ELSEVIER

Soil & Tillage Research 61 (2001) 61–76

Soil & Tillage Research

www.elsevier.com/locate/still

Tillage systems and soil ecology

Eileen J. Kladivko*

Department of Agronomy, Purdue University, 1150 LILY, West Lafayette, IN 47907-1150, USA

Abstract

Tillage systems affect the soil physical and chemical environment in which soil organisms live, thereby affecting soil organisms. Tillage practices change soil water content, temperature, aeration, and the degree of mixing of crop residues within the soil matrix. These changes in the physical environment and the food supply of the organisms affect different groups of organisms in different ways. One of the challenges of research in soil ecology is to understand the impacts of management on the complex interactions of all organisms at the soil community level. In addition to the response of organisms to soil manipulations, agriculturalists are interested in the actions of soil organisms on the physical and chemical environment in the soil. Soil organisms perform important functions in soil, including structure improvement, nutrient cycling, and organic matter decomposition. This paper discusses the effects of tillage practices on soil organism populations, functions, and interactions. Although there is a wide range of responses among different species, most organism groups have greater abundance or biomass in no-till than in conventional tillage systems. Larger organisms in general appear to be more sensitive to tillage operations than smaller organisms, due to the physical disruption of the soil, burial of crop residue, and the change in soil water and temperature resulting from residue incorporation. Variations in responses found in different studies reflect different magnitudes of tillage disruption and residue burial, timing of the tillage operations, timing of the measurements, and different soil, crop, and climate combinations. The paper concludes with a discussion of challenges for tillage researchers.

Keywords: No-till; Tillage; Soil fauna; Microflora; Biodiversity

1. Introduction

Tillage and cropping systems have complex effects on the soil physical, chemical, and biological environment. The degree of tillage disturbance of the soil and the resulting location of the crop residues affects soil water content, soil temperature, aeration, and the degree of contact between organic materials and mineral soil particles. These changes in the soil physical environment affect the organisms that live within that environment, with different soil organisms responding in different ways. Populations, diversity, and activity may all be affected by changes in tillage systems.

Although soil organisms respond to tillage-induced changes in the soil physical environment, they also have an impact on soil physical and chemical conditions. Larger organisms such as earthworms burrow through the soil, producing large pores that are important for water flow and retention, aeration, and root development. They help mix organic materials into the soil and aid in aggregate formation. Microorganisms as well as microfauna, mesofauna, and macrofauna play essential roles in nutrient cycling and organic matter decomposition in the soil. Interactions among different organisms can have either beneficial or

---

* Tel.: +1-765-494-6372; fax: +1-765-496-2926.
E-mail address: kladivko@purdue.edu (E.J. Kladivko).

0167-1987/01/$ – see front matter © 2001 Elsevier Science B.V. All rights reserved.
PII: S0167-1987(01)00179-9

harmful effects on crops. Thus soil organisms are both affected by tillage and the soil physical/chemical environment and have an effect on the physical/chemical environment. Greater understanding of soil ecology could lead to more precise management of soil organisms for beneficial purposes in agriculture.

This paper will discuss the effects of tillage practices on soil organism populations, functions, and interactions. The major focus will be on soil fauna rather than soil microorganisms, and only brief mention will be made of organisms usually considered to be "pests" (soil-borne plant pathogens, insect pests, plant-parasitic nematodes). Earthworms will be discussed in greater detail than some of the other organisms, to provide in-depth examples of some of the main topics discussed in the paper. Recent reviews are cited where possible, and readers are referred to those reviews for more in-depth treatment of specific studies on each topic. The paper concludes with discussions of the importance of soil fauna in conservation tillage systems and of the research challenges awaiting tillage researchers.

2. Soil organisms

Before considering the effects of tillage systems on soil organisms, a brief description of the groups and a conceptual framework for discussion will be presented. Cochran et al. (1994) present a concise description of the different groups of organisms found in the soil, and they summarize the impacts of tillage practices on each of these groups. Bacteria, fungi, and green algae are included in the microflora. The remaining groups of interest are usually referred to as *soil fauna*, although Cochran et al. (1994) comment that protozoa have little relationship to true animals and thus they consider them in a separate category in their review.

For the purposes of this paper, the system described by Lavelle (1997) for discussion of soil fauna will be adopted. Three groups are distinguished, based on their size and their adaptation to living in either the water-filled pore space or the air-filled pore space of soil and litter. The microfauna are small (less than 0.2 mm body width on average), live in the water-filled pore space, and are comprised mainly of protozoa and nematodes. The mesofauna include microarthropods (mainly mites (acarids) and springtails (collembolans)) and the small Oligochaeta, the enchytraeidae. They have an average size of 0.2–2 mm and live in air-filled pore space of soil and litter. The macrofauna are larger than 2 mm and include termites, earthworms, and large arthropods. They have the ability to dig the soil and are sometimes called "ecosystem engineers" because of their large impact on soil structure.

In the review by Lavelle (1997), these three groups of fauna are classified into three functional guilds of organisms, based on the relationship they have with microorganisms and the kind of excrement they produce. He discusses that soil invertebrates in general have a limited ability to digest many of the complex organic substrates present in soil and litter, but that many invertebrates have developed interactions with microflora in order to utilize the resources. The first guild of organisms considered are *microfoodwebs*, which are defined as the part of the foodweb that links microorganisms to their predators (Lavelle, 1997). These *microfoodwebs* are comprised mainly of the microfauna that are predators of bacteria and fungi, and their predators. Thus bacteria, fungi, protozoa, nematodes, and some predacious Acarina are included. The microfauna significantly affect population dynamics of the bacteria and fungi and subsequent nutrient release from microbial biomass. The specific structure of microfoodwebs at a site is determined largely by whether the system is dominated by bacteria or fungi, which is in turn affected by management practices and abiotic factors.

The second functional guild recognized by Lavelle (1997) is the *litter transformers*, comprised of the mesofauna and large arthropods. They usually ingest purely organic material and do not ingest mineral soil or dig the soil. They physically fragment the litter and have an effect on soil structure by deposition of fecal pellets. Many litter arthropods have an "external rumen" type of digestion (Lavelle, 1997) in which microflora in the fecal pellets digest the complex organic compounds after deposition of the fecal pellet. The arthropod later reingests the fecal pellet and absorbs the assimilable compounds released. Although the fecal pellets are distinct structures that regulate microbial activity, they are usually small and do not have significant mineral soil within them. Thus their impact on soil structure is limited.

The third functional guild is the *ecosystem engineers*, comprised mainly of earthworms and termites (Lavelle, 1997). These macrofauna develop mutualistic relationships with the microflora within their gut, enabling them to digest complex substrates. They usually ingest a mixture of organic matter and mineral soil. Their fecal pellets are comparatively large and contain an intimate mixture of mineral materials and partially decomposed organic materials. Microbial activity may be increased or decreased within these pellets, depending on the time scale of observation, and they are a major contributor to soil structure and aggregation. Macrofauna dig burrows or build nests, thereby affecting soil porosity and water and air flow.

Lavelle (1997) contends that whenever conditions are suitable for macrofaunal activity, they become important regulators of microbial activity within their spheres of influence. This type of ‘‘top-down’’ influence of the larger organisms on the smaller ones reflects the mixing and redistribution of organic resources in the soil and the overarching effect of the physical environment created by the ecosystem engineers. However, ‘‘bottom-up’’ influences also exist, whereby organisms at the lower end of the hierarchy affect those at upper levels (Lavelle, 2000).

