Small but powerful:

Nematodes as model to disentangle the structure, function and carbon allocation in the soil micro-food web

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Erklärung

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbstständig verfasst und keine anderen Hilfsmitte als die angegebenen Hilfsmittel genutzt habe. Alle wörtlich und inhaltlich übernommenen Stellen habe ich als solche gekennzeichnet.

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1. Zusammenfassung

In Agroökosystemen nehmen die Organismengemeinschaften in den verschiedenen Bodentiefen eine wichtige Rolle im Kohlen- und Nährstoffkreislauf ein, wobei nur wenig über die Nahrungsnetzdynamik unterhalb der Pflugsohle bekannt ist. In der hier vorliegenden Arbeit wurden die Einflüsse der landwirtschaftlichen Nutzung auf die Struktur und Biomasse von Nematoden im Oberboden, in der Wurzelzone und der wurzelfreien Zone innerhalb zweier Vegetationsperioden an einem Ackerstandort nahe Göttingen (Niedersachsen) untersucht. In einem Feldexperiment wurde die Ressourcenqualität über die Pflanzenart (Mais oder Weizen) und zusätzliche Streuausbringung (mit oder ohne Maisstreu) verändert, um den Kohlenstofffluss - von den Wurzeln, Bakterien und Pilzen kommend - zu manipulieren. Die Analyse der Nematodengemeinschaft wies auf ein mit Nährstoffen angereichertes und gestörtes Bodenökosystem, mit einer geringen Biodiversität, hin. Entlang des Tiefengradienten bildeten die Nematoden sogenannte Metacommunities, d.h. Gruppen von ökologischen Gemeinschaften, welche Umweltgegebenheiten wie Nahrungsquellen und abiotischen Faktoren widerspiegeln. Signifikant höhere Biomassen der Nematoden wurden unter Weizen im Vergleich zu Mais als Ackerfrucht beobachtet. Die Streuapplikation induzierte einen „bottom-up“ Effekt im Mikro-Nahrungsnetz mit größeren Biomassen in den niedrigen als in den höheren trophischen Stufen. Die Nematoden Biomassen sowie die faunistischen Indizes (Channel Index, Enrichment Index) zeigten, dass der Kohlenstofffluss im Bakterienkanal des Bodens dominierte. Allerdings deckte das ^{13}C Pulse-Labelling Experiment im Feld auf, dass der Kohlenstofffluss durch die Pilzgemeinschaft sowie die pilzfressenden Nematoden wesentlich höhere Umsatzraten aufweist. Dies steht im Kontrast zur generellen Annahme, dass der bakterielle Kanal in einem landwirtschaftlichen Boden dominiert. Für zukünftige Untersuchungen wäre daher eine Kombination aus Biomasse- und Umsatzratebestimmung sinnvoll.

In einem Laborexperiment wurden radioaktive ^{14}C Isotope eingesetzt, um ein vollständiges Budget des Flusses von wurzelbürtigem Kohlenstoff im Nahrungsnetz der Nematoden zu bestimmen. Hierbei wiesen die pflanzenparasitären Nematoden die höchsten ^{14}C-Gehalte innerhalb weniger Tage auf, da sie direkt an den Wurzeln fressen und über die Herbivorenkette den Nährstoffzyklus im Boden eröffnen.

Erfolgreich zeigt die vorliegende Arbeit, dass Nematoden ein gutes Werkzeug darstellen um die Struktur und Funktion von Mikronahrungsnetzen im Boden zu entschlüsseln, sowie den Kohlenstofffluss in ackerbaulich genutzten Böden zu bestimmen.

