## Soil food web controls on nitrogen mineralization are influenced by agricultural practices in humid temperate climates

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## Abstract

Agricultural crop production depends upon judicious use of nitrogen (N) fertilizers to sustain yields. Globally, the N recovery rate by crops is about 60%, meaning that the rest of the N applied to agroecosystems is transformed to forms that are not available for crop uptake or are lost to the environment. Considering that part of the soil N supplied to crops comes from biological  $N_2$ fixation and mineralization of soil organic N, quantifying these contributions could reduce our reliance on exogenous N inputs. This review examined how the microbially mediated reactions of N mineralization and nitrification contribute to the soil N supply, and biotic controls on these reactions in the soil food web. Potential N mineralization by heterotrophic bacteria and fungi can exceed 10% of the total soil N per year, and ammonium released by mineralization is rapidly transformed to nitrate through the action of chemoautotrophic ammonia oxidizers (bacteria and archaea) followed by heterotrophic and chemoautotrophic nitrifiers (bacteria and fungi). Predation of these micro-organisms, primarily by soil microfauna, accounts for additional release of ammonium, estimated at 32-38% of the annual N mineralization. Soil meso- and macro-fauna also contribute to N mineralization and nitrification by accelerating the decomposition of organic substrates and modifying the soil habitat in ways that favour microbial activity. Tillage, application of organic amendments and improving soil drainage in humid temperate regions should favour N mineralization and nitrification processes in soil food web, whereas agrochemical use is expected to have a negligible effect. In summary, the soil food web contribution to N mineralization needs to be included in the soil N supply concept, which requires the development of field-based measurements and models of the soil N supply.

Keywords: Soil nitrogen cycle, Soil fauna, Soil nitrogen supply

## Introduction

Agricultural crop growth and yield depends on the availability of nitrogen (N) for protein synthesis, chlorophyll formation, photosynthesis and other essential functions. Some agricultural crops, notably legumes, benefit from associations with symbiotic and free-living N<sub>2</sub>-fixing bacteria that supply a portion of the N required for primary production. Globally, N<sub>2</sub> fixation provides an estimated 50–70 Tg N/year to support the growth of pasture and fodder legumes, rice, sugarcane, non-legumes and savannahs [1]. In humid temperate climates, the N<sub>2</sub>

fixation is from 30 to 50 kg N ha/ year for common bean (*Phaseolus* sp.) and may reach 170 kg N ha/ year for soybean (*Glycine max* (L.) Merr.), while forage legumes such as lucerne (*Medicago sativa* L.) fix an estimated 50–300 kg N ha/ year with symbiotic N<sub>2</sub>-fixing bacteria [1, 2]. These N<sub>2</sub> fixation rates represent 36–88% of the crop N requirements; the rest of the N required for crop production is absorbed from the soil solution as ammonium (NH<sub>4</sub><sup>+</sup>) and nitrate (NO<sub>3</sub><sup>--</sup>), with free amino acids making a minor contribution to plant N nutrition [3, 4]. Since biological N<sub>2</sub> fixation accounts for only 15–20% of the N input in agroecosystems [1, 5] and most crops grow on soils

where the naturally-occurring concentrations of plantavailable  $NH_4^+$  and  $NO_3^-$  are insufficient to achieve maximum yields, other N inputs are needed.

Chemical fixation of  $\mathsf{N}_2$  through the Haber–Bosch process is the starting point for synthesis of inorganic N fertilizers, the cornerstone of modern agriculture. Globally, inorganic N fertilizer consumption increased from 10.8 million tonnes N/year in the 1960s to an estimated 97.9 million tonnes N/year in 2012 [6, 7]. Other N inputs to agroecosystems include manure (13% of global N input), wet and dry atmospheric deposition (11% of global N input), sedimentation (2.4% of global N input) and crop residue (8.3% of global N input), based on estimates from the year 2000 [8]. The fact that inorganic N fertilizers account for about 50% of the N input for global agricultural production is cause for concern. The chemical N<sub>2</sub> fixation process generally relies on natural gas (methane), a non-renewable energy source, to generate  $H_2$  for the chemical reaction and to heat the reaction vessel. Hence, agricultural systems that depend heavily on inorganic N fertilizers require more energy to sustain in the long term. Global assessment of N flows in cropland showed an average N recovery rate of 59% in crop biomass, indicating that more than 40% of N inputs are transformed into forms that are not available for plant uptake or lost from agroecosystems [8]. This imbalance in the global N cycle means that reactive N is emitted to the atmosphere or entering aquatic ecosystems, resulting in unintentional fertilization of non-agricultural ecosystems [5, 9, 10].

One way to counteract these undesirable environmental consequences of agricultural production is to increase the N recovery rate, and this can be done by following good management practices with respect to fertilizer use (e.g., soil testing, diagnostic plant analysis, choice of appropriate fertilizer compounds, selection of proper nutrient ratios, attention to timing and placement of fertilizers). These good management practices can be fine-tuned for particular crops according to the 4R nutrient stewardship approach [11] or integrated nutrient management planning [12]. Another way to improve N recovery rate is to apply fewer N inputs to an agroecosystem and rely on the N supplied from mineralization of soil organic N, resulting from soil biological activity. Research dating from the 1980s suggests that more complex soil food webs increase N mineralization from soil organic matter [13, 14], which implies that agroecosystems with such soil food webs will require less inorganic N fertilizer to achieve optimal crop production. But how does the soil food web contribute to the soil N supply, which is defined as the amount of N in the soil (in addition to that from N inputs) that is available for uptake by the crop during the growing season, taking account of N losses? Can agricultural soils under particular management support an active soil food web community that mineralizes N from organic matter in synchrony with crop N requirements, thereby reducing reliance on N inputs and improving the N recovery rate? This paper will explore these and other questions related to how the soil food web controls N mineralization in agricultural soils, with emphasis on findings from humid temperate agroecosystems.

The objectives of this review are: (1) to investigate how N mineralization and nitrification processes contribute to the soil N supply, (2) to determine how the soil food web controls N mineralization and nitrification, (3) to determine how agricultural management practices affect the structure and functions of the soil food web related to N mineralization and nitrification, and (4) to give recommendations about how to integrate soil food webs into our concept of the soil N supply.

## Microbial Basis of N Transformations Contributing to the Soil N Supply

The soil N cycle is a dynamic, multi-trophic cascade involving abiotic and biotic controls that govern the rates at which organic N compounds are transformed to inorganic N forms, and vice versa. In agroecosystems, biological N<sub>2</sub> fixation, N mineralization and nitrification reactions are the most relevant for crop production because these microbially mediated reactions produce inorganic N compounds that can be assimilated by plants. The next sections will focus mainly on how the soil food web affects N mineralization and nitrification, given the contribution of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> from these reactions to the soil N supply (kg N/ha), defined as [15]:

Soil N supply = Mineral N+Crop N+Mineralizable Soil N

 $(\mathbf{I})$ 

Mineral N (kg N/ha) is the NH<sub>4</sub>-N plus NO<sub>3</sub>-N concentration of the soil in the potential rooting depth of the crop, Crop N (kg N/ha) is the N concentration in the crop at the time that soil was sampled for Mineral N measurement, and Mineralizable Soil N (kg N/ha) is the estimated amount of N that becomes available for crop uptake from mineralization of soil organic matter during the growing season, after the time that soil was sampled for Mineral N determination.