3. Tillage impacts on soil organisms

With this background conceptual framework on soil organisms, we are ready to look at the impact of different tillage practices on soil organisms and the impact of soil organisms on soil properties and processes. Although most of the studies reviewed compared the two extremes of no-till and ‘‘conventional’’ tillage, intermediate forms of ‘‘conservation tillage’’ or ‘‘reduced tillage’’ are likely to give intermediate results. The main areas to be considered in this paper are the effects of tillage practices on organism populations and activity, and the impacts of soil organisms on organic matter decomposition, nutrient cycling, and soil structural alteration. Some limited discussion of the role of soil organisms in pest/predator interactions within cropped fields is included. The relationship between biodiversity and soil function is also discussed.

When considering the impact of tillage practices on soil organisms, many studies have focused on one group or a few closely related groups of organisms and have not studied the interactions among different groups. An alternative approach has been to study the detrital food webs, which include microflora and microfauna and perhaps some of the mesofauna and macrofauna as well, depending on the system. In a review on ecological challenges for soil science research, Lavelle (2000) suggests that studying at the scale of ‘‘functional domains’’ within soils is one way in which interdisciplinary approaches can be used to study the complex interactions among organisms and the physical environment. Examples of functional domains (Fig. 1) include the ‘‘drilosphere’’ (influenced by earthworms), ‘‘rhizosphere’’ (influenced by roots), and ‘‘detritusphere’’ (influenced by plant litter) (Beare et al., 1995). Lavelle (2000) further describes functional domains as specific sites that may be physically separated from the soil matrix and that are defined by their main organic resource (e.g. leaf litter, soil organic matter, root exudates), a major ‘‘regulator’’ (e.g. roots, invertebrate ‘‘engineers’’, freeze/thaw processes), a set of structures created by the regulator (channels, fecal pellets, cracks), and a community of dependent, smaller invertebrates and microorganisms that live within these structures. Within each functional domain, processes may be studied at different scales of time and space, which often explains apparently conflicting results. For example, earthworm casts (fecal pellets) often show enhanced mineralization during the first few hours to days after deposition but then have reduced mineralization rates for subsequent months, due to formation of stable organic matter-mineral complexes (Lavelle, 1997). The high spatial and temporal variation of soil properties and processes, even within functional domains, makes generalizations about the impact of tillage systems on soil ecology very difficult.

A comprehensive review by Wardle (1995) does an excellent job of discussing the impacts of tillage disturbance on detritus food webs. Readers are referred to this paper for in-depth discussion of studies up until 1995 and the relationship of the results to ecological theory. A few main points from the Wardle (1995) review will be highlighted here along with a few examples from studies published since that time.

Wardle (1995) compiled the results of 106 studies of tillage impacts on soil organisms or on soil carbon

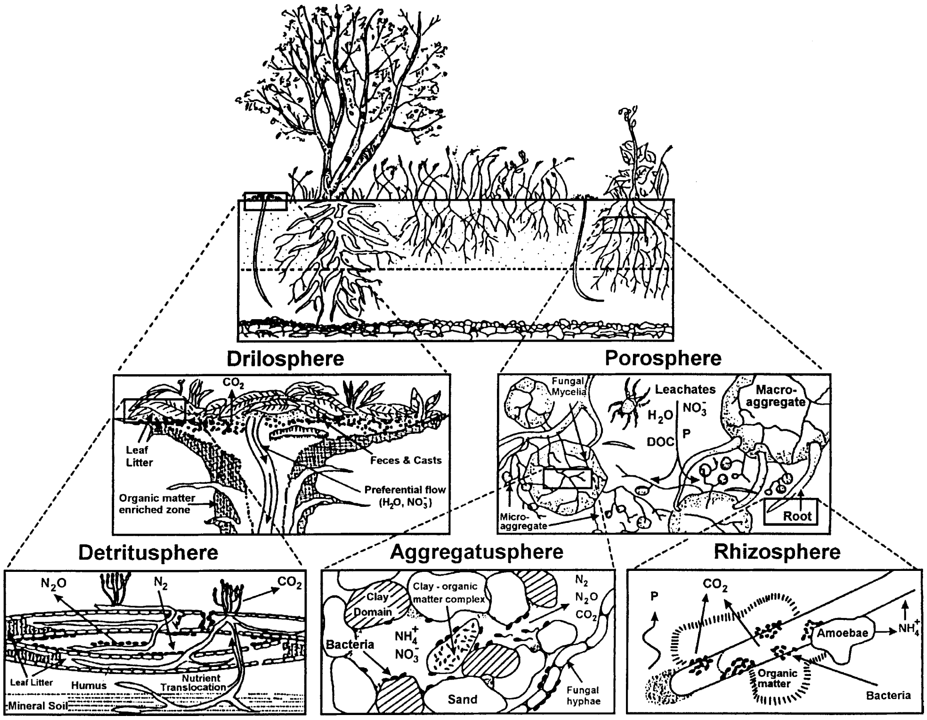

Fig. 1. Example functional domains in the soil ecosystem (reprinted from Beare et al., 1995).

and nitrogen levels. Most of the studies pooled for this analysis investigated only one or two trophic levels. Although there is a wide range of responses among different species, most organism groups have greater abundance or biomass in no-till than in conventional tillage systems. Larger organisms in general appear to be more sensitive to tillage operations than smaller organisms, due to the physical disruption of the soil, burial of crop residue, and the change in soil water and temperature resulting from residue incorporation. Variations in responses found in different studies reflect different magnitudes of tillage disruption and residue burial, timing of the tillage operations, timing of the measurements, and different soil, crop, and climate combinations. More detailed discussions of the individual groups will follow in the next sections.

Wardle (1995) also calculated an index of change *V* for each group of organisms considered in each of the compiled studies, to compare the relative increase or decrease in organism abundance or biomass (or percent soil carbon or nitrogen) between conventional tillage (CN) and no-tillage (NT). The index *V* was calculated as (Wardle, 1995):

$$V = \frac{2M_{\mathrm{CN}}}{M_{\mathrm{CN}} + M_{\mathrm{NT}}} - 1 \qquad (1)$$

where M_{CN} and M_{NT} are the abundance or mass of organisms, or percent carbon or nitrogen, under CN and NT, respectively. The index *V* ranges from -1 when organisms occur only under NT to $+1$ when organisms occur only under CN with 0 representing equal abundance under both NT and CN. Wardle (1995), constructed the following categories to express the magnitude of response to tillage:

extreme inhibition by tillage: $V < -0.67$;
moderate inhibition by tillage: $-0.33 > V > -0.67$;
mild inhibition by tillage: $0 > V > -0.33$;
mild stimulation by tillage: $0 < V < 0.33$;
moderate stimulation by tillage: $0.33 < V < 0.67$;
extreme stimulation by tillage: $V > 0.67$.

