Soil & Tillage Research 111 (2010) 33–40

Contents lists available at ScienceDirect

Soil & Tillage Research

journal homepage: www.elsevier.com/locate/still

Review

Tillage and soil ecology: Partners for sustainable agriculture

Jean Roger-Estrade [a,b,*], Christel Anger [b], Michel Bertrand [b], Guy Richard [c]

[a] AgroParisTech, UMR 211 INRA/AgroParisTech., Thiverval-Grignon, 78850, France
[b] INRA, UMR 211 INRA/AgroParisTech. Thiverval-Grignon, 78850, France
[c] INRA, UR 0272 Science du sol, Centre de recherche d'Orléans, Orléans, 45075, France

A R T I C L E I N F O

Keywords:
Tillage
Soil ecology
Agroecosystems
Soil biota
No tillage
Plowing

A B S T R A C T

Much of the biodiversity of agroecosystems lies in the soil. The functions performed by soil biota have major direct and indirect effects on crop growth and quality, soil and residue-borne pests, diseases incidence, the quality of nutrient cycling and water transfer, and, thus, on the sustainability of crop management systems. Farmers use tillage, consciously or inadvertently, to manage soil biodiversity. Given the importance of soil biota, one of the key challenges in tillage research is understanding and predicting the effects of tillage on soil ecology, not only for assessments of the impact of tillage on soil organisms and functions, but also for the design of tillage systems to make the best use of soil biodiversity, particularly for crop protection. In this paper, we first address the complexity of soil ecosystems, the descriptions of which vary between studies, in terms of the size of organisms, the structure of food webs and functions. We then examine the impact of tillage on various groups of soil biota, outlining, through examples, the crucial effects of tillage on population dynamics and species diversity. Finally, we tackle the question of the design of tillage systems to enhance biological control in cultivated fields. Identification of the optimal tillage system requires a global consideration of soil management, rather than an analysis focusing on tillage alone, taking into account soil ecology. Organic residue management, the prevention of compaction, crop rotation and the timing of cultivation must all be considered together, taking into account their impact on pest populations and on the natural enemies of pests and ecosystem engineers. This approach requires more detailed research and careful experimental design than traditional comparisons of conventional and reduced tillage systems. We propose the development of population modeling in cultivated fields, as the available ecological models rarely include parameters linked to the soil management system.

Contents

* Corresponding author at: INRA, UMR 211 INRA/AgroParisTech. Thiverval-Grignon, 78850, France. Tel.: +33 130815412; fax: +33 130815425.
E-mail address: estrade@grignon.inra.fr (J. Roger-Estrade).

0167-1987/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.still.2010.08.010

1. Introduction

Soil is the most diverse and important ecosystem on the planet. A tremendous number of biological processes continually active in soils are of crucial importance for the maintenance of other ecosystems in the continental biosphere. Most of the biodiversity of agroecosystems lies in the soil (Young and Crawford, 2004), and the functions performed by soil biota have large, direct and indirect effects on crop growth and quality, soil and residue-borne pests, disease incidence, the quality of nutrient cycling and water transfer and the sustainability of soil productivity. They also determine the resistance and resilience of agroecosystems to abiotic disturbance and stress (Brussaard et al., 2007).

The rationale of sustainable crop management systems is based on the achievement of multicriterion objectives: crop yield is only one of a number of factors to be considered when evaluating the functioning of a crop management system. Consequently, the soil is no longer seen purely as a medium for plant growth, but also as a habitat for a number of organisms. A fundamental consequence of this change in approach is that ecological concepts and theories are now required for the design of new tillage systems, together with a knowledge of soil science, agronomy, ecophysiology and soil mechanics.

Farmers use tillage, consciously or inadvertently, to manage soil biodiversity. However, several literature reviews (e.g. House and Parmelee, 1985a,b; Stinner and House, 1990; Kladivko, 2001; Lakshman et al., 2006; Miura et al., 2008) have highlighted the difficulties involved when trying to identify trends concerning the effect of tillage on soil biota. The identification of keys to help us to understand and predict the relationships between tillage regime and soil ecology therefore remains an important challenge in tillage research. When taking up this challenge, two key points must be addressed.

1. Firstly, improvements in the assessment of the impact of tillage on soil organisms and functions are required. Unlike above-ground biodiversity, soil biodiversity can mostly be managed only indirectly, through tillage and other cropping practices (crop rotation, organic and mineral fertilization), complicating the design of new crop management systems.
2. Secondly, we need to determine which tillage systems make the best use of soil biodiversity. Given the large number of functions of soil biota, we require biodiversity to fulfill many services, and tillage must be designed such that those services are optimized, even if the intrinsic value of soil biodiversity is, in many cases, difficult to assess (Brussaard et al., 2007).

This paper will focus on these two points, after a short presentation of the conceptual framework for soil biota studies. We will not deal here with weed control by tillage, focusing only on the soil microflora and fauna and the biological control of crop pests.

2. The soil ecosystem

2.1. Diversity of soil biota

The complexity of soil biota may be characterized in several ways, the most commonly used method being based on organism size. Excluding plant roots, soil biota consist of the soil microflora (bacteria, fungi, green algae, etc.) and the soil fauna. The soil fauna is also usually divided into three groups, on the basis of mean organism size and adaptation to life in either the water-filled pore space or the air-filled pore space (Cochran et al., 1994; Lavelle, 2000). The organisms of the soil microfauna are generally less than 0.2 mm long. This group consists mostly of protozoa and nematodes, predominantly living in the water-filled pore space. The mesofauna consists of organisms 0.2–2 mm in length, living in the air-filled pore space of the soil and within the litter. The mesofauna includes microarthropods (e.g. acarids, springtails) and enchytraeid worms (small Oligochaeta). The macrofauna consists of individuals more than 2 mm in length, including termites, earthworms and large arthropods.

