

Quantifying the Effects of Earthworms on Soil Aggregation and Porosity

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INTRODUCTION

The potential for earthworms to improve soil aggregation and porosity and the subsequent effects of these changes in soil structure on plant growth and soil hydrology were perhaps first recognized by Gilbert White in 1777 when he wrote “worms seem to be great promoters of vegetation, which would proceed but lamely without them; by boring, perforating, and loosening the soil, and rendering it pervious to rains and the fibres of plants; by drawing straws and stalks of leaves and twigs into it; and, most of all, by throwing up such infinite numbers of lumps of earth called worm-casts, which, being their excrement, is a fine manure for grain and grass” (White 1789). Prior to these observations, earthworms were often regarded as pests by farmers and as detrimental to crop growth.

One hundred years later, the first scientific observations on the effects of earthworms on soil structure were conducted by Darwin (1881) and centered mostly on how earthworms contribute to the geologic evolution of soils and landscapes. Like White, he recognized that earthworms promote the growth of vegetation by creating an intimate mixture of organic and mineral matter that aids in water retention and nutrient release and provides a medium suitable for root proliferation. He also recognized that deep-burrowing earthworms affect water movement in the soil and “materially aid in its drainage.” Darwin also postulated that earthworm activity can have negative aspects by contributing to “denudation” (soil erosion) by both wind and water. This was based on observations that casting activity by earthworms can result in the deposition of weakly aggregated material at the soil surface that can flow or be washed or blown downslope.

In the ensuing years since these pioneering naturalists published their findings, a number of scientific studies have confirmed their observations, and there now is detailed data on the effects of earthworms on soil aggregation and soil porosity. We are also beginning to understand the chemical and physical processes by which earthworms affect soil structure and the consequences of their activity, both positive and negative, and the interrelationships between soil management and earthworm activity.

ECOLOGICAL CLASSIFICATION OF EARTHWORMS

Earthworms affect soil physical properties when they ingest and excrete soil to construct burrows and as part of their feeding activities. Because different earthworm species have different ecological strategies, their effects on soil aggregation and porosity can vary considerably. Most earthworms are placed in one of three ecological groups: epigeic, anecic, or endogeic (Bouché 1977).

Epigeic species of earthworms generally forage within accumulations of organic matter and rarely burrow into or ingest much soil. Typical habitats include forest litter or manure piles; thus, they have little direct effect on the structure of mineral soils. For example, Hamilton and Dindal (1989) noted that the epigeic earthworm *Eisenia fetida* had no effect on aggregation in a sludge-amended soil.

In the same study, however, the anecic earthworm *Lumbricus terrestris* improved aggregation. *Anecic* earthworm species normally live in permanent or semipermanent burrows that can extend deep into the soil. They feed primarily on decaying surface organic residues, which they frequently pull into their burrows or mix with excrement to form a midden. The midden promotes further decay of the incorporated organic residues and covers the burrow entrance.

Endogeic earthworm species burrow extensively belowground and obtain their nutrition by ingesting a mixture of soil and organic matter. They form extensively branched, subhorizontal networks of burrows in search of food, but most of their activity is in the upper 10 to 15 cm, where organic matter levels are generally highest. Portions of their burrows are often occluded with their casts, and they occasionally cast on the soil surface. These classifications are not absolute because the behavior of many species is intermediate to these groupings and can vary with environmental conditions (C.A. Edwards and Bohlen 1996).

AGGREGATION

INGESTION RATES AND PROPERTIES OF CASTS

Although earthworms feed on decaying organic matter and the microorganisms that colonize it, the material ingested by endogeic and anecic species during feeding and burrowing is predominantly mineral matter. This mineral and organic material is mixed thoroughly in their digestive tracts and excreted as casts on the soil surface or belowground, depending on the species of earthworm, location of the food source, and soil bulk density (Binet and Le Bayon 1999). The amount of soil ingested is highly dependent on the size, composition, and activity of the earthworm population

and is hard to measure accurately because subsurface activity is difficult to monitor. Nevertheless, estimated soil ingestion rates for earthworms in temperate regions are usually less than 100 Mg ha⁻¹ year⁻¹ (Tomlin et al. 1995). In tropical areas, such as the Ivory Coast, where climatic conditions are less likely to seasonally inhibit activity, Lavelle et al. (1989) reported a cast production rate of 1200 Mg ha⁻¹ year⁻¹. High cast production rates such as this are attributable to the fact that geophagous, endogeic earthworms can ingest 5 to 30 times their body weight per day (Lavelle 1988). According to Lee (1985), earthworms can process up to 25% of the Ah horizon in 1 year and thus can be important aggregate-forming agents through the production of casts in the soil and on the surface. In a laboratory study, Ziegler and Zech (1992) showed that *E. fetida* could bind up to two thirds of the beech litter and unstructured artificial soil into 200 to 2000 µm diameter aggregates in 446 days.

