



The Role of Soil Biology in Crop Nutrition

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AGRICOLOGY





Contents

Sum	mary	3
Introduction		3
1.	Bacteria	5
2.	Fungi & Mycorrhizae	7
3.	Protozoa	9
4.	Nematodes	11
5.	Arthropods	13
5a.	Arthropods at the Allerton Project	15
6.	Earthworms	17
6a.	Allerton Project Earthworms	20
Soil	Biology encouraged by Agroecology	21
Conclusions		22
Refe	eferences	

All photographs taken by Dr Felicity Crotty, unless otherwise stated.





Summary

This review looks at the importance of soil biology in plant nutrition and how it aids crop growth and yield. The report emphases the importance of **soil biology in recycling plant nutrients** and looks in detail at bacteria, fungi and mycorrhizae, protozoa, nematodes, arthropods and earthworms.

Where the Allerton Project has conducted **soil biology studies** in cover crops, they have been included to illustrate some of the aspects of soil activity.

Most of the biodiversity within agricultural systems resides in the soil (Brussaard et al., 2007) and arable cultivations will have an impact on soil biology.

Agroecological and Integrated Farm Management (IFM) approaches can help enhance soil structure, soil fertility and assist soil water infiltration. Such principles include natural fertilizers, wide crop rotation including legumes and the use of cultural control wherever possible, an emphasis on more biology and less chemistry.

Introduction

Nitrogen is the most yield defining nutrient in arable farming systems. It has long been recognised that Nitrogen, Phosphate and Potassium (N, P, K) should be replaced in the soil following crop harvest. The amount is determined by numerous nutrient calculators and rates will also depend on whether crop residues are removed from fields, but usually in the UK, it is applied to meet guidelines in the Fertiliser Manual RB209 (Defra, 2010).

Manures from livestock have been used historically, however due to the separation of farming systems – arable or livestock, rarely mixed, there is not enough to supply all arable areas with current farming practices. This has led to worldwide development and use of manufactured synthetic nitrogen, to produce and maintain yields at a level which will feed the rising population globally. It is also recognised that economically, income from fertiliser-generated high yields, outweighs the cost of the application of fertilisers.

Agricultural crop cultivars are not always the most efficient at converting all NPK applications into crop growth and this has led the surplus from arable systems entering water courses through leaching. With a greater focus on farming sustainably, reducing agricultural pollution is top of many policy and environmental agendas. We need to look again at ways of replacing nutrients in arable soils whilst retaining them within the field, to be available for the next crop.

Soil is made up of five component parts – air, water, mineral, organic matter and biota. These living organisms play a key role within the soil. Soil is the most diverse habitat that exists on earth, with millions of species inhabiting the same space within the soil. Soil fauna are ubiquitous and can be found in any soil from the arctic to the equator, and from arable farmland to pristine natural habitats. The organisms that inhabit the soil range over multiple scales – micro, meso and macro (Figure 1). Here, in this report we examine each taxon that co-exists together within the soil as part of the soil biology, these organisms co-exist together within the soil linked through feeding relationships and a variety of interactions (Figure 2), we will also be highlighting their contribution to maintaining soil nutrients. How we can work with them harmoniously, in an integrated approach to maximise nutrient release, minimise nutrient loses, maintain and increase yields whilst limiting the damaging effects of nutrient pollution to the wider environment, will be key.







Figure 1: Size classification of organisms living in the soil, by body width (Swift et al., 1979).

Whilst we don't know what is an "optimal" balance of all soil biota in terms of agricultural productivity, research has shown that diversity is beneficial for the following reasons (Thiele-Bruhn, 2012):

- Nutrient cycling
- Nutrient retention
- Improved structure, infiltration, and water-holding capacity
- Disease suppression
- Degradation of pollutants
- Biodiversity
- Carbon sequestration







Figure 2: Food webs are used to show the linkages and feeding relationships between the different organisms within the same community. This diagram shows the soil food web, which is based on organic matter and detritus that is utilised by bacteria and fungi as two separate energy channels within the soil food web. (Diagram from Ingham, 2016).

1. Bacteria

Intro:

The rhizosphere is the area of soil immediately surrounding plant roots that is directly influenced by these roots. Exudates such as amino acids and sugars from the plant roots provide an energy-rich medium for the proliferation of many microorganisms including bacteria (Bhattacharyya and Jha, 2011).

Most soil dwelling bacteria are decomposers, breaking down organic nutrients and detritus into forms which can then be further utilised by other soil biota, turning it into mineral nutrients that are more readily usable by crops. Some bacterial exudates help to bind soil aggregates, improving the hydrology and oxygen flow through the soil and therefore nutrient retention. The function of some bacteria can also include the decomposition of pesticides and pollutants and pathogen suppression through resource competition. Generally, important soil dwelling bacteria fall into the following functional categories (Orgiazzi, et al., 2016):

- Nitrogen fixing bacteria form a symbiosis (relationship) with the roots of plants. The plant provides food for the bacteria in the form of carbon compounds (sugars and starches) and the bacteria convert nitrogen from the air into a form that the plant can use in return. The most well-known relationship is between rhizobium bacteria and leguminous plants which create nodules on the roots of these plants where nitrogen fixation occurs. However, there are actually two types of these bacteria, known as plant growth promoting rhizobacteria (PGPR), (Khan, 2005);
 - Symbiotic bacteria (iPGPR) living within plant root cells such as the rhizobia, which produce nodules and are associated with leguminous crops.





• Free-living bacteria (ePGPR) i.e. those which exist within the rhizosphere which colonise plant root surfaces.

PGPR's are known to have three main functions:

- Pathogen antagonism.
- Facilitate nutrient uptake.
- Compound synthesis.
- Nitrifying bacteria are aerobic microbes which convert ammonium (nitrite) into nitrate, the form of nitrogen which plants can use. Farmers aim to harness these action, when applying ammonia as a fertiliser to their fields, it can then be converted by these bacteria for the crops to utilise. This process can be restricted by both too much water content within the field (waterlogging) and too little (drought). If bacteria are too efficient at nitrification, leading to an excess of nitrate which is more readily leached from the soil, farmers may have to use nitrification inhibitors to suppress their activity and prevent nutrient losses from the field. Research has shown that a greater organic matter content and reduced tillage practices generally tend to favour the proliferation of these bacteria, whose primary food source is decomposing organic matter.
- **Denitrifying bacteria** are anaerobic microbes, thriving where oxygen is not present such as waterlogged soils. They convert nitrate, the useful form of nitrogen used by plants, into nitrous oxide gas, which is released into the atmosphere (and often referred to as a greenhouse gas, causing pollution and potentially leading to climate change). Therefore, avoiding and alleviating waterlogged and compacted soils, which would promote these bacteria, will help to retain the nitrate within soils for plant use (Orgiazzi, et al., 2016, lpni2016b)
- Actinomycetes, are the bacteria responsible for the characteristic "earthy" smell of soil, they are a diverse group of decomposers which breakdown dead plant material and convert it into organic matter, they are of particular importance as they utilise some plant compounds which are more difficult to break down by other organisms e.g. cellulose.

