Chapter 4

Role of Fauna in Soil Physical Processes

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1. INTRODUCTION

Soils are formed through the interactions of several factors: climate, parent material, organisms and topography (relief), all acting through time (Jenny 1941). Soil is the outer layer of the crust that covers the land surface of the earth and is the product of mechanical, chemical and biological weathering of parent material. For instance, in the Negev desert in Israel three species of snails feed on endolithic lichens, which grow in the limestone rocks. In order to eat the lichens, the snails must ingest rock, excreting the rock materials as faeces. Snails, at a density of 21/m^2, convert rock to soil at a rate of ca. 70 to 110 g/m^2/yr (Shachak *et al*. 1987, 1995).

Besides the weathering process, water and the activities of soil organisms cause movement of organic and inorganic materials in the soil profile, thereby contributing to the formation of soils. The end product is a physical mixture of inorganic particles, organic matter, air and water. Porosity, which is that portion of the soil occupied by air and water, is a very important property of soils and strongly depends on and affects abiotic and biotic conditions. Very large pores, with a diameter greater than 100 μm,

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conduct water only during flooding or ponding rain; they are empty under drier conditions. Smaller pores almost always contain capillary (diam. 25-100 μm) and bound water (diam < 0.2 μm).

Soil texture, soil structure and porosity are interconnected and influence water transport, soil temperature, air transport and mechanical impediment of soil seedling emergence and root penetration. Soil structure cannot be measured directly and is therefore often described by size and shapes of aggregates, porosity and pore-size distribution (Koorevaar 1983). Effects of soil fauna on soil physical processes are therefore also expressed as effects on aggregation, porosity and pore-size distribution of the soil.

Soil provides a habitat for a huge array of small and large organisms. Some organisms complete their entire life cycle within the soil, while others take temporary refuge in the soil environment, which tends to be more constant than conditions above ground (Wood 1988). The effect that organisms have on the soil ecosystem depends on the number present and the time that the organisms reside in the soil. Hole (1981) classified organisms that participated in the dynamics of the soil ecosystem into the following categories: permanent, temporary, periodic, alternating, transient and accidental (see Table 1). The last three groups hardly have any influence on the properties of a soil ecosystem and will not be discussed in this chapter.

Table 1 Classification of animals in soil on basis of incidence in the soil (Hole 1981).

Category	Explanation	Representative fauna
permanent	all stages of the animal reside in the soil	Acari (mites), Collembola (springtails), earthworms
temporary	one active stage of the animal lives in the soil; another active stage does not or is periodic	larvae of many insects
periodic	the animal moves in and out of soil frequently	active forms of many insects
alternating	one or more generations of the animal live in the soil, the other generation(s) live(s) above the soil	potato aphid (*Rhopalosiphonius*), oak apple gall wasp (*Biorhiza*)
transient	inactive stages (eggs, pupae, hibernating stages) of the animal live in soil; active stages do not	many insects
accidental	the animal falls or is blown or washed into the soil	insect larvae of the forest canopy, surface animals that fall into cracks of vertisols

Soil fauna are divided into three groups according to their activities and distribution in the soil: i) epigeics that process organic matter on or near to the soil surface, ii) endogeics, which live in the mineral soil and feed on humus, and iii) anecics, which transfer materials between the soil and litter habitats (Bouché 1977). Through their location in the soil profile, these groups of animals have different effects on soil structure and physical processes.

In the first part of this chapter, we will discuss the possible effects that soil fauna can have on physical properties and processes. We conclude with an overview of the importance of soil fauna for soil physical processes in agricultural ecosystems and consider how different management strategies will influence the relationship between soil fauna and physical processes.

2. FAUNAL INFLUENCES ON SOIL PHYSICAL PROPERTIES

Activities of soil fauna that significantly affect soil structure result from the following (Lee and Foster 1991):

- burrowing and excavation in search of food, or for construction of living spaces or storage chambers within the soil or above the soil surface (e.g. earthworms, termites, ants)
- active transport of excavated or ingested soil which is deposited elsewhere (e.g. ants, earthworms)
- ingestion of soil materials (e.g. earthworms, termites)
- production of faecal pellets (e.g. microarthropods)
- use of excreta, mucus, or salivary secretions to line burrows/galleries or for gluing materials (e.g. termites, earthworms)
- collection of plant litter, animal dung, carrion from the soil surface and incorporating this into the soil with or without prior digestion (e.g. earthworms, dungbeetles).