Soil biota may also be described through the structure of soil food webs (Moore, 1994). For instance, considering the detritus microfoodweb, the microflora and microfauna break down the organic matter. The protozoa, nematodes and microarthropods forage on fungi and bacteria and have their own predators, which in turn serve as a food resource for organisms at higher levels. This approach to studying soil biota highlights the importance of cultivated areas for biodiversity conservation: organisms living in agricultural soils are part of larger food webs, serving as a reservoir of food for animals belonging to higher orders in the food web. For instance, in organic rice-based cropping systems, recent studies have shown that spiders depend on detritivores for food during fallow periods (Sidsgaard, 2000). It has been suggested that, given the low prey quality of pest species, alternative preys serve as important food supplement for spiders and other beneficial organisms. Thus, changes in crop management practices, such as direct drilling, mechanization or the replacement of manual weed control by chemicals, may have a significant impact on spiders and other beneficial organisms.

It is also possible to classify soil organisms according to their function. For instance, considering the role of soil fauna in nutrient cycling in agro-ecosystems, Lavelle (1997) suggested classifying invertebrates into three functional groups, based on the nature of their relationship with the microflora and their ability to create various structures. The first functional group defined consists of the organisms of the aforementioned *microfoodweb*, corresponding to the part of the general soil foodweb linking microorganisms to their predators. This group corresponds principally to the part of the microfauna predating on bacteria and fungi, and their predators. These organisms create no structures. The second functional group consists of the mesofauna and large arthropods and was described by Lavelle as *litter transformers*. These organisms ingest purely organic material, physically fragmenting the litter and releasing fecal pellets with an important role in microbial activity ("external rumen digestion", Aira et al., 2003). These digestion processes release nutrients, which may subsequently be reabsorbed by the decomposers. The fecal pellets are also involved in the stabilization of soil structure and aggregation (Balesdent et al., 2000). The final functional group consists of *ecosystem engineers*, most of which are members of the macrofauna: earthworms (endogeic and anecic species), termites and ants. These organisms create diverse organomineral structures and interact with microorganisms through an internal rumen-type digestion. They alter the physical and chemical conditions in the soil, modifying the flow of water and nutrients, thereby indirectly affecting the growth and development of other living organisms, including the crop, in particular. Ecosystem engineers not only contribute to soil aggregation by releasing fecal pellets and casts, they also make a major contribution to soil structure, by creating nests or digging burrows, thereby affecting air, water and nutrient transfers and root development and function.

These different ecological groups exert several functions in the soil, thereby controlling the efficiency of several ecosystem services (e.g. the capacity of the soil to degrade pesticides (Holtze et al., 2008), the biological control of numerous pathogens (Bailey and Duczek, 1996) and nutrient cycling (Sooksa-nguan et al., 2009)).

2.2. Complexity of the soil habitat

The soil biota lives in a complex structure, the mineral and organic components of which determine habitat conditions and the availability of food resources. As a physical habitat, soil is characterized by spatial and temporal heterogeneities, whatever the measurement scale used (Young and Ritz, 2000). The geometric characteristics of the pore space (size distribution, connectivity) are of crucial importance for the biochemical processes governing life in the soil. Porosity and the extent to which the pores are saturated and connected depend on and affect abiotic and biotic conditions. The structural heterogeneity of the soil is a key element underlying the diversity of the soil biota. Indeed, it has an exceptional potential for niche partitioning, resource and habitat specialization. This key soil characteristic makes it possible for several functional groups to co-exist in the soil. The soil thus provides a habitat for a vast array of small and large organisms residing permanently or temporarily within it.

As highlighted by Young and Crawford (2004), the structure of the pore system in a cultivated field is determined not only by the chemical nature of the material and the action of climate, but also by life itself (roots, fauna, and tillage). In addition to weathering, the activity of soil organisms causes the movement of organic and inorganic materials in the soil profile, thereby contributing to the formation and stability of soil structure.

Moreover, although crop rotation and the application of organic fertilizers determine the nature and amount of fresh organic matter provided annually to the soil biota, the distribution of this organic matter within the soil profile depends on the tillage regime. Thus, tillage affects not only the amount of organic matter available as a trophic resource for soil biota, but also its arrangement and utility as a shelter for numerous soil organisms, pathogens or natural enemies of pests.

3. Effects of tillage on soil ecology

Tillage induces significant biophysical and biochemical changes, of various intensities, over short time scales. In addition to disturbing the soil habitat, it also has a direct effect on the organisms themselves, by killing or injuring them or exposing them to the risk of predation (Fig. 1). Tillage also modifies the relationships between soil organisms within the soil ecosystem, with changes in tillage regime affecting species dominance, relative population size and the diversity of communities (Altieri, 1999). This may have detrimental effects (e.g. rapid expansion of populations of phytophagous species following the decline of predator populations). However, it may also be highly beneficial in situations in which the new tillage regime favors the predator populations. We will illustrate this below, through the example of the effect of tillage on slug populations (see Section 4.2).

Many studies of the impact of tillage on soil biota have shown that different communities respond differently to tillage regime. However, despite the importance of other elements of crop management systems (organic manure application, crop sequence, pesticide spraying, etc.), it is possible to identify a number of effects specific to tillage. In general, both the abundance and diversity of soil communities increase with decreasing tillage intensity (El Titi, 2003a). However, regardless of the organism considered, responses to tillage regime are highly variable (Kladivko, 2001). Another effect of changes in tillage regime is the major modifications observed in the vertical distribution of organisms when plowing is abandoned. In many studies, the size of the total population per unit soil volume is similar in plowed and unplowed treatments (e.g. for earthworms, Pelosi et al., 2009).

