or chemical methods. Access to and experience with equipment for electrical extractions was not feasible for this study. Historically there have been numerous chemicals used to extract earthworms from soils. Currently hot mustard solution is widely used because it is apparently effective on a number of earthworm species with minimal adverse effects on soil. However, it was decided not to attempt a chemical extraction of earthworms from the microcosms for a number of reasons. The response of the three earthworm species to hot mustard solution has not been experimentally evaluated and it was reasonable to expect that some individuals would likely not find their way to the soil surface in a reasonable amount of time, if at all. Furthermore, since other soil variables were to be measured following the earthworm extraction, it was decided to limit the potential confounding effects by hot mustard solution.

After saturated hydraulic conductivity was determined for all microcosms, each were cut in half along the length of the tubes in order to release the soil with minimal disturbance for the determination of water stable aggregates (WSA). Soil color differences between the upper and lower portions of the soil column were observed and seemed to show similar patterns for each

earthworm species. The microcosms with the two *Diplocardia* species were more distinctly partitioned into an upper brown (oxidized) region and a lower gray (reduced) region. Most *Diplocardia* specimens after the 70 d incubation period were observed in the upper brown region of the soil when the tubes were cut open. Apparently macropores engineered by the *Diplocardia* species occurred in the first weeks of the experiment when oxygen in the soil microcosm was not as limited. Typically *A. diffringens* microcosms had a uniform brown (oxidized) soil column from top to bottom. These differences in soil column partitioning by the native and non-native earthworm species merits future quantifiable investigations.

The presence of medium-sized native and non-native earthworms significantly contributes to the formation of large (>4.75 mm) water stable aggregates when compared to the control and the small native earthworm species (Fig. 2). There is no significant difference of the means in the formation of large WSA between the non-native *A. diffringens* and native *D. komareki*, even though *D. komareki* has a mean wet biomass 1.4 times greater than *A. diffringens*. When *A. diffringens* is combined with each of the two native species this invasive species of earthworm does not significantly influence the formation of large water stable aggregates. The formation of small water stable aggregates (< 2.00 mm to > 1.00 mm) did not differ significantly in microcosms treated exclusively with either *D. komareki* or *A. diffringens* (Fig. 3). However, while *A. diffringens* did not significantly influence the production of small water stable aggregates when in the same soil as *D. komareki*, *A. diffringens* did significantly decrease this size class of WSA in combination with *D. eiseni*, yet apparently only to the same degree as when both native earthworm species worked the same soil. Again, even though *D. komareki* has a mean wet biomass 1.4 times greater than *A. diffringens*, the smaller non-native earthworm species has an apparent equal influence on WSA formation.

It was soon realized after microcosm processing began that there were several measurable soil column variables that would have contributed to a greater understanding of the potential influence on natural soils by these three earthworm species. For example, these data do not reveal the depth and uniformity of distribution of large and small WSA in the microcosm based on species-specific earthworm activity, yet the ecological implications of these delineations could significantly influence hydrology and plant community structure. Also, the proportion of large oxidized aggregates was observed to be greater than large gleyed aggregates.

The presence of earthworms significantly decreases bulk density when mean values were compared to soil that is free of earthworms, while the non-native invasive *A. diffringens* significantly decreased bulk density to the greatest extent when compared to treatments of native only microcosms (Fig. 4). Although *D. komareki* has a mean weight biomass 6.7 times greater than *D. eiseni* there was no significant difference in mean values for bulk density between these two native species. And while *A. diffringens* did not significantly decrease bulk density values when combined with *D. komareki* in comparison to microcosms with only *D. komareki*, the non-native invasive *A. diffringens* did significantly reduce the bulk density of the soil in combination with *D. eiseni* when compared to all other treatments that were devoid of *A. diffringens*.

Unincorporated leaf litter was significantly different between microcosms with only the non-native invasive *A. diffringens* and the microcosms set up with each of the isolated native earthworm species (Fig. 5). The converse implication of these data is that unincorporated leaf litter is proportional to incorporated leaf litter, especially given the relatively short duration (70 d) of this experiment that would minimize the effect of decomposer organisms such as bacteria, fungi, and microfauna. Based on this assumption, then, exclusive treatments of *A. diffringens* incorporated three to four times more leaf litter into the mineral soil than either of the exclusive

native earthworm species. The control and native species only microcosm treatments were not significantly different from each other and there is no significant difference of the means between the two native species, even though *D. komareki* has a mean weight biomass 6.7 times greater than *D. eiseni*.