2. Summary

The organismic assemblages inhabiting the different soil horizons are important drivers for carbon and nutrient cycle in arable ecosystems, yet knowledge on food web dynamics below the plough zone is scarce. The present research considered the effects of agricultural management practice on the nematode community structure and biomass in the top soil, rooted zone below plough layer, and root free deeper soil in two successive vegetation periods at an arable field site near Göttingen (Niedersachsen). In a field experiment, the resource quality was manipulated by crop plant (maize or wheat) and organic amendment (with or without maize litter), to investigate the major soil carbon pathways based on roots, bacteria and fungi. The analysis of the nematode community pointed to a highly enriched and disturbed ecosystem with low biodiversity. Along the depth gradient the nematodes formed distinct metacommunities, which are local assemblages reflecting resource availability and abiotic environmental factors. Wheat supported significantly greater nematode biomass than maize. The litter amendment induced bottom-up effects in the micro-food web, with greater biomass allocation at lower than at higher trophic levels. The biomass of nematode families as well as faunal indices (Channel Index, Enrichment Index) revealed a predominance of the bacterial carbon channel in the arable soil. On the other hand, a ^{13}C pulse-labelling experiment in the field investigating the flux of root- derived C into the soil food web revealed high turnover rates in the fungal carbon pathway. This was evident for soil fungi as well as for fungal-feeding nematodes and contradicts general assumptions of a more active bacterial pathway in arable soils. For future research a combination of biomass and turnover rates would be helpful.

A laboratory experiment with the radioactive ^{14}C isotope was used to compile a complete budget for the root-derived carbon in the nematode micro-food web. Here plant-feeding nematodes, which feed on living plant roots, thereby opening the root C cycling into the food web, showed highest amounts of ^{14}C allocation within a few days.

In sum, the present study successful shows the use of nematodes as model to disentangle the structure and function of a soil micro-food web and the carbon allocation and flow in an arable soil.

3. Introduction

3.1 Soil ecosystems

Imagine: a dark place full of hard working labourers, permanently under construction and a buffer for environmental stress - a factory of life - THE SOIL. Soil systems regulate the water and nutrient cycle; containing more than twice the amounts of carbon than the atmosphere ((Jeffery, et al., 2010). It is acknowledged that one-quarter of all species worldwide occur in soil. These organisms are key drivers of pedogenesis and soil fertility. Abundance and diversity of soil biota is important to maintain soil health, whilst on the other hand soil animals are depended in soil texture, pH, organic matter supply and, moreover, are influenced by human impact like management practices (Jeffery, et al., 2010). Soil animals are divided in three groups: microfauna, mesofauna and macrofauna. Microorganisms (bacteria and fungi) are the most abundant and diverse groups within the soil consortium (Bardgett, 2008).

Herbivore animals, bacteria and fungi are primary consumers of root tissue, plant litter and root exudates (rhizodeposits). They build the major resources for the soil food web, by decomposing and mineralizing the organic matter (Moore, et al., 2005). While bacteria predominantly degrade labile organic substrates (e.g. plant exudates - sugar, carboxylic acids, amino acids), fungi are able to break down recalcitrant compounds (e.g. lignin, cellulose). A fungal-dominated energy channel characterizes a slow nutrient circle (Fig.1), which depends on recalcitrant resources leading to a slower decomposition rate (Scheu & Setälä, 2002). In contrast, the bacterial-based energy channel is fast with a rapid nutrient transfer to plants due to a high turnover rate of bacteria and their consumers (Ruess & Ferris, 2004).