3.1. Tillage and soil microbiology

The effects of tillage regime on the microflora can be illustrated by the case of mycorrhizal fungi (particularly arbuscular mycorrhizae—AM). Several studies (e.g. Jasper et al., 1991; Sujan, 2003; Usuki et al., 2007) have shown that tillage is a major stress factor leading to a decrease in inoculum potential. The fungal hyphae form extended networks in cultivated soils and are activated by contact with the seedlings. These networks are fragmented by tillage, potentially resulting in a loss of cell contents. Moreover, tillage affects fungal sporulation, depositing the propagules at the soil surface, where they are subjected to higher temperatures and stronger antagonist pressure. In no-till fields, the mycorrhizal system is more stable (Souza-Andrade et al., 2003). Moreover, McGonigle and Miller (1993), as cited by Douds et al. (2007),

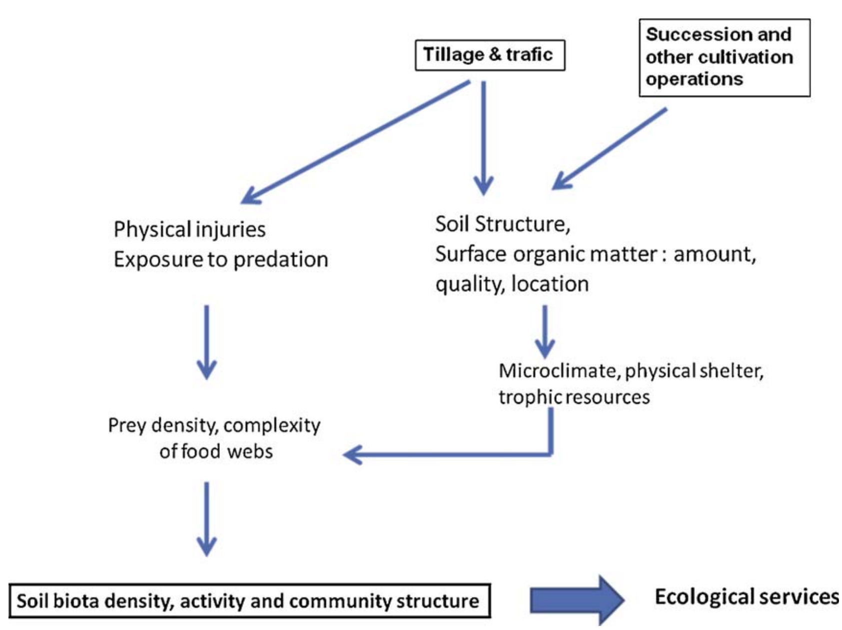

Fig. 1. Effects of tillage on soil ecology.

showed that no-till systems resulted in more extensive root growth with AM, improving the nutrition of maize seedlings early in the growth of the crop. Another interesting experiment showed that increases in aggregate stability were linked to glomalin content, an indicator of the degree of hyphal network development (Wright et al., 1999 in Douds et al., 2007). Tillage exerts a selective pressure on AM fungi communities, with conventional tillage favoring the proliferation of a specific group of species and no-till conditions favoring the proliferation of other species in an environment in which it is possible to establish a more permanent network of external hyphae and colonized roots, increasing the potential infectivity of the soil (De Miranda and de Miranda, 2007).

The main factor determining the size of the microbial component of the microfauna is the availability of carbon and nitrogen resources (Six et al., 2004). Tillage (especially conventional tillage) promotes the release and decomposition of previously protected organic matter, initially increasing soil microbial biomass. However, the long-term effects are less clear, because they depend on the amount of carbon re-injected into the soil each year, to compensate for mineralization (Anderson and Domsch, 1989). When no-till systems are adopted, N availability may decrease temporarily due to an increase in microbial activity in terms of straw decomposition and the absence of residue incorporation into the soil. However, some studies have suggested that there may be a significant long-term increase in the quantity of organic C or microbial biomass throughout the topsoil in various reduced tillage systems (Balesdent et al., 2000; Vian et al., 2009).

Tillage effects are also of crucial importance for other organisms of the microfauna, including the primary consumers in soil nutritional food webs. The effects of tillage on nematode communities have been studied in detail, focusing particularly on plant parasitic nematodes (Minton, 1986), although a growing number of studies (e.g. Lenz and Esenbeis, 2000) are now considering other components of the nematode fauna in the soil food web. This food web is complex, as illustrated in Fig. 2. This may account for the conflicting results published concerning the effects of tillage on nematodes. Nematode density seems to be affected principally by the nature and amount of crop residues. In addition, field studies are difficult to perform, due to the heterogeneous distribution of nematodes in soils. Like many microorganisms, nematodes feeding on bacteria and fungi tend to cluster in pockets of organic matter in the soil, whereas plant-feeding nematodes are distributed within the rhizosphere. Finally, the indirect effects of tillage mediated through soil structure are complex. For instance, changes in porosity exert a selective pressure on nematodes, based on body size (Lenz and Esenbeis, 2000). Furthermore, changes in water availability affect the diversity of nematode communities (Kaya and Gaugler, 1993). A wide range of responses to different types of tillage has thus been reported (see for instance the review of El Titi, 2003a), depending on nature, number or timing of cultivation operations.

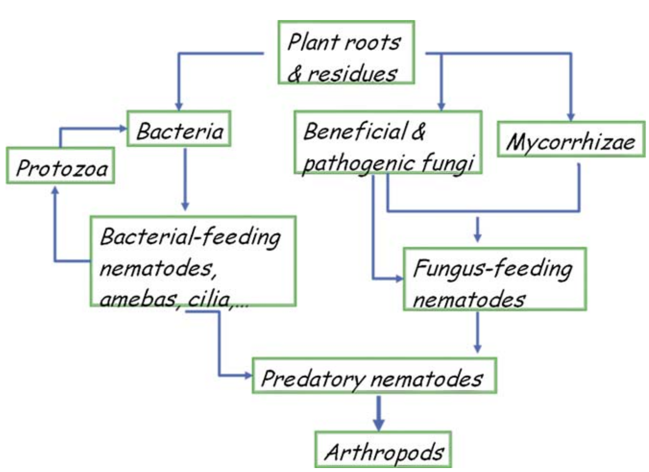

Fig. 2. Simplified diagram of the soil food web (from Holtkamp et al., 2009).