Each of these activities has different effects on soil physical properties. Litter removal from the soil surface increases temperature gradients in the topsoil, increases evaporation of soil water, increases the possibilities for soil crusting and surface flow, and decreases infiltration (Anderson 1988). For instance, the removal of vegetation cover by grass-harvesting termites in Australia has been reported to increase sheet erosion (Wood and Sands 1978). Comminution of litter increases the active surface of the organic matter in and on the soil thereby affecting the wettability and water-holding capacity of the soil. Burrowing in the soil increases the porosity of the soil, which can have positive effects on infiltration, aeration and rooting depth of the soil. Some animals, such as earthworms, while burrowing, mix organic matter in the soil thereby increasing the water-holding capacity and aggregate stability. Certain soil fauna deposit their casts elsewhere in the soil profile or on the surface, causing a mixing of soil horizons. Casts deposited on the soil surface create a heterogenous soil surface, which limits surface flow and positively affects infiltration. However, casts can be less stable than other soil aggregates and can increase sediment erosion (Shipitalo and Protz 1988).

Figure 1 summarises the influences of soil biota on one another and on soil structure in terrestrial ecosystems. Microflora (bacteria and fungi) produce organic compounds that bind aggregates and hyphae entangle particles onto aggregates. Microfauna (protozoa and nematodes) do not have a direct effect on soil structure processes; they affect aggregate structure through their regulation of bacterial and fungal populations. The mesofauna (microarthropods and enchytraeids) affect soil structural processes through their production of faecal pellets and biopores. Some animals in this group contribute significantly to the comminution of litter material. This has a strong effect on structural stability and water-holding capacity of the soil. The macrofauna (earthworms, termites and ants) have the largest influence on soil structural processes. They create biopores and mix organic material and mineral particles. Their burrows often stimulate infiltration and aeration of the soil.

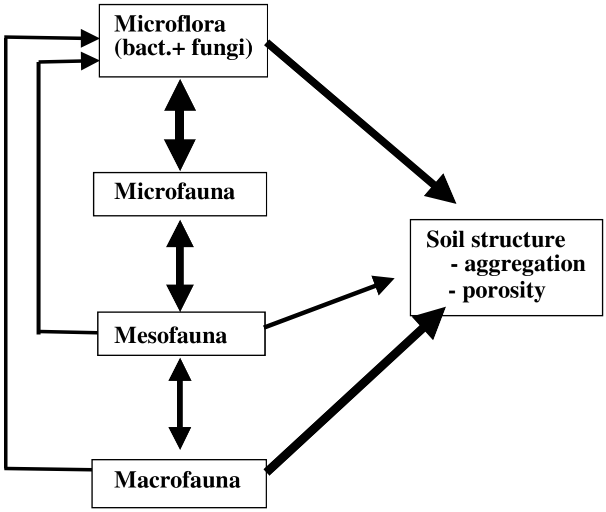

Figure 1 Direct and indirect influences of microflora, microfauna, mesofauna and macrofauna on soil structure. The magnitude of the influence is indicated by the thickness of the solid line between the boxes. Bact = bacteria

The ultimate effect of soil fauna on soil physical properties is often the result of the balance between compaction and decompaction processes (Lavelle 1997). Some invertebrates generate large aggregates that can compact the soil. Other invertebrates break these aggregates into smaller ones, by eating them and releasing small faecal pellets or by simply digging their way through these structures; this can be described as a decompaction process. In the following paragraphs the effects of several soil faunal groups on soil structure through their faecal pellets and burrowing behaviour are discussed.

2.1 Organisms which affect Soil Structure Through the Production of Faecal Pellets

Animal groups whose contribution to the formation of soil structure is limited to the production of faecal pellets are discussed. These animals hardly ingest any mineral particles and move through the soil using existing pores/burrows, thereby mixing organic matter into the topsoil. Their faecal pellets (microaggregates) may, in turn, serve as building blocks for macroaggregates (Tisdall and Oades 1982).

2.1.1 Diptera and macroarthropods

Larvae of Diptera that occur in the soil ecosystem mostly form spherical, cylindrical or spindle-like droppings, which contain large pieces of plant tissues, sometimes mixed with mineral particles. Droppings of litter-consuming diplopods and isopods contain large pieces of litter fragments, droppings of smaller soil animals or a great quantity of mineral particles, and are not very compact (size 0.5-4 mm). Because these animals occur mostly on the soil surface, their faecal pellets may accumulate to form the H-horizon of specific humus type soils (Delecour 1980). These ‘organic’ faecal pellets contribute to the water-holding capacity of the soil.