The soil N supply concept is illustrated in Figure 1. In soil with no exogenous N inputs, the soil N supply comes from the soluble  $NH_4^+$  and  $NO_3^-$  pool in the root zone, which is derived primarily from N mineralization, ammonia oxidation and nitrification reactions and supplemented by the biological N<sub>2</sub> fixation of free-living, associative and symbiotic bacteria. Since the inherent soil N supply is generally insufficient to achieve optimal economic yields in humid temperate agroecosystems, it becomes important to consider the contribution of N inputs to the soluble  $NH_4^+$  and  $NO_3^-$  pool, and to the mineralizable soil organic matter pool (Figure 1). In humid temperate regions, the inherent soil N supply comes



**Figure 1** The nitrogen cycle in agroecosystems, illustrating major exogenous inputs (atmospheric N, inorganic N fertilizer, manure N and crop residue N; the sediment N input is not shown). The soil N supply to crops includes  $NH_4^+$  originating from biological N<sub>2</sub> fixation and from the  $NH_4^+$  and  $NO_3^-$  pools, which are replenished by N mineralization and nitrification reactions

mostly from N mineralization during the growing season (spring and summer), since N mineralized during fall and winter is susceptible to loss in the environment [16]. The  $NH_4^+$  and  $NO_3^-$  concentration in the root zone declines with crop N uptake and when these reactive N forms are transformed through abiotic reactions (e.g.,  $NH_4^+$  fixation on clays), biotic processes (e.g., immobilization in microbial biomass) or lost in gaseous forms and water (Figure 1).

## **Nitrogen Mineralization**

In the cool humid soils of eastern Canada, the soil organic matter contains 4408–11 455 g organic C/m<sup>2</sup> and between 359 and 1008 g total N/m<sup>2</sup> [17]. Only a fraction of the organic N pool is mineralized during the growing season, as most of the organic N is physically or chemically protected from decomposition. In potato fields on sandy soils, the potentially mineralizable N pool was 3.8-13% of the total N pool [18], while the potentially mineralizable N pool on medium – to heavy-textured soils under forage grass production with a history of manure application [19]. In those studies, the potentially mineralizable N pool was determined after aerobic soil incubation for 24 weeks at  $25^{\circ}$ C, one of the laboratory-based methods used to evaluate N mineralization [20].

Nitrogen mineralization is intricately linked to the decomposition of organic matter, since the heterotrophic micro-organisms responsible for the reaction need carbon (C), N and other nutrients derived from organic matter to support their metabolic functions, growth and reproduction. As described by Schimel and Bennett [21], decomposition of organic matter is the depolymerization of organic soil polymers by extracellular enzymes, followed by their degradation to monomeric compounds such as amino acids, amines, amino sugars and urea (Figure 2). Since less than 15% of the total N pool is potentially mineralizable, this suggests that depolymerization is the rate-limiting step in the reaction. The regulatory gate hypothesis [22] indicates that abiotic factors such as those listed in Figure 2 control the rate limiting step in the reaction, which seems to be the case for C mineralization [23] but is not yet confirmed for N mineralization.

After monomeric compounds are cleaved from complex polymers, they may be degraded to  $NH_4^+$  through the action of abiotic enzymes (e.g., urease) present in soil solution or associated with soil organo-mineral complexes [24]. Monomeric compounds are also absorbed by microbial cells and undergo ammonification to yield  $NH_4^+$  as the end product of the reaction. Soil microbes are proposed to assimilate N via two pathways: (1) the mineralization-immobilization-turnover (MIT)



**Figure 2** Soil N mineralization and nitrification reactions, showing depolymerization as the rate limiting step in the conversion of soil organic matter to monomeric N compounds, a small fraction of which is absorbed directly by plants, and the remainder is transformed by microbes directly or through the MIT (mineralization-immobilization-turnover) route to  $NH_4^+$  (adapted from [21]). Soil fauna control microbial communities through predation, which releases additional  $NH_4^+$  into the soil solution. Other biotic and abiotic factors controlling these reactions are listed

route, indicated in Figure 2, and (2) the direct route. The MIT route involves extracellular deamination of organic N and ammonification of  $NH_4^+$  before it is assimilated by soil bacteria, which is thought to occur when mineral N availability is high [25]. The direct route occurs when monomers (e.g., amino acids, amino sugars) are directly assimilated and deaminated inside bacterial cells, and N exceeding physiological requirements is actively excreted into the soil  $NH_4^+$  pool [25, 26]. It is hypothesized that both pathways operate concurrently, but within different microsites in heterogeneous soils [27, 28]. Surplus  $NH_4^+$  released from microbial biomass enters the  $NH_4^+$  pool, where it is available for plant uptake or undergoes other transformations.

When organic N is transformed via the direct route, the N immobilized in microbial cells can be released as  $NH_4^+$  when those micro-organisms are consumed (predated) by protists and nematodes [29], as illustrated in Figure 2. Predation by soil fauna contributes an

estimated 30% of N mineralization under field conditions [30]. Soil protists assimilate 10-40% of the microbial C consumed and nematodes use an estimated 50-70% of microbial C consumed [31, 32], which results in lysed microbial cells and cellular contents returning to the soil organic matter and monomeric N pools (Figure 2). When protists and nematodes prey on N-rich bacteria, they consume more N than their nutritional requirements and release excess  $NH_4^+$  into the soil solution (Figure 2), which is available for plant uptake or other transformations in the N cycle. Predation by larger soil fauna may alter the growth pattern and enzyme production of soil micro-organisms, leading to higher protease and arginine deaminase activities in forest soil mesocosms with mesofauna [33, 34]. However, the stimulation or suppression of N mineralization and other functions of the soil microbial community by predators appears to depend on the composition of available substrates and the mineral N concentration [34, 35]. Another way that soil fauna

affect N mineralization is by fragmenting, mixing and redistributing organic matter in the soil, which can bring the microbial community in contact with substrates or create habitats (e.g., faecal pellets, burrow linings) that are favourable microsites for decomposition and N mineralization [36]. Soil food web interactions that moderate microbially mediated N transformations will be discussed in more detail below.