Fig. 2 presents the percent of reviewed studies with change index values in each of the different categories, for each group of organisms included. Following

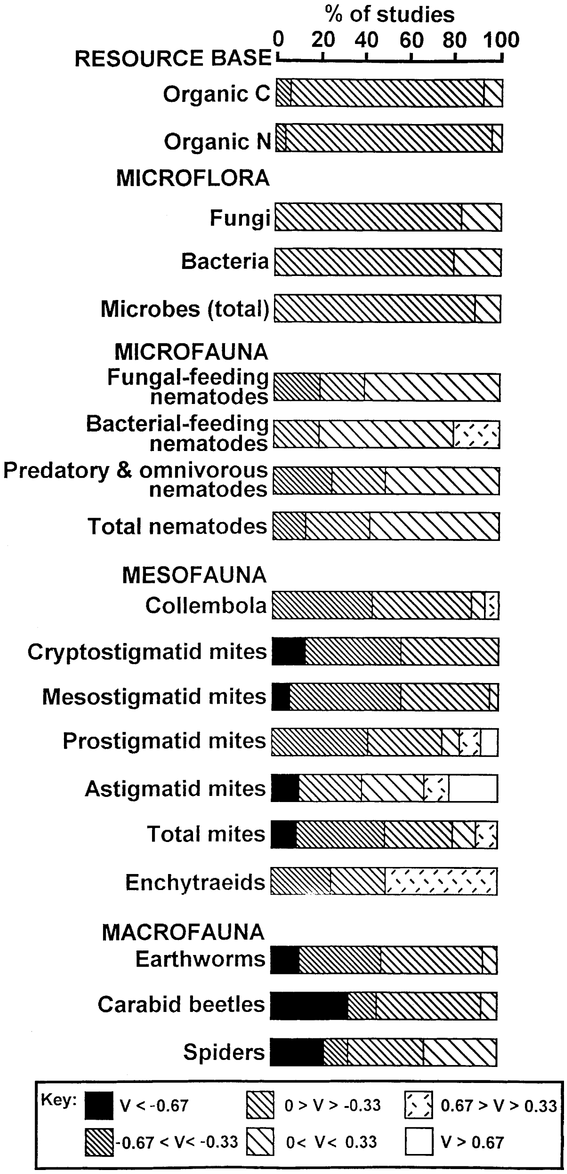

Fig. 2. Results of studies compiled by Wardle (1995), in which the index V (as described in text) represents the relative difference in abundance or biomass of organism groups between no-till and CN. The index V ranges from -1 to $+1$ and is increasingly negative or positive as the group is increasingly harmed or enhanced, respectively, by tillage operations (adapted from Wardle, 1995).

Wardle (1995), the next sections will construct the detritus food web from the bottom-up, looking at progressively larger organisms and their interaction with other groups.

3.1. Soil microflora

Most of the studies of microflora found less soil microbial biomass (defined as mass of living microbial tissue) in CN than in NT (Wardle, 1995), although differences were usually small (Fig. 2). Greater microbial biomass under NT than CN is likely due in part to cooler, wetter conditions and less fluctuation in temperature and moisture in NT. Although bacteria and fungi both appear to have greater biomass in the soil under NT than CN (Wardle, 1995), the crop residues at the soil surface under NT tend to be fungal-dominated (Hendrix et al., 1986). Thus one generalization often made is that at the microfoodweb scale, NT systems tend to be fungal-dominated whereas CN systems tend to be bacterial-dominated, although this certainly depends on whether measurements are made near the soil surface or deeper in the soil profile.

After no-till systems have been established for a number of years, many studies have found an increase in soil organic matter in no-till compared to CN systems (Logan et al., 1991; Karlen et al., 1994; Reeves, 1997). At first glance, the higher microbial biomass with no-till may appear to be contradictory to a buildup of soil organic carbon content. However, some studies have found a decrease in the efficiency of use of carbon sources by soil microorganisms under CN, as evidenced by greater carbon dioxide evolution per unit microbial biomass under CN compared with NT systems (Haynes, 1999). In addition, many studies have not explicitly considered the seasonality of tillage operations and microbial activity, in particular the flush of microbial growth and activity directly after tillage and residue incorporation (Logan et al., 1991). Current interest in C sequestration has focused attention on the dynamics of organic matter accumulation and decomposition in different tillage management systems. Discussion of the different total amount and the different pools of organic carbon and nitrogen in the soil and their interactions with microbial biomass are beyond the scope of this paper, but readers are referred to the review of carbon sequestration and tillage (Follett, 2001) and papers by Cambardella and Elliott (1992), Franzluebbers and Arshad (1996), Angers et al. (1997), and Wander et al. (1998) for discussion of these issues.

3.2. Soil microfauna

The effects of tillage practice on microfauna have been varied. Wardle (1995) states that few tillage studies have assessed protozoa, so that insufficient data are available to make generalizations. Cochran et al. (1994) suggest that management practices that favor bacteria would also be expected to favor protozoa, since bacteria are their main food source. Total nematode numbers have been found to either increase or decrease with tillage, with both mild and moderate stimulation or inhibition having been found (Fig. 2) (Wardle, 1995). The wide range of responses probably reflects the wide range of functional groups and trophic levels (fungivores, bacterivores, omnivores, predators, and plant parasites) and also the wide range of physical conditions present in either conventional or no-till systems. The effect of tillage practice on soil pore sizes, and the persistence of water films needed for microfaunal motility, are direct effects that may be important. In addition, however, there are likely indirect effects due to the influence of tillage on lower trophic levels (Wardle, 1995). Often it has been found that there are no predictable relationships between microfloral groups and their associated microfauna. In some cases an increase in microorganism growth causes an increase in the associated microfauna, which then subsequently causes a suppression in the microorganisms. This grazing pressure appears to be more pronounced for bacteria than for fungi, and the ratio of bacterial-feeding nematodes to bacterial biomass is usually higher than the ratio of fungal-feeding nematodes to fungal biomass (Wardle, 1995). In addition, the intermediate trophic levels of the microfauna have top-down effects of predators above them in the hierarchy, leading to highly variable impacts of different tillage systems. Wardle (1995) contends that there are insufficient data from field studies of NT vs. CN to make meaningful predictions about the effects of the top predatory nematodes on regulating lower trophic levels.

3.3. Soil mesofauna

As a major part of the mesofauna, soil microarthropods consist mainly of springtails (Collembola) and mites (Acari). These groups span a range of trophic levels, consuming plant litter, microflora, microfauna, and other mesofauna (Wardle, 1995). Springtails are usually inhibited by tillage disturbances, although some studies have shown the opposite effect. Mites exhibit a wider range and more extreme responses to tillage than microbial groups, with moderate to extreme increases or decreases having been found (Fig. 2) (Wardle, 1995). The different taxonomic groups of mites appear to respond differently to tillage disturbance, which explains some of the varied responses. The cryptostigmatid (Oribatid) and mesostigmatid mites are often moderately to extremely inhibited by tillage compared with NT practices (Wardle, 1995), whereas the astigmatid mites may be either inhibited or enhanced by tillage and appear to recover from tillage disturbances more rapidly (Wardle, 1995; Behan-Pelletier, 1999).

The effects of tillage on microarthropod populations are caused in part by the physical disturbance of the soil by tillage. Some individuals may be killed initially by abrasion during the tillage operation or by being trapped in soil clods after tillage inversion (Wardle, 1995). The longer-term effects of tillage practices on soil moisture, pore continuity, and litter accumulation are probably significant, with different orders of mites or species assemblages of springtails responding differently to these factors. It is also probable that microarthropod numbers are affected to some extent by the overall biomass of the trophic levels below them. The overall populations of both mites and springtails are decreased by tillage more often than they are increased (Fig. 2).

The other main group within the mesofauna are the enchytraeids. They are small, colorless worms that burrow extensively in the soil and can increase aeration, water infiltration, and root growth (Cochran et al., 1994). They may be either inhibited or stimulated by tillage (Fig. 2). The apparent stimulation of enchytraeids by tillage, which contrasts with most of the other groups discussed, may be due to their ability to recover rapidly from disturbances (Wardle, 1995). In addition, the food resources are more available to them when they are incorporated into the soil rather than remaining at the soil surface (Cochran et al., 1994).

3.4. Soil macrofauna

In tropical regions, termites (Isoptera) can cause significant alterations in soil physical and chemical properties (Lavelle, 1997). They tunnel extensively and build elaborate nests, altering soil porosity and water and air flow. As with earthworms, the other major "ecosystem engineer", termites ingest both mineral and organic material and contribute to organic matter and nutrient cycling, as well as soil aggregation. Most termites must stay within the protection of their nests and burrows to maintain their internal water content (Cochran et al., 1994). Thus tillage or other physical disturbances greatly reduce termite populations, due to destruction of their nests and burrows.