2.1.2 Microarthropods (mites and collembola)

Faecal pellets of oribatid mites are egg-shaped or spherical, with a smooth surface, very compact and without mineral particles inside, light brown coloured and up to 140-200 µm in size, depending on the species and life-stage (Rusek 1985). Droppings of collembola are usually compact, 30-90 µm in diameter, irregularly round, with a rugged, irregular surface, usually containing some mineral particles and usually black. Collembola have a leading role in the formation of soil microstructure in some arctic, alpine and weakly developed soils. Microarthropod faeces contribute to the water-holding capacity and aggregation of a soil.

Rusek (1985) found that some Onychiurid collembola and oribatid mites can make “microtunnels” in the soil matrix. These channels are important for capillary rise of moisture in the soil, aeration and fast drainage.

2.2 Ecosystem Engineers

Organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, thereby causing physical state changes in biotic and abiotic materials, are called ‘ecosystem engineers’ (Lawton and Jones 1995). These organisms modify, maintain and/or create habitats by transforming living or non-living materials from one physical state to another via mechanical or other means. Ecosystem engineers have the ability to move through soil and to build organo-mineral structures.

2.2.1 Enchytraeids

Several researchers have concluded that enchytraeids create burrows (Jegen 1920, Rusek 1985, van Vliet *et al.* 1993). Didden (1990) suggested that enchytraeids increase pore continuity and pore volume according to their body size (50-200 µm). Activities of the enchytraeids result in significant effects on air permeability, pore structure and aggregate stability. The impact of enchytraeids on hydraulic conductivity depends on the incorporation of organic matter in the soil, on the number of enchytraeids present and on the duration of the experiment (van Vliet *et al.* 1998).

Enchytraeids produce faecal pellets containing fine particles with little cellulosic plant residues. In mineral soils the faecal pellets are sponge-like structures with humus and loamy material combined (Kasprzak 1982). Didden (1990) concluded that enchytraeids have a positive effect on aggregate stability in the 600-1000 µm fraction. These aggregates might have been partly composed of enchytraeid excrements with a size of about 200 µm. However, he observed no significant effects of enchytraeids on the distribution of water-stable aggregates.

Many researchers have reported considerable amounts of mineral particles in the gut contents of enchytraeids (e.g. Babel 1968, Toutain *et al.* 1983, Didden 1990, van Vliet *et al.* 1995). Together with mineral particles attached to the body surface (Ponge 1984), enchytraeids transport these particles and may in this way influence soil structure. The amount of soil turned over by enchytraeids differs greatly between systems (Table 2). Environmental conditions, which influence enchytraeid abundances and species composition, seem to have a major influence on the soil turnover by the enchytraeid community in an ecosystem.

2.2.2 Earthworms

Numbers of earthworm burrows per unit area vary with the population density. Many researchers report about 100-300 burrows/m^2. Bouché (1971) counted more than 800 burrows/m^2 in a French pasture soil. In an irrigated orchard soil in Australia, Tisdall (1978) reported more than 2000 burrows/m^2. The diameter of the burrows varies with the size of the earthworm; generally the diameter of the burrows fits in the range of 1-10 mm. Due to their large size, earthworm burrows are important for fast drainage and aeration. Burrows of anecic species are open at the surface and may penetrate more than 1m deep into the soil. Each burrow is a distinct structure (Lee and Foster 1991). Burrows of endogeic species are often more or less randomly distributed through the soil, progressively decreasing in number with depth. The burrow system of endogeics changes continuously as the earthworms forage for food and fill certain sections with their casts (Lee and Foster 1991).

Table 2 An overview of soil turnover rates of several ecosystem engineers.