Key facts:

- Extensive research has been undertaken to identify effects of Rhizobium sp. on leguminous crops and N² fixation. There is growing interest in other plant growth promoting Rhizobacteria (PGPR's) and their contribution towards sustainable agricultural practices through their use as bio-fertilisers. However, there has been limited field-scale research undertaken to identify cost-effective seed treatments or soil inoculant which conventional UK farmers could utilise. Although some PGPR seed treatments are available on the UK market for leguminous crops such as soya, lupin, lucerne and clover.
- A meta-analysis, concluded that only two types of bacteria Azospirilium and Azotobacter have been shown to positively impact wheat yields, particularly when used together (however this was in the absence of N fertiliser) (Veresoglou and Menexes, 2010). It was suggested that crop varieties and soil type are the most important influencing factor on the effectiveness of these bacteria as a biofertiliser.
- Phosphorous harvesting bacteria increase the amount of P available to plants, by solubilising the mineral from the soil particles therefore increasing plant uptake. Field trials have proven that the application of a bacteria (M-13) positively influenced the grain yield of barley and sugar beet particularly when used in conjunction with an N-fixing bio-fertiliser (Sahin et al., 2004). However, P fixation and precipitation in soils is highly dependent upon soil type and pH (Hayat et al., 2010).





- Rapeseed yield has been shown to increase following the application of N fixing bacteria (Azotobacter Chroococcum and 1-Pseudomona Putid) in field trials, and suggests that chemical N fertiliser application could be reduced if used in conjunction with this PGPR inoculation (Naseri et al., 2013).
- Inefficient or over abundant use of N fertilisers could lead to an excess of N being available, this is a catalyst for denitrification. Splitting fertiliser applications, using controlled release fertilisers, or nitrifying inhibitor additives such as Didin and fertigation (water soluble/irrigation application) can reduce the risk of N losses (Ipni, 2016a) and increase nutrient use efficiency (NUE).
- Some bacteria (e.g. Pseudomonas and Xanthomonas species) promote plant growth by pathogen antagonism this is where the bacteria suppress or interfere with the normal growth and activity of the plant pathogen, reducing its virulence and/or abundance. These bacteria can also increase plant growth compound generation.

Current UK Relevance:

- Use a legume -> non-legume crop rotation to utilise the residual N² generated by the leguminous plant-microbe interactions that remains in the soil after the legumes are harvested (Hayat et al., 2010, Hayat et al., 2008).
- Use non-harvested leguminous cover crops and green manures to maximise the return of the N² fixed by the plants to the soil for following crops.
- Reduce the risk of denitrification through:
 - Well timed fertiliser applications, i.e. those which correspond to the time the plant is actively growing and needs the nutrient (this is plant specific)
 - Splitting fertiliser applications,
 - o Controlled release fertilisers,
 - Nitrifying inhibitor additives e.g. Didin.
 - Fertigation (injection of fertiliser / water-soluble products into an irrigation system).
- Aim to maintain soil quality which promotes the proliferation of bacteria useful to crop nutrition, i.e. increase soil organic matter and reduce tillage where possible.
- Alleviate compacted soils to maintain good water infiltration and improve drainage to prevent waterlogging and maintain soil organic matter to help reduce further compaction and aid infiltration
- Increase and maintain soil organic matter to improve soil structure in sandy, free-draining soils, in order to maintain moisture levels in support of soil bacteria.

2. Fungi & Mycorrhizae

Intro:

Fungi within soil can be split into three groups dependent upon how they obtain their energy; pathogens and parasites, decomposers (saprotrophic fungi) and mutualists (mycorrhizal fungi). It is unknown just how many species of fungi there are living together within the soil, but estimates are in excess of 1.5 million different species globally (Hawksworth, 1991).

The decomposers break down hard to digest organic compounds into simpler forms which can be used by other soil organisms and plants. Their hyphae, long strand-like structures, help to physically bind soil particles together which aids water infiltration and retention. The filamentous structure of the hyphae provides an extensive pathway for nutrients to flow between fungi and plants through the soil, often exceeding tens of metres of fungal hyphae per gram of soil (Leake et





al., 2003). Decomposers also immobilise nutrients within the soil, reducing the risk of leaching and retaining them for use by the crop (USDA, 2016b). Decomposers exude compounds which helps to retain and build-up soil organic matter. This further improves soil structure and contributes towards carbon sequestration (Orgiazzi, et al., 2016).

Mycorrhizal fungi make up between 20-30% of the total soil microbial biomass (Leake et al., 2003) and are known to have positive effects on plant growth through their symbiosis with them (Orgiazzi, et al., 2016). There are two major mycorrhizal groups:

- Endomycorrhiza also known as arbuscular mycorrhizal fungi (AMF) penetrate the plant roots intracellularly (into cortical cells).
- Ectomycorrhiza colonise the external surface of the plant roots.

The fungal mycelium of mycorrhizae act as an extension to the roots of plants, and are between 10-100 times the root length (Leake et al., 2003) enabling the plant to access more nutrients within the soil, particularly beneficial for phosphorous absorption. Other benefits include pathogen antagonism, soil aggregate stabilisation, stress alleviation from both biotic and abiotic factors and preventing erosion (Vosatka et al., 2012) as well as yield increases and biofortification of crops.

Mycorrhizal associations are found in many mainstream agricultural crops such as maize, wheat, barley, potatoes, beans, clover etc. (but not in brassicas i.e. rapeseed or amaranths i.e. sugar beet). The use of domesticated mycorrhizal fungi as a commercial bio-fertiliser to promote plant growth is increasing across the world, particularly in developing countries (Vosatka et al., 2012). However, a cost-effective, consistent quality inoculum for large-scale crops such as cereals is elusive and more development is required.