Earthworm casts, deposited on the burrow walls, within the burrow, or on the soil surface (Brown et al. 2000), usually contain more clay and less sand than the surrounding soil because of selective ingestion, with this effect more prominent with endogeic species, which tend to be smaller than anecic species of earthworms. This concentration of fine particles in earthworm casts may need to be taken into account when using methods such as dispersible clay or turbidity to compare the stability of casts to uningested soil. Moreover, the relative differences in texture between casts and uningested soil are probably dependent on the coarseness of the parent soil. For example, Shipitalo and Protz (1988) noted that casts of *Lumbricus rubellus*, an epigeic/endogeic species, contained less sand than those of *L. terrestris* (anecic species), and both had less sand than the uningested soil (18% sand). Whereas Schrader and Zhang (1997) reported small differences in the texture between the casts of *L. terrestris* and *Aporrectodea caliginosa* (endogeic) and parent soils with initial sand contents less than 4%.

Likewise, the amount of organic matter incorporated into casts is dependent on whether the earthworms are actively burrowing or feeding and the food source. Shipitalo et al. (1988) reported that food ingestion rates and organic carbon contents of casts were higher for more palatable food sources, as reflected in earthworm weight gains, and that casts of *L. rubellus* were generally higher in organic carbon than those of *L. terrestris*. In a study by Schrader and Zhang (1997), however, *L. terrestris* casts were enriched in organic carbon to a greater extent than *A. caliginosa* casts. Specific organic compounds such as reducing sugars, amino sugars, phenolic materials (Mora et al. 2003), and carbohydrates (Scullion and Malik 2000) can also be concentrated by earthworms in their casts. Earthworm casts also usually have higher bulk density than the uningested soil (C.A. Edwards and Bohlen 1996; Görres et al. 2001), unless the soil is already compacted (Joschko et al. 1989), and are higher in pH, contain more available nutrients, and have higher levels of microbial activity.

REMOLDING OF SOIL AGGREGATES BY EARTHWORMS

The muscular contractions of the earthworm crop and gizzard, the peristalsis of the gut wall, and contractions of the body wall create a great range of pressures that mechanically disrupt soil microaggregates during passage through the digestive tract. The mean pressure applied to soil by *Aporrectodea rosea* was estimated as 259 Pa (McKenzie and Dexter 1987). For *L. terrestris*, Newell (1950) reported that the average coelom pressure was 1.6 kPa in segment 28 and 0.8 kPa near the tail region. Such pressures, concomitant to the addition of large amounts of watery mucus (Barois et al. 1993), can lead to the mobilization of clay (Marinissen et al. 1996) and the disruption of existing interparticle water and cation bridges in the aggregates (Shipitalo and Protz 1988, 1989). Conversely, soil remolding also brings clay minerals into close association with newly formed or released bonding agents originating from the ingested organic matter (Shipitalo and Protz 1989). Consequently, the soil fabric is reorganized in the posterior intestine of earthworms (Barois et al. 1993), with resistant organic fragments becoming the foci for new microaggregates (Shipitalo and Protz 1989). Earthworm gut transit time probably also affects the degree of microaggregate disruption. It reportedly takes 2 to 24 hours for soil to pass through the digestive tract of lumbricid earthworms (Barley 1959; Pearce 1972; Bolton and Phillipson 1976).

To gain further insights into the physical processes occurring in the earthworm gut, a number of researchers have compared the stability of artificial casts to those made by earthworms. In some cases, the artificial casts were less stable than natural casts, which may be related to applying forces to the soil greater than those normally encountered within the earthworm gut (Zhang and Schrader 1993; Hindell et al. 1994, 1997a; Schrader and Zhang 1997). This may be a particular concern when artificial casts are made by forcing soil material through a syringe (Hindell et al. 1997a). Zhang and Schrader (1993) also suggested that earthworm casts were more readily stabilized than artificial casts because the organic and mineral fractions were mixed more intimately within the earthworms than when the soil was artificially remolded. On the other hand, Marinissen and Dexter (1990) reported that fresh casts produced by *A. caliginosa* were up to two times more dispersible than artificial casts made by extruding the same soil through a syringe. In this instance, they suggested that the results were probably attributable to less intensive remolding in the artificial casts than in the earthworm casts. Despite the difficulties in replicating the physical forces encountered by soil material during passage through earthworms, Hindell et al. (1997a) pointed out that artificial casts can be a useful model against which changes in soil structure that result from earthworm activity can be tested.