Ecosystem engineer	**System/Country**	**Soil turnover rate**	**Reference**
Enchytraeids	Arable field (The Netherlands)	0.75 t/ha/yr	Didden 1990
Enchytraeids	Arable field (USA)	21.8 t/ha/yr	van Vliet *et al.* 1995
Enchytraeids	Forest (USA)	4.2 t/ha/yr	van Vliet *et al.* 1995
Earthworms	Moist savanna (Ivory Coast)	500-1000 t/ha/yr	Lavelle 1978
Earthworms	Mexico	400 t/ha/yr	Barois *et al.* 1993
Earthworms	Temperate pasture	40-70 t/ha/yr	Bouché 1982
Humivorous termites	Moist savanna (Ivory Coast)	45 t/ha/yr	Lavelle *et al.* 1997
Termites	Guinean savanna (Niger)	0.9 t/ha/yr (litter)	Collins 1981
Termites	Senegal	2 t/ha/yr	Lepage 1974
Subterranean termites	Sonoran desert	0.75 t/ha/yr	Nutting *et al.* 1987
Mound building termites	Tropical Australia	0.3-0.4 t/ha/yr	Coventry *et al.* 1988
Ants	Subtropical regions	10 t/ha/yr	Paton *et al.* 1996
Ants	Desert (Australia)	0.42 t/ha/yr	Briese 1982
Ants	Argentina	2.1 t/ha/yr	Folgarait 1998
Ants	USA	0.842 t/ha/yr	Whitford *et al.* 1986
Tubificids	Lake sediments	2.4 t/ha/yr	Davis 1974

Many researchers have found that water infiltration increases 2 to 10 times if earthworms are present (see Lee 1985). However, this depends on the species present and environmental conditions (especially soil texture, organic matter content and climate). Burrows of anecic species might be tightly sealed by the earthworm's body; the burrow is in that case not significant for the infiltration of ponded surface water. Elimination of earthworms from a pasture resulted in a 3-fold reduction in water infiltration (Sharpley *et al.* 1979).

Inoculations of lumbricids in a Dutch polder resulted after 10 years in a significant change in soil physical properties. Uninoculated areas were covered with inactive organic mats, the mineral soil had a high penetration resistance and infiltration of water was low. In the areas with earthworms, the organic mat had disappeared, there was a high water permeability and low penetration resistance (Hoogerkamp *et al.* 1983). Twenty years of absence of earthworms in a grassland soil lead to a build-up of a litter layer and caused a compacted soil (Clements *et al.* 1991).

The size, structure and internal composition of earthworm casts depend on the ecological group that produces them. Epigeic animals usually produce cylindrical or irregular droppings containing plant material of different stages of degradation mixed with some mineral particles. These faecal pellets are not stable for a very long time (Lavelle. 1997). Burrowing (anecic) and soil feeding (endogeic) earthworms, ingest a mixture of organic and mineral debris. Casts are wet and pasty when egested, very fragile and may be easily dispersed (Shipitalo and Protz 1988). They may strongly contribute to soil loss and crust formation, especially in places where rainfall can be intense (Blanchart *et al.* 1999). In a study by Sharpley *et al.* (1979), the sediment load of surface runoff increased through splash dispersal of earthworm casts. But as the burrows of the earthworms acted as sinks for the suspended material, net sediment losses were lower in plots with earthworms than when earthworms were absent. With time and drying or drying-rewetting cycles, casts become more stable (Shipitalo and Protz 1988, Marinissen and Dexter 1990, Hindell *et al.* 1994) and become more important for aeration and drainage in soils. Dried earthworm casts are 2.5 times more resistant than similar sized dried soil aggregates (McKenzie and Dexter 1987). Stable casts increase the roughness of the soil surface, thereby reducing runoff and improving infiltration.

Earthworms in temperate pastures and grasslands deposit on average 40-50 t/ha/yr of cast material on the surface (Lee 1985). Some species in the humid tropics feed on the soil in the deeper horizons (20-50 cm) and egest casts in the soil profile; in the humid savannas of Lamto (Ivory coast), only 3 to 18% of the soil was egested as surface casts, depending on the species (Lavelle 1978). Lavelle estimated the casting rate of *Millsonia anomala* in these systems as 22-28 t/ha/yr. This equals the creation of 30-40m^3/ha of pore space.

Through their foraging activities, anecic earthworms can decrease the area of soil surface protected by residual organic matter. Without residue cover, the soil surface is exposed to 'the elements' (Freebairn *et al.* 1991) and surface crusts or seals can be formed (Shuster *et al.* 2000).