Key facts:

- In a meta-analysis, potato yield was shown to significantly increase following a liquid application to seed of the AMF Rhizophagus irregularis when compared to no application control (Hijri, 2016).
- Some wheat cultivars have a greater ability to form mycorrhizal symbiosis than others (Cameron, 2014) and some varieties depend more upon mycorrhizal symbiosis than others.
- Organic farming (characterised by the lack of chemical fertilisers and pesticides used) supports a greater number and diversity of mycorrhiza than conventional farming (Verbruggen et al., 2010).
- Tillage has a negative impact on the number and diversity of mycorrhizae and P concentrations in Maize (Kabir et al., 1998), through the disruption of the hyphal network. Some AMF can protect cereals (e.g. barley) against the impact of fungal pathogens such as take-all (Castellanos-Morales et al., 2011) and a high diversity can suppress agricultural weeds (Rinaudo et al., 2010).
- SAMF can improve the drought tolerance of wheat (Al-Karaki et al., 2004).
- Mycorrhizal abundance is positively linked to greater aggregate size which is influential in the movement and storage of water and oxygen in the soil (Wilson et al., 2009).
- Macro-aggregates, linked to a healthy mycorrhizal population, can be restored quickly within 5 years, by the use of grass leys, which in turn improves carbon sequestration (Jastrow, 1996).
- Soil organic matter content promotes soil microbial activity, including mycorrhizae, which help to bind soil aggregates (Tebrugge and During, 1999), which reduces the risk of soil erosion (Matson et al., 1997, Tebrugge and During, 1999).





Current UK Relevance:

- Reduce tillage where possible to maximise mycorrhizal associations.
- Alleviate compaction and poor drainage to prevent anaerobic soil conditions which are unfavourable to mycorrhizae.
- Avoid broad spectrum fungicides where possible, which are toxic to mycorrhizae.
- Avoid high levels of nitrogen and phosphorous fertilisers with leguminous plants which can reduce associations.
- Maintain good levels of soil organic matter.

3. Protozoa

Intro:

Protozoa are single-celled organisms (Figure 3), they are a highly diverse and abundant group, occupying many niches within the soil, their primary food source is bacteria although some species consume soluble organic matter, fungi and each other. They represent the greatest biomass of all soil organisms. Protozoa live within the water films covering soil aggregates and within water-filled soil pores. Protozoa also form a large food source for many different organisms within the soil food web (Crotty et al., 2012).



Figure 3: Drawing of a range of protozoa – the larger protozoa are different ciliate species, whilst the smaller protozoa are flagellates (Finlay et al., 2001).

Their consumption of bacteria significantly contributes to the nutrient cycling process, by releasing available nitrogen and phosphorous for use by crops, within the soil (microbial loop effect). The microbial loop is the positive effect of protozoan grazing on rhizosphere bacteria (stimulated to multiply by root exudates) that releases more nutrients which can then be taken up and used by the plant for increased growth (Coleman, 1994). Other soil functions also include suppression of pathogens through resource competition or consumption.

Key facts:

• Protozoa have a direct effect on soil nutrient cycling due to their abundance, diversity and assimilation rates of bacterial biomass (Crotty et al., 2013).





- Some insecticides and fungicides can be toxic to protozoa (Foissner, 1997), therefore the benefits of application may be outweighed by the loss of mineral N generation from the reduced protozoa abundance (Ekelund, 1999).
- Herbicides effect the activity of protozoa indirectly by influencing the plant cover thereby influencing bacterial populations that largely make up protozoan diets. This can be counteracted by maintaining a good level of soil organic matter (Bamforth, 1997).
- Tillage has been shown to decrease protozoa abundance, reducing tillage increases the favourability of the environment (Bamforth, 1997).
- Fertiliser application generally reduces protozoa abundance, however increasing organic fertiliser can increase protozoan abundance and diversity (Bamforth, 1997).
- Increasing crop spacing will increase the microhabitat mosaic favouring greater species diversity. Limited rotations (two crop) or long fallow periods will reduce protozoan abundance (Bamforth, 1997).
- Compaction reduces soil pore space which impacts upon the biomass and activity of protozoa (Bamforth, 1997).

Current UK Relevance:

- Maintain good soil organic matter content in order to support the bacteria which forms the main diet of protozoa.
- Use organic fertiliser inputs instead of mineral fertilisers.
- Reduce the use of insecticides, fungicides and herbicides where possible, particularly nonspecific ones.
- Reduce tillage where possible.
- Maintain surface residues.
- Alleviate and avoid compaction.





4. Nematodes

Nematodes are tiny unsegmented, transparent worms (Figure 4), barely visible with the naked eye and reside naturally within the soil (Orgiazzi, et al., 2016). They are the most abundant metazoan and are found throughout all soil environments (Ferris et al, 2001).



Figure 4: Fungal feeding nematode found in agricultural grassland.

They operate on a number of different trophic levels and can actually be classified into eight different feeding guilds (Yeates et al., 1993).

- Bacterial-feeders
- Fungal-feeders
- Herbivores
- Detritivores
- Protistovores
- Omnivores
- Parasitic
- Predatory nematodes (eat all types of nematodes and protozoa)

There is much research undertaken on the impact of plant parasitic nematodes (PPN's) on agricultural crops but there is limited knowledge on ways in which can predatory nematodes can be harnessed, in agricultural context, to control PPN's and other crop pests. There are several well-known detrimental nematode induced conditions suffered by cereals (Smiley and Nicol, 2009):

- Heterodera (cyst),
- Pratylenchus (root-lesion),
- Meloidogyne (root knot),
- Ditylenchus (stem),
- Tylenchorhynchus and Merlinius (stunt),
- Paratrichodorus (stubby-root),
- Anguina (seed-gall)





Functions performed relevant to soil quality and crop nutrition include:

- Mineralisation of organic matter for plant use.
- Release of ammonium, the available form of nitrogen for plants, through ingestion of bacteria and fungi.
- Support populations of other beneficial soil biota such as soil arthropods, fungi and insects.
- Their feeding, at low levels stimulates population growth of their prey such as bacteria and fungi, but at high levels it reduces populations.
- Dispersal of bacteria and fungi through the soil.
- Disease suppression if consuming disease-causing nematode species or bacterial / fungal pathogens.

Agricultural soils support similar numbers of nematodes compared to grassland and forest soils, however the species diversity is greatly different. Less disturbed soils are known to contain more predatory nematodes, with tillage being found to increase abundance of bacterial feeding nematodes (Crotty et al., 2016).