## Nitrification

In well-aerated mineral soils, including those in humid temperate agroecosystems, the  $NH_4^+$  concentration is generally less than 10 mg NH<sub>4</sub>-N/kg [personal observation] because  $NH_4^+$  is rapidly converted to  $NO_3^$ through nitrification [37]. Two groups of chemoautotrophic micro-organisms are involved: (1) ammonia oxidizers, which catalyse the ammonia oxidation and hydroxylamine oxidation reactions (converts  $NH_4^+$  to  $NH_2OH$  and then  $NO_2^-$ ), and (2) nitrifiers that oxidize  $NO_2^-$  to  $NO_3^-$ . There is considerable diversity in the chemoautotrophs that derive energy from these reactions, with representative species from the autotrophic bacteria, archaea and heterotrophic bacteria among the ammonia oxidizers; nitrifiers include autotrophic bacteria, heterotrophic bacteria and heterotrophic fungi [38]. The diversity in these groups implies that ammonia oxidation and nitrification should occur over a wide range of soil conditions, although these biological reactions will be affected by abiotic and biotic soil factors, as listed in Figure 2. The ammonia oxidation reaction is of interest because it generates byproducts - nitroxyl radicals (HNO), nitric oxide  $(NO_{(g)})$  and nitrous oxide  $(N_2O_{(g)})$  – and the gaseous byproducts are susceptible to loss from soil. Nitrification produces  $NO_3^-$ , which can be assimilated by plants or immobilized in microbial biomass, but is not strongly bound to the soil matrix and therefore is prone to loss via leaching or denitrification after rainfall and irrigation events.

## Soil Food Web: Moderating the Microbially Mediated N Transformations

How does the soil food web moderate microbially mediated N transformations that are important for the soil N supply? As illustrated in Figure 2, soil fauna interact with heterotrophic micro-organisms to accelerate the N mineralization rate and increase the amount of  $\rm NH_4^+$ released in the soil solution, which can undergo further transformation by chemoautotrophic ammonia oxidizers and nitrifiers. Predation of soil micro-organisms by soil microfauna (mainly protists and nematodes [31, 32]) can alter the metabolic activity, population structure, competitive and mutualistic interactions in the soil microbial community. Larger meso- and macro-fauna also consume soil micro-organisms, but whether this is predation or a consequence of their preference for palatable, partially decomposed organic substrates with certain physical size (because of ease of ingestion) is not clear. Feeding rates are consistently high at lower trophic levels (e.g., micro-fauna) and relatively low at the higher trophic levels [39]. For this reason, we consider microfauna to be the primary predators of soil micro-organisms involved in N cycling (Figure 3).

The other way that soil fauna influence the activity of heterotrophic and chemoautotrophic micro-organisms involved in N transformations is through the alteration of organic substrates and the soil habitat (Figure 3). Soil meso- and macro-fauna are well known for their manipulation of surface litter - they fragment fresh and partially decomposed residues, then mix some of those residues with soil by burying them [36, 38]. Later, they may return to eat the well-decomposed residue. Ingesting fresh or partially decomposed residues, along with mineral soil, is another way that residues come into contact with decomposer micro-organisms. Faunalmediated inoculation of residue is expected to speed depolymerization and release of soluble substrates as the residue passes through the intestinal tract, or after faecal pellets are deposited on the soil surface or within the soil profile [40]. Finally, soil meso- and macro-fauna can physically modify the soil environment because their faecal deposits are newly-formed macroaggregates, a favourable habitat for soil micro-organisms, particularly aggregates with mean diameter from 250 to  $425\,\mu\text{m}$ [41]. In addition, macrofauna burrows are macropores (>10 $\mu$ m diameter) that serve as conduits for water infiltration and gas exchange in the soil profile, which can indirectly affect the activity of micro-organisms involved in soil N transformations [38].

# Predation as a Control on Soil N Mineralization and Nitrification

A classic microcosm experiment by Ingham et al. [42] demonstrated a 30% increase in soil mineral N concentration and 60% greater plant biomass (shoots and roots of Bouteloua gracilis, a perennial C4 grass) when bacterial-feeding nematodes were introduced to microcosms with plants and bacteria. However, the addition of fungal-feeding nematodes had negligible impact on the soil mineral N concentration and plant biomass [42]. In a shortgrass prairie, Hunt et al. [43] estimated that bacteria were primarily responsible for N mineralization, releasing 4.5 g N/m<sup>2</sup>/year, while fungi contributed 0.3 g N/m<sup>2</sup>/year. Predation by amoebae and bacterial-feeding nematodes also contributed to N mineralization, with an additional 2.9 g N/m<sup>2</sup>/year released by these predators [43]. Protists are the most effective bacterial predators because they have short generation times (minimum of 2-4h), large populations and high production rates (10-12 times



**Figure 3** Soil food web controls on the microbially mediated N mineralizaton and nitrification reactions, showing the importance of predation dominated by the microfauna (protists, bacterial – and fungal-feeding nematodes, underlined) as well as substrate quality and soil habitat modification by soil meso- and macrofauna, predominantly earthworms (under-

the standing biomass per year) [44]. In a dryland wheat agroecosystem, N mineralization from bacteria and fungi released 10.1 g N/m<sup>2</sup>/year and an additional 4.9 g N/m<sup>2</sup>/year came from predation, probably by protists because they were more abundant (7-fold more biomass) than nematodes and microarthropods [45]. A portion of the N consumed by a microfaunal predator is retained within its biomass and may be recycled when the organism dies, or transferred to higher trophic levels within the soil food web. Only 2–3% of N was transferred from lower to higher trophic levels (e.g., from bacter-

ivorous nematodes to predaceous nematodes, then to nematophagous mites, and finally to predaceous mites) in a shortgrass prairie [43], which implies that food webs with predators at several trophic levels will stimulate  $\rm NH_4^+$  release to the soil solution, since very little of it is retained in their biomass.

The N mineralization from predation contributes to the soil N supply, as demonstrated in controlled studies where plant N uptake and biomass accumulation were enhanced in the presence of predators such as protists [46], microbial-feeding nematodes [47], enchytraeids and

microarthropods [48]. Yet in experimental microcosms with simulated forest soil and poplar (*Populus trichocarpa*), soil microfauna did not seem to be important for N mineralization because greater plant N uptake and biomass accumulation occurred when soil micro-, meso- and macrofauna were present [49]. This suggests that predation is often, but not always, controlling soil N mineralization.

The previous examples demonstrate the net effect of predation on the soil N supply, but we also need to consider the interspecific interactions between predators and their prey. Changes in bacterial morphology in response to predation by protists can lead to larger or smaller cell sizes, outgrowths of filamentous bacterial cells and microcolonies that the protists apparently cannot digest effectively [50]. Selective predation on older, larger bacterial cells can provide opportunities for the growth of younger cells with higher metabolic activity [30]. Predation by protists often stimulates nitrifying bacteria and leads to high  $NO_3^-$  concentrations in the rhizosphere [51], which could be the result of greater availability of  $NH_4^+$ , selective removal of fast-growing bacterial competitors, or sensory signals exchanged between bacteria and plants when predators are present. Phillips et al. [52] proposed that the  $N_2$ -fixing bacteria Sinorhizobium meliloti would respond to nematode predation by producing sensory signals, warning signals and exudation factors that could induce a response from a host plant (e.g., secretion of nematode-repelling compounds by the plant, induction of nodulation genes) and thereby protect some of the bacterial population from the predator. This concept is consistent with the idea of bacterial quorum sensing, in which the production, detection and response to specific molecular signals (bacteria-bacteria, plant-bacteria and others) regulates gene expression [53]. The soil N supply may be partially controlled by plant-bacteria signalling since proteobacterial signal molecules (acyl-homoserine lactones) were linked to the production and activity of extracellular chitinase and protease enzymes responsible for organic N depolymerization in the rhizosphere of oat seedlings [54]. Future research into bacterial contributions to the soil N supply should consider the multi-trophic interactions in the soil food web and plant systems, from molecular to community levels.