Changes in the composition of the earthworm community can have far reaching effects on soil structural properties. Chauvel *et al.* (1999) showed that the invasion of the earthworm *Pontoscolex corethrurus* into soil converted from forest to pasture reduced macroporosity by 50%. Large earthworms such as *P. corethrurus* or *M. anomale* egest large and compact casts, resulting in an increase in large soil aggregates and an increase in bulk density ('compacting species'). Small earthworms such as eudrilid worms, feed at least partly on large compact casts and egest smaller, less stable aggregates, resulting in a decrease in large aggregates and a decrease in bulk density ('decompacting species') (Blanchart *et al.* 1999). The effect of the compacting species seems linked to the presence of organic residues at the surface. If organic residues are low, the presence of 'compacting' earthworms results in a lower infiltration and an increased water retention and even crust formation can occur (Blanchart *et al.* 1999, Ester and van Rozen 2002, Shuster *et al.* 2000). The introduction of decompacting species and an increase in organic residues at the soil surface will cancel these effects (Blanchart *et al.* 1999).

2.2.3 Termites

Termites are social insects living in colonies; their impact on soil structure is largely concentrated in discrete areas. Termites construct burrows to make nests, food stores or chambers for fungal gardens. They will also build vertical shafts that may penetrate several metres deep to find suitable building material or to give access to water. Horizontal burrows are constructed to provide protected access to food sources; often an extensive network of these burrows can be found (Lee and Foster 1991). The diameter of termite galleries is in the range of 1-20 mm and the network may comprise up to 7.5 km/ha (e.g. Wood 1988). Certain termite species have galleries that extend more than 50 m from the mound (Ratcliffe and Greaves 1940).

The amount of soil transported by termites is difficult to quantify because termites build a wide range of structures which are heterogeneously spaced that includes mounds (aboveground), nests (belowground), galleries and sheetings, (Anderson *et al.* 1991). Also, the soil in these structures has variable textural and chemical characteristics depending on where the soil was collected (from the soil surface or from 10-12 meters deep), if the soil was orally transported or if the soil was faecal in origin (Wood 1988). The amount of soil in surface mounds and sheetings, originating from deeper soil layers can be up to 2400 Mg/ha and cover 10% of the soil surface (Meyer 1960). Lepage (1974) found that the termite *Macrotermes subhyalinus* brought 2000 kg of soil per ha per year to the soil surface, of which between

675 and 950 kg/ha was used for the construction of foraging runways on the soil surface (Table 2). These runways rapidly erode, but are also rapidly rebuilt. Nutting *et al.* (1987) recorded a soil turnover of two species of subterranean termites of 750 kg/ha/yr (Table 2).

Soil-feeding termites ingest a mixture of organic and mineral debris. The faeces formed contain organo-mineral complexes and are stable over periods ranging from months to decades (Wood 1996). Termites generally select the smaller particles from within the soil profile and bring to the surface significant amounts of clay materials (Williams 1968, Boyer 1982). Termite mounds are often enriched with clay in comparison with unaffected soils (Lobry de Bruyn and Conacher 1990).

The effects of termite burrows on macroporosity, water infiltration and aeration are not well studied. There seem to be two contrasting theories applicable. In the first theory, termites repack the soil in such a way that it forms a compact structure which reduces water infiltration and aeration. The other theory states that termites increase infiltration and aeration by incorporating organic matter into the soil and by constructing galleries through the soil. More research is needed to determine which theory is most plausable (Lobry de Bruyn and Conacher 1990). A few studies have been done and point toward the second theory. Elkins *et al.* (1986) found that in plots in which termites were present, water infiltration rates were much higher than in plots without termites. Casenave and Valentin (1989) found that if termite sheetings covered about 30% of the soil surface infiltration increased maximally. This is probably due to increased surface roughness and the presence of galleries below the surface structures (Lavelle 1997). Others state that because the entrances to the termite galleries (burrows) are mostly closed to the surface, the effect on water infiltration is minimal (Lee and Foster 1991).

2.2.4 Ants

Ants can be found in any type of habitat in the world; they are only lacking in Iceland, Greenland, Antarctica and a few small islands (Hölldobler and Wilson 1990). Their pedobiological influence is largely through the construction of nests, galleries, soil sheetings and mounds.

As a result of the network of galleries and chambers, the porosity of a soil is increased and the soil is less compact, resulting in better drainage and aeration (Baxter and Hole 1967, Rogers 1972, Gotwald 1986, Majer *et al.* 1987, Cherrett 1989). Certain ant species fill underground cavities with a porous mixture of aggregates (750-2000 μm) (Humpreys 1994). Majer *et al.* (1987) found that the mean infiltration rate on ant nests was much faster compared with unaffected soil. However, ants expose bare soil around their burrows (Thorp 1967), which could impede water infiltration and encourage water erosion.