These data indicate that *Amynthas diffringens* has the potential to significantly re-engineer the forest floor and the physical structure of the mineral soil in East Texas bottomland hardwood forest soils. In particular, the activity of *A. diffringens* in a soil promotes changes in hydraulic conductivity, formation of water stable aggregates, a decrease in bulk density, and increased leaf litter incorporation. A change in leaf litter incorporation alone could promote changes in soil microclimate, erosion, condition of seedbed, rate of nutrient cycling, and depth of the A horizon (Nielsen and Hole 1964.) Often these transformations are not proportional to the body sizes of the three earthworm species investigated in this study. Based on these observations it is reasonable to suspect that chemical and biological alterations could also occur wherever *A. diffringens* invades soils. The results of this microcosm study elicit questions related to the history, degree of change, and future of forest soils in East Texas, as well as the entire Southeastern USA. Since the presence of *A. diffringens* has been documented in the Southeast refugium of the United States for the past five decades or more, what "engineered" changes in the forest soil ecosystems have not been documented that are attributable to the highly aggressive species? Have there been or will there be similar forest ecosystem changes as reported in Minnesota and New York? Has the invasion of non-native species in the SE USA, including East Texas, reached equilibrium? For example, in the upper reaches of Harrison Bayou at the LHAAP-CLNWR in Harrison County Texas, some of the bottomland hardwood forest soils are dominated by *D. eiseni*, yet also there are areas that apparently are absent of earthworm populations. Based on these data from the microcosm study, if *A. diffringens* invaded these soils then it is reasonable to expect significant changes like those described above, both in the presence and absence of *D. eiseni*. As for the other two locations, SFAEF in Nacogdoches County and LSNWR in Wood County, where reproducing populations of *A. diffringens* occur among a community exclusively comprised of native earthworm species, these data help speculate as to how forest soil ecosystems may have been altered over past decades by this non-native invasive species of earthworm.

Unfortunately, from continued surveys for earthworm species in East Texas it is apparent that the invasion of non-native earthworm species is still in flux. In the past two years a reproducing population of *Octolasion tyrtaeum* (Savigny, 1826) has been documented in a mixed pine-hardwood forest adjacent to La Nana Creek in Nacogdoches County, Texas; this species has never been reported in Texas. Even more recently, a reproducing population of *Lumbricus rubellus* Hoffmeister, 1843 has been identified in a wooded urban lot in the city of Marshall in Harrison County, Texas. As with *O. tyrtaeum*, *L. rubellus* has never been recorded in Texas, nor was it considered possible to become established in Texas, because it is considered to be intolerant of the hot dry summer soil temperatures. After this discovery, an inquiry made in response to a bait supply sign in small rural East Texas town, it was revealed that *L. rubellus* has recently been introduced to fishermen in Texas and surrounding states. *L. rubellus* is one of the principal earthworm species that has been documented in promoting change in the forest soil ecosystem of Minnesota.

Several management approaches have been suggested which are similar to strategies for other invasive invertebrate organisms. Minimizing or avoiding habitat disturbance is often cited as a key strategy in the prevention of invasive species establishment; this, however, is not always

effective, and it certainly seems to be the case with *A. diffringens*. The Harrison Bayou watershed associated with the newly established Caddo Lake National Wildlife Refuge has an opportunity to establish baseline data for bottomland hardwood forests of Texas that are currently free of non-native invasive earthworms species, including *A. diffringens*. Apparently this is a rare occurrence based on collections at the SFA Experimental Forest, the Little Sandy National Wildlife Refuge, and elsewhere. Caddo Lake has been designated a RAMSAR site (Wetlands of International Importance) and managers of this site should incorporate measures to insure continued forest soil ecosystems that are free of non-native invasive earthworms species.

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Table 1. Saturated hydraulic conductivity (*K*) means and standard deviations for earthworm microcosms with silty clay loam A horizon.