The bacterial-dominated food web described above is linked to a faster rate of N cycling than fungal-dominated food webs [55]. A bacterial-dominated food web could be advantageous when growing annual grain, oilseed or vegetable crops in humid temperate climates since most of those crops will require ample N and reach physiological maturity within 100–120 days under field conditions. Depending on when the bacterial-mediated N mineralization occurs during the growing season and where in the soil profile, relative to the rhizosphere and particularly young unsuberized root tips that actively assimilate NH4<sup>+</sup> through root interception, the mineralized  $NH_4^+$  may be taken up by the crop or it could undergo nitrification. Still, most annual crops can access  $NO_3^-$  that moves to the rhizosphere by mass flow. Nitrate assimilated is a highly regulated energy-dependent process that involves active transport of  $NO_3^-$  through epidermal and cortical cells into the cytosol; next  $NO_3^$ crosses the endodermis and moves through the xylem to leaf cells where it is reduced to ammonia and then incorporated into glutamine for protein synthesis and other metabolic functions [56]. However,  $NO_3^-$  losses from leaching and denitrification during the growing season and in the post-harvest period are common in annually cropped agroecosystems in humid temperate regions of Canada [57, 58], which implies that the soil N supply from N fertilizer and from N mineralization with a bacterial-dominated food web provides more  $NH_4^+$  and  $NO_3^-$  than needed for plant uptake and often leads to N losses.

In contrast, a fungal-dominated food web has a slower N mineralization rate and retains more N in the soilplant system [59, 60], which led de Vries and Bardgett [61] to propose a variety of management options to promote fungal-based soil food webs and plant-microbial linkages, thereby reducing N losses from agroecosystems. Not only do larger fungal populations have substantial capacity to immobilize added NH<sub>4</sub>NO<sub>3</sub> fertilizer in their biomass [60], but fungal predators such as fungivorous nematodes and collembola have longer generation times, smaller populations and biomass than bacterial predators [44]. This further lengthens the time that N is retained within the soil food web and hence protected from loss. Restructuring the soil microbial community to favour greater fungal abundance in agroecosystems can be achieved by manipulating abiotic factors such as the amount and chemical composition of C and N contained in detritus, inorganic N inputs, tillage intensity and other agricultural practices [61]. However, it is not clear whether such interventions can be accomplished without compromising crop yields. In humid temperate regions, ideally the soil food web structure would be dynamic and shift from bacterialdominated during the growing season (i.e., to promote N mineralization for crop production) to fungal-dominated in the post-harvest and overwinter period (i.e., to increase N retention). Selecting management practices that promote such soil food web dynamics requires a deeper understanding of interactions between fungi and bacteria, such as competition for simple and complex substrates such as root exudates and cellulose, mutualistic interactions (e.g., cometabolism in lignocellulosic degradation, bacteria that consume fungal exudates, endosymbiosis) and parasitism (e.g., mycophagy, decomposition of fungal cell walls) [62]. Also, we do not know how predators in the soil food web affect the activities of recently discovered ammonia-oxidizing soil archaea in the phyla Crenarchaeota and Thaumarchaeota [63, 64], so this remains an open research question.

## Substrate Quality and Habitat Modification as Controls on Soil N Mineralization and Nitrification

Heterotrophic micro-organisms involved in N mineralization require ample substrates for growth and reproduction, primarily organic C as an energy source and for metabolic processes. Soil organic matter, root exudates, manure, crop litter and other organic substrates may be used, as long as they are physically accessible and the micro-organism can produce the necessary exoenzymes to cleave simple substrates from complex polymers. Microbial metabolism also requires C and N in fixed proportions, based on the C: N ratio of the microbial cell (from 5:1 to 8:1 in bacterial cells; between 9:1 and 22:1 in fungal cells [38]). Consequently, micro-organisms may not degrade a C-rich substrate if they cannot obtain sufficient N from the substrate or immobilize enough  $NH_4^+$  and  $NO_3^-$  from the soil solution to support their metabolic processes. In model soil food webs, increasing the C:N ratio of organic matter from 10:1 to 12.5:1 reduced the N mineralization rates because more NH4<sup>+</sup> was immobilized, whereas N mineralization rates increased by 38% when the C:N ratio of bacterial biomass increased from 4:1 to 5:1 [65].

Fragmentation, consumption and mixing organic substrates with soil are ways that soil meso- and macro-fauna speed up decomposition and N mineralization processes. Increasing the surface area of litter and other organic materials allows it to be more readily colonized by heterotrophic bacteria and fungi [66]. In humid temperate regions, earthworms are responsible for this process, with collembola and microarthropods contributing to a lesser extent. Soil meso- and macro-fauna also facilitate contact between soil micro-organisms and organic substrates. For example, earthworms consume soil, which contains micro-organisms, along with fresh or partially decomposed organic matter. After grinding in the gizzard, the mixture is bathed in a solution of intestinal mucus containing water, electrolytes, glycoproteins, mucopolysaccharides, lectins and haemocyanin [67]. Some of water and nutrients are resorbed in the hindgut and proctodeum, but fresh casts excreted by the earthworm are generally wetter and enriched in NH4<sup>+</sup> and NO3<sup>-</sup> relative to the bulk soil [68]. Soil leaving the earthworm gut has more gram positive bacteria, gram negative bacteria and eukaryotes than the bulk soil, as well as fewer fatty acids derived from plant material [69]. Faecal pellets from oribatid mites had a lower lignin: N ratio than the original litter and the presence of mites increased  $NH_4^+$  concentration by 4.9 times and  $NO_3^-$  concentration by 35 times, after 34 d incubation with corn litter [70]. This indicates that ingestion of organic substrates by soil meso- and macro-fauna favours N mineralization and nitrification.

Physical modification of the soil habitat by soil fauna can bring soil micro-organisms in contact with organic substrates or change the structure and porosity of the soil

environment [38], which is often favourable for heterotrophs and chemoautotrophs involved in N mineralization and nitrification. For example, the casts deposited by earthworms on the soil surface or within the soil profile support larger microbial populations owing to higher organic matter content and moisture than the bulk soil. Greater microbial biomass, higher N mineralization rates and higher nitrification rates are reported in casts [71, 72] and middens [73], relative to bulk soil. The lining of earthworm burrows is cemented with mucus, which serves as a substrate for microbial growth. Under laboratory conditions, nitrification rates were 20-fold higher in the burrow lining than in bulk soil [74]. Since burrows function as macropores, the environment is well aerated, which should favour ammonia oxidation by the chemoautotrophic bacteria and archaea, followed by nitrification by chemoautotrophic and heterotrophic micro-organisms.