The nematofauna is highly diverse, containing organisms with different feeding habits and reproduction strategies. This diversity was described on a colonizer-persister (cp) scale by Bongers (1999). Nematodes can be assigned to five classes (cp-1 to cp-5), according to their generation time, reproduction rate and tolerance of disturbance. Nematode feeding habits and life-history characteristics are not necessarily correlated. The first two groups (cp-1 and cp-2) may be considered to correspond to colonizer organisms, comparable to r-strategists. The cp-1 group predominates in nutrient-rich conditions, whereas cp-2 is more common in disturbed environments. The other groups are favored by the absence of stress and are more equivalent to persisters or K-strategists. This cp scale is therefore sensitive to the soil management system. Indeed, the impact of disturbance on the below-ground ecosystem is often assessed with the nematode maturity index—based on the proportion of colonizers and persisters in samples (Ivezic et al., 2000; Sanchez-Moreno et al., 2006).

3.2. Tillage effects on the meso- and macrofauna

The effects of tillage on the meso- and macrofauna can be illustrated with earthworm populations, which have been studied in detail. The mechanisms underlying the effects of tillage on earthworm communities are reported in Table 1, with examples of field studies given for each. Earthworm abundance is strongly affected by tillage intensity, particularly when the soil management system includes moldboard plowing, and these effects are mediated by several mechanisms (Chan, 2001). The amount, type and location of organic matter influence the relative sizes of the various ecological groups in the community. Deep tillage, in which the soil is inverted, is not systematically detrimental to all species. Anecic and epigeic species are known to be adversely affected by the incorporation of crop residues into the soil, but endogeic species benefit from the burial of surface organic matter (Nuutinen, 1992). The death of earthworms wounded by the plow, the destruction of earthworm habitats and exposure to predators also affect the abundance of earthworms. A less frequently cited effect of tillage is the negative effect of soil compaction. Larink and Schrader (2000) and Capowiez et al. (2009) have reported that the passage of farm vehicles may directly kill the earthworms located under the wheel tracks. Finally, Boström (1995) showed that 64% of the earthworms present were killed by the rotary harrow used in a Swedish pasture.

Pelosi et al. (2009), in a study of several crop management systems with different levels of productivity, intensities of soil tillage and pesticide use, showed a clear effect of tillage regime on the balance between the various ecological groups: anecic worms were favored by a direct drilling system with a permanent cover-crop maintained throughout the year, whereas endogeic worms tended to be favored by conventional crop management (including pesticide use and plowing) and organic crop management systems (with moldboard plowing).

4. Tillage for the optimal use of soil biodiversity in sustainable agriculture

When trying to develop tillage systems for improving biological control in cultivated fields, the potentially opposite effects of tillage must be considered: intensive tillage, including moldboard plowing, buries the plant residues and consequently destroys

Table 1
Examples of mulching effects on the biological control of insect crop pests.

Mechanism	Experimental conditions	Preys and/or Natural enemies studied		References
		Preys	Predators	
Reduce intra-specific competition between predators	Various types of mulch (residues of straw, corn stalks or paper fiber), incorporated into the soil or applied to the surface, in oats and soybeans crops, Southern Ontario, USA.		Various spider (Arachnidae) species	Manns et al. (2008)
Increase intra-guild predation	Soybean cropped with and without alfalfa (*Medicago sativa* L.) living mulch.	Soybean aphid (*Aphis glycines*, Matsumura)		Schmidt et al. (2007)
	Sunn hemp (*Crotalaria juncea*) and cowpea (*Vigna unguiculata*) organic mulches under turnip (*Brassica rapa*) and lima bean (*Phaseolus lunatus*) crops.	Various root-knot nematode species		Wang et al. (2008)
Increase availability of alternative food for predator	Three types of living mulch with mixed species in cherry orchards in Michigan (USA).		Several arthropod species	Sirrine et al. (2008)
Provide shelter and favorable microclimate for natural enemies	A living mulch (buckwheat, *Fagopyrum esculentum*, Moensch) in a zucchini squash crop in Florida.	Silverleaf whitefly (*Bemisia tabaci*, Gennadius) and Melon aphid (*Aphis gossypii*, Glover)	Various beetle species: *O. nubilalis* (Coleoptera: Carabidae), *Poecilus chalcites*, Say and *Scarites quadriceps*, Chaudior.	Nyoike and Liburd (2010)
	Alfalfa (*Medicago sativa* L.) and kura clover (*Trifolium ambiguum* M. Bieb.) living mulches in a corn–soybean–forage rotation.	European corn borer (*Ostrinia nubilalis*, Hubner)		Prasifka et al. (2006)

pathogens that overwinter in infected residues at the soil surface (Jordan and Hutcheon, 2003). However, the mulches left at the soil surface in no-till systems create stable and favorable conditions for several organisms, including some predators of various pests (Kendall, 2003). Both these aspects must be considered.

4.1. Effects of mulches on predators and biological control

Reduced tillage (with residues left on the soil surface) creates a stable environment, encouraging the development of more diverse species (including decomposers, in particular). A few studies have reported that mulches have no effect (e.g. Szendrei and Weber, 2009), but most studies have shown that, for several crops at least, the presence of permanent mulches increases the diversity of generalist predators, such as ground beetles, spiders and hoverflies (Schmidt et al., 2004; Pullaro et al., 2006).

The mechanisms underlying the positive effects of mulches on pest regulation are diverse. Some examples of field studies are provided in Table 2.