Key facts:

- Less than 10% of nematodes that exist within the soil are plant pests.
- Free living nematodes are very important and beneficial in the decomposition of organic material and the recycling of nutrients in soil (Neher, 2001).
- Nematodes enhance soil quality in four main ways: regulate populations of other soil organisms, mineralise nutrients into plant available forms, provide a food source for other soil organisms and consume disease-causing organisms (Ferris and Matute, 2003; Ferris et al., 2004).
- Nematodes are grazers, living within the water filled pore space in the soil. The move through the soil pores consuming bacteria, fungi but also distributing bacteria and fungi.
- Nematodes (unlike earthworms) can be found in all soils globally, and certain species are frequently the last animals to die in polluted or disturbed areas (Neher, 2001).
- However, the potato cyst nematode is one of the most economically important pests in temperate agricultural regions.
- An integrated pest management approach is recommended to control PCN as implementation of single measures of control, such as resistant strains sown as a monoculture, have limited longevity and success (Fourie et al., 2016).
- Nematicide application has been found to reduce numbers of all trophic groups of nematodes, with lingering effects on both bacterivores and fungivorous nematodes the following year (Timper et al., 2012).
- Using brassicas as a cover crop or an inter crop or as part of a rotation can significantly reduce the viability and abundance of pest nematodes (Fourie et al., 2016, Defra, 2016).
- Some cover crops, particularly cruciferous varieties such as oilseed radish, mustards and rockets can act as biofumigants for the following crops when incorporated prior to crop drilling, and can interrupt the lifecycle of pathogenic nematodes reducing the population and therefore threat to the following crop (Gleadell, 2016).

Current UK Relevance:

- Maintain soil conditions which support a healthy nematode population.
- Reduce tillage where possible to maintain a stable environment for soil organisms.
- Take an integrated approach to effectively manage nematode problems nematicide application will affect all non-target nematodes as much as the target.
- Include brassicas in cover crops and incorporate their residues.





 Introduce longer rotations where possible to reduce the build-up of parasitic nematodes.

5. Arthropods

Intro:

Arthropods are the largest group of soil fauna (both in diversity of species and size range of organisms) (Coleman and Crossley, 2003). Soil arthropods can be classified by their degree of presence in soil e.g. transient (e.g. hibernates in soil over winter), temporary (e.g. egg and juvenile stage), periodic (e.g. most of lives spent within the soil, although adult stage may emerge to reproduce), and permanent (e.g. all life stages and time spent within the soil) (Coleman and Crossley, 2003). Arthropods can be categorised into two main groups – microarthropods (springtails and mites) and macroarthropods (fly and beetle larvae, centipedes, millipedes and other insects). Microarthropods inhabit the air-filled pore spaces and are largely restricted to existing ones; whereas the macroarthropods (and earthworms) have the ability to create their own spaces through burrowing (Coleman and Crossley, 2003). Microarthropods can be found at densities of 50,000 – 300,000 individuals per metre square in UK soils (Bardgett and Cook, 1998) (Figure 5).



Figure 5: Acari extractions from agricultural grassland.

Many arthropods act as ecosystem engineers. The functions they perform are beneficial for cultivation – including the processing of organic matter, increasing aeration, infiltration and water retention through their burrowing, improving soil structure and predation of crop pests. The movement of these creatures through the soil redistributes the organic matter from the surface of the soil through the soil profile.

Arthropods have many different feeding preferences (Crotty, 2011):

- Microbivores consume fungi and bacteria from around the plant roots, changing decomposing material into usable nutrients for plants; includes springtails and mites.
- Decomposers consume the decaying organic material, breaking it down into smaller pieces to be consumed by smaller arthropods; includes woodlice, millipedes, some mites.
- Predators Can be either specialist or non-specialist feeders, many feed upon crop pests; includes spiders, centipedes, ground beetles, ants and some mites.
- Herbivores Live mostly within the soil. Can be pests when large numbers occur, such as symphyla, a relative of the centipede.





Key facts:





Small and wingless, they are numerous in soils and leaf litter globally. Have a wide diet of bacteria, fungi, decaying plant materials & humus, other springtails, moss, algae, faeces etc. As much as 20% of annual litter input may be processed by this arthropod. Collembola have been shown to have important impacts on nitrogen mineralisation, soil respiration, leaching of dissolved organic carbon and plant growth (Filser, 2002).

• Acari (Mites)

Are the most abundant microarthropod in soils and have a spiderlike appearance, there is a huge diversity of species leading to a varied range of food sources - including fungi, bacteria, faeces, decaying plants, nematodes, springtails, other mites etc. but are also prey to other fauna. Soil functions performed focus mainly upon the processing of decaying plant material. There are three main subgroups of mites – Mesostigmata (mainly predatory mites), Oribatida (mainly decomposers) and Prostigmata (broadest range of feeding habits and includes both predators and decomposers).

• Other microarthropods – Protura, Diplura and Pauropoda Protura are small wingless primitive insects, can be found deep within the soil profile (25cm), feeding on fungal hyphae. Diplura are small elongate primitive insects, some have large cerci with modified pinchers – used to catch prey of small microarthropods. Pauropoda resemble tiny centipedes, but have branched antennae; they are white and blind. They are thought to be fungal feeders, but may also be predaceous



• Myriapoda (Millipedes and Centipedes)

This group is characterised by elongated segmented bodies with many sets of legs. Millipedes (Diplopoda) are mainly plant litter feeders / fungal feeders; prefer calcareous soils and moist conditions. Centipedes (Chilopoda) are predatory and much more active. They have been seen to actively pursue and capture small prey.



• **Symphala** (primitive centipedes)

Small, white, eyeless many legged invertebrate that resembles tiny centipedes. They are very dependent on a high soil moisture. They are omnivorous and can feed on both plants and animals.







• Insecta (Insects)

This is the most diverse group and includes beetle larvae and adults, fly larvae, bugs and ants.

Beetles: largest order of insects – can be predatory, herbivorous or a fungal feeder living both temporarily to permanently in soils. Rove beetles (staphylinidae) are common soil predators, whilst wireworms (elateridae) can be significant herbivorous pests.

Flies: can be considered soil insects as the larvae of many species develop within the soil. Fly larvae have a major impact on the decomposition of carrion, as well as consuming fungi, plant material and some are predatory. Ants: have a large influence on soil structure through the formation of ant hills / burrows. They are predators of small invertebrates. Based on Coleman and Crossley (2003) and Brussaard (1998).