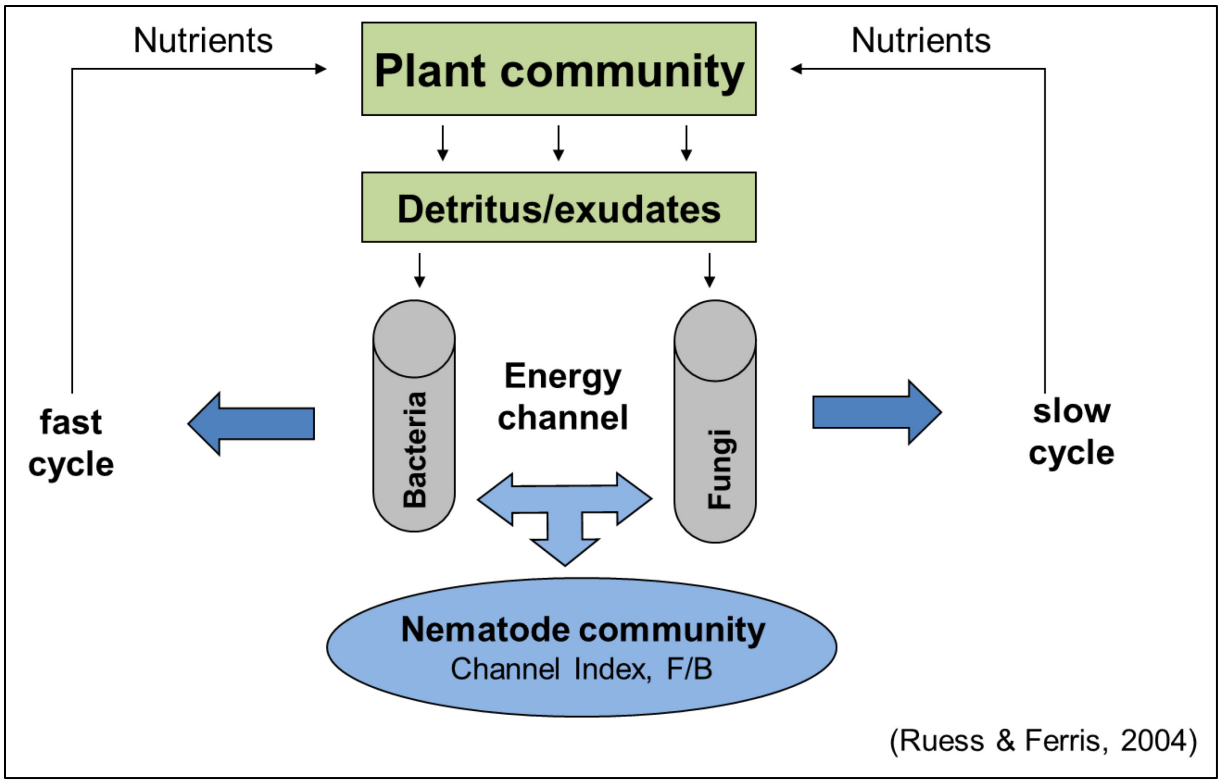


Figure 1: The nutrient pathway through the bacterial and fungal energy channel. Nematodes act as indicator for fluxes via community based indices (Channel Index, fungal to bacterial feeder ratio - F/B). Graph from Ruess & Ferris (2004).

3.2. Nematodes as indicators for soil conditions

Soil nematodes play a significant role in regulating the composition of the microflora, litter decay rates and element cycles (Freckman, 1988; Neher, 2010; Bardgett, et al., 1999). Nematodes hold a central position in soil food webs, with the highest density among multicellular animals and species at all trophic levels (Yeates, 1979). Based on their morphology, especially the mouth structure, nematodes are separated into five trophic groups: fungivores, bacterivores, plant feeder, omnivores and predators (Yeates, et al., 1993). Nematodes have been used as valuable bioindicators to analyze the structural and functional conditions of soil (Bongers & Ferris, 1999; Neher, 2001).

Nematodes life strategy can be characterize as colonizer (c) and persister (p) that are ranked on a *c-p*-scale from 1 to 5, respectively (Bongers, 1990). Nematodes with smaller *c-p* value have a short lifecycle, high fecundity and feed on enriched resources can be referred to as *r*-strategists, whereas those with a *c-p* value close to five have a longer life span, large body size, lower fecundity and are sensitive to disturbances (*k*-strategists) (Bongers, 1990; Ferris & Bongers, 2006). To get information about soil condition, various indices for nematodes were

established. Using the nematode *c-p* scale Bongers (Bongers, 1990) created the Maturity Index *(MI)* to predicate the disturbance of a soil ecosystem.