Treatment	*K* (cm h^{-1})	SD
Control	0.1	0.1
Amynthas diffringens (Ad)	49.9	50.9
Diplocardia komareki (Dk)	537.8	668.7
Diplocardia eiseni (De)	24.5	28.9
AdDk	209.4	409.4
AdDe	275.6	266.2
DkDe	3.8	5.8

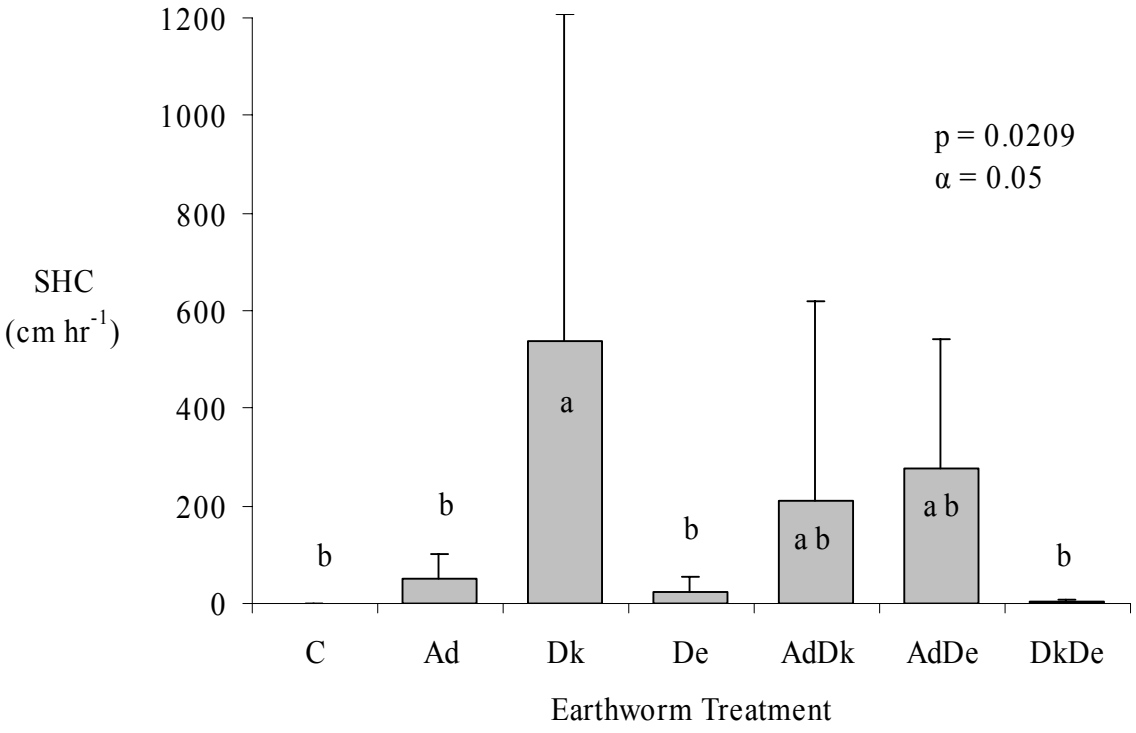

Figure 1. ANOVA of mean values for saturated hydraulic conductivity (SHC) of the control and six earthworm treatments in microcosms with silty clay loam A horizon soil. Error bars are standard deviation of the mean. (n = 7)