## Agricultural Practices Impacting Soil Food Web Structure and Functions

The previous sections described how predation and modification of substrate quality and habitat by soil fauna can accelerate microbially mediated N mineralization and nitrification. Much of the evidence to support this notion is based on controlled laboratory experiments in homogenous (sieved) soils without much disturbance (i.e., constant soil temperature and moisture) and often without plants. Field soils have heterogeneous physical, chemical and biological properties, even at relatively small spatial scales, while agroecosystems in humid temperate regions are subject to changing temperatures and irregular rainfall events, and are planted with crops of economic importance such as corn, soybean and other oilseeds, cereals, forages and potatoes. In addition, agricultural activities such as tillage, organic residue management, agrochemical application and water management may cause disturbance to the soil food web, or they may favour some organisms disproportionately. For better predictions about the soil N supply, we require information about how these agricultural practices influence the soil food web structure and its functions related to N mineralization and nitrification.

## Tillage

Tillage is the mechanical manipulation of soil to prepare the seedbed, control weeds and incorporate agricultural chemicals and amendments in soil [75, 76]. Plough pans, rotary harrows and other tillage machinery are used to reduce soil compaction and remove excessive surface residues prior to planting the field. Thorough mixing of surface residues and other materials in the plough layer (generally 10–20 cm depth, depending on the machinery used) can mitigate stratification of nutrients and soil organic matter, thereby homogenizing soil conditions in this part of the crop root zone. Tillage practices may be intensive (e.g., mouldboard ploughing in the fall, following by one or more harrowing events in the spring) or producers may choose to employ conservation tillage, for instance with a chisel plough or disk harrow, or even no-tillage where the soil is undisturbed except for small slots opened to plant seeds and apply fertilizer [76]. Tillage replaces the functions of soil macrofauna by fragmenting and mixing surface litter in the plough layer and aerating the soil.

Intensive tillage has a pronounced effect on macrofauna, particularly earthworms and beetles. For example, abrasion by plough pans and rotary harrows can kill earthworms [77], while soil compaction in wheel tracks of farm machinery can crush earthworms to death [78]. Turning the soil exposes soil-dwelling earthworms to direct sunlight and warmer, drier conditions at the soil surface, which can cause desiccation [76] and they also become vulnerable to predators, particularly birds. Carabid beetles are surface dwelling macroarthropods that live in surface litter; when this litter is incorporated into deeper soil horizons during tillage, beetles may be buried as well and those that survive the tillage operation will find their preferred habitat reduced or eliminated [79]. The intensity and frequency of tillage events, as well as the organism's response to tillage, determines whether tillage will have a temporary or persistent impact on the soil food web. Boström [80] reported a 73-77% reduction in earthworm populations dominated by the endogeic earthworm Aporrectodea caliginosa following the rotary cultivation and ploughing of meadow fescue and alfalfa hayfields. One year later, the earthworm biomass (predominantly individuals of A. caliginosa) was the same as in the undisturbed, unploughed alfalfa hayfield. It appeared that crop residues incorporated by tillage provided ample organic substrates to support reestablishment of this endogeic earthworm species. However, intensive and frequent tillage generally reduces populations of anecic earthworms, likely because the surface litter that serves as their primary food source is fragmented and mixed into the topsoil by tillage implements [81].

Soil micro- and mesofauna can also be affected by tillage, owing to modification or destruction of the soil habitat, exposure to frost, dryness or heat, and changes in the availability of organic substrates [82]. Soil mesofauna, including collembola, cryptostigmatid mites and mesostigmatid mites, tend to be impacted negatively by tillage because they cannot tolerate changes in the soil physical environment and become trapped in the soil profile when pores are disrupted [83]. However, enchytraeid populations often increase following tillage, perhaps because they are normally constrained by competition for food resources with larger detritivores such as earthworms, and the decrease in earthworm numbers following tillage gives the enchytraeids access to more organic substrates [83]. No-till and strip-tillage alters the trophic structure of soil nematodes, favouring bacterivorous and fungivorous nematodes and inhibiting herbivorous nematodes, likely the result of the presence of predatory mites [84, 85] and detritivorous isopods and amphipods that aid in the decomposition of recalcitrant substrates [85]. Tillage temporarily modifies the soil structure by disrupting macroaggregates and causes localized compaction, so amoeba and other protists that inhabit the aggregate pore space will be impacted in the shortterm [86].

A review of more than 100 studies of soil biota in intensively tilled and no-till agroecosystems [83] revealed that soil fauna with larger body size are more inhibited by tillage than those with a smaller body size. In addition to the physical disturbance to large soil fauna caused by tillage, two other reasons have been proposed to explain this observation: (1) after organic substrates incorporated by tillage are metabolized by bacteria, food availability declines, inducing a tropic cascade that results in diminished food supply for their predators, as well as top-level detritivores, and (2) smaller organisms have a short life spans and recover quickly from tillage disturbance.

Intensive tillage generally favours bacterial decomposers due to the mixing of fragmented surface litter in the soil profile, increasing the surface area for colonization, with a corresponding increase in predatory protists that creates a positive feedback for decomposition and N mineralization [87]. The burst of soil respiration following tillage points to rapid growth of heterotrophic bacteria in response to substrate availability and favourable soil conditions. Ammonia oxidizers and nitrifiers also respond positively to tillage, which generates a peak in the  $NO_3^$ concentration following tillage operations. Whereas tillage mechanically disrupts the fungal hyphal network, the conditions in no-tillage agroecosystems (intact surface litter, undisturbed soil profile) lead to soil organic C accumulation, larger soil microbial biomass and support fungal-mediated decomposition and N mineralization [87, 88]. In the field, N mineralization and nitrification rates should be greater in intensively tilled than no-till agroecosystems owing to positive response of bacteria and their protist predators to tillage [43]. The decline in soil meso- and macro-fauna populations resulting from intensive tillage probably have relatively little effect on the N mineralization rate, according to Andrén et al [89]. Reports of greater potential N mineralization in soils under long-term no-tillage compared with intensive tillage [90-92] probably reflect the accumulation of labile soil organic N in no-till soils that is transformed to  $NH_4^+$  and  $NO_3^-$  when soils are disturbed (i.e., sieved to disrupt macro-aggregates) and incubated under favourable conditions for microbial growth in the laboratory. In conclusion, tillage is expected to alter the soil food web structure and increase the bacterial contribution to N mineralization and nitrification in humid temperate regions.

#### **Organic amendments**

Depletion of soil organic C in intensively cultivated agroecosystems can be counteracted by applying organic amendments such as green manure, animal manure, farmyard compost and retaining a greater proportion of crop residues in the field [93, 94]. Organic amendments contain organic C, N and other essential plant nutrients, so can be used to partially meet the nutritional requirements of agricultural crops if they can be decomposed to yield  $NH_4^+$  and  $NO_3^-$  or solubilized to release noncovalently bound cations and anions (e.g.,  $K^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$ and most micronutrients). Organic amendments become accessible to soil micro-organisms after they are incorporated in the soil by tillage or processed by soil macrofauna, so these organic substrates should promote growth of soil microbial populations and create a positive feedback in the soil food web. Organic amendments increase the abundance of soil micro-organisms [95–97], protists, nematodes, microarthropods and earthworms [98–100]. Reports of greater microbial diversity following application of organic amendments could be related to laboratory methods (i.e., microbial populations grew large enough to be detected when they received ample organic substrates) or introduced species coming from manure and off-farm amendments [101].