Beetles (Coleoptera) and spiders (Araneae) are important members of the macrofauna that are usually much reduced by tillage operations (Wardle, 1995). Beetles include groups that are predators as well as those that are "litter transformers" whereas spiders are mainly predators (Wardle, 1995). Reduced populations under CN are likely due in part to physical disturbance and abrasion from the tillage operation itself, but the reduction in surface residue cover is probably more significant. Spiders and beetles are active mostly near the soil surface and litter layers, and depend upon the litter or the surface-associated prey as a feed source (Wardle, 1995). In addition, the larval stage of many beetles live in the soil, and surface residue cover is important for maintaining appropriate soil moisture and temperature conditions (Cochran et al., 1994).

Wardle (1995) discusses that the predator soil macrofauna are likely the groups where the detritus food web and the above-ground (foliage-based) food web meet; but that this linkage is poorly understood. Research is needed to determine the nature and magnitude of the top-down effects of these predators on the lower trophic levels, particularly in no-till systems.

The potential role of within-field diversity of microhabitats on spider populations was reviewed by Samu et al. (1999). Spider abundance and diversity were increased when within-field heterogeneity was increased, such as with intercropping or "living mulches", reduced tillage, or weedy patches. Management of field edges for spatial diversity was not generally very effective in increasing spider populations within fields. Samu et al. (1999) suggest that strategically-timed manipulation of within field microhabitats or field edges might promote seasonal transfer of spiders from senescing plants to young crops, thus aiding pest control within fields.

A recent review by Kromp (1999) discusses the role of carabid beetles in pest control. Carabids are known to be predators of several insect pests, but many taxa are "generalist" predators and will ingest plants, weed seeds, and fungi (Stinner and House, 1990; Kromp, 1999). The linkages between the predators and detrital food webs are not well understood and may be particularly important in reduced tillage systems. Carabid populations are increased under reduced tillage systems, and the presence of weedy patches and vegetated field edges may also enhance populations. Data are limited regarding the degree of increase of pest control efficiency corresponding to the increase in numbers, however. More field-scale research is needed to determine the role that carabids could play in pest control under conservation tillage systems.

While a review of insect pests is beyond the scope of this paper on soil biology and tillage systems, the predacious macrofauna discussed above have a role in regulating some of these pests (Cochran et al., 1994). A review of 45 studies of tillage and invertebrate pests (Stinner and House, 1990) showed that of the 57 arthropod pest species represented in the studies, 28% of the species and their associated crop damage increased with decreasing tillage, 29% showed no change with tillage systems, and 43% showed decreases with decreased tillage.

3.5. *Earthworms*

Earthworms are a significant part of the macrofauna in many soils, affecting soil properties and processes through their feeding, casting, and burrowing activities. Earthworms will be discussed in more detail in this paper than some of the other groups of organisms, as an example of the types of processes and interactions that may be important in reduced tillage systems. Much of the general information about earthworm biology and ecology can be found in books by Edwards and Lofty (1977) and Lee (1985). Studies on earthworm ecology, their responses to tillage practices, and their impacts on soil nutrient cycling, structure formation, and microbial interactions are reviewed in two recent books (Hendrix, 1995; Edwards, 1998).

Although there are thousands of species of earthworms in the world, terrestrial earthworms are often categorized into three major behavioral groupings: litter-dwellers (epigeic), shallow soil-dwellers (endogeic), and deep-burrowers (anecic) (Bouché, 1977 as described by Lee, 1995). The litter-dwellers live in the litter layer of a forest, e.g., and are often absent from agricultural fields. The shallow-dwelling earthworms live primarily in the surface 30 cm of the soil, although they may move to deeper layers during summer (aestivation) and winter (hibernation) resting phases. They generally do not construct permanent burrows, but rather they burrow throughout the topsoil, ingesting mineral soil and plant residues in the process. The deep-burrowing species build large, vertical, permanent burrows that may extend 1–2 m deep or more. The predominant deep-burrowing species in northern temperate climates, *Lumbricus terrestris*, pulls plant residues down several centimeter into the opening of its burrow, where it feeds on it after some initial softening or microbial decomposition. *L. terrestris* also may form ''middens'', or small mounds of castings and residues, over the mouth of their burrow (Kladivko, 1993). These middens may be localized ''hot spots'' of microbial activity affecting organic matter and nutrient cycling, pesticide sorption and degradation (Akhouri et al., 1997), and other processes, but little research has focused on these structures which are quite common in some no-till fields (Kladivko et al., 1997; Schmidt, 1997).

Tillage and other soil management practices affect earthworm populations by affecting food supply (amount, quality, location), mulch protection (affects soil water and temperature) and chemical environment (fertilizers and pesticides). This review focuses on the first two aspects of tillage practices, and readers are referred to Lee (1985) for discussion of pesticide impacts on earthworms. By considering how the first two factors are changed under different management systems, one can often predict the general effects on earthworm populations for systems that have not been studied.

Earthworm populations are almost always higher under no-till than under CN practices (Wardle, 1995). Numerous examples from research plots (Barnes and Ellis, 1979; Edwards and Lofty, 1982; Mackay and Kladivko, 1985; House and Parmelee, 1985) and producers' fields (Table 1) support the conclusion that reduction of tillage intensity encourages earthworm populations. Moldboard plowing and no-till represent the two extremes of tillage systems, and systems with intermediate levels of soil disturbance and surface residue usually have populations intermediate between the two extremes. In no-till systems, the residues on the soil surface are available as a food supply to the earthworms for a longer period of time

Table 1
Total number of shallow-dwelling earthworms, and evidence of *L. terrestris* activity under 14 no-till and conventional tillage sites in Indiana and Illinois, sampled in April, 1992 (adapted from Kladivko et al., 1997)

Site No.	Years no-till	Texture[a]	Drainage[b]	Earthworms (m^{-2})[c]		*L. terrestris* middens present?	
				NT	CN	NT	CN
5	9	SiL	SPD	159	63	Yes	No
6	7	SiL	SPD	58	29	Yes	Yes
7	6	SL	WD	41	39	No	No
8	2	SiL	WD	2	16	No	No
9	3	SiL	WD	39	70	Yes	Yes
10(1)	7	L	SPD	27	26	No	No
10(2)	ND	SL	MWD	24	50	Yes	Yes
11	6	SiCL	PD	168	107	Yes	No
12	8	SiL	SPD	296	115	No	No
13	7	SiCL	PD	343	35	Yes	No
15(1)	17	SiL	SPD	259	119	Yes	No
15(2)	12	SiL	SPD	170	19	Yes	No
15(3)	8	SiCL	PD	109	16	Yes	No
20	9	SiCL		237	196	No	No

[a] L: loam, SL: sandy loam, SiL: silt loam, SiCL: silty clay loam.
[b] PD: poorly drained, SPD: somewhat poorly drained, MWD: moderately well drained, WD: well drained.
[c] NT: no-till, CN: conventional.

than if the residues are incorporated with a tillage implement. In addition, the surface residues serve as a mulch and slow the rate of soil drying in late spring and freezing in late autumn. This can lengthen the active periods for the earthworms, allowing them to feed and reproduce a little longer in both spring and autumn. Surface residue also gives the earthworms more time to acclimate to the summer or winter and move down into their resting state. No-till is even more important for deep-burrowing species than for shallow-dwelling earthworms. Because the deep-burrowers feed primarily on residues at the surface, pulling them into their permanent burrows, a clean-till system is not conducive to deep-burrowers. The surface food supply is not present in plowed soils, and the top portion of the permanent burrow must be reformed after any tillage operation. Although a few deep-burrowers may be present in plowed fields, often they will not be present at all.