According to Landis et al. (2000), the presence of decomposing organic matter at the soil surface may provide predators with alternative preys when there are no crop pests present in the plot. This would account for the greater abundance of generalist predators in crop management systems including no tillage and direct drilling. Furthermore, some studies have suggested that mulches may disturb prospecting and approach behavior, rendering pests being less efficient at localizing plant hosts, due to physical barriers and the release of allelochemical substances from the decomposing residues (Mabbett, 1991) or living mulch (Finch and Collier, 2000). The structure of the vegetation may also affect the lurking behavior or web attachment of spider species (Rypstra et al., 1999).

However, this general trend does not ensure the systematic effective regulation of pest populations (Symondson et al., 2002). Indeed, although many studies have shown that predator populations increase if a mulch is left at the soil surface, with rare exceptions showing the contrary (e.g. Collins et al., 2002), very few studies have considered whether mulches effectively decrease pest populations. Finally, it is also necessary to determine the balance between a possible positive effects on pest populations and other negative effects (on emergence or the warming of the soil surface in spring).

Table 2
Main mechanisms involved in the effects of tillage on earthworm communities. Examples of field studies.

Mechanism	Description	References
Physical injuries caused by tillage tools	Worms located near the plough pan wounded by the plough share.	Gerard and Hay (1979)
	Earthworms located in the 0–5 cm layer destroyed by rotary harrow	Edwards and Lofty (1975) and Boström (1995).
Compaction	Earthworms avoid compacted zones and could be killed by compaction due to wheels; species are more sensitive to soil compaction when tillage is reduced; species react differently to compaction.	Cuendet (1992), Capowiez et al. (2009), Cluzeau et al. (1992) and Larink and Schrader (2000)
Habitat destruction	Anecic species are more affected by frequent destruction of burrows than endogeic species.	Ivask et al. (2007)
Exposure to frost and dryness	Soil inversion due to ploughing brings cocoons and juveniles to soil surface, where they are destroyed by frost and dryness.	House and Parmelee (1985a,b)
Exposure to predation	Destruction by seagulls immediately after ploughing.	Tomlin and Miller (1988)
Changes in organic matter availability	Crop residue burial at ploughing removes food resources for anecic worms.	Chan (2001)
	Organic matter burial increases the food supply for endogeic worms.	Lee (1985)
	Old crop residues favor *A. caliginosa*	Nuutinen (1992) and Briones and Bol (2003)

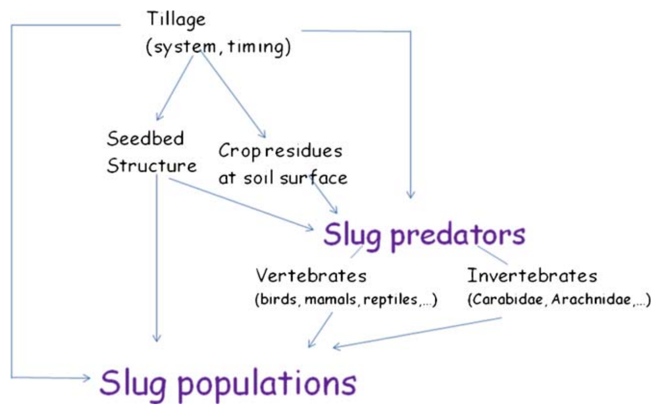

Fig. 3. Effects of tillage and other cultivation techniques on slugs and their enemies.

Thus, mulches should not be seen as the sole alternative solution for pest control. The efficacy of this approach is highly variable, because interactions with other practices and other pests must be taken into account.

4.2. Positive effects of tillage on pest control

Simplified soil cultivation techniques may also favor pest development. Indeed tillage, through its direct action on slug populations and indirect effects on habitat, is an efficient way of controlling slugs. Ploughing buries slug eggs and seed bed preparation also has an important effect, with coarse seed beds favoring slug populations (Chabert and Gandrey, 2005). These effects are summarized in Fig. 3.

Thus, an increase in the slug (e.g. *Deroceras reticulatum*) population is often observed when plowing is abandoned (Mabbett, 1991). This increase may result from a lack of natural enemies, including large ground beetles, due to the generally heavier use of insecticides in no-till systems (Chabert and Gandrey, 2005). Another possible explanation is provided by the so-called "deficiencies in the ecological infrastructure" of tilled fields. When regular plowing ceases, slugs are favored by the presence of crop residues at the soil surface. Indeed, the overabundance of alternative prey, such as springtails, aphids, fly eggs, and larvae, may favor pest populations (Mair and Port, 2002; Symondson et al., 2006).

Tillage has also long been recognized as an efficient way of controlling pathogenic fungi. Phoma stem canker, or blackleg, is one of the most damaging fungal diseases of rapeseed (*Brassica napus* var. *oleifera*) worldwide. The causal fungus (*Leptosphaeria maculans,* asexual stage *Phoma lingam*) can survive saprophytically for several years on rapeseed stubble (Schneider et al., 2006). In autumn, epidemics are initiated by air-borne ascospores released from stubble at the soil surface. Tillage is therefore of crucial importance, determining the vertical distribution of stubble and the production of blackleg primary inoculum from infected residue fragments.

Another example of the positive effects of tillage on pest control is the decrease in the risk of wheat streak mosaic virus infection. This virus spends the summer period on the wheat curl mite (*Aceria tosichella*). This mite takes refuge on wheat volunteers, resulting in the re-infestation of autumn-sown winter wheat. The study by Thomas et al. (2004) provides a good example of the efficacy of tillage for reducing mite populations, thereby preventing infection. Many other examples are provided in the review by El Titi (2003a,b).