MEASUREMENT OF THE STABILIZATION OF AGGREGATES IN CASTS

Prior to the mid-1980s, most studies suggested that freshly excreted earthworm casts were immediately more stable than uningested soil (Hopp and Hopkins 1946; Dutt 1948; Swaby 1950; Teotia et al. 1950; Parle 1963; Lal and DeVleeschauwer 1982; Lal and Akinremi 1983). These results, however, were mainly attributable to the fact that the samples were dried before analysis. Most recent studies indicated that fresh, moist casts are less water stable than uningested soil because of the intense remolding that occurs during passage through earthworms (Shipitalo and Protz 1988; Marinissen and Dexter 1990; Barois et al. 1993; Schrader and Zhang 1997; Decaëns et al. 2001).

As casts age, they are stabilized by a combination of physical, chemical, and biological processes, which explains why some casts can persist at the soil surface for more than a year when protected from raindrop impact and trampling by animals (Decaëns 2000). Although several studies have shown that aging or drying fresh casts reduced their dispersibility (Shipitalo and Protz 1988; Marinissen and Dexter 1990), this conclusion has not been universal (Haynes and Fraser 1998). To understand these seemingly contradictory findings, the methodology used to measure the stability of earthworm casts (e.g., wet or dry sieving, clay dispersion, turbidimetric analysis), as well as the effects of other treatments to which the casts have been subjected (wetting and drying cycles, simulated rainfalls, sterilization and chemical treatments), must be taken into account.

Water-stable aggregation is an index for aggregate stability under wet conditions, whereas tensile strength (determined by a crush test) is an index for aggregate stability under dry conditions. The tensile strength of aggregates is influenced by their water and clay contents (Gill 1959) and decreases with increased porosity (Dexter et al. 1984). In studies in which tensile strength was measured (Schrader and Zhang 1997; Garvin et al. 2001), earthworm casts were significantly stronger than natural aggregates. The tensile strength of casts, however, appears to be species dependent because Flegel et al. (1998) observed a lower tensile strength for the casts of *Dendrobaena octaedra* compared to those of *L. terrestris*. Similarly, Schrader and Zhang (1997) noted that water-stable aggregation was significantly higher in casts of *L. terrestris* than in casts of *A. caliginosa*.

STABILIZATION OF AGGREGATES IN CASTS: PHYSICAL, CHEMICAL, AND BIOLOGICAL PROCESSES

One of the physical processes thought to contribute to the stabilization of casts with age is thixotropic hardening (Shipitalo and Protz 1989). Thixotropic or age hardening is described by Utomo and Dexter (1981) as a rearrangement of particles and water films and a restoration of

edge-to-edge contacts between clay domains with time, but without water loss. These processes are reversible, and organic matter reportedly slows or has no effect on thixotropic hardening (Blake and Gilman 1970; Molope et al. 1985). As Marinissen et al. (1996) pointed out, however, thixotropic process normally occur within hours, so cannot be solely responsible for the stabilization that occurs in casts over much longer time frames.

In addition to the physical processes, chemical processes can contribute to stabilization of earthworm casts. Earthworms are known to secrete amorphous calcium carbonate (C.A. Edwards and Bohlen 1996), a possible binding agent (Tisdall and Oades, 1982). In addition, by using selective chemical pretreatments, Shipitalo and Protz (1989) gathered indirect evidence that calcium, and to a lesser extent magnesium, are involved in the clay-polyvalent cation-organic matter linkages that stabilize soil microaggregates within casts. In fact, the change in CaCO_3 content in casts compared to uningested soil (Zhang and Schrader 1993) might be useful as an index of the capacity of various earthworm species to bond soil particles and reform new stable aggregates. When they compared casts from various soils, Schrader and Zhang (1997) found positive correlations between tensile strength and the clay and CaCO_3 contents of the soil. These parameters, however, correlated negatively to water-stable aggregation. Hindell et al. (1997a) hypothesized that the greater dispersibility of artificial casts compared to natural casts was because of a greater loss of calcium ions from the artificial casts, which reduced coagulation of clay particles.

The production of microbial polysaccharides in casts (Chapman and Lynch 1985; Emerson et al. 1986; Robertson et al. 1991) and polysaccharides that are added to casts in the mucus secreted by earthworms and by mucilages produced by microorganisms living in their digestive tract (Barois and Lavelle 1986; Kristufek et al. 1992) may also affect aggregate stability. The role these polysaccharides play in cast aggregation, however, is still uncertain.

Hindell et al. (1997a) suggested that the secretion of soluble carbohydrates in the earthworm gut initially facilitates the dispersion of clay. On the other hand, Swaby (1950) showed that, as populations of intestinal bacteria increased, the production of gums and glues increased, and cast stability increased. Altemüller and Joschko (1992) also showed that carbohydrates produced by bacteria can serve as cementing agents, and Flegel et al. (1998) report a significant correlation between phosphomonoesterase activity and the water-stable aggregation of earthworm casts.