The diversity of earthworms at any site is relatively low. Lee (1995) summarized findings from a wide variety of locations and vegetation types, which showed between one to 15 species but more commonly two to five per site. Lee (1995) suggested that looking at functional groups, rather than species, might be a better way to assess earthworm diversity at a site. For example having one species from each of the three functional groups (epigeic, endogeic, anecic) may be more beneficial than having three species all from one group. The concepts of redundancy and ecological plasticity may apply to earthworm populations, particularly in agricultural fields. While European grasslands may have up to 15 earthworm species, the two or three species present in New Zealand soils appear to occupy all the niches available (Lee, 1995). The earthworms in New Zealand are apparently exhibiting plasticity of behavior, and will modify and expand their behavior to include some aspects of all three functional groups. Thus, the typically endogeic species will also feed on dead plant material and animal dung on the soil surface, and deposit casts both within the soil and at the surface. Although this type of assessment of apparent "redundancy" may be helpful for devising management practices for earthworms and other soil biota, Lee (1995) also cautions that this concept is limited by our anthropocentric view of the function or "usefulness" of any particular species in a particular ecosystem.

When earthworms are present in sufficient numbers, they can have significant impacts on soil properties and processes. The deep, vertical burrows of *L. terrestris* can increase water infiltration and root growth, while the shallow burrows of endogeic species generally increase the porosity of the topsoil (Edwards and Shipitalo, 1998). The effects of earthworm feeding and casting on soil aggregation varies with earthworm species, the type of food source, and many soil and environmental factors, but often the presence of earthworms contributes to formation and maintenance of stable soil structure (Tomlin et al., 1995). Earthworms are also important for mixing plant residues and other materials into the soil, which may be particularly important in no-till systems due to lack of mechanical mixing by tillage implements (House and Parmelee, 1985).

The impacts of earthworms on nutrient cycling, microbial activity, and organic matter decomposition and stabilization are quite complex. Earthworm casts are usually higher in carbon, available nutrients, and microbial populations than the surrounding mineral soil, because they contain a mixture of mineral soil and partially decomposed organic materials (Blair et al., 1995; Edwards et al., 1995). Populations of many microorganisms are increased during gut passage, although some organisms may be decreased. Although freshly deposited casts may have higher microbial activity and carbon dioxide evolution than surrounding soil, microbial activity often declines with time, and carbon may be stabilized by the close association of carbon and clay minerals. Blair et al. (1995) stress that the age of the casts, along with the earthworm species, soil type, and food source, all affect the experimental results.

The interactions of earthworms with other soil invertebrates is an area that requires much more study. As discussed by Blair et al. (1995), few studies have assessed the effects of earthworms on both other soil fauna and the soil microorganisms at the same time. Changes in the soil decomposer community induced by earthworms may have significant impacts on nutrient cycling processes, particularly in reduced tillage systems, and may be an area for fruitful manipulation by agriculturalists.

The earthworm communities of agricultural soils in New Zealand and the glaciated region of North America, are examples of large-scale introductions of non-native species. As discussed by Reynolds (1977, pp. 116–117) and Lee (1995), the glaciated regions of North America are thought to have been devoid of earthworms at the beginning of European settlement. As European settlers came to North America and brought various plants with them, the European lumbricid earthworms were apparently accidentally introduced as well. The common species in agricultural fields in much of North America are now the common European lumbricids.

European lumbricids have also been intentionally introduced into New Zealand pasture soils for decades. Observations by a farmer in 1940s led Stockdill (1966, 1982) to study introductions of *Aporrectodea caliginosa* into pasture soils (Lee, 1985, 1995). Pasture productivity increased as a result of earthworms breaking down the dead root mat and increasing the infiltration rate on these soils. Commercial machinery exists to harvest turfs from pastures with high earthworm populations and to distribute those turfs in fields without earthworms (Lee, 1995). Although these results are from pasture soils, they suggest that incorporation and mixing of surface residues into the soil profile by earthworms may be important benefits in no-till cropping systems as well.

In southern Australia, Baker (1998) found improved nutrient availability and improved pasture and crop production from the presence of the common European lumbricids *A. caliginosa* or *A. trapezoides*. Baker (1998) suggests that management practices such as reduced tillage and stubble management, be used to enhance earthworm populations where they are currently present. He also comments that distribution of the anecic species *A. longa* is currently very patchy, but that it has been shown to further increase pasture production above the level achieved with the endogeic species *A. caliginosa* alone. This suggests that no-till cropped fields might also be improved by a wider distribution of *A. longa* in Australia.

The topic of earthworm introductions has become of great interest to many farmers using no-till in parts of the US "Cornbelt." This region is characterized by large fields devoted to corn (*Zea mays* L.) and soybean (*Glycine max*) rotations, without growth of hay crops or use of manures. In conventionally tilled fields, *L. terrestris* is often absent. When farmers change tillage practices from moldboard plow or some intermediate form of tillage to no-till, the shallow-dwelling earthworm populations usually increase within several years, but the deep-burrowing species *L. terrestris* may or may not reappear in large numbers in the field (Table 1) (Kladivko et al., 1997). Many farmers are convinced that *L. terrestris* are important for water infiltration and drainage in no-till fields, and they are anxious to encourage repopulation of their fields by these deep-burrowers. One hypothesis concerning the lack of return of *L. terrestris* to some no-till fields, has been that *L. terrestris* may not have survived the many years of CN on these fields, due to its greater sensitivity to tillage disturbance and litter burial and its slower reproductive rate. Once no-till has begun, the shallow-dwelling earthworm populations are able to increase quickly, but *L. terrestris* may have no resident population from which to begin. They may colonize from adjacent edges of undisturbed vegetation, but these "edges" are limited for many large fields in this region. Thus the limit to reestablishing viable *L. terrestris* populations may be the limited source area from which colonization can take place. In this case, introduction of *L. terrestris* at various locations within the field, may provide a source for further colonization of the field (Kladivko, unpublished data).

The role of earthworms in tropical agroecosystems has received intensive study over the past few decades, and recent results of large, interdisciplinary studies are compiled in a book by Lavelle et al. (1999). Fragoso et al. (1999a,b) suggest that in contrast to temperate agricultural systems, in the tropics it appears that exotic species are not the only important species in the system. They contend that earthworm communities rather than individual species, should be the focus of management efforts. Brown et al. (1999) show significant increases in plant growth due to earthworm inoculations in 72% of the studied cases, with the effects varying with earthworm species, plant species, and soil type. Beneficial impacts included enhanced microbial activity, nutrient availability, and rhizosphere processes (Brown et al., 1999) as well as larger-scale improvements in soil physical properties (Blanchart et al., 1999).

4. Overall food web responses to tillage

Summarizing the foregoing sections on different organisms, the overall response is that most organism groups have greater abundance or biomass in no-till than in CN systems. Tillage generally has greater negative impacts on large organisms than on smaller organisms (Fig. 3), suggesting that responses to tillage are scale-dependent (Wardle, 1995). The larger organisms appear to be more sensitive to physical disruption, abrasion by the tillage operation itself, and the loss of surface residues than are the smaller organisms. Although a reduction in populations of smaller organisms can have a bottom-up effect on larger organisms, the habitat modification from litter burial and physical disturbances appears to be of greater significance for determining the population of larger organisms. Therefore intensive tillage often severely limits the actions of the litter transformers and the ecosystem engineers in the soil. Wardle (1995) also found a greater variability of response to tillage as organism size increased (Fig. 3), suggesting that their responses are less predictable than those of smaller organisms. This may be related to variations in the timing of field operations as well as the degree of physical disturbance and litter burial in different studies.