Current UK Relevance:

- Research has found that soil arthropods have greater diversity and abundance under reduced tillage regimes than in conventional tillage systems (House and Parmelee, 1985). As tillage disturbs the fungal networks and reduces the amount of organic matter available for consumption.
- Some organic fertilisers have been found to increase soil arthropods (including biogas digestate (Platen and Glemnitz, 2016).
- Maintain levels of surface residue and soil organic matter.
- Create beetle banks to offer habitat to beneficial predatory arthropods.

5a. Arthropods at the Allerton Project

In studies conducted in autumn 2015 and spring 2016 below ground arthropod numbers were present in cover crop mixes and in the no cover control. Numbers were greater in the autumn when soil conditions were more favourable to arthropod movement. In early spring, arthropods may have been deeper underground and less active due to colder soil temperatures. There was no difference between abundance of arthropods in the autumn between the cover crop and bare stubble control, however there was a greater abundance of millipedes in the spring cover crop treatment in comparison to the bare stubble.





Figure 6: Macroarthropod abundance in cover crop mixes versus bare stubble at the Allerton Project 2015 Autumn (left); and Spring (right).







6. Earthworms

In recognition of the importance of the biological activity of earthworms in the soil, the ancient Chinese named earthworms as "angels of the soil" (Blakemore, 2002). It is believed that having a high abundance of earthworms is an indication of a healthy soil. Earthworms are often referred to as ecosystem engineers, as they change the whole soil habitat, effecting all other organisms within the soil. Earthworms improve soil structure through their burrowing and casting, increasing the amount of water infiltration possible as well as the aeration of the soil. Plant roots are known to preferentially grow down the vertical burrows of earthworms, as it is the path of least resistance. Without earthworm burrows, it is thought that 93% of all water infiltration would be reduced (Cuddington, et al., 2011). Soil organic matter is also fragmented by the ingestion and digestion of the earthworms (Chan, 2001) making it more readily available for further decomposition by other soil microbes; and releasing mineral nutrients for use by plants directly. It is therefore widely recognised that earthworms are a soil quality bioindicator (Frund, et al., 2011).

Earthworms can be categorised into three groups depending upon where they reside within the soil and how they feed (Figure 7):

- Surface dwellers (Epigeic species) these are usually found in leaf litter and rotting logs on the soil surface, feeding directly on decaying matter. They are usually small and dark red in colour, relatively short lived, with fast reproductive cycles. E.g. *Lumbricus rubellus*
- Horizontal burrowing species (Endogeic species) these are soil dwellers that create horizontal burrows, they rarely appear on the surface and mainly consume the soil itself. They are much less pigmented (grey/pink or greenish), small to medium sized with midlength life-spans, with relatively fast reproductive cycles. E.g. *Allolobophora chlorotica*
- Deep vertical burrowing species (Anecic species) these species move up to the surface at night to pull leaves and other dead plant material into their burrows for it to decompose, before they consume it. They are usually dark red and large worms, that are long living, with slow reproductive cycles. E.g. *Lumbricus terrestris.*

From Sherlock (2012).





Figure 7: Pictorial representation of three main functional groups of earthworms and their characteristics. Based on Brown (1995) and Coleman and Crossley (2003).



Enchytraeidae

have significant effects on and soil structure.



Figure 8: Enchytraeid worm Key facts:

- Reduced tillage and cover cropping, particularly cereal-clover intercropping, supports significantly greater earthworm populations, than conventional tillage and mono-cropping (Schmidt et al., 2003).
- Diversity as well as abundance of earthworms can be negatively impacted by tillage (Chan, 2001).
- Growing white clover has been found to increase earthworm abundance (in comparison to ryegrass, chicory and red clover) (Crotty et al., 2015).





- Intensive soil cultivations grubbing, ridging, bed-tilling and destoning, which are performed to prepare for potatoes, can almost eliminate earthworm populations (Curry et al., 2002) which will struggle to recover through the rest of the rotation.
- The reduction in earthworm abundance following intensive cultivations is a result of mortality through direct injury, habitat destruction (cutting up of permanent burrows), altered abiotic conditions (soil moisture reduction and extreme temperature fluctuations), as well as loss of food supply (Curry et al., 2002, Chan, 2001).
- Earthworm activity increases crop residue incorporation into the sub-soil, improving soil organic matter content (Parmelee et al., 1990).
- Mineral nutrients in soil organic matter are released and made available for plant use by the ingestion and digestion of the earthworm (Chan, 2001) significantly contributing towards N-cycling particularly in conservation tillage regimes (Parmelee et al., 1990).
- Conversely, compaction and poor drainage can restrict the populations of earthworms (Chan, 2001).
- Soil acidification has been found to effect earthworms detrimentally (Springett and Syers, 1984).
- Some mineral N fertiliser types can decrease the numbers and biomass of some earthworm species more than others (Ma et al., 1990).
- A reduction in pesticide applications would increase earthworm population density (Pelosi et al., 2013).
- Earthworms have been found to contribute significantly to the control of mycotoxins in wheat straw (Wolfarth et al., 2016).

Current UK Relevance:

- Reduce tillage to maintain a stable environment which supports earthworms throughout their lifecycles.
- Alleviate compaction and poor drainage to prevent anaerobic soil conditions which are unfavourable to earthworms.
- Avoid high levels of mineral fertilisers which can cause unfavourable soil acidification
- Maintain good levels of soil organic matter.
- Retain surface residues, which can provide a food supply to earthworms
- Avoid high levels of pesticides where possible, think about the toxicity of pesticides used to non-target organisms.
- Maintain soil conditions which are supportive of other soil microbes, particularly fungi, protozoa, bacteria and soil organic matter, in order to support a healthy food web, which will lead to larger numbers and diversity of earthworms.





6a. Allerton Project Earthworms

A recent metaanalysis (van Groenigen et al. 2014), found positive differences in plant growth occurred when earthworm abundance was 400 or more per metre square. This paper states that, *"on average earthworm presence in agroecosystems leads to a 25% increase in crop yield and a 23% increase in aboveground biomass. The magnitude of these effects depends on presence of crop residue, earthworm density and type and rate of fertilization"* At the Allerton Project our earthworm counts are around 750 per metre square – this is similar in fields with cover crops and those with bare stubble (although all reduced tillage) Figure 9. Overall there was no difference in total abundance in earthworm numbers, however there were significantly greater numbers of surface dwelling earthworms (epigeic) in the cover cropped strips in comparison to the bare stubble.