Agricultural producers generally apply organic amendments with low C:N ratios to avoid immobilization of  $NH_4^+$  and  $NO_3^-$  from the soil solution as the material decomposes in the field. Animal manure and farmyard compost have C:N ratios between 3:1 and 25:1 (lower values from liquid manure and slurry, higher values from well-decomposed compost). In humid temperate agroecosystems, organic amendments with these characteristics are decomposed by micro-organisms and other soil food web organisms during the growing season, releasing from 15 to 75% of the total organic N into soil solution as  $NH_4^+$  and  $NO_3^-$  [102]. Variation in N mineralization is the result of the C:N ratio of the organic amendment (less N mineralization from materials with higher C:N ratio), soil type (greater N mineralization from sandy and loamy soils than clayey soils) and the crop grown in the field (maize, oilseed rape and grass-based hayfields have greater N recovery than potatoes and cereal crops) [103]. Decomposition and N mineralization from green manure probably follows the same trend as animal manure, since green manures are generally N-rich legumes with C:N ratios below 15:1, but it depends on the lignocellulose content of the green manure at the time of incorporation because lignocellulose acts as a barrier to decomposition [38].

Mineralizable N contained in organic amendments is transformed to  $NH_4^+$  and  $NO_3^-$  during the growing season, as part of the soil N supply for plant uptake or subject to other transformations in the N cycle. Feedbacks between well-fertilized plants and soil food web organisms are expected to be positive, owing

to greater root growth and exudation during the growing season and more residues left in the field after harvest [38]. Non-mineralized organic C and N from organic amendments is retained in soil, contributing to the formation of macroaggregates that are a preferred habitat for certain micro-organisms and microfauna, improving soil structure and aeration, and increasing the soil organic matter content [103, 104]. In conclusion, organic amendments are predicted to increase the size and activity of the soil food web, primarily by serving as an input of organic N that can readily undergo N mineralization and nitrification in humid temperate regions.

## Agrochemicals

Agrochemicals such as inorganic N fertilizers and pesticides are popular inputs in agroecosystems of humid temperate regions owing to the demand for plant-available N to achieve economic crop yields and the need to control weeds and other pests that compete with or damage crops. When applied in sufficiently large doses, some agrochemicals may prove toxic to organisms in the soil food web, which can alter population dynamics, community structure and diversity in the soil food web [9, 55, 87]. However, soil food web organisms are seldom the target of agrochemicals applied for crop nutrition and crop protection, so effects on the soil food web are expected to be indirect and the result of feedbacks in the soil-plant system [105]. Regardless, inorganic N fertilizers and pesticides applied to agroecosystems alter interactions between the aboveground and belowground soil food web, which can reduce [106] or increase [107] soil N mineralization rates, thereby impacting the soil N supply.

#### **Inorganic N Fertilizers**

Although minerals can be mined to produce inorganic N fertilizer (notably sodium nitrate or 'Chile saltpetre'), most agricultural producers rely on inorganic N fertilizers derived from the Haber–Bosch process to fertilize their crops. A variety of inorganic N fertilizers can be purchased, including anhydrous ammonia, ammonium sulphate, calcium ammonium nitrate and mixed nitrogen–phosphorus fertilizers such as monoammonium phosphate and diammonium phosphate [38]. Inorganic N fertilizers are water soluble, meaning that they are quickly dissolved and release NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> into the soil solution. Urea (CO(NH<sub>2</sub>)<sub>2</sub>) produced by the Haber–Bosch process is an organic N fertilizer that must be hydrolysed by urease before releasing NH<sub>4</sub><sup>+</sup> into the soil solution.

When applied to agroecosystems at agronomic rates (generally less than 200 kg N/ha [15, 94]), inorganic N fertilizers are not expected to have a direct effect on soil food web organisms because  $NH_4^+$  and  $NO_3^-$ 

solubilized from inorganic N fertilizers at these rates are not toxic to soil organisms. Inorganic N is utilized as a substrate by ammonia oxidizers and nitrifiers in wellaerated mineral soils when their preferred C substrates are available (depending on whether their metabolism is heterotrophic or chemoautotrophic). The conversion of  $NH_4^+$  to  $NO_3^-$  through these microbially mediated reactions appears to occur rapidly and dominate in agricultural soils in the humid temperate regions, based on evidence from natural abundance  $\delta^{15}N$  stable isotopes and the fact that more than 50% of the  $NO_3^-$  leaching from these systems was the product of nitrification, not lost directly from applied fertilizers [108].

By contributing to the soil N supply, inorganic N fertilizers stimulate crop growth and yield, which generates a positive feedback for the soil food web (more root growth, more rhizodeposition, more crop residues remaining in the field after harvest), similar to the effect described for organic amendments. However, long-term application of NH<sub>3</sub>-based fertilizers like anhydrous ammonia and urea can lower soil pH owing to  $H^+$  generation during the nitrification process [109], which could be deleterious to soil food web organisms that are sensitive to acidic conditions (e.g., actinobacteria, earthworms) as well as biochemical processes in the N cycle [38]. In plots receiving ammonium nitrate fertilizer, N mineralization was not affected by soil pH (ranged from 4.7 to 6.6), but nitrification was reduced by 75-85% at pH 4.7 compared with pH 6.6 [110]. Similarly, plots that were acidified to pH 4.5 by 10 years of anhydrous ammonia showed no difference in N mineralization but a 42% drop in the potential nitrification rate measured in the laboratory [111]. The decline in nitrification in soils with low pH is likely due to inhibition of ammonia oxidation, as chemoautotrophic bacteria and archaea seem to be sensitive to pH [112, 113]. In conclusion, application of inorganic N fertilizers is expected to stimulate nitrification directly and contribute indirectly to N mineralization and nitrification reactions in the soil food web, except when fertilization results in a decline in soil pH that reduces the nitrification rate.

#### Pesticides

Herbicides are the most widely used pesticides in Canada, representing 56% of the active ingredients purchased from 1998 to 2003 [114]. They are applied to control weeds that compete with field and vegetable crops for light, water and nutrients. Fungicides (11% of active ingredients purchased [114]) and insecticides (7% of active ingredients purchased, [114]) are generally applied to field and vegetable crops when pest populations reach economic thresholds according to the principles of integrated pest management. A limited number of soil fumigants are registered for use as pre-plant soil fumigants in Canada, but include those containing the active ingredients chloropicrin, dazomet, metam sodium and metam potassium and may be applied prior to planting crops, in woodlots, nurseries, seed beds and turf [114].