Data on several taxonomic groups were too limited for Wardle (1995) to include in the correlation of organism size and the change index *V*, but it appears that several mesofaunal groups may respond positively to tillage. The enchytraeids and the astigmatid mites were found to increase with tillage. Wardle (1995) suggested these groups have high reproductive rates and are able to colonize quickly, but would be reduced by competition from other mesofauna once a system remains untilled for some time.

The index of change discussed above was calculated at the level of functional groups or major

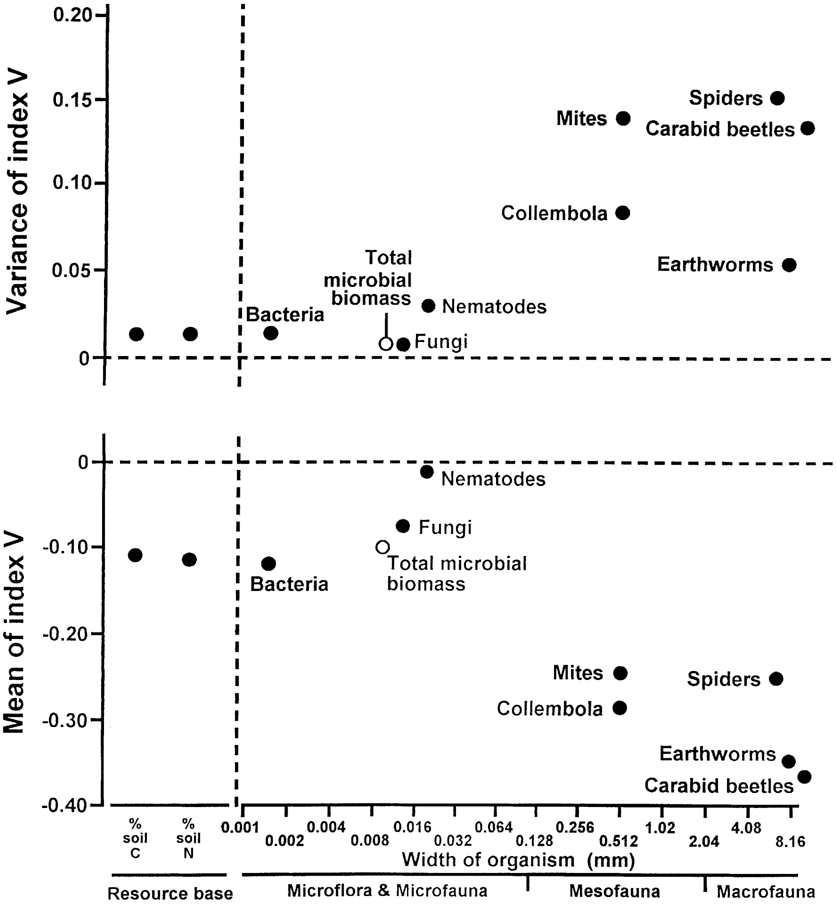

Fig. 3. Variance and mean of the index *V* (as described in text) for the studies compiled in Fig. 2, plotted against mean organism width (width derived from Swift et al., 1979) (reprinted from Wardle, 1995).

taxonomic entities (Wardle, 1995). However, a wide range of taxonomic species are contained within each functional group, and they may respond differently to tillage. Wardle (1995) also calculated diversity indexes for each taxonomic group represented in 20 reviewed studies. When comparing CN to NT, there was a relationship between the diversity at the species assemblage level and the mean organism size. Diversity of microfauna was relatively unaffected by tillage, but the macrofauna showed a wide range of response with diversity sometimes increasing and sometimes decreasing. The current unpredictability of the effects of tillage on macrofauna diversity, may be due in part to different levels of disturbance (Wardle, 1995) as well as timing of tillage operations, compared to the life cycles of the fauna and the timing of field sampling. As noted by Samu et al. (1999) for spiders, intermediate levels of disturbance sometimes increase the diversity of a spider community, presumably by increasing the diversity of microhabitats.

5. Importance of organisms in no-till systems

By definition, no-till systems have less mechanical mixing of crop residues into the mineral soil than do CN systems. From that standpoint, the no-till systems are a little more like undisturbed natural ecosystems (House and Parmelee, 1985; Wardle, 1995) and may depend more on soil organisms for proper functioning. When there is no mechanical loosening of soil or mixing of soil and residues, the actions of the ecosystem engineers and the litter transformers may become much more important than in systems disturbed and mixed by a moldboard plow. Interdisciplinary research is needed on ways to stimulate optimal populations and activity under no-till and other reduced tillage systems, and to document the quantitative impacts of the soil faunal and microbial communities on nutrient cycling, organic matter decomposition and retention, and soil physical properties and processes.

6. Challenges for tillage researchers

Although the relative importance of soil mesofauna and macrofauna in agricultural systems is not well understood, in general it appears to be beneficial to have larger populations and perhaps increased diversity of faunal groups present in a field. Given this premise, there are a number of research areas that need interdisciplinary efforts.

6.1. Design of tillage and planting equipment

When designing or modifying tillage and planting equipment, the primary goal is usually to prepare an adequate seedbed for germination and growth of the crop. Other objectives may include leaving a rough surface or adequate residue cover for erosion control, or burial of crop residues for pest control, depending on the system. If the enhancement of soil faunal populations is also a goal, what would the design objectives be? From the data currently available, it appears that the main objectives would probably be to (a) leave as much surface residue cover as possible, and (b) do as little physical disruption (tillage) as possible. On soils where intermediate levels of tillage are desirable from an agronomic viewpoint, residue cover may be more important for soil faunal populations than the amount of soil disturbance. Tillage or planting equipment that loosens the soil but leaves most of the residue on the soil surface, may be the best. Systems such as strip-tillage, where a fine seedbed is prepared in a narrow strip but the remainder of the soil is left covered and undisturbed, may also provide benefits. These latter systems might actually provide greater spatial heterogeneity of habitats on a small-enough scale to enhance faunal diversity, as suggested by Samu et al. (1999) for spiders. There is also some evidence that low levels of weeds in a field may contribute to greater numbers and diversity of fauna. Evaluation of different levels of residue cover, physical disruption, and spatial arrangement of plants and residues on soil organisms, plant growth, and soil physical conditions would be a fruitful area for interdisciplinary research.

6.2. Characterization of the tillage zone

When characterizing the tillage zone in tillage research studies, it would be helpful to document factors that affect soil faunal populations and activity. Measurements should include the percent of the soil surface covered by residue and the mass of residue, as well as perhaps some measurement of the spatial distribution of the residue (i.e. in strips, or in irregular patches separated by large bare areas, or relatively uniform). Some parameters to characterize the degree of physical disruption from tillage might be the change in bulk density after tillage, macroporosity, the degree of contact or isolation between adjacent large clods of soil, and some assessment of the area of freshly exposed soil surfaces for microbial activity. The resulting sizes and depth distributions of the residues, along with the degree of contact between residues and the mineral soil, would help when studying the overall soil foodweb and the interactions between microorganisms and the soil faunal groups. Soil water and temperature fluctuations also affect populations and activity and could be monitored.

6.3. Soil physical properties

The burrowing, aggregate formation, and mixing activities of soil macrofauna are well known, but additional research is needed on the rate of these processes in the field and the duration of the effects. Is there an optimal soil structure that can be identified for different soil/cropping systems? What level of faunal populations and diversity is needed in different tillage systems, to achieve an optimal structure?