The *MI* is a weighted mean frequency of free-living soil nematode taxa with their different *c-p*-scale. The *MI* is used to assign the soil quality and conditions with low values (less than 2.0) indicate a disturbed and nutrient-enriched ecosystem with high rates of r-strategists and a decrease of higher trophic levels (Bongers, 1990; Bongers & Ferris, 1999). In agricultural soils the distribution of plant-feeding nematode guilds can display an inverse relationship compared to free-living taxa, because sensitive persisters (*k*-strategists) like Trichodoridae can increase under stress conditions (Bongers, et al., 1997). Therefore the plant-parasitic nematodes are separately considered by the calculation of the plant parasite index *(PPI)* using the same formula as for the *MI* (Bongers, 1990). In arable ecosystems *MI* values around 2.1 and 2.3 indicate undisturbed and disturbed agroecosystems, respectively, whereas *PPI* values around 2.9 suggest either an undisturbed or disturbed agroecosystem (Neher, et al., 2005). With fertilizer (manure) application the *MI* tends to decrease whilst the *PPI* increases (Neher & Olsen, 1999; Bongers, et al., 1997).

The nematode micro-food web has basal, enrichment and structural components, indicating the carbon and energy flow through root, bacterial and fungal energy channel (Ferris et al., 2001). To describe food web conditions, Ferris & Bongers (2009) established the Enrichment Index (*EI*) and the Structure Index (*SI*) using functional guilds of nematodes characterized by the same feeding habit and life strategy. The Enrichment Index provides information on nutrient availability and soil fertility, while the Structure Index informs about the stability and structure of the soil food web and the regeneration stage after a disturbance (Ferris, et al., 2001). These indices, calculated on the frequency of nematode families, are generally displayed in a squared plot graph as presented in Fig. 2.

By plotting the *EI* against the *SI* the data are assigned to four quadtrats (Fig.2)