The movement of subterranean soil to the surface through ant activity can be very high. Paton *et al.* (1996) recorded mounding rates of 10 t/ha/yr in moist tropical and temperate ecosystems (Table 2). From a comparison of global rates of animal bioturbation, ants scored second (ca. 50 t/ha/yr) after earthworms (ca. 150 t/ha/yr), but ants have a wider geographical distribution than earthworms (Paton *et al.* 1996).

Ants also bury organic matter into the soil, thereby increasing the water-holding capacity of the soil, and mix soil layers by moving small particles from deeper layers to the surface (Petal 1978). Some researchers reported an enrichment of ant mounds with clay compared to undisturbed soil nearby, while others found the opposite (Lobry de Bruyn and Conacher 1990).

2.2.5 Tubificidae

In ricefields, tubificid worms feed with their heads downward in a burrow and deposit their faeces on the sediment surface. This leads to a vertical distribution of soil particles. Larger particles and plant residues are gradually concentrated in the lower soil layer, while finer particles are concentrated in the upper layer. Through the activities of the tubificids, the seeds of weeds are moved to a layer of about 3-5 cm below the soil surface where the oxygen concentration is too low for seed germination. Soil turnover of tubificid worms in a lake was estimated at 2.4 t/ha/yr (Table 2) (Davis 1974).

3. INFLUENCES OF MANAGEMENT ON SOIL FAUNA

The impact of soil fauna on soil structure development and stabilisation depends on the spatial and temporal scale of its actions. The following characteristics are therefore important:

- the lifetime of the individual organisms,
- the population density,
- the spatial distribution (local and regional) of the population,
- the length of time that the population has been present at the site,
- the durability of the structures in the absence of the original ‘ecosystem engineers’,
- the number of attributes of the ecosystem changed through the activities of the engineer (Lawton and Jones 1995).

Effects of agricultural practices on soil fauna will carry through in their influence on soil physical processes. A decrease in abundances will translate into a reduced effect of soil fauna on soil physical properties.

Table 3 shows abundances of certain soil faunal groups in different ecosystems. Most groups, which can exercise significant effects on soil structural properties, have lower abundances in arable land compared to forest and/or grassland ecosystems, depending largely on the intensity of management. Isopods are very sensitive to cultivation compared to other soil animals (Curry 1986). Their densities are often low in agricultural soils. Loss of shelter for isopods in arable land is a major factor reducing abundances (Wolters and Ekschmitt 1997). Reduced tillage operations such as minimum or no-tillage result in an increase in the biomass of isopods, compared with conventional tillage (Stinner and House 1990).

Agricultural practices (including heavy grazing, irrigation, drainage, fertilisation, mowing, ploughing) reduce ant biodiversity and or ant biomass (Folgarait 1998) and the number of colonies present. However ants can tolerate disturbances and recover and reinvade the same areas after the disturbance (Folgarait 1998). Tillage disturbs nest and channel structures of termites and certain species will disappear if they experience too much stress (Wielemaker 1984). Due to their sensitivity to disturbances, effects of termites on soil structure and soil physical processes will only be found in low-input, minimum tillage agriculture.

Table 3 Abundances (number/m^2) of different soil fauna groups in different ecosystems.

Ecosystem Soil fauna group	**Forest**	**Grassland**	**Arable land**	**References**
Isopoda	286	1200	5	Wolters and Ekschmitt 1997
Isopoda	155	nd	0	Abbott and Parker 1980
Microarthropods	208727	61885	39584	Hendrix *et al.* 1990
Enchytraeids	16200	23800	18000	Andrén and Lagerlöf 1983
Earthworms	85[a]	250	90	Paoletti 1999
Termites	2110	nd	0	Abbott and Parker 1980
Ants	155	nd	0	Abbott and Parker 1980

[a] average of deciduous, coniferous and tropical forests; nd = not determined

Soil cultivation affects soil fauna either directly or indirectly. The most obvious direct effect is the immediate killing or confinement of many epigeic and endogeic species. Indirect effects are due to repeated habitat destruction by destroying the surface layer, disturbing the natural macropores and cavities in soil, eliminating the systems of passageways created by burrowing invertebrates and, particularly in heavy soils, blocking the interstices of deeper layers by an accompanying accumulation of clay particles below the plough sole (Wolters and Ekschmitt 1997).