Soil fumigants generally act as a broad-spectrum control for pests or pathogens such as insects, nematodes, bacteria and fungi, thereby directly impacting these groups of soil food web organisms. A study of N mineralization and nitrification rates in soils fumigated with a mixture 1,3-dichloropropane and 1,3-dichloropropene showed both short- and long-term N mineralization rates were stimulated by fumigation, whereas nitrification was inhibited completely for at least 3 weeks in all soils, and the reduction in nitrification was maintained for up to 17 weeks in one soil [115]. In contrast, most of commonly used pesticides in Canada (herbicides, fungicides and insecticides) are non-target for soil food web organisms, but they should alleviate crop stress and thereby elicit a positive feedback with the soil food web community (healthier plants produce more roots, more rhizodeposits and leave more crop residues in the field after harvest); as well, dead weed biomass constitutes an organic substrate for the soil food web. In this regard, herbicide application may have a similar effect on the soil food web as the application of surface mulch, although the organic input from dead weed biomass is probably lower and patchy in the field, compared with mulch. Modern pesticides have a half-life of days, weeks or months in the soil-plant system, which implies that they are rapidly degraded as organic substrates by soil micro-organisms. A few pesticides are more persistent or susceptible to loss from soil, such as chlorothalonil (fungicide) and the insecticides azinphosmethyl, permethin, chlorpyrifos and diazinon, which were found in Canadian aquatic ecosystems in concentrations that exceeded water quality and science-based benchmark limits [114].

Glyphosate is the most commonly applied herbicide in Canada [114] and has a C:N ratio of 3:1 [116]. Although glyphosate is not directly applied to soil, exposure in the rhizosphere can significantly stimulate N mineralization without affecting microbial biomass [109, 117]. A 19-year field trial studying the effect of annual field application of five pesticides (benomyl, chlorfenvinphos, aldicarb, triadimefon and glyphosate) on soil processes found that soil microbial biomass, N mineralization and nitrification rates were not affected by long-term exposure to single pesticides or combined pesticide applications [118]. In conclusion, herbicides and other pesticides containing N may be degraded by soil micro-organisms and cause a small temporary increase in N mineralization and nitrification, but are not expected to contribute directly to the soil N supply.

#### Water management

Soil moisture varies in humid temperate regions, with flooding common after snowmelt and heavy spring rains;

at the other extreme, soils may reach the wilting point during dry spells in the summer. Field crop production in humid temperate regions generally relies on rainfall as the main water source, with irrigation reserved for specialty vegetable and small fruit crops. Flooding in spring can delay planting, especially on heavy clay soils, so many producers install artificial tile drainage to remove excess water from the subsurface layer, thereby facilitating water infiltration and drainage from surface soils as well. There are approximately two million hectares of croplands with artificial tile drainage in Quebec and Ontario, Canada [119]. Controlled drainage and free-outlet drainage are the two most common drainage systems in part of eastern Canada. Controlled drainage maintains the water table level at a desired level, which gives more control over soil moisture. In contrast, free-outlet drainage continuously removes excess water in the field by carrying it to a series of resistance-free conduits via gravity. While free-outlet drainage gives slightly drier soil conditions, however, both systems improve the overall water-holding capacity of soil but exaggerate the wetting-drying cycle within a field.

Fluctuating wet-dry cycles cause selective pressure on soil food web organisms. The oligochaeta (enchytraeids and earthworms) are among the most sensitive to dry conditions because they require sufficient water to move through soil and avoid desiccation [38]. Under excessively dry conditions, they may die, enter diapause or aestivate, which reduces their metabolism to a basal level. Soil macrofauna and microarthropods belonging to the phylum Arthropoda are more tolerant of dry conditions, since most possess an exoskeleton and have behavioural adaptations to avoid desiccation (e.g., hiding in soil crevices, retreating to deeper soil layers, anhydrobiosis) [38]. Gergócs and Hufnagel [120] reported that oribatid mites can survive in dry soils, but are affected by drought because of a reduction in fungi that serve as food; therefore the effect of drought on some arthropods may be due to food limitation rather than a lack of water. Prolonged flooding can be deleterious for soil meso- and macrofauna, as they may eventually drown from the lack of oxygen.

Soil microfauna (amoebas and other protists, nematodes) live and swim through water films surrounding soil particles [30], so are highly active in moist and flooded soils and become inactive when water films evaporate in very dry soils. Protists did not grow in soils with 11.4% moisture content, but grew rapidly and preyed on bacterial populations when moisture content increased to 18.6% [121]. Following drought, fungal- and bacterialfeeding nematodes and their prey (fungi, bacteria) recovered more rapidly in C-rich grassland than arable soil under wheat production [122], which highlights predator-prey relationships that are relevant for N mineralization. When soils are saturated, the movement of gravitational water towards tile drainage may facilitate the movement of soil microfauna and also stimulates germination of fungal spores and their distribution in the soil profile [123], which could also favour predator-prey relationships.

Soil micro-organisms tolerate extreme wetting and drying events due to their ability to osmoregulate [124], but soil drying and rewetting can also create osmotic stress leading to microbial death and cell lysis. Consequently, soil drying and rewetting causes a flush of C, N and phosphorus (P) in the soil solution, probably from cell lysis and an increase in soil respiration due to greater microbial activity and metabolism of organic substrates when soils are rewetted [125]. The integrity of fungal-rich communities is maintained during drying-rewetting cycles, which resulted in less dissolved organic N and inorganic N losses from fungal-rich unimproved grassland soils compared with a bacterial-rich intensively managed grassland soils [126]. Schimel et al. [125] suggested that adaptation may increase the microbial resistance and resilience to drought, but experimental results are not consistent in this regard [122]. Furthermore, the presence of growing plants, which supply readily-mineralizable organic substrates in their rhizodeposits, can compensate for the depletion of organic substrate following multiple or prolonged drying-rewetting cycles [122].

Biochemical reactions catalysed by micro-organisms depend on soil redox conditions (related to the concentration of oxygen and other electron acceptors) that are influenced by soil moisture. The heterotrophic and chemoautotrophic micro-organisms responsible for N mineralization and nitrification are facultative aerobes with maximum reaction rates around 60–70% water-filled pore space [127]. Due to the strong dependence of soil food web organisms on soil moisture for survival, availability of organic substrates and biochemical reactions such as N mineralization and nitrification, water management is expected to exert an important control on the soil N supply.

#### Integrated crop management systems

The previous sections have examined how selected agricultural practices could individually affect the size, composition and activity of the soil food web in relation to N mineralization and nitrification. However, agricultural producers select a suite of agricultural practices based on their values and production goals, in the context of local site factors such as climate and weather, agricultural policies, land tenure, technologies, markets, soil conditions, crop demands and ecosystem vulnerability [11]. It is informative to compare some contrasting crop management systems to determine how these may affect the soil food web and ultimately the soil N supply.