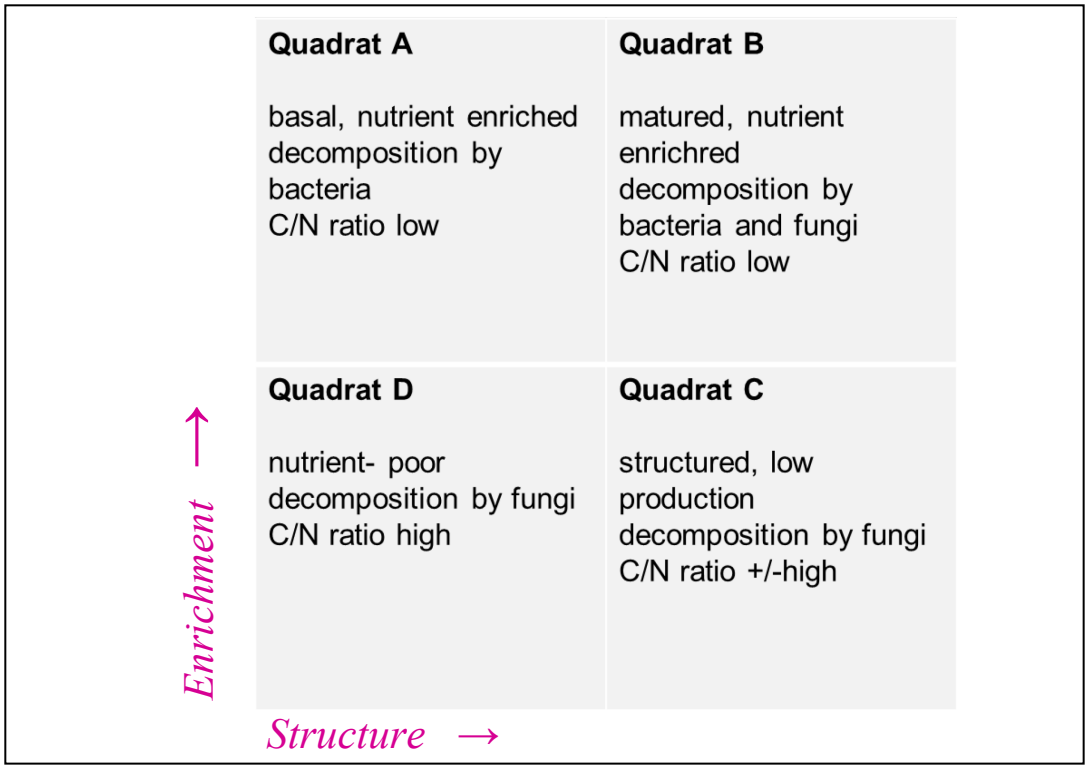


Figure 2: Nematode faunal profile to assign soil food web conditions. After Ferris & Bongers (2009), modified.

In addition, the Channel Index (*CI*) and the ratio of fungal and bacteria feeders (*F/B*), provide information about the dominant decompositions and carbon pathways (Ferris & Bongers, 2009; Ferris, et al., 2001; Ruess & Ferris, 2004). The decomposition pathways can vary between different soils; arable soils are usually dominated by the bacterial pathway whereas forest soils by the fungal pathway. The Channel Index in forest soils shows mostly high values (>50), while the CI is low (<50) at crop sites (Ruess, 2003). Briar et al. (2007) compared the nematode community in organic and conventional farming systems and reported that the *EI, SI* and *CI* differ with season and years but less in management practices (Briar, et al., 2007). In general the faunal profile pointed to a highly enriched and moderately high structured food web with a dominant bacterial decomposition channel (Briar, et al., 2007). Correspondingly, Ugarte, et al. (2013) found similar differences between season, however, the Structure Index rose in the spring in all three different managements (ley, row crop, vegetable) (Ugarte, et al., 2013). The *CI* showed high values with a peak around 80 in July in conventional (row crop) and organic (vegetable) production. In the opposite ley management had low *CI* values with under 20 in April and around 60 in July.

In sum, the various indices offer a powerful tool to analyse soil and food web conditions with the use of nematodes and provide an easy way to gain knowledge about soil health and decomposition pathways.

3.2 Nematode biomass as a measure of belowground carbon flow

A further powerful key to encrypt the complexity of soil food webs is to analyse the carbon cycling in the soil food web and the interactions among trophic groups. About 80% of global terrestrial organic carbon (C) is stored in soil and minor changes in this carbon pool could have strong impact on atmospheric CO_2 concentrations and related climate processes (IPCC, 2007). Regarding the increasing concentration of atmospheric CO_2 and climate change plenty of studies about carbon flow, its sinks and sources, stabilization and sequestration been carried out (Curtis, et al., 1998; Mosier, 1998; Kaiser, et al., 2002; Janzen, 2006; Lützow, et al., 2006). However, the carbon exchange between plant and soil compartments, especially the carbon flow through the food web, are still poorly known. Moreover, the transfer of organic compounds from top soil into deeper horizons was rarely investigated. Jaesche, et al. (2006) observed a flush from microorganisms from top soil to the vadose zone and further to groundwater, where they still were active. In addition to the transfer down to the aquifer, the internal soil ecosystem C cycle is an important component to understand carbon flow in belowground food webs (Jaesche, et al., 2006). In agroecosystems this internal C flux is constantly interrupt by harvesting crop biomass, which also impacts on the soil community, which is more depend on root-derived resources than plant litter (Albers, et al., 2006). Therefore, it is necessary to analyse carbon cycling in the soil food web for a better understanding and prognostication of the impact of human activities, such as advancement of agricultural managements. Nematode biomass is an ideal tool to assign carbon allocation to obtain valuable information about food web carbon flow (Ferris, 2010; Zhang, et al., 2015). Nematode assemblages build separate metacommunities depending on nutrient availability and soil abiotic factors (Yeates, 1999; Liang, et al., 2005; Wilson, 1992). Due to their vermiform, cylindrical shape and standardized morphological attributes nematodes biomass can be easily calculated and used as production component. The biomass C of a taxon or trophic group of nematodes is assigned based on nematode body weights (Andrássy, 1954) taking into account the coefficients for dry weight and carbon content (Sohlenius, et al., 1997). The C allocation in the trophic groups of nematodes can be used as a measure of C flow in the food web and of the carbon flow in the bacterial or fungal channel. Additionally, by combination of nematode biomass with respiration data a metabolic footprint is created,