Other research, however, has demonstrated that microbial activity is not necessary for casts to stabilize (Marinissen and Dexter 1990; Marinissen et al. 1996; Haynes and Fraser 1998). In fact, microbial activity may be reduced in some casts because of limited gaseous exchange caused by their high bulk density (Blanchart et al. 1993). In some instances, poor correlations of aggregate stability in casts with the size of the microbial populations and polysaccharide content are probably because the arrangement and location of these constituents within casts is more important than the absolute quantities (Shipitalo and Protz 1989; Haynes and Fraser 1998).

Microbial activity can also physically stabilize earthworm casts. Fungal hyphae have been reported to stabilize soil aggregates and casts (Tisdall and Oades 1982; Molope et al. 1987; Marinissen and Dexter 1990; Lee and Foster 1991; Tisdall 1991; Tisdall et al. 1997; Kabir and Koide 2002). Using scanning electron microscopy, Haynes and Fraser (1998) observed that fungal hyphae emanating from within casts enmeshed aggregates. Tiunov and Scheu (2000) found that most fungi can survive passage through *L. terrestris*, but the dominance structure of the fungal community changes with time and remains cast specific for up to 100 days.

ROLE OF ORGANIC MATTER

In most studies, the amounts and source of organic matter incorporated into the soil by earthworms has been shown to have a significant affect on aggregate stability within casts; thus, a positive correlation between cast organic carbon content and cast stability is frequently noted (Shipitalo and Protz 1988; Zhang and Schrader 1993; Schrader and Zhang 1997; Flegel et al. 1998). Earthworms play a large role in litter comminution and its repartitioning into the smaller aggregate size

fractions. For example, the organic matter in the fraction larger than 2000 μm decreased from 97 to 27% in the presence of the *E. fetida*, leading to a predominant 630- to 2000- μm fraction after 446 days of incubation (Ziegler and Zech 1992). This litter-derived organic matter can serve as a bonding agent or promote microbial activity that leads to the production of bonding agents (Guggenberger et al. 1996).

Beare et al. (1994) suggested that the incorporation of organic matter promotes the formation of stable microaggregates within macroaggregates. Kladvko et al. (1986) found that, after drying, aggregate stability was mainly determined by the type of plant remains, although the effect of earthworms was still significant. Once incorporated into casts and if not subject to further disturbances, the organic matter can persist for many years (McInerney et al. 2001), with organic carbon persistence and dynamics in earthworm casts dependent on complex interactions among soil texture, temperature, and wetting cycles (McInerney and Bolger 2000). In some instances, however, cast stabilization has been observed in the absence of a source of organic residue (Marinissen and Dexter 1990; Marinissen et al. 1996). Similarly, although Haynes and Fraser (1998) observed fragments of decomposing organic material adhering to aggregate surfaces, they noted stabilization in the absence of a source of organic residue. It is likely that the type and extent of bonding will depend on properties of the soil materials and on the quality and the quantity of the ingested organic debris.

Thus, several physical, chemical, and biological mechanisms probably contribute to the stabilization of aggregates within casts, and their relative importance can vary under different conditions and with different earthworm species. The continued stability of these aggregates can be influenced by wetting and drying cycles and whether other soil organisms disrupt them. Successive wetting and drying cycles contribute to the stability of natural aggregates by creating bonds of different nature between the contact points of soil particles over time (Dexter et al. 1988).

In casts, Marinissen and Dexter (1990) assumed that the effects of drying-rewetting would be more persistent with time than the effects of fungal hyphae. In newly remolded aggregates, Utomo and Dexter (1982) showed that wetting and drying increased the percentage of water-stable aggregates two- to fourfold. Nevertheless, Hindell et al. (1997b) reported opposite results for initially air-dried casts and uningested soil. Air-dried samples slaked severely when immersed in water, and they speculated that surface casts are the most subject to slaking following sudden rain or irrigation.

In a laboratory microcosm study, Shaw and Pawluk (1986) noted that soil structure development was maximized when anecic and endogeic earthworm species were allowed to interact. In a field study in a tropical region, however, Blanchart et al. (1997) noted that small eudrilid earthworms accelerated the destruction of aggregates created by larger earthworms. This prevented accumulation of large casts at the soil surface and, in some cases, led to the formation of a compact and impermeable layer and to negative effects on plant growth (Blanchart et al. 1999; Chauvel et al. 1999). In temperate region soils, Ge et al. (2001) noted that casts near the soil surface degraded rapidly unless protected by a mulch cover, and Shuster et al. (2000) noted that foraging and midden building by anecic earthworm species reduced residue cover and exposed more soil and casts to raindrop impact.