Figure 9: Spring earthworm abundance in cover crop versus bare stubble, including differences in functional group (epigeic, endogeic, anecic) at the Allerton Project 2016







Soil Biology encouraged by Agroecology

Maintaining a healthy soil, with a large diversity of species and large abundance of organisms is known to increase agricultural productivity (DuPont et al., 2009; van Groenigen et al. 2014).

What is agroecology? Agroecology involves understanding ecological processes and applying these concepts to the design and management of agricultural production systems.

"Agroecology is concerned with the maintenance of a productive agriculture that sustains yields and optimizes the use of local resources while minimizing the negative environmental and socio-economic impacts" (Miguel Altieri).

Agroecological approaches: Agroecology is not associated with any one particular method of farming. Approaches to farming that fall under the umbrella of agroecology can include: organic farming, biodynamic farming, agroforestry and permaculture.

Integrated farming and conservation agriculture, also adopt agroecological principles and practices, but may also use external inputs (depending on how the approach is implemented).

Agroecological principles:

- Promoting recycling of biomass (e.g. plant material and agricultural residues) and optimizing nutrient availability.
- Ensuring favorable soil conditions for plant growth, particularly soil organic matter and biota.
- Minimizing losses from the agricultural system e.g. through water harvesting, soil and energy management.
- Maximizing species and genetic diversity (plants and livestock).
- Enhancing biological interactions and synergies to promote ecological processes and services.

Agroecological management practices:

- Relying on soil biota, e.g. earthworms, to enhance soil structure and fertility, the formation of water stable aggregates and soil water infiltration.
- Using legumes and symbiotic N-fixing bacteria to create nitrogen that is utilizable by the current crop and following crops.
- Using biologically active soil amendments (e.g. composts) to suppress soil-borne diseases and enhance soil structure and fertility.
- Practicing passive biological control of pests using field margins or beetle banks to encourage presence of beneficial insects.
- Designing cropping systems to disrupt pest life cycles or attract pests away from sensitive crops (including push-pull systems).
- Using crop rotation to manage soil fertility, weeds, pests and diseases.
- Using diverse cultivar and species mixtures (including combining crops and livestock), to improve resource use efficiency and reduce the spread of pests and diseases.
- Combining livestock species with different grazing behaviors and ensuring effective resource utilization to maximize nutrition and health benefits.
- Relying on minimal artificial inputs from outside the farm system.

Common features within agroecological management practices are:

- A strong biological rather than technological focus, with reliance on knowledge, skills and experience for effective management;
- Emphasizing the diversity of the farming system and its components, because complex relations between components help to deliver system resilience and stability.





• Aiming for reduced and efficient use of industrial/technological/synthetic agrochemical inputs through reuse and recycling.

Agroecological practices, case studies and information can be found at; <u>http://www.agricology.co.uk/</u>

Conclusions

This review of the function of soil biology in agriculture has highlighted that there is a need to support many aspects of soil biology in order to maintain conditions which are beneficial to crop nutrition. The existence of one organism within the soil can support many others so a holistic approach is vital in order to maintain the complex food web. Such an approach to encourage soil biology can be found in agroecological principles at http://www.agricology.co.uk/

In relation to specific improvements to soil biology the following practices should be encouraged;

- Reduced tillage.
- Reduced mineral inputs.
- Increased organic inputs.
- Maintenance of organic matter and promoting the increase of organic matter.
- Maintenance of soil surface organic residues.
- Compaction avoidance and alleviation.
- Maintenance of good drainage and avoidance of waterlogging.
- Maintain soil cover throughout the year, i.e. through using cover-crops over the winter.

Maintaining conditions and undertaking integrated farming practices, many of which are advocated by LEAF, will enable farmers to balance food production and the environment.







References

- Al-Karaki, G., Mcmichael, B. & Zak, J. (2004) Field response of wheat to arbuscular mycorrhizal fungi and drought stress. *Mycorrhiza*, **14**, (263-269).
- Bamforth, S. S. (1997) Protozoa: Recyclers and Indicators of Agroecosystem Quality. *In:* Benckiser, G. (ed.) *Fauna in soil ecosystems: recycling processes, nutrient fluxes, and agricultural production.* [s.l.]: CRC Press.
- **Bardgett, R.D., Cook, R.,** (1998). Functional aspects of soil animal diversity in agricultural grasslands. Applied Soil Ecology 10, 263-276.
- Bhattacharyya, P. N. & Jha, D. K. (2011) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World Journal of Microbiology and Biotechnology*, **28**, (1327-1350).
- **Blakemore, R.J.,** (2002). Cosmopolitan Earthworms: An Eco-taxonomic guide to the peregrine species of the world. VermEcology, Australia, 426 pp.
- Brown, G.G., (1995). How do earthworms affect microfloral and faunal community diversity? Plant and Soil 170, 247-269
- Brussaard, L., Behan-Pelletier, V.M., Bignell, D.E., Brown, V.K., Didden, W., Folgarait, P., Fragoso, C., Freckman, D.W., Gupta, V., Hattori, T., Hawksworth, D.L., Klopatek, C., Lavelle, P., Malloch, D.W., Rusek, J., Soderstrom, B., Tiedje, J.M., Virginia, R.A., (1997). Biodiversity and ecosystem functioning in soil. Ambio 26, 563-570.
- **Brussaard, L., de Ruiter, P.C., Brown, G.G.,** (2007). Soil biodiversity for agricultural sustainability. Agriculture Ecosystems & Environment 121, 233e244.
- Cameron, D., Hughes, B., Burrell, M., Leake, J. R., Summers, R. (2014) Wheat cultivars differ in their ability to form mycorrhizal symbiosis. [s.n.]: White Rose Sustainable Agriculture Consortium.
- Castellanos-Morales, V., Keiser, C., Cardenas-Navarro, R., Grausgruber, H., Glauninger, J., Garcia-Garrido, J. M., Steinkellner, S., Sampedro, I., Hage-Ahmed, K., Illana, A., Ocampo, J. A. & Vierheilig, H. (2011) The bioprotective effect of AM root colonization against the soil-borne fungal pathogen Gaeumannomyces graminis var. tritici in barley depends on the barley variety. *Soil Biology & Biochemistry*, **43**, (831-834).
- **Chan, K. Y.** (2001) An overview of some tillage impacts on earthworm population abundance and diversity implications for functioning in soils. *Soil & Tillage Research*, **57**, (179-191).
- **Coleman, D.C. (1994).** The microbial loop concept as used in terrestrial soil ecology studies. Microbial Ecology 28, 245-250.
- Coleman, D.C., Crossley, D.A.J., (2003). Fundamentals of soil ecology, Second ed. Academic Press New York.
- **Crotty, F.V.,** (2011). Elucidating the relative importance of the bacterial and fungal feeding channels within the soil food web under differing land managements. Centre for Agricultural & Rural Sustainability. Plymouth University, Plymouth, UK.