which was successful applied for a quantitative carbon analysing of ecosystems. (Ferris, 2010; Zhang, et al., 2015).

Generally, the dynamics of soil food webs depend on inputs from plants in the form of litter (slowly decomposable) and rhizodeposits (readily available C), which results in three major nutrient pathways based on bacteria, fungi and roots (Scheu, et al., 2005; Moore, et al., 2005; Ruf, et al., 2006). In the present study nematodes with their functional groups at each trophic level were used to analyse the nutrient input of rhizodeposits and maize litter or their combination. The bacterial community reduces soluble organic matter (e.g. rhizodeposits), fosters bacterial-feeding nematodes while enhancing mineralization and nutrient availability for the plants (Ingham, et al., 1985; Neher, 2010). Recalcitrant compounds such as litter and detritus are degrade by saprophytic fungi which serve as food-source for fungal-feeding nematodes (Ruess, et al., 2000). Plant-feeding nematodes are important in agricultural production due to the contribution to crop yield losses (Yeates, et al., 2009). At low density of plant parasites, the infestation of nematodes is accomponied by the leakage of cell metabolites, which can foster microbial biomass build up and in turn the plant growth via nutrient mineralization (Yeates, et al., 1998; Poll, et al., 2007). Omnivorous nematodes with their broad prey pattern (algae, enchytraeids, bacteria, fungi, nematodes, plant tissue) have also an important influence on soil C fluxes as top down regulators predatory nematodes affect soil food web interactions and nutrient cycle (Yeates, et al., 1993; Ferris, 2010; Neher, 2010).

3.3 Stable carbon isotopes as tool for soil food web analyses

Stable isotopes (e.g. C, N) are a widespread tool used to analyse the food web structure and the quantitative characterization of carbon dynamics. The analysis of carbon is used to determine the respective food sources, whereas nitrogen analysis can differentiate the relative trophic levels, both methods provide an insight into soil food webs and their trophic links (Scheu, et al., 2005; Tiunov, 2007). A lot of studies clarified trophic levels using ^{15}N, and C resources using ^{13}C, by the shifts in natural abundance (Albers, et al., 2006; Tiunov, 2007; Crotty, et al., 2014). The use of $\delta^{13}C$ as a signal to assign the trophic levels of soil food webs depends on the carbon source, i.e. the organic matter either derived from C_3 or C_4 plants. In temperate zones C_3 plants (e.g. wheat, rye, rice) are most abundant and fix CO_2 via the C_3 pathway with the key enzyme Ribulose-1, 5-bisphosphat-Carboxylase (Rubisco). Its enzymatic discrimination against the lighter isotope ^{12}C results in products with a $\delta^{13}C$ value ranging between -18 and -26‰.