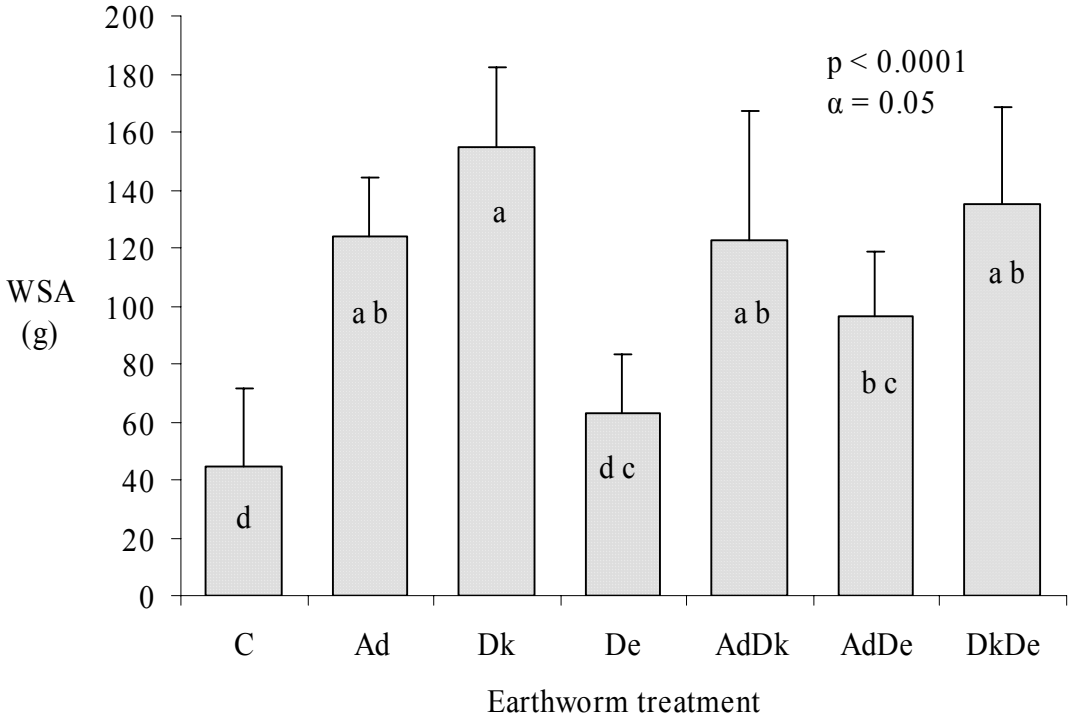

Figure 2. ANOVA of mean values for water stable aggregates (WSA) > 4.75 mm for six earthworm treatments and control in microcosms with silty clay loam A horizon soil and 70 d incubation. (n = 7)