SURFACE CASTING, SOIL EROSION, AND NUTRIENT TRANSPORT

Although Darwin (1881) speculated that earthworms contribute to soil erosion, it is now known that the net effect of their activity on soil losses depends on a number of interacting factors. By burrowing into the soil and creating macropores, earthworms can increase infiltration rates 2- to 15-fold, which should lead to a reduction in runoff (Ehlers 1975; Joschko et al. 1989; W.M. Edwards et al. 1990; Kladvko and Timmenga 1990; Bouché and Al-Addan 1997; Willoughby et al. 1997). This, in turn, should contribute to a reduction in soil loss. In addition, earthworms can increase surface roughness by casting on the soil surface, and their burrowing activity can disrupt soil crusts, which should further increase infiltration and reduce runoff (Kladvko et al. 1986).

However, because freshly deposited casts are of low stability, they are subject to dispersion if deposited on the soil surface and not protected from raindrop impacts (Van Hoof 1983). This detached material is then subject to transport, which can contribute to soil losses and the loss of sediment-associated nitrogen (Parle 1963; Binet and Tréhen 1992; Buck et al. 1999), phosphorus (Graff 1970; Sharpley and Syers 1976; Ganeshamurthy et al. 1998), and potassium (Tiwari et al. 1989; Ganeshamurthy et al. 1998). Hence, surface casts have been shown to be a source of sediment and particulate and dissolved P in surface runoff from a permanent pasture (Sharpley and Syers 1976; Sharpley et al. 1979). In temperate regions, surface-casting activity can increase sediment losses from fields used to grow row crops, particularly in maize fields, where compacted soils can contribute to increased surface casting activity and increased surface runoff (Binet and Le Bayon 1999; Le Bayon and Binet 1999). In a tropical forest, Nooren et al. (1995) estimated that $0.12 \text{ kg m}^{-2} \text{ year}^{-1}$ of organic suspended sediment originated from the disintegration of earthworm casts because of the combined effect of rain splash and surface runoff.

Field plot research conducted by Le Bayon and Binet (2001) using simulated rainfall highlighted the complexity of the dynamic interrelationships among earthworm surface casting activity, runoff, and erosion in temperate region agroecosystems. Although these experiments confirmed some of the findings of static measurements, such as cast water stability and tensile strength, they also indicated that a number of other factors must be taken into account to understand the potential contributions of earthworm casts to soil erosion and nutrient transport. They found that recently deposited earthworm casts were more susceptible to dispersion by raindrops and transport in surface runoff than older casts, probably because of enhanced stability with time caused by the mechanisms discussed here. The resistance of casts to dispersion with time also appeared to be species dependent (anecic vs. endogeic). Casts were enriched in particulate phosphorus compared to uningested soil. Nevertheless, soil and particulate phosphorus losses in runoff were less from plots with earthworm casts than from control plots without surface casts. This was attributed to a reduction in surface runoff because of enhanced infiltration from earthworm burrowing activity and the casts acting as a physical barrier to runoff by increasing surface roughness, thereby ponding water and further delaying the onset of runoff (Figure 10.1). By following the fate of individual earthworm casts, they also determined that cast morphology (base/height ratio), weight, bulk density, and abundance could affect cast susceptibility to dispersion and transport, factors that would not be evident based on water stability or tensile strength measurements. Moreover, factors external to earthworm activity, such as rainfall intensity and slope, can also affect the fate of surface casts (Figure 10.1).

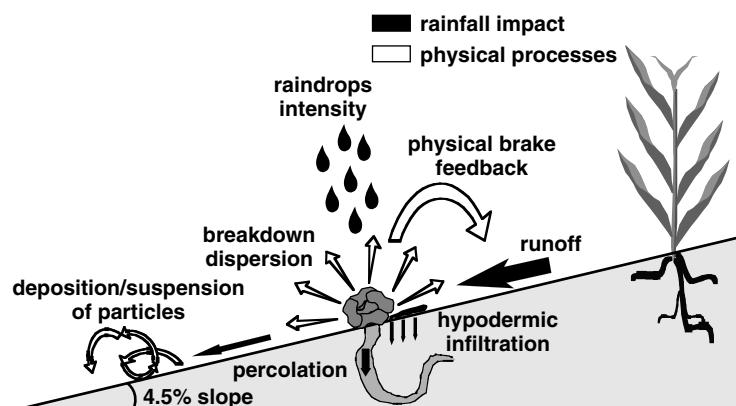


FIGURE 10.1 Interrelationships between earthworm surface casting activity, rainfall, surface runoff, infiltration, and soil erosion. (From Le Bayon, R.C. and F. Binet, 2001, *Pedobiologia*, 45:430–442.)

POROSITY AND INFILTRATION

CHARACTERIZATION OF BURROW MORPHOLOGY

Because they burrow extensively into mineral soil, endogeic and anecic earthworms can substantially alter soil porosity. Estimates of the number of burrows in temperate region soils range as high as 100 to 800 m⁻² (Lavelle 1988). Although these burrows usually account for a small fraction of the soil volume, because of their continuity, stability, and relatively large size compared to pores formed by most other mechanisms, these macropores have the potential to affect greatly the movement of air, water, and solutes. Moreover, unlike cracks, earthworm burrows tend to remain open and continue to function as preferential flow paths under wet soil conditions (Friend and Chan 1995) and are less likely to be closed by vehicle-induction compaction than other soil macropores (Alakukku et al. 2002). Quantifying burrow numbers and morphology is difficult, however, and a number of techniques have been used to accomplish this task.