In arid areas C_4 plants (e.g. maize, sugarcane) dominate, with products of photosynthesis ranging between –7 to –18‰ due to the high ^{13}C affine key enzyme Phosphoenolpyruvate-Carboxylase (PEP) (Tieszen & Boutton, 1989; Heldt & Piechulla, 2008). Organisms which feed on two or more isotopically distinct carbon resources mirror the $\delta^{13}C$ signal of the individual food sources. For instance, Ekblad & Högberg (2000) measured the microbial respiration of C_4-sucrose, which was added in a C_3-ecosystem and were able to distinguish between CO_2 evolved from endogenous carbon sources (roots, microbial respiration) and from microbial mineralisation of C_4 (Ekblad & Högberg, 2000). Also, Henn & Chapela (2000) used C_4-sucrose to measure the $\delta^{13}C$ signal in the fungi community in a lab experiment (Henn & Chapela, 2000). Albers, et al. (2006) used stable isotopes to analyze the incoporation of plant carbon into the meso- and macrofauna by measuring their ^{13}C and ^{15}N content. A number of studies on use of stable isotopes analysed the C flow in a whole community (protists) or a single species (Neilson & Brown, 1999; Crotty, et al., 2011; Darby & Neher, 2012). Crotty, et al. (2011) traced the flow of stable isotopes from protists into the whole soil food web.

However, most studies have focused on meso- and macrofauna, whereas the microfauna especially nematodes have been relatively neglected due to the difficulties collecting measurable biomass (Semenyuk & Tiunov, 2011; Potapov, et al., 2013). Pausch, et al. (2016a) reported that the different soil carbon pools can be separated by analysing the flux of plant derived $\delta^{13}C$ in organic matter, microorganisms and animals. In case of the lack in a natural ^{13}C difference in food web resources or at limited biomass of the investigated organisms (especially nematodes) ^{13}C pulse- labelling can be used to introduce a strong signal. In the present study nematodes were used as a part of a carbon budget analysis, in which the incorporation of root derived ^{13}C into different food web compartments was assigned within a $^{13}CO_2$ pulse-labelling experiment. In Figure 3 the entire budget of C pools and shifts, dissolved organic carbon (DOC) and turnover rates are illustrated at the experimental arable field site (Pausch, et al., 2016a).

The present study contributed to a complete C budget of a soil ecosystem, whereas an entire food web (except protists) and their trophic interactions were measured and summed up.