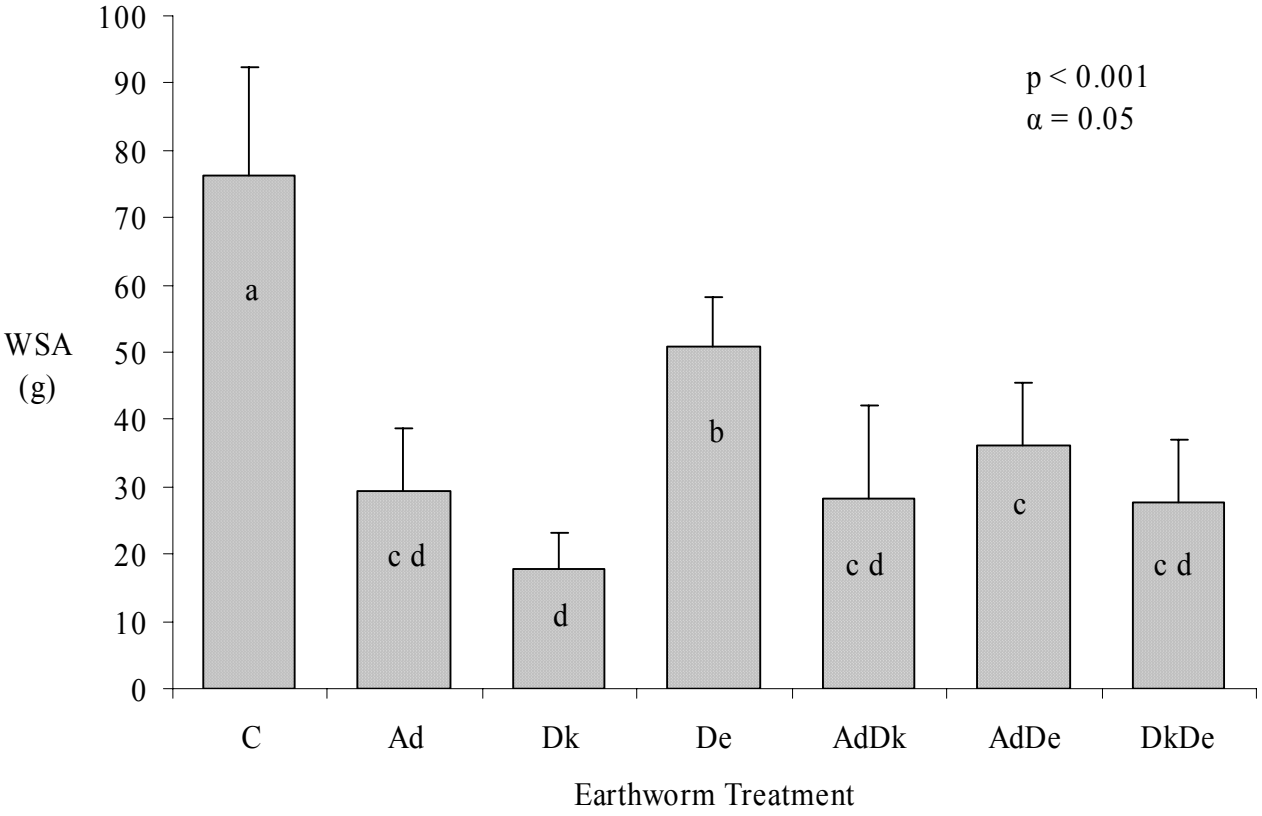

Figure 3. ANOVA of mean values for water stable aggregates (WSA) from < 2.00 mm to > 1.00 mm of six earthworm treatments and control in microcosms with silty clay loam A horizon soil and 70 d incubation. Error bars are standard deviations of means. (n = 7)