- Crotty, F.V., Adl, S.M., Blackshaw, R.P., Murray, P.J., (2012). Protozoan pulses unveil their pivotal position within the soil food web. Microbial Ecology 63, 905-918.
- Crotty, F.V., Adl, S.M., Blackshaw, R.P., Murray, P.J., (2013). Measuring soil protist respiration and ingestion rates using stable isotopes. Soil Biology and Biochemistry 57, 919-921.
- Crotty, F.V., Fychan, R., Scullion, J., Sanderson, R., Marley, C.L., (2015). Assessing the impact of agricultural forage crops on soil biodiversity and abundance. Soil Biology & Biochemistry 91, 119-126.
- Crotty, F.V., Fychan, R., Sanderson, R., Rhymes, J.R., Bourdin, F., Scullion, J., Marley, C.L., (2016). Understanding the legacy effect of previous forage crop and tillage management on soil biology, after conversion to an arable crop rotation. Soil Biology and Biochemistry 103, 241-252.
- **Cuddington, K., Byres, J.E., Wilson, W.G., Hastings, A.,** (2011). Ecosystem Engineers: Plants to Protists. Academic Press, London, UK, 432 pp.
- Culliney, T. W. (2013) Role of arthropods in maintaining soil fertility. Agriculture, 3, (629-659).
- Curry, J. P., Byrne, D. & Schmidt, O. (2002) Intensive cultivation can drastically reduce earthworm populations in arable land. *European Journal of Soil Biology*, **38**, (127-130).DEFRA, (2010). Fertiliser Manual (RB209). In: DEFRA (Ed.), Fertiliser Manual. The Stationery Office (TSO), Norwich, p. 257.
- DEFRA. (2016) The impact of shortened rotations on rhizosphere microbial diversity IF0128 [Online]. [s.l.]: DEFRA. Available: http://sciencesearch.defra.gov.uk/Default.aspx?Menu=Menu&Module=More&Location=No ne&Completed=0&ProjectID=14950 [Accessed: 5th September 2016].
- **DuPont, S.T., Ferris, H., Van Horn, M.,** (2009). Effects of cover crop quality and quantity on nematode-based soil food webs and nutrient cycling. Applied Soil Ecology 41, 157-167.
- **Ekelund, F.** (1999) The impact of the fungicide fenpropimorph (Corbel[®]) on bacterivorous and fungivorous protozoa in soil. *Journal of Applied Ecology*, **36**, (233-243).
- Ferris, H., Bongers, T., de Goede, R.G.M., (2001). A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Applied Soil Ecology 18, 13-29.
- Ferris, H., Matute, M.M., (2003). Structural and functional succession in the nematode fauna of a soil food web. Applied Soil Ecology 23, 93-110.
- Ferris, H., Venette, R.C., Scow, K.M., (2004). Soil management to enhance bacterivore and fungivore nematode populations and their nitrogen mineralisation function. Applied Soil Ecology 25, 19-35.
- Finlay, B.J., Fenchel, T.M., (2001). Protozoan community structure in a fractal soil environment. Protist 152, 203-218.
- Foissner, W. (1997) Protozoa as bioindicators in agroecosystems, with emphasis on farming practices, biocides, and biodiversity. *Agriculture, ecosystems & environment*, **62**, (93-103).





- Fourie, H., Ahuja, P., Lammers, J. & Daneel, M. (2016) Brassicacea-based management strategies as an alternative to combat nematode pests: A synopsis. *Crop Protection*, **80**, (21-41).
- Frund, H.C., Graefe, U., Tischer, S., (2011). Earthworms as bioindicators of soil quality. In: Karaca, A., (ed). Biology of Earthworms. Springer-Verlag, Berlin, Germany, 316 pp.
- **Gleadell**. (2016) *Soil Health RAGT* [Online]. Gainsborough: Gleadell Agriculture Ltd. Available: http://store.gleadell.co.uk/pages/soil-health [Accessed: 5th September 2016].
- Hawksworth, D. L., (1991). The fungal dimesnion of biodiversity magnitude, significance and conservation. Mycological Research 95, 641-655.
- Hayat, R., Ali, S., Amara, U., Khalid, R. & Ahmed, I. (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. *Annals of Microbiology*, **60**, (579-598).
- Hayat, R., Ali, S., Siddique, M. T. & Chatha, T. H. (2008) Biological nitrogen fixation of summer legumes and their residual effects on subsequent rainfed wheat yield. *Pakistan Journal of Botany*, 40, (711-722).
- Hijri, M. (2016) Analysis of a large dataset of mycorrhiza inoculation field trials on potato shows highly significant increases in yield. *Mycorrhiza*, **26**, (209-214).
- House, G. J. & Parmelee, R. W. (1985) Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. *Soil and Tillage Research*, **5**, (351-360).
- Ingham, E. R. (2016) *Soil Food Web* [Online]. [s.l.]: USDA. Available: http://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/soils/health/biology/?cid=nrcs142p2_ 053868 [Accessed: 26th August 2016].
- IPNI (2016a) Nitrogen Notes: Denitrification. In: (IPNI), IPNI. (ed.) http://www.ipni.net/publication/nitrogenen.nsf/0/668099AE825517CB85257DD600054B8C/\$FILE/NitrogenNotes-EN-5.pdf. Georgia: IPNI.
- IPNI (2016b) Nitrogen Notes: Nitrification. In: (IPNI), IPNI (ed.) http://www.ipni.net/publication/nitrogenen.nsf/0/7F7F448C4D064A5985257C13004C83A3/\$FILE/NitrogenNotes-EN-04.pdf. Georgia: IPNI.
- Jastrow, J. (1996) Soil aggregate formation and the accrual of particulate and mineral-associated organic matter. *Soil Biology and Biochemistry*, **28**, (665-676).
- Kabir, Z., O'halloran, I. P., Widden, P. & Hamel, C. (1998) Vertical distribution of arbuscular mycorrhizal fungi under corn (Zea mays L.) in no-till and conventional tillage systems. *Mycorrhiza*, 8, (53-55).
- Khan, A. G. (2005) Role of soil microbes in the rhizospheres of plants growing on trace metal contaminated soils in phytoremediation. *Journal of Trace Elements in Medicine and Biology*, 18, (355-364).
- Leake, J. R., Johnson, D., Donnelly, D. P., Muckle, G. E., Boddy, L. & Read, D. J. (2003) Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and





agroecosystem functioning. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **82**, (1016-1045).