A commonly used technique is to count the number of burrows open at various depths in the soil and measure their diameters. These counts can be performed manually or by taking photographs and using image analysis techniques (Shipitalo and Protz 1987; W.M. Edwards et al. 1988a, 1988b). If accurate information on burrow continuity is to be obtained, the observations must be made at relatively narrowly spaced vertical intervals. This can be accomplished by serially sectioning the soil either *in situ* or with impregnated soil thin sections (Ehlers 1975; Lighthart et al. 1993; McKenzie and Dexter 1993; Schrader 1993; Hirth et al. 1996; Lighthart 1997; Pitkänen and Nuutinen 1997; Sveistrup et al. 1997; Springett and Gray 1998). These techniques, however, are laborious and are often only partially successful, particularly in the soil layers near the surface, because of loose soil aggregates and interference by plant roots (Lighthart et al. 1993). For example, McKenzie and Dexter (1993) were only successful 20% of the time when they used a grid coordinate system and manual excavation to measure earthworm burrow geometry.

A modification of the excavation technique that reduces some of the difficulties encountered in trying to track the continuity of individual earthworm burrows and that can result in more accurate characterization of their morphology is through the use of replicas of burrows made *in situ* (Figure 10.2). These replicas can be made using materials such as molten lead (Teotia et al. 1950), plaster (Bouma et al. 1982; Wang et al. 1994), wax (Smettem 1986), or fiberglass resin (Shipitalo and Butt 1999; Shipitalo and Gibbs 2000). Like excavation, this technique is not always successful because of an inability to fill the burrows completely with the impregnating media. Additional drawbacks are that the technique works best only on burrows of relatively large diameter (i.e., >5 mm), and removal of the replicas is a tedious operation.

More recently, x-ray computed tomography has been used to characterize earthworm burrow morphology (Golabi et al. 1995; Daniel et al. 1997; Perret et al. 1997; Jegou et al. 1998; Capowicz et al. 1998, Langmaack et al. 1999). A major advantage of this technique, compared to procedures involving excavation, is that the soil is not disturbed during the analysis. Consequently, the dynamics of burrow construction can be investigated. Besides the limited availability and high expense of this equipment, a major disadvantage is that the resolution of the current generation of equipment is such that only the morphology of large diameter burrows can be accurately assessed. Another concern is that the samples are usually obtained by incubating earthworms in columns of soil that will fit within the instruments rather than examining burrows formed by earthworms in the field under natural conditions. As Springett and Gray (1998) noted when they manually excavated burrows, there can be major differences between those formed in laboratory columns and those formed in the field because of restriction of the available space in columns.

EFFECTS OF EARTHWORM BURROWS ON INFILTRATION

A variety of field and laboratory techniques have been used to determine the effects of earthworm burrows on infiltration. These techniques include dye and tracer studies, studies in which movement



FIGURE 10.2 Example of a fiberglass replica of an *L. terrestris* burrow photographed against the backdrop of a monolith of the soil from which it was obtained. Approximate length 1 m.

of water coming from individual earthworm burrows is monitored, and studies in which the overall effect of earthworm presence on infiltration rate of the bulk soil is investigated. These studies have shown that burrows made by anecic and endogeic species of earthworms can effectively conduct water (Zachmann et al. 1987; Trojan and Linden 1992; Joschko et al. 1992; Shipitalo et al. 2000).

Because most of their activity is confined to surface soil horizons, however, endogeic earthworms probably do not directly influence water movement deep into the profile (Ela et al. 1992). The fact that portions of their burrows are often occluded with casts probably further limits their effectiveness in water transport.

Thus, most research has centered on the effects of anecic earthworm species on infiltration and on *L. terrestris* in particular. Burrows created by *L. terrestris* are normally single, nearly vertical channels, up to 12 mm in diameter and 2.4 m deep (C.A. Edwards and Bohlen 1996). These burrows can have several entrances directly underneath the midden, but these usually coalesce into a single channel within the upper few centimeters of soil. Nevertheless, Shipitalo and Butt (1999) and Shipitalo and Gibbs (2000) found that about 5% of the *L. terrestris* burrows they investigated were Y shaped, with the two channels intersecting as deep as 69 cm below the soil surface.