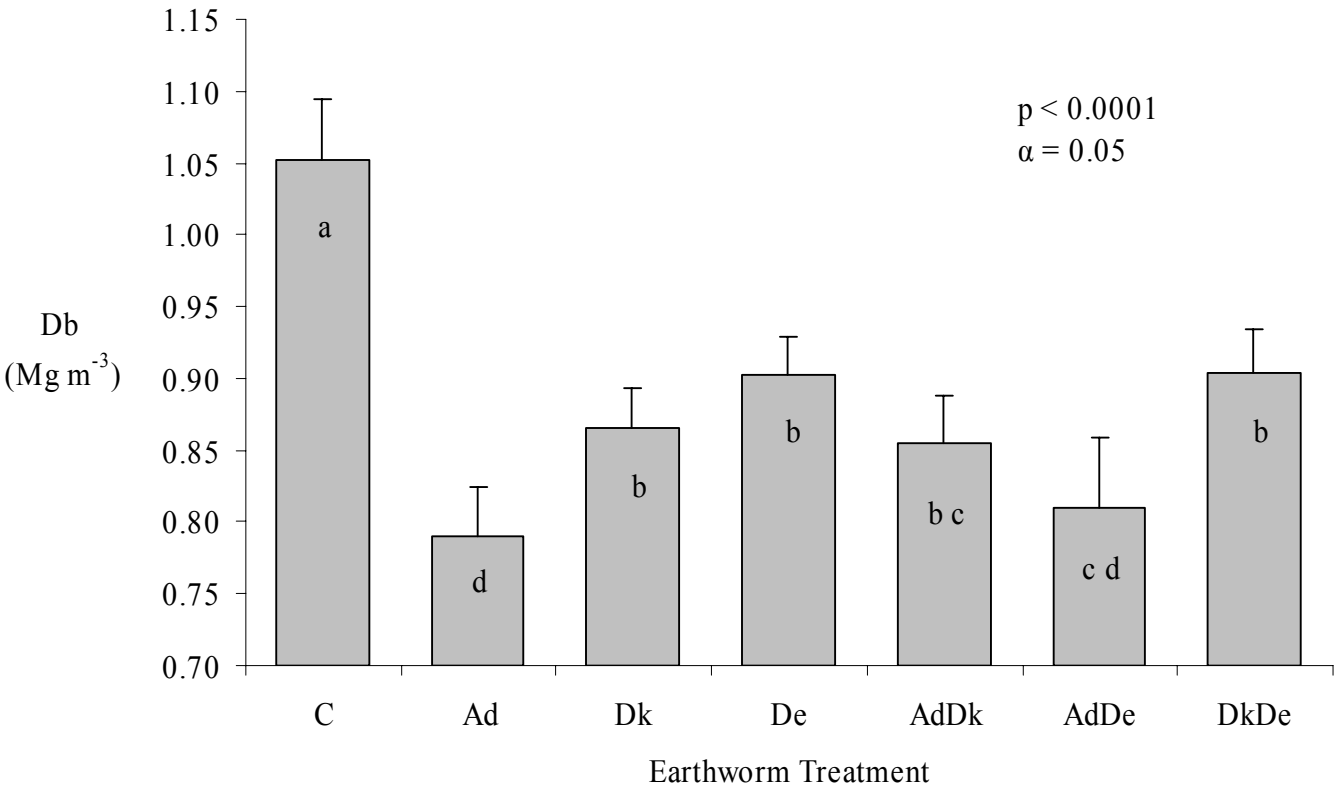

Figure 4. ANOVA of mean values for bulk density (Db) for control and six earthworm treatments in silty clay loam A horizon soil and 70 d incubation. Error bars are standard deviation of the mean Db value for each treatment (n = 7).

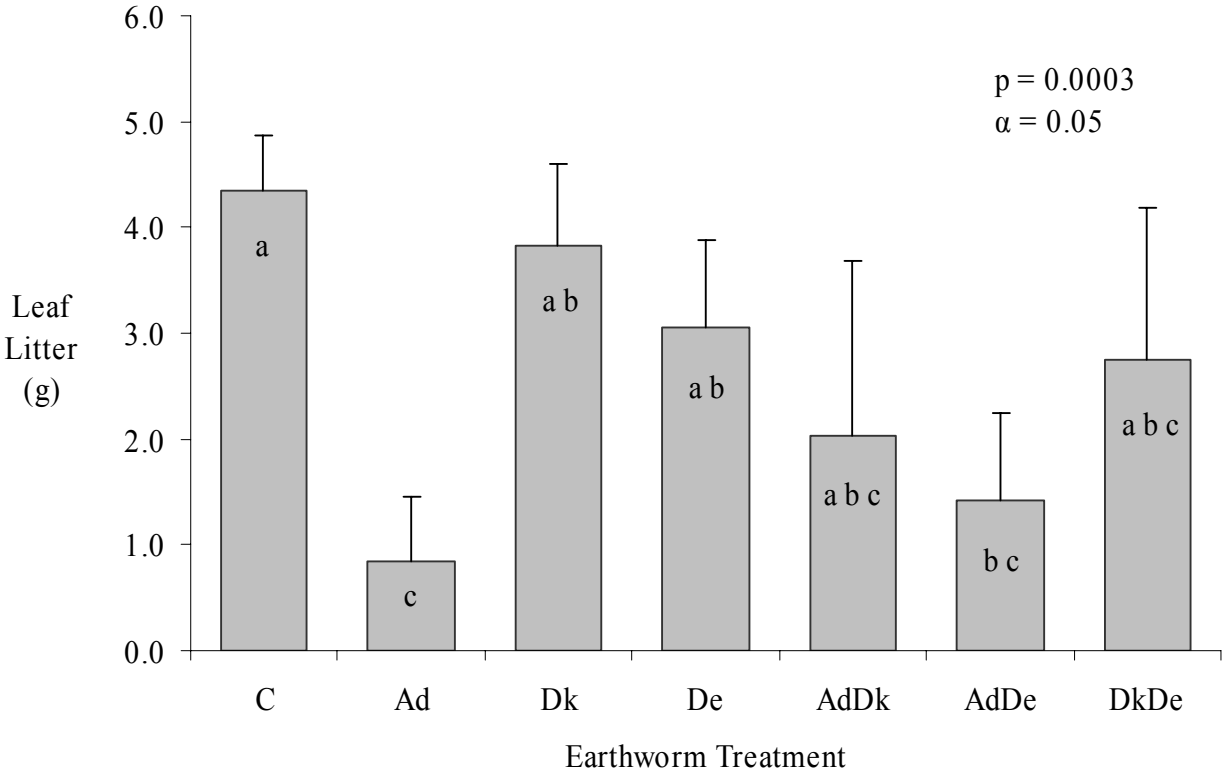

Figure 5. GLM of mean values for unincorporated leaf litter in earthworm-treated microcosms and the control with silty clay loam A horizon soil and a 70 d incubaton. Error bars are standard deviations of means. (n = 4, 5, or 6)