6.4. Nutrient cycling

The effect of more complex soil food webs on the availability, storage, and loss of plant nutrients on a field-scale is a practical application of soil biological research to tillage systems. Most fertilizer recommendations made in modern agricultural systems are based upon research conducted under conventional moldboard plowed systems. In no-till systems with greater presence of soil fauna, nutrient and organic matter cycling differ from when systems include only microorganisms. Soil fauna such as earthworms may increase nitrogen availability over the short-term, e.g., in their casts and mucus secretions, but their longer-term effect on nutrient storage or loss from the system is not known (Blair et al., 1995). The synchronization of release of available nutrients by soil organisms and the crop uptake requirements is a challenge that needs to be addressed (Edwards et al., 1995). In northern temperate climates, e.g., earthworms are most active in the spring and autumn, at a time when summer annual crops are not growing or taking up nutrients. Although the implications of a more complex soil food web for reduced tillage management are not clear, there may be more potential for modification of nutrient release within the multiple trophic levels present in such systems.

6.5. Soil organic matter dynamics

The interactions of soil microorganisms and soil fauna in different tillage systems also have an impact on organic matter cycling. As with nutrient cycling, the net effect of a more complex foodweb on field-scale carbon storage or release is poorly understood. It is not known, e.g., whether the long-term net effect of earthworm activity is to increase organic matter decomposition or to stabilize organic matter through cast formation (Blair et al., 1995). With the great interest in C sequestration as affected by tillage systems, it is essential that the soil faunal communities be included in detailed research studies, along with the microbial component. In addition, many models of crop residue decomposition do not include earthworms or other macrofauna and mesofauna, and this needs to be addressed in models that compare different tillage systems.

6.6. Soil-borne pests

The adoption of conservation tillage is sometimes restricted by concerns about potential increases in certain pests, particularly plant pathogens and insect pests. More interaction of tillage researchers with plant pathologists, entomologists, and soil ecologists is needed, in order to understand the interactions between the detrimental organisms and potential beneficial or antagonist organisms. The complex interactions within a more diverse soil community in no-till may provide protection from the pest organisms, but the time required for this shift in communities may be too long for farmers' economic requirements. Another avenue for study is to look for ways to modify the no-till environment so that plants are less susceptible to stress during their early growth stages. Discussions of specific pest strategies include Bockus and Shroyer (1998) for plant pathogens, Barker and Koenning (1998) for nematodes, and Stinner and House (1990) for insects.

6.7. Sustainable crop production and faunal diversity

There is a great need for studies that assess both the smaller and larger soil organisms at the same time. Especially in no-till systems, the macrofauna and mesofauna can affect the biomass and activity of microorganisms and microfauna, thereby affecting nutrient and organic matter cycling. The role of soil fauna in controlling pest populations is also an area that needs more work. A more complex soil biotic system in no-till, may provide more potential points to modify organism functions without completely eliminating whole groups of organisms.

6.8. Additional research questions

The effects of intermediate tillage systems as well as ‘‘rotational tillage’’ need to be assessed. Many farmers in the US Cornbelt, e.g., may use no-till for soybeans but some intermediate tillage practice for corn. How does this rotation of the tillage practice affect the soil community and its activity? Relatedly, the differences between short-term and long-term no-till, and the time required for soil community shifts to occur, need documentation on sites with different soils, crops, and climate. Are there ways to hasten the development of the more complex soil community, when a farmer changes from conventional to no-till systems? The effects of related management practices such as residue chopping, wheel traffic, cover crops, and intercropping should also be assessed. Finally, the *timing* of measurements should be carefully considered. Soil organisms may respond to season, tillage/planting practice, or short-term weather. Basic knowledge of the life cycles of different organisms and their impact on soil and plant processes is essential when planning sampling and measurement strategies for tillage studies.

7. Conclusions and future research needs

Conversion of agricultural fields from CN practices to no-till or other reduced tillage systems usually stimulates populations of soil fauna and microorganisms. The increased soil moisture and smaller fluctuations in soil temperature under no-till are generally beneficial for microbial activity as well as some of the faunal groups. In addition, the mesofauna and macrofauna groups are sensitive to tillage-induced physical disturbances and the removal of a surface litter layer. These larger organisms may be completely absent or present only in very low numbers in tilled systems, but no-till provides appropriate habitats for their survival. No-till systems may therefore encourage greater biological complexity in agricultural fields and begin to approach the structure of ‘‘natural’’ ecosystems a little more closely than CN fields.

The potential benefits of a more complex biological system within the context of a simplified agricultural system have rarely been explored. While it is often hypothesized or assumed that greater complexity and diversity of the soil community are better, the quantitative benefits of increased faunal populations in no-till systems are not well understood. Research is needed on the interactions among the different groups of organisms at the community level. This is especially true for the interactions between the macrofauna and all other smaller soil organisms within detrital food webs (Wardle, 1995). The impacts of soil macrofauna on multiple functions in the soil, including soil physical properties, organic matter stabilization, and nutrient cycling, require further investigation in linkage with work on smaller soil organisms. The relationship of above-ground biodiversity to below-ground biodiversity needs to be determined, and this information applied to the practical aspects of encouraging optimal levels of below-ground biodiversity within agricultural fields. Relatedly, it would seem useful to define some minimal level of functional diversity that is optimal for no-till soils, and to investigate different methods to achieve such a level. The inclusion of grass strips within fields, intercropping or relay-cropping, or other methods to diversify the field, may be methods that can stimulate a diverse soil fauna and improve overall soil functioning within agricultural systems.

Acknowledgements

The author thanks colleagues Cindy Nakatsu, Tony Vyn, and John Graveel for helpful discussion on an earlier draft of this paper.

References

Akhouri, N.M., Kladivko, E.J., Turco, R.F., 1997. Sorption and degradation of Atrazine in middens formed by *Lumbricus terrestris*. Soil Biol. Biochem. 29, 663–666.

Angers, D.A., Bolinder, M.A., Carter, E.G., Gregorich, E.G., Drury, C.F., Liang, B.C., Voroney, R.P., Simard, R.R., Donald, R.G., Beyaert, R.P., Martel, J., 1997. Impact of tillage practices on organic carbon and nitrogen storage in cool, humid soils of eastern Canada. Soil Till. Res. 41, 191–201.

Baker, G.H., 1998. Recognising and responding to the influences of agriculture and other land-use practices on soil fauna in Australia. Appl. Soil Ecol. 9, 303–310.

Barker, K.P., Koenning, S.R., 1998. Developing sustainable systems for nematode management. Annu. Rev. Phytopathol. 36, 165–205.

Barnes, B.T., Ellis, F.B., 1979. Effects of different methods of cultivation and direct drilling and disposal of straw residues on populations of earthworms. J. Soil Sci. 30, 669–679.

Beare, M.H., Coleman, D.C., Crossley Jr., D.A., Hendrix, P.F., Odum, E.P., 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. Plant and Soil 170, 5–22.

Behan-Pelletier, V.M., 1999. Oribatid mite biodiversity in agroecosystems: role for bioindication. Agric. Ecosyst. Environ. 74, 411–423.

Blair, J.M., Parmelee, R.W., Lavelle, P., 1995. Influences of earthworms on biogeochemistry. In: Hendrix, P.F. (Ed.), Earthworm Ecology and Biogeography in North America. Lewis Publishers, Boca Raton, FL, pp. 127–158.

Blanchart, E., Albrecht, A., Alegre, J., Duboisset, A., Gilot, C., Pashanasi, B., Lavelle, P., Brussaard, L., 1999. Effects of earthworms on soil structure and physical properties. In: Lavelle, P., Brussaard, L., Hendrix, P. (Eds.), Earthworm Management in Tropical Agroecosystems. CABI Publishing, New York, pp. 149–172.