4.3. Negative effects of tillage on natural pest enemies

Parasitoid populations are also very sensitive to tillage when they overwinter either in the soil or on crop residues. Tillage has been shown to have a large effect on the survival and emergence rates of parasitoids in the following year (Nilsson, 1994). The timing of tillage has a major effect on predator populations. For instance, House and Rosario-Alzgaray (1989), working on maize, have shown that the diversity of soil arthropod species is greater in no-till systems than in the presence of plowing only during the April–May period. No difference was found during the second part of the maize crop cycle. It is assumed that, in late season, most of the predators have moved to overwintering sites, mostly in uncultivated areas, or to sites deeper in the soil.

Tillage may have unanticipated effects on biological control, due to the complexity of the soil food web. Indeed, some generalist predators, which are favored by the absence of soil disturbance, may disrupt other biological control mechanisms. For instance, according to Snyder and Ives (2001), a generalist carabid beetle (*Pterostichus melanarius*) may act as an intraguild predator, interfering with aphid (*Acyrthosiphon pisum*) population control by a specialist parasitoid wasp (*Aphidius ervi*).

5. Conclusion

Soil management plays a key role in the design of sustainable cropping systems minimizing pesticide use. It must be considered in a global fashion extending beyond tillage: organic residue management, prevention of compaction, crop rotation and the timing of cultivation, must be considered together, with an assessment of their impact on pests and their natural enemies and on ecosystem engineers. The use of this approach requires more detailed research and careful experimental design than the traditional comparison of conventional and reduced tillage. A more precise analysis taking into account the characteristics of tillage and residue management, as suggested by El Titi (2003b), would be more appropriate for field studies in the domain of tillage and soil ecology.

Future soil ecology studies should focus on population modeling in the cultivated field like in Pelosi et al. (2008). Indeed, many of the available ecological models do not include the tillage regime and its interaction with other cropping practices and this area of research is potentially very large. The examples presented here highlight the complexity of the problem. For many of the pests considered, tillage may have both beneficial and detrimental effects. Modeling is essential to determine which tillage system will give the best trade-off for the ecosystem services provided by soil biota, establishing a real partnership between tillage and soil ecology.

Some farmers have themselves established innovative crop management systems (including new crop rotations, diverse associations and new tillage tools). Scientific research would benefit from an analysis of these innovations, including their experimental evaluation, and their possible wider diffusion.

References

Aira, M., Monroy, F., Dominguez, J., 2003. Effects of two species of earthworms (*Allobophora* spp.) on soil systems: a microfaunal and biochemical analysis. Pedobiologia 47, 877–881.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74, 19–31.

Anderson, T.H., Domsch, K.H., 1989. Ratios of microbial biomass carbon to total organic carbon in arable soils. Soil Biology and Biochemistry 21, 471.

Bailey, K.L., Duczek, L.J., 1996. Managing cereal diseases under reduced tillage. Canadian Journal of Plant Pathology 18, 159–167.

Balesdent, J., Chenu, C., Balabane, M., 2000. Relationship of soil organic matter dynamics to physical protection and tillage. Soil and Tillage Research 53, 215–230.

Bongers, T., 1999. The maturity index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. Plant and Soil 212, 13–22.

Boström, U., 1995. Earthworm populations (Lumbricidae) in ploughed and undisturbed leys. Soil and Tillage Research 35, 125–131.