One method that has been used to investigate water movement through natural *L. terrestris* burrows in the field involves placing surface-vented collection bottles beneath individual burrows 30 to 50 cm below the soil surface (W.M. Edwards et al. 1989; Shipitalo et al. 1994). Because the portions of the burrows above the samplers are not disturbed, this technique can be used to investigate infiltration into burrows with intact middens. Although middens would seem to inhibit entry of water, these studies indicated that *L. terrestris* burrows could transmit substantial amounts of water. In fact, Darwin (1881) did not consider middens to be a barrier to water movement. These studies also indicated that the fraction of rainfall collected increased with rainfall intensity. With an intense rainfall on a dry soil surface, W.M. Edwards et al. (1989) estimated that the monitored burrows collected 10% of the rainfall and an average of 13 times more water than expected based on the diameter of the burrows at the soil surface.

Problems with the bottle sample technique include concern that interception of flow with the samplers may allow more water to move through the burrows than would naturally occur because infiltration characteristics of the soil surrounding the lower reaches of the burrow might limit infiltration (Lee and Foster 1991; Golabi et al. 1995). In addition, after initially high rates of infiltration, soil air pressure might restrict further water entry under field conditions (Linden and Dixon 1976; Edwards et al. 1979; Baird 1997), a consequence precluded by the sampler design. These concerns appear to be unfounded in most soils under most conditions because procedures in which infiltration has been measured by introducing water directly into the openings of individual *L. terrestris* burrows at the soil surface have demonstrated average infiltration rates in the range of several hundred milliliters per minute, well in excess of the amounts measured using the bottle sampler technique, for soils in Germany (Ehlers 1975), the Netherlands (Bouma 1982), Wisconsin (Wang et al. 1994), the U.K., and Ohio (Shipitalo and Butt 1999). Moreover, the study by Shipitalo and Butt (1999) indicted that the presence of live *L. terrestris* in the burrows did not have detectable effects on infiltration. This addressed the concern of Lee and Foster (1991) that anecic earthworms might tightly seal their burrows with their bodies and limit infiltration. In fact, Shipitalo and Butt (1999) speculated that occupied burrows might be more effective in transmitting water than abandoned burrows because they are more likely to maintain near-surface continuity.

The effects of earthworms on infiltration have also been investigated in the laboratory using intact or repacked soil columns with resident or inoculated earthworms. Although these studies have provided insight into mechanisms affecting infiltration, one concern, particularly with repacked soil columns inoculated with earthworms, is that the burrows formed are not representative of those constructed under more natural conditions (Springett and Gray 1998). Similarly, studies in which artificially constructed macropores are used to investigate water movement through earthworm burrows can have significant limitations and must be interpreted with caution (Joschko et al. 1989; Roth and Joschko 1991; Ela et al. 1992; Li and Ghodrati 1995). In this case, an additional limitation is that the artificial burrows lack the organic matter-rich lining or drilosphere, composed of earthworm excrement, mucus secretions, and plant remains, that can affect water and chemical movement (Stehouwer et al. 1993, 1994).

Models have also been used to determine the impact of earthworm burrows and other macropores on infiltration (Ehlers 1975; W.M. Edwards et al. 1979; Smettem and Collis-George 1985; Smettem 1986; Wang et al. 1994, Li and Ghodrati 1995). Although this approach is useful in investigating the factors affecting infiltration in earthworm burrows, collection of the burrow data needed to obtain parameters (i.e., burrow depth, length, diameter, volume) for the models is difficult. Moreover, although most of these models indicate that the aforementioned parameters should affect infiltration capacity, Shipitalo and Butt (1999) were unable to detect any significant correlations between these geometrical properties and infiltration rates through *L. terrestris* burrows. In addition, not all earthworm burrows conduct water (Ela et al. 1992; Trojan and Linden 1992; Shipitalo et al. 2000). In fact, Bouma et al. (1982) stated that theoretical models are unlikely to predict infiltration in earthworm burrows successfully given the complexity and variability of the morphological factors affecting hydraulic performance.

EFFECTS OF EARTHWORM BURROWS ON WATER QUALITY

Increased infiltration attributable to earthworm activity in soils is generally regarded as beneficial because it can reduce surface runoff, thereby increasing plant-available water and reducing the potential for overland transport of sediment, nutrients, and agrochemicals (Shipitalo et al. 2000). Earthworm burrows can also increase the efficiency of subsurface drainage systems (Urbánek and Doleňal 1992) and may help restore the infiltration capacity of clogged septic system leach beds (Jones et al. 1993). However, this increased infiltration can increase the quantity and rate of solute movement through the soil profile. This is of particular concern with *L. terrestris* burrows because they are often deep enough to penetrate the entire soil profile (Figure 10.2). Thus, solutes transported through these burrows can rapidly bypass the upper reaches of the profile, where uptake is most likely to occur and biological activity and the potential for degradation are greatest. In addition, because the velocity at which water moves through these macropores is much greater than when the entire soil matrix is involved in the flow process, the amount of soil a solute encounters and its contact time with the soil are reduced.