Bloem et al. [106] described a long-term study at the Lovinkhoeve Experimental Farm (Marknesse, the Netherlands) where soil food web and N dynamics were compared in integrated and conventional crop management systems. Integrated crop management systems received nearly twice as much organic matter each year as farmyard manure, green manure and crop residues, whereas conventional crop management systems received crop residues only. During the winter wheat production year of the crop rotation, the N mineralization rate was on average 30% greater in the integrated crop management system, which received 40% lower inorganic N fertilizer inputs, reduced soil tillage (10 cm depth in the integrated crop management system versus 20 cm depth in the conventional crop management system), lower pesticide use and no soil fumigation compared with the conventional crop management system. Greater N mineralization was attributed to greater organic matter content in the integrated crop management system, which also received with 30 tonnes/ha of mushroom compost (C:N ratio=14) following winter wheat harvest in August. According to Bloem et al. [106], the presence of easily decomposable organic matter from organic amendments increased bacterial growth rates, and supported more amoebae (64% higher) and nematode (22% higher) biomass, which presumably preyed upon the bacteria and increased N mineralization in the integrated crop management system, especially during the growing season (April-August). No soil fumigants were applied to the integrated crop management system, and this led to larger populations of bacterivorous fauna [106]. Their study confirms that predator-prey relationships in the soil food web control N mineralization and the soil N supply, especially in agroecosystems where organic amendments contribute to the annual N input. However, N mineralization was not enough to achieve the potential yield at this site, as grain yield was 23% lower and N removal in harvested grain and straw was also less in the integrated crop management system (111 kg N/ha) than the conventional crop management system (165 kg N/ha) [106].

Lower crop yields are not unusual in farming systems that rely on N mineralization from organic amendments to furnish part of the soil N supply, but in some cases the low yields seem to be the result of inadequate N input rather than an inability of the soil food web organisms to efficiently convert organic N to  $NH_4^+$  and  $NO_3^-$ . Mäder et al. [128] reported 20% lower crop yield in organic (biodynamic and bioorganic) than conventional production systems in Switzerland over a 21-year period, and a follow-up study after 27 years found 23% lower wheat grain yield in the organic than conventional production systems [129]. However, crop yields were likely constrained by the fact that NPK inputs were 34-51% lower in the organic than conventional production systems. This suggests that mineralization (N and P) and solubilization (P and K) reactions liberated a supply of plant-available NPK that was efficiently transferred from soil to plants. Although symbiotic mycorrhizal fungi were proposed to facilitate nutrient transfer and improve crop nutrition [128], no difference in hyphal biomass of saprophytic and mycorrhizal fungi or the biomarker for mycorrhizal fungi was detected between organic and conventional production systems [129]. Greater microbial biomass (particularly bacterial biomass), more bacterivorous, herbivorous and omnivorous nematodes, enchytraeids, earthworms, spiders, fly larvae (Diptera and Brachycera) and surface-dwelling arthropods in the organic production systems [128, 129] suggests that a bacterial-dominated food web was responsible for N and P mineralization. This is supported by greater enzyme activity linked to N and P mineralization in the organic than conventional production systems in this study [128].

## Conclusions

The concept of the soil N supply expands previous notions of soil fertility because it acknowledges the potential of the soil food web to furnish part of the crop N requirements through N mineralization and nitrification processes. Better estimates of the soil N supply from the soil food web should allow us to reduce N fertilizer inputs and to adjust the timing of N inputs so that exogenous N sources are applied when crops really need them. For instance, a cold wet spring may hinder soil food web organisms from supplying enough  $NH_4^+$  and  $NO_3^-$  for early crop growth, necessitating a larger input of starter N fertilizer under these conditions. Extra N fertilizer inputs may be needed to achieve target yields when managing agroecosystems with a fungal-dominated soil food web that retains N and keeps plant-available N concentrations low. Since N mineralization and nitrification can continue after harvest in humid temperate climates, producers can consider planting cover crops to deplete the NH4<sup>+</sup> and  $NO_3^{-}$  produced during this period or avoid fall tillage and manage surface residues to support more N retention in fungal-based soil food webs, thereby minimizing overwinter N losses to the environment. Some of these ideas were already proposed by de Vries and Bardgett [61].

At present, most research on the soil N supply focuses on developing quick laboratory methods to measure the fraction of total N or organic N in soil that is potentially mineralizable. Aerobic incubations to determine the potentially mineralizable N (No) are lengthy (20-40 weeks) but considered to be the best predictor of the soil N supply, with chemical methods (e.g., hot KClextractable N, UV absorbance of NaHCO<sub>3</sub> extract at 205 or 260 nm, Illinois soil test for N) showing very poor to very good relationships with  $N_o$  ( $R^2 = 0.11-0.83$ ) and crop N uptake under field conditions ( $R^2 = 0.09-0.87$ ) [20]. In-field measurements of soil N supply such as the preplant and pre-sidedress nitrate tests, and anion/cation exchange membranes appear to be more robust indicators of crop N uptake ( $R^2$ =0.34–0.91) [20], which argues for the use of field-based tests or development of soil tests that mimic field conditions, because this is the only way to truly account for soil food web structure and its functions related to the soil N supply.

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The fundamental difficulty with chemical methods of measuring the soil N supply is that those methods do not account for soil biological processes and physical properties governing N mineralization and nitrification. All organisms will consume substrates as fast as possible [130], but their activities are restrained by physical barriers and other constraints (e.g., temperature, moisture, redox conditions). Aerobic incubations may be better for determining potentially mineralizable N because the experiments are relatively long in duration and use sieved soil (<2 mm mesh) that probably contains soil microorganisms, their primary predators (protists, nematodes) and some of the mesofauna, but not earthworms and other macrofauna. Yet, potentially mineralizable N is not a direct measure of soil N supply - it overestimates the  $NH_4^+$  and  $NO_3^-$  pools because sieving removes physical barriers to potentially mineralizable substrates that are not accessible to the soil food web in the field [90-92] and the incubations are run under constant temperature and moisture conditions (35°C, 55-65% water-filled pore space) [20].

How do we reconcile these challenges in determining the soil N supply with the fact that we wish to measure the contribution to N mineralization and nitrification of soil food web organisms under field conditions, to be able to make practical recommendations about fertilizer use in agroecosystems without compromising producers' yield objectives? Addiscott [130] wrote 'if mineralization is an emergent process, it will be characterized by bottom-up behaviour' and this is consistent with our view that the microbially-mediated N transformations are the key to understanding the soil N supply, with microfaunal predators showing strong and consistent control on the N mineralization and nitrification processes. Soil mesoand macro-fauna also contribute to the soil N supply by moderating substrate quality and soil habitat, but sporadically because of their sensitivity to environmental conditions and relatively small, patchy populations (compared with micro-organisms and microfauna). Ideally the soil food web structure and functions would be measured and modelled in the field, but this does not necessarily call for large research teams to collect and enumerate a multitude of soil organisms. Functional genomics targeting genes involved in soil N transformations (e.g., amo, hao and nrx genes in the ammonia oxidation and nitrification pathways [10]) and quorum sensing of chemical signals involved in the depolymerization of organic N (e.g., acylhomoserine lactones from proteobacteria [54]) can give us insight into microbial activities and responses in the soil environment. These approaches may hold promise for linking the soil food web to the soil N supply in the future.

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