Bockus, W.W., Shroyer, J.P., 1998. The impact of reduced tillage on soilborne plant pathogens. Annu. Rev. Phytopathol. 36, 485–500.

Bouché, M.B., 1977. Stratégies lombriciennes. In: Lohm, U., Persson, T. (Eds.), Soil Organisms as Components of Ecosystems. Biol. Bull. (Stockholm) 25, 122–132.

Brown, G.G., Pashanasi, B., Villenave, C., Patron, J.C., Senapati, B.K., Giri, S., Barois, I., Lavelle, P., Blanchart, E., Blakemore, R.J., Spain, A.V., Boyer, J., 1999. Effects of earthworms on plant production in the tropics. In: Lavelle, P., Brussaard, L., Hendrix, P. (Eds.), Earthworm Management in Tropical Agroecosystems. CABI Publishing, New York, pp. 87–147.

Cambardella, C.A., Elliott, E.T., 1992. Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Sci. Soc. Am. J. 56, 777–783.

Cochran, V.L., Sparrow, S.D., Sparrow, E.B., 1994. Residue effects on soil micro- and macroorganisms. In: Unger, P.W. (Ed.), Managing Agricultural Residues. CRC Press, Boca Raton, FL, pp. 163–184.

Edwards, C.A. (Ed.), 1998. Earthworm Ecology. St. Lucie Press, Boca Raton, FL, 389 pp.

Edwards, C.A., Bohlen, P.J., Linden, D.R., Subler, S., 1995. Earthworms in agroecosystems. In: Hendrix, P.F. (Ed.), Earthworm Ecology and Biogeography in North America. Lewis Publishers, Boca Raton, FL, pp. 185–213.

Edwards, C.A., Lofty, J.R., 1977. Biology of Earthworms, 2nd Edition. Chapman & Hall, London, 333 pp.

Edwards, C.A., Lofty, J.R., 1982. Nitrogenous fertilizers and earthworm populations in agricultural soils. Soil Biol. Biochem. 14, 515–521.

Edwards, W.M., Shipitalo, M.J., 1998. Consequences of earthworms in agricultural soils: aggregation and porosity. In: Edwards, C.A. (Ed.), Earthworm Ecology. St. Lucie Press, Boca Raton, FL, pp. 147–161.

Follett, R.F., 2001. Soil management concepts and carbon sequestration in cropland soils. Soil Till. Res., 61, 77-92.

Fragoso, C., Kanyonyo, J., Moreno, A., Senapati, B.K., Blanchart, E., Rodriguez, C., 1999a. A survey of tropical earthworms: taxonomy, biogeography and environmental plasticity. In: Lavelle, P., Brussaard, L., Hendrix, P. (Eds.), Earthworm Management in Tropical Agroecosystems. CABI Publishing, New York, pp. 1–26.

Fragoso, C., Lavelle, P., Blanchart, E., Senapati, B.K., Jimenez, J.J., Martinez, M.A., Decaens, T., Tondoh, J., 1999b. Earthworm communities of tropical agroecosystems: origin, structure and influence of management practices. In: Lavelle, P., Brussaard, L., Hendrix, P. (Eds.), Earthworm Management in Tropical Agroecosystems. CABI Publishing, New York, pp. 27–55.

Franzluebbers, A.J., Arshad, M.A., 1996. Soil organic matter pools during early adoption of conservation tillage in northwestern Canada. Soil Sci. Soc. Am. J. 60, 1422–1427.

Haynes, R.J., 1999. Size and activity of the soil microbial biomass under grass and arable management. Biol. Fertil. Soils 30, 210–216.

Hendrix, P.F. (Ed.), 1995. Earthworm Ecology and Biogeography in North America. Lewis Publishers, Boca Raton, FL, 244 pp.

Hendrix, P.F., Parmelee, R.W., Crossley Jr., D.A., Coleman, D.C., Odum, E.P., Groffman, P.M., 1986. Detritus food webs in conventional and no-tillage agroecosystems. BioScience 36, 374–380.

House, G.J., Parmelee, R.W., 1985. Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. Soil Till. Res. 5, 351–360.

Karlen, D.L., Wollenhaupt, N.C., Erbach, D.C., Berry, E.C., Swan, J.B., Eash, N.S., Jordahl, J.L., 1994. Long-term tillage effects on soil quality. Soil Till. Res. 32, 313–327.

Kladivko, E.J., 1993. Earthworms and crop management. Purdue University Cooperation Extension Service, West Lafayette, IN, pp. 1–5.

Kladivko, E.J., Akhouri, N.M., Weesies, G., 1997. Earthworm populations and species distributions under no-till and conventional tillage in Indiana and Illinois. Soil Biol. Biochem. 29, 613–615.

Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agric. Ecosyst. Environ. 74, 187–228.

Lavelle, P., 1997. Faunal activities and soil processes: adaptive strategies that determine ecosystem function. In: Begon, M., Fitter, A.H. (Eds.), Advances in Ecological Research. Academic Press, New York, pp. 93–132.

Lavelle, P., 2000. Ecological challenges for soil science. Soil Sci. 1651, 73–86.

Lavelle, P., Brussaard, L., Hendrix, P. (Eds.), 1999. Earthworm Management in Tropical Agroecosystems. CABI Publishing, New York.

Lee, K.E., 1985. Earthworms: Their Ecology and Relationships with Soils and Land Use. CSIRO, Sydney, Australia, 411 pp.

Lee, K.E., 1995. Earthworms and sustainable land use. In: Hendrix, P.F. (Ed.), Earthworm Ecology and Biogeography in North America. Lewis Publishers, Boca Raton, FL, pp. 215–234.

Logan, T.J., Lal, R., Dick, W.A., 1991. Tillage systems and soil properties in North America. Soil Till. Res. 20, 241–270.

Mackay, A.D., Kladivko, E.J., 1985. Earthworms and the rate of breakdown of soybean and maize residues in soil. Soil Biol. Biochem. 17, 851–857.

Reeves, D.W., 1997. The role of soil organic matter in maintaining soil quality in continuous cropping systems. Soil Till. Res. 43, 131–167.

Reynolds, J.W., 1977. The Earthworms of Ontario. Royal Ontario Museum, Toronto, 141 pp.

Samu, F., Sunderland, K.D., Szinetár, C., 1999. Scale-dependent dispersal and distribution patterns of spiders in agricultural systems: a review. J. Arachnol. 27, 325–332.

Schmidt, B., 1997. Size and spatial distribution of *Lumbricus terrestris* middens in no-till fields. M.S. Thesis. Purdue University, 73 pp.

Stinner, B.R., House, G.J., 1990. Arthropods and other invertebrates in conservation-tillage agriculture. Annu. Rev. Entomol. 35, 299–318.

Stockdill, S.M.J., 1966. The effect of earthworms on pastures. Proc. NZ Ecol. Soc. 13, 68–75.

Stockdill, S.M.J., 1982. The effects of introduced earthworms on the productivity of New Zealand pastures. Pedobiologia 24, 29–35.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley, 372 pp.

Tomlin, A.D., Shipitalo, M.J., Edwards, W.M., Protz, R., 1995. Earthworms and their influence on soil structure and infiltration. In: Hendrix, P.F. (Ed.), Earthworm Ecology and Biogeography in North America. Lewis Publishers, Boca Raton, FL, pp. 159–183.

Wander, M.M., Bidart, M.G., Aref, S., 1998. Tillage impacts on depth distribution of total and particulate organic matter in three Illinois soils. Soil Sci. Soc. Am. J. 62, 1704–1711.

Wardle, D.A., 1995. Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. In: Begon, M., Fitter, A.H. (Eds.), Advances in Ecological Research, Vol. 26. Academic Press, New York, pp. 105–185.