It is difficult, however, to quantify the effects of earthworm burrows on chemical transport because, as just discussed, it is difficult to measure their effects on infiltration. An additional complication is that the burrow linings can serve as both a source and a sink for various solutes. For example, W.M. Edwards et al. (1992b) found that when nitrate-free water was poured into *L. terrestris* burrows and immediately collected 45 cm below the soil surface, it contained as much as 40 mg of nitrate-nitrogen per liter. They speculated that the nitrate originated from the decomposition of the organic matter lining the burrows. This contention is supported by the work of Parkin and Berry (1999), in which higher microbial populations as well as higher nitrification and denitrification rates were noted in *L. terrestris* burrow linings than in bulk soil. W.M. Edwards et al. (1992b) also noted a fivefold reduction in the concentration of alachlor and a ninefold reduction in the concentration of atrazine when solutions of these two herbicides were poured into burrows and collected at the bottom. When these solutions were poured through man-made artificial burrows, the concentrations were only reduced by about half. In this instance, the decreased herbicide concentrations were attributed to sorption of the herbicides by the organic matter-rich linings of the burrows, a contention supported by the work of Stehouwer et al. (1993, 1994). For this reason, chemical tracers are often used to investigate solute movement in earthworm burrows.

The results of a number of field and laboratory chemical transport and tracer studies suggested that earthworm burrows can increase overall water movement through the soil and contribute to a slight increase in the leaching of surface-applied agrochemicals, particularly when intense storms occur shortly after application on residue-covered no-till soils (Germann et al. 1984; Bicki and Guo 1991; W.M. Edwards et al. 1992a; Trojan and Linden 1992). The potential for this to occur is greatly reduced with time (W.M. Edwards et al. 1993, 1997; Logsdon 1995) and low intensity intervening rainfalls (Shipitalo et al. 1990; Propes et al. 1993; Golabi et al. 1995). Ingestion of

herbicide-coated residues by earthworms can also reduce leaching losses (Farenhorst et al., 2000a,b).

Other potential adverse effects of earthworm burrows on water quality and water utilization include fostering nonuniform distribution of water during furrow irrigation and loss of water through unlined irrigation ditches. Possible remedies for these concerns include compacting the ditches and removing vegetation to reduce earthworm burrowing (Kemper et al. 1988) and adding ammonia at low rates to the irrigation water to repel earthworms (Trout and Johnson 1989). Burrowing by earthworms can also contribute to leakage of earthen-lined manure storage lagoons by increasing the hydraulic conductivity of the berms (McCurdy and McSweeney 1993). Presumably, the procedures used to reduce water movement through unlined irrigation ditches would help alleviate this concern.

Earthworm burrows can also affect the movement of the constituents in animal wastes applied to soils. Joergensen et al. (1998) noted greater movement of fecal indicator organisms in cattle slurry applied to grassland than to plowed soil; they attributed this increased movement to greater numbers of *L. terrestris* burrows in the grassland. Similarly, the results of a study by Shipitalo and Gibbs (2000) suggested that *L. terrestris* burrows, in close proximity to subsurface drains, can contribute to rapid movement of injected animal wastes off-site. In this instance, rapid movement of the tracer to the buried drains was limited to burrows 0.5 m to either side of the drain. This suggests that disrupting the burrows in this region prior to slurry application or avoiding application in this region might reduce this concern.

CONCLUSIONS

Despite the large number of studies that have been conducted on the effects of earthworm activity on soil structure, a number of important gaps in knowledge remain. Factors contributing to this problem include a lack of appropriate techniques to assess aggregation and porosity and often-inappropriate extrapolation of laboratory findings to the field.

In general, earthworm activity improves soil aggregation, but their casting activity initially destabilizes the soil. Although laboratory studies can elucidate some of the factors affecting the improvement of aggregation with time, only when the fate of earthworm casts is investigated in the field or in microcosms that reflect the complexity of natural systems and managed agroecosystems will a more complete understanding be obtained. One approach that shows promise is to manipulate earthworm populations in long-term field plots to assess the effects of different population levels on soil structural dynamics (Bohlen et al. 1995).

Similarly, quantification of earthworm burrow morphology and the effects of earthworm burrows on water movement and water quality are hampered by limitations in methodology. Earthworm burrows, particularly those formed by anecic species of earthworms, can function as preferential flow pathways. Although enhanced infiltration is normally desirable, in rare instances it can result in increased chemical movement through the soil or inappropriate distribution of irrigation water and liquid animal wastes. Although there are some management options available to reduce this concern, the dynamics of water movement through earthworm burrows at the field scale are still poorly understood. Once problems with limited resolution are overcome, x-ray computed tomography holds considerable promise for increasing knowledge of the mechanisms affecting water and solute transport in earthworm burrows.

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