Briones, M.J.I., Bol, R., 2003. Natural abundance of ^{13}C and ^{15}N in earthworms from different cropping treatments. Pedobiologia 47, 560–567.
Brussaard, L., de Ruiter, P.C., Brown, G.G., 2007. Soil biodiversity for agricultural sustainability. Agriculture Ecosystems and Environment 121, 233–244.
Capowiez, Y., Cadoux, S., Bouchand, P., Roger-Estrade, J., Richard, G., Boizard, H., 2009. Experimental evidence for the role of earthworms in compacted soil regeneration based on field observations and results from a semi-field experiment. Soil Biology and Biochemistry 41, 711–717.
Chabert, A., Gandrey, J., 2005. Impact of some insecticides on Carabidae beetles. Bulletin OILB/SROP 28, 111–113.
Chan, K.Y., 2001. An overview of some tillage impacts on earthworm population abundance and diversity—implications for functioning in soils. Soil and Tillage Research 57, 179–191.
Cluzeau, D., Binet, F., Vertes, F., Simon, J.C., Riviere, J.M., Trehen, P., 1992. Effects of intensive cattle trampling on soil–plant–earthworms system in two grassland types. Soil Biology and Biochemistry 24, 1661–1666.
Cochran, V.L., Sparrow, S.D., Sparrow, E.B., 1994. Residues effects on soil micro- and macroorganisms. In: Unger, P.W. (Ed.), Managing Agricultural Residues. CRC Press, Boca Raton, FL, USA, pp. 163–184.
Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M., Chaney, K., 2002. Influence of beetle banks on cereal aphid predation in winter wheat. Agriculture, Ecosystems and Environment 93, 337–350.
Cuendet, G., 1992. Effect of pedestrian activity on earthworm populations of two forests in Switzerland. Soil Biology and Biochemistry 24, 1467–1470.
De Miranda, J.C., de Miranda, L.N., 2007. Impact of no Till Systems on the Diversity of Native Arbuscular Mycorrhizal Fungi Species in Cerrado Soils. Comunicado Tecnico No. 135, Embrapa, Cerrados, Brasil, 4 pp.
Douds Jr., D.D., Nagahashi, G., Reider, C., 2007. Inoculation with arbuscular mycorrhizal fungi increases the yield of potatoes in a high P soil. Biological Agriculture and Horticulture 25, 67–78.
Edwards, C.A., Lofty, J.R., 1975. The influence of cultivation on soil animal populations. In: Vanek, J. (Ed.), Progress in Soil Zoology. Academia, Prague, pp. 399–407.
El Titi, A., 2003a. Effects of tillage on invertebrates in soil ecosystems. In: El Titi, A. (Ed.), Soil Tillage in Agroecosystems. CRC Press, Boca Raton, FL, USA, pp. 261–296.
El Titi, A., 2003b. Tillage in agroecosystems, the synthesis. In: El Titi, A. (Ed.), Soil Tillage in Agroecosystems. CRC Press, Boca Raton, FL, USA, pp. 261–296.
Finch, S., Collier, R.H., 2000. Host-plant selection by insects; a theory based on 'appropriate/inappropriate landing' by pest insects of cruciferous plants. Entomologia Experimentalis et Applicata 96, 91–102.
Gerard, B.M., Hay, R.K.M., 1979. The effect on earthworms of ploughing, tined cultivation, direct drilling and nitrogen in a barley monoculture system. Journal of Agricultural Science of United Kingdom 93, 147–155.
Holtkamp, R., Kardol, P., van der Wal, A., Dekker, S.C., van der Putten, W.H., de Ruiter, P.C., 2009. Soil food web structure during ecosystem development after land abandonment. Applied Soil Ecology 39, 23–34.
Holtze, M.S., Sørensen, S.R., Sørensen, J., Aamand, J., 2008. Microbial degradation of the benzonitrile herbicides dichlobenil, bromoxynil and ioxynil in soil and subsurface environments—insights into degradation pathways, persistent metabolites and involved degrader organisms. Environmental Pollution 154, 155–168.
House, G.J., Parmelee, R.W., 1985a. Comparison of soil arthropods and earthworms from conventional and no tillage agroecosystems. Soil and Tillage Research 5, 351–360.
House, G.J., Rosario-Alzgaray, A.L., 1989. Influence of cover-cropping and no-tillage practices on community composition of soil arthropod in North Carolina, USA agroecosystems. Environmental Entomology 18, 302–312.
House, G.J., Parmelee, R.W., 1985b. Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. Soil and Tillage Research 5, 351–360.
Ivask, M., Kuu, A., Sizov, E., 2007. Abundance of earthworm species in Estonian arable soils. European Journal of Soil Biology 43, 539–542.
Ivezic, M., Raspudic, E., Brmez, M., 2000. Structure of nematode communities in different agroecosystems in Croatia. Helminthologia 37, 165–169.
Jasper, D.A., Abbot, L.K., Robson, A.D., 1991. The effect of soil disturbance on vesicular-arbuscular mycorrhizal fungi in soils from different vegetation types. New Phytologist 118, 471–485.
Jordan, W.L., Hutcheon, J.A., 2003. Influence of cultivation practices on arable crop diseases. In: El Titi, A. (Ed.), Soil Tillage in Agroecosystems. CRC Press, Boca Raton, FL, USA, pp. 187–206.
Kaya, H.K., Gaugler, R., 1993. Entomopathogenic nematodes. Annual Review of Entomology 38, 181–200.
Kendall, D.A., 2003. Soil tillage and epigeal predatory arthropods. In: El Titi, A. (Ed.), Soil Tillage in Agroecosystems. CRC Press, Boca Raton, FL, USA, pp. 297–342.
Kladivko, E.J., 2001. Tillage systems and soil ecology. Soil and Tillage Research 61, 61–76.
Lakshman, Lal, R., Gangwar, S.K., 2006. Effect of tillage on population density of soil biota. Indian Journal of Entomology 68, 62–65.
Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropods in agriculture. Annual Review of Entomology 45, 175–201.
Larink, O., Schrader, S., 2000. Rehabilitation of degraded compacted soils by earthworms. Advances in Geoecology 32, 284–294.
Lavelle, P., 1997. Faunal activities and soil processes: adaptive strategies that determine ecosystem functions. In: Begon, M., Fitter, A.H. (Eds.), Advances in Ecological Research. Academic Press, New York, USA, pp. 93–132.
Lavelle, P., 2000. Ecological challenges for soil science. Soil Science 165, 73–86.
Lee, K.E., 1985. Earthworms their Ecology and Relationships with Soils and Land Use. Academic Press, 389 pp.
Lenz, R., Esenbeis, G., 2000. Short-term effects of different tillage in a sustainable farming system on nematode community structure. Biology and Fertility of Soils 31, 237–245.
Mabbett, T., 1991. Straw incorporation trials reveal arable slug damage will increase. Agriculture International 43, 304–306.
Mair, J., Port, G.R., 2002. The influence of mucus production by the slug *Deroceras reticulatum* on predation by *Pterostichus madidus* and *Nebria brevicollis* (Coleoptera: Carabidae). Biocontrol Science and Technology 12, 325–335.
Manns, H.R., Murray, D.L., Beresford, D.V., 2008. The use of mulch to increase spider (Arachnidae) numbers; a habitat approach to biological insect control. In: Neuhoff, D., Halberg, N., Alfoldi, T., Lockeretz, W., Thommen, A., Rasmussen, I.A., Hermansen, J., Vaarst, M., Lueck, L., Caporali, F., Jensen, H.H., Migliorini, P., Willer, H. (Eds.), Proceedings of the Second Scientific Conference of the International Society of Organic Agriculture Research (ISOFAR), Modena, Italy, 18–20 June 2008, pp. 648–651.
Minton, N.A., 1986. Impact of conservation tillage on nematode populations. Journal of Nematology 18, 135–140.
Miura, F., Nakamoto, T., Kaneda, S., et al., 2008. Dynamics of soil biota at different depths under two contrasting tillage practices. Soil Biology and Biochemistry 40, 406–414.
Moore, J.C., 1994. Impact of agricultural practices on soil food web structure: theory and application. Agriculture, Ecosystems and Environment 51, 239–247.
Nilsson, C., 1994. Pollen beetle and rape: interactions and crop losses. Vaxtskyddsnotiser 58, 56–57.
Nuutinen, V., 1992. Earthworm community response to tillage and residue management on different soil types in southern Finland. Soil and Tillage Research 23, 221–239.
Nyoike, T.W., Liburd, O.E., 2010. Effect of living (buckwheat) and UV reflective mulches with and without imidacloprid on whiteflies, aphids and marketable yields of zucchini squash. International Journal of Pest Management 56, 31–39.
Pelosi, C., Bertrand, M., Makowski, D., Roger-Estrade, J., 2008. WORMDYN: A model of *Lumbricus terrestris* population dynamics in agricultural fields. Ecological Modelling 218, 219–234.
Pelosi, C., Bertrand, M., Roger-Estrade, J., 2009. Earthworm community in conventional, organic and direct seeding with living mulch cropping systems. Agronomy for Sustainable Development 29, 287–295.
Prasifka, J.R., Schmidt, N.P., Kohler, K.A., O'Neal, M.E., Hellmich, R.L., Singer, J.W., 2006. Effects of living mulches on predator abundance and sentinel prey in a corn–soybean–forage rotation. Environmental Entomology 35, 1423–1431.
Pullaro, T.C., Marino, P.C., Jackson, D.M., et al., 2006. Effects of killed cover crop mulch on weeds, weed seeds and herbivores. Agriculture, Ecosystems and Environment 115, 97–104.
Rypstra, A.L., Carter, P.E., Balfour, R.A., Marshall, S.D., 1999. Architectural features of agricultural habitats and their impact on the spider inhabitants. Journal of Arachnology 27, 371–377.
Sanchez-Moreno, S., Minoshima, H., Ferris, H., Jackson, L.E., 2006. Linking soil properties and nematode community composition: effects of soil management on soil food webs. Nematology 8, 703–715.
Schmidt, M.H., Thewes, U., Thies, C., Tcharntke, T., 2004. Aphid suppression by natural enemies in mulched cereals. Entomologia Experimentalis et Applicata 113, 87–93.
Schmidt, N.P., O'Neal, M.E., Singer, J.W., 2007. Alfalfa living mulch advances biological control of soybean aphid. Environmental Entomology 36, 416–424.
Schneider, O., Roger-Estrade, J., Aubertot, J.N., Doré, T., 2006. Effect of seeders and tillage equipment on vertical distribution of oilseed rape stubble. Soil and Tillage Research 85, 115–122.
Sidsgaard, L., 2000. Early season natural biological control of insect pests in rice by spiders—and some factors in the management of the cropping system that may affect this control. European Arachnology 57–64.
Sirrine, J.R., Letourneau, D.K., Shennan, C., Sirrine, D., Fouch, R., Jackson, L., Mages, A., 2008. Impacts of groundcover management systems on yield, leaf nutrients, weeds, and arthropods of tart cherry in Michigan, USA. Agriculture, Ecosystems and Environment 125, 239–245.
Six, J., Ogle, S.M., Breidt, F.J., Conant, R.T., Mosier, A.R., Paustian, K., 2004. The potential to mitigate global warming with no-tillage management is only realized when practised in the long term. Global Change Biology 11, 155–160.
Snyder, W.E., Yves, A.R., 2001. Generalist predators disrupt biological control by a specialist parasitoid. Ecology 82, 705–716.
Sooksa-nguan, T., Thies, J.E., Gypmantasiri, P., Nantakorn, B., Neung, T., 2009. Effect of rice cultivation systems on nitrogen cycling and nitrifying bacterial community structure. Applied Soil Ecology 43, 139–149.
Souza-Andrade, D., Collozzi-Filho, A., Giller, K.E., 2003. The soil microbial community and soil tillage. In: El Titi, A. (Ed.),Soil Tillage in Agroecosystems. CRC Press, Boca Raton, FL, USA, pp. 267–296.
Stinner, B.R., House, G.J., 1990. Arthropods and other invertebrates in conservation tillage agriculture. Annual Review of Entomology 35, 299–318.
Sujan, Singh, 2003. Role of mycorrhiza in disturbed lands. Part 1. Effect of soil disturbance and tilling on mycorrhiza. Mycorrhiza News 151, 2–10.

Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47, 561–594.

Symondson, W.O.C., Cesarini, S., Dodd, P.W., et al., 2006. Biodiversity vs. biocontrol: positive and negative effects of alternative prey on control of slugs by carabid beetles. Bulletin of Entomological Research 96, 637–645.

Szendrei, Z., Weber, D.C., 2009. Response of predators to habitat manipulation in potato fields. Biological Control 50, 123–128.

Thomas, J.A., Hein, G.L., Lyon, D.J., 2004. Spread of wheat curl mite and wheat streak mosaic virus is influenced by volunteer wheat control methods. Plant Health Progress 23, 1–6.

Tomlin, A.D., Miller, J.J., 1988. Impact of ring-billed gull (*Larus delawarensis* ord.) foraging on earthworm populations of Southwestern Ontario agricultural soils. Agriculture, Ecosystem and Environment 20, 165–173.

Usuki, K., Yamamoto, H., Tazawa, J., 2007. Effects of previous cropping and tillage system on growth of maize and symbiotic association with arbuscular mycorrhizal fungi in central region of Japan. Japanese Journal of Crop Science 76, 394–400.

Vian, F.J., Peigné, J., Chaussod, R., Roger-Estrade, J., 2009. Effects of four tillage systems on soil structure and soil microbial biomass in organic farming. Soil Use and Management 25, 1–10.

Wang, K.H., McSorley, R., Gallaher, R.N., Kokalis-Burelle, N., 2008. Cover crops and organic mulches for nematode, weed and plant health management. Nematology 10, 231–242.

Young, I.M., Crawford, J.W., 2004. Interaction and self-organization on the soil–microbe complex. Science 304, 1634–1637.

Young, I.M., Ritz, K., 2000. Tillage, habitat, space and function of soil microbes. Soil and Tillage Research 53, 201–213.