- Ma, W., Brussaard, L. & De Ridder, J. (1990) Long-term effects of nitrogenous fertilizers on grassland earthworms (Oligochaeta: Lumbricidae): their relation to soil acidification. *Agriculture,* ecosystems & environment, **30**, (71-80).
- Naseri, R., Maleki, A., Naserirad, H., Shebibi, S. & Omidian, A. (2013) Effect of plant growth promoting rhizobacteria (PGPR) on reduction nitrogen fertilizer application in rapeseed (Brassica napus L.). *Middle-East Journal of Scientific Research*, **14**, (213-220).
- Neher, D.A., (2001) Role of nematodes in soil health and their use as indicators. Journal of Nematology 33, 161-168.
- Orgiazzi, A., Bardgett, R.D., Barrios, E., Behan-Pelletier, V., Briones, M.J.I., Chotte, J.-L., De Deyn,
 G.B., Eggleton, P., Fierer, N., Fraser, T., Hedlund, K., Jeffery, S., Johnson, N.C., Jones, A.,
 Kandeler, E., Kaneko, N., Lavelle, P., Lemanceau, P., Miko, L., Montanarella, L., Moreira,
 F.M.S., Ramirez, K.S., Scheu, S., Singh, B.K., Six, J., van der Putten, W.H., Wall, D.H., (2016).
 Global Soil Biodiversity Atlas. Publications Office of the European Union, Luxembourg.
- Parmelee, R. W., Beare, M. H., Cheng, W., Hendrix, P. F., Rider, S. J., Crossley, D. A. & Coleman, D.
 C. (1990) Earthworms and Enchytaeids in Conventional and No-Tillage Agroecosystems a Biocide Approach to Assess their Role in Organic-Matter Breakdown. *Biology and Fertility of Soils*, **10**, (1-10).
- Pelosi, C., Toutous, L., Chiron, F., Dubs, F., Hedde, M., Muratet, A., Ponge, J.-F., Salmon, S. & Makowski, D. (2013) Reduction of pesticide use can increase earthworm populations in wheat crops in a European temperate region. *Agriculture, ecosystems & environment,* 181, (223-230).
- Platen, R. & Glemnitz, M. (2016) Does digestate from biogas production benefit to the numbers of springtails (Insecta: Collembola) and mites (Arachnida: Acari)? *Industrial Crops and Products*, 85, (74-83).
- Rinaudo, V., Bàrberi, P., Giovannetti, M. & Van Der Heijden, M. G. (2010) Mycorrhizal fungi suppress aggressive agricultural weeds. *Plant and soil*, **333**, (7-20).
- Sahin, F., Cakmakci, R. & Kantar, F. (2004) Sugar beet and barley yields in relation to inoculation with N(2)-fixing and phosphate solubilizing bacteria. *Plant and Soil*, 265, (123-129).
- Schmidt, O., Clements, R. O. & Donaldson, G. (2003) Why do cereal-legume intercrops support large earthworm populations? *Applied Soil Ecology*, 22, (181-190).
- Smiley, R. W. & Nicol, J. M. (2009) Nematodes which challenge global wheat production. Wheat Science and Trade. BF Carver, ed. Wiley-Blackwell, Ames, IA, 10, (171-187).
- Springett, J. & Syers, J. (1984) Effect of pH and calcium content of soil on earthworm cast production in the laboratory. *Soil Biology and Biochemistry*, **16**, (185-189).
- Swift, M., Heal, O.W., Anderson, J.M., (1979). Decomposition in terrestrial ecosystems. Blackwell Scientific Publications, Oxford, 362 pp.





- **Tebrugge, F. & During, R. A.** (1999) Reducing tillage intensity a review of results from a long-term study in Germany. *Soil & Tillage Research*, **53**, (15-28).
- Thiele-Bruhn, S., Bloem, J., de Vries, F.T., Kalbitz, K., Wagg, C., (2012). Linking soil biodiversity and agricultural soil management. Current Opinion in Environmental Sustainability 4, 523-528.
- **Timper, P., Davis, R., Jagdale, G., Herbert, J., (**2012). Resiliency of a nematode community and suppressive service to tillage and nematicide application. Applied Soil Ecology 59, 48-59.
- Van Groenigen, J.W., Lubbers, I.M., Vos, H.M.J., Brown, G.G., De Deyn, G.B., van Groenigen, K.J., 2014. Earthworms increase plant production: a meta-analysis. Scientific Reports 4, 6365
- Verbruggen, E., Röling, W. F. M., Gamper, H. A., Kowalchuk, G. A., Verhoef, H. A. & Van, D. H.
 (2010) Positive effects of organic farming on below-ground mutualists: large-scale comparison of mycorrhizal fungal communities in agricultural soils. *The New Phytologist*, 186, (968-979).
- Veresoglou, S. D. & Menexes, G. (2010) Impact of inoculation with Azospirillum spp. on growth properties and seed yield of wheat: a meta-analysis of studies in the ISI Web of Science from 1981 to 2008. *Plant and Soil*, **337**, (469-480).
- Vosatka, M., Latr, A., Gianinazzi, S. & Albrechtova, J. (2012) Development of arbuscular mycorrhizal biotechnology and industry: current achievements and bottlenecks. *Symbiosis*, **58**, (29-37).
- Wilson, G. W., Rice, C. W., Rillig, M. C., Springer, A. & Hartnett, D. C. (2009) Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. *Ecology Letters*, **12**, (452-461).
- Wolfarth, F., Schrader, S., Oldenburg, E. & Brunotte, J. (2016) Mycotoxin contamination and its regulation by the earthworm species Lumbricus terrestris in presence of other soil fauna in an agroecosystem. *Plant and Soil*, **402**, (331-342).