Ploughing or tilling reduces the earthworm population considerably (see Table 4), especially when the cultivation is followed by dry or frost periods (House and Parmelee 1985, Henke 1987). Compared to grassland, tilled areas have significantly lower numbers of burrows per area (Graff 1967, Ehlers 1975).

Soil tillage has little detrimental effect on enchytraeid abundances in contrast to earthworms, in certain systems (Table 4). There are even indications that soil tillage may positively influence enchytraeid abundances (Fründ *et al.* 1992, Didden *et al.* 1994). The smaller size of enchytraeids, their higher growth rates and less disturbance of microhabitats by tillage probably make them less vulnerable than earthworms to tillage.

Compaction of soil due to intensive traffic with heavy machinery leads to lower abundances of soil fauna (Aritajat *et al.* 1977). After slight soil compaction, recovery of the soil fauna was observed 1 month later and 3 months later when the compaction was more severe. Recovery of the soil fauna was not completed until at least 6 months after the disturbance.

Table 4 Examples of studies in which the effect of tillage on earthworm and enchytraeid abundances was determined.

Soil fauna group	**Country**	**Conventional tillage** (number/m^2)	**Minimum or no tillage** (number/m^2)	**Reference**
Earthworms	Indiana and Illinios, USA	64	138 (NT)	Kladivko *et al.* 1997
Earthworms	Georgia, USA	149	967 (NT)	Hendrix *et al.* 1986
Enchytraeids	Georgia, USA	15270	16830 (NT)	van Vliet *et al.* 1995
Enchytraeids	The Netherlands	23845	43007 (MT)	Didden 1991

*NT = no tillage; MT = minimum tillage.

Sustainable agriculture aims to reduce external inputs, enhance internal recycling of nutrients by reducing tillage, and use organic instead of mineral fertilisers (Doran and Werner 1990). Agricultural production systems emphasising minimum or zero tillage or direct drilling obviously promote earthworm populations in arable land (Table 4). These reduced soil cultivation techniques compared to conventional cultivation systems increase population densities by a factor of 2-3 (Makeschin 1997). Deep burrowing species such as *Lumbricus terrestris*, especially benefit from reduced cultivation (Edwards and Lofty 1982, Lavelle 1997). The burrows made by these species are very important for aeration and drainage during and after heavy rainfall. A few endogeic species benefit from cultivation and mixing of organic residues in arable soils. The availability of sufficient organic food seems to override the influence of cultivation practices (Doube *et al.* 1994).

In an agroecosystem with reduced tillage, more favourable habitats are created and a greater soil faunal diversity develops. Higher densities of soil fauna, and especially of the soil ecosystem engineers, result in a larger influence of these animals on soil physical processes. Conversely, reduced densities of these organisms, as a result of certain management practices, can be expected to reduce their influences on soil processes and possibly cause longer-term changes in soil physical properties. The best documented effects have been observed following reductions in earthworm population densities (e.g. Parmelee *et al.* 1990, Clements *et al.* 1991), which often result in decreased organic matter decomposition, thatch or litter accumulation, and possibly soil compaction. Similar or perhaps more subtle effects may result from population declines in other soil faunal groups (e.g. Microarthropods: Crossley *et al.* 1989) but these smaller animals may operate as engineers at a much finer scale; further research is needed to assess their influences on soil physical processes in response to management.

4. CONCLUSIONS

In this chapter, the potential contribution of several soil animal groups to soil physical processes has been described. Through their feeding, excrements and burrowing activities the influence of soil biota on soil structural properties can be substantial. Soil ecosystem engineers, which burrow through a soil, can contribute significantly to the better functioning of physical processes. However, for these influences to be significant, abundances of the different soil fauna need to be much larger than they are currently found in conventional tillage systems. The less ecosystem engineers are disturbed by a particular tillage system, the greater their influence on physical processes.

Sustainable agriculture, which reduces the use of non-renewable resources and protects the environment (Pankhurst and Lynch 1994), stimulates many biological soil processes. In low-input, minimum tillage or no-tillage systems, soil biota have a more important role in the maintenance and development of soil structure and soil physical processes, contributing to agricultural sustainability.

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