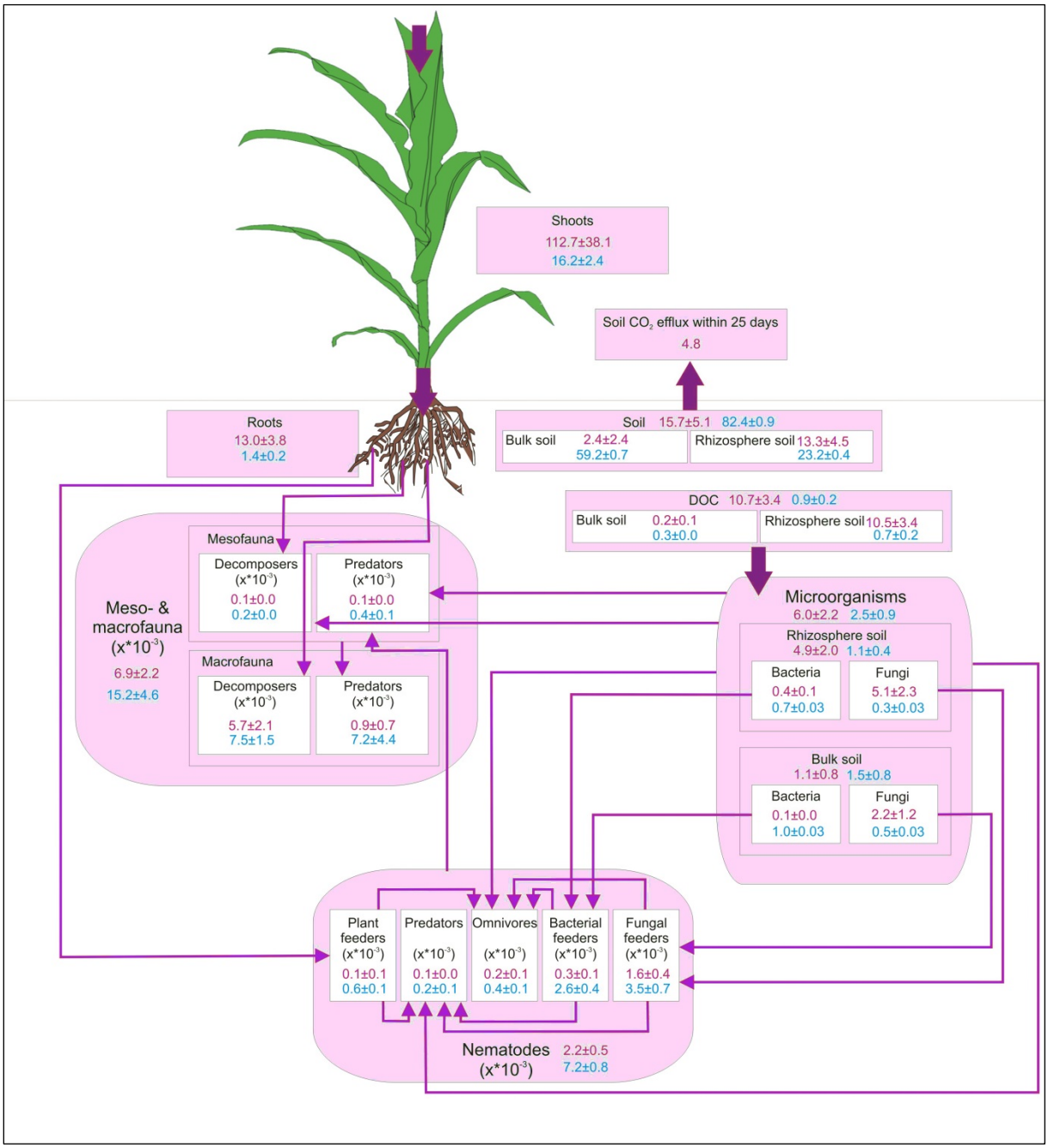


Figure 3: Carbon budget presented as % of total C per m² (blue values) and minimal tracer flux through each C pool of the food web after $^{13}CO_2$ pulse labelling of maize (red values) within 25 days in the first 10cm of an arable soil. The minimal tracer flux is given as % of total recovered ^{13}C on day 2 after labelling and was calculated based on the maximal ^{13}C recovered in each pool. Graph from Pausch, et al. (2016a)

3.4 Unstable carbon isotopes in soil food web research

The use of unstable carbon isotopes, i.e. radioactive markers like ^{14}C, is less restricted by abundance – in contrast of the stable isotopes ^{13}C and ^{12}C - for encrypting the trophic interactions in soil food web. With ^{14}C as tracer minimal fluxes even at low biomass as well as dynamics of rhizodeposits and root-derived carbon effluxes in the fauna can be detected. The combination of nematode identification and labelling of plants with ^{14}C enables C flux quantification from roots into the different compartments of the micro-food web. This allows measuring the ^{14}C activity and recovery, and the C flow through the herbivore and detritivore food chain can be clarified as well as their linkage at higher trophic levels.

In a previous study, Yeates et al. (1998) used $^{14}CO_2$ labelling on white clover to describe the flux of recent plant photoassimilates into the plant-feeding nematode *Heterodera trifolii,* and detected an increase of root cell metabolites in the rhizosphere caused by the plant-parasitic nematode. Further studies clarified relationships of C incorporation for specific trophic groups of nematodes or compared nematode density and composition of different managed agroecosystems (Yeates, 1999; Fu, et al., 2000; Fu, et al., 2001). However, to the best of our knowledge there has been no investigation on the whole nematode community or the entire food web and trophic links in an agroecosystem.

In the present work, a closed chamber system was used to pulse-label *Zea mays* with $^{14}CO_2$ and the allocation pattern of plant C in the fauna and the dynamics of rhizodeposition and root-derived carbon efflux were investigated. The C flux from $^{14}CO_2$ pulse labelled maize plants into the entire nematode micro-food web was measured; thereby identifying the ^{14}C activity of each trophic group. The gained data were used to generate a complete C-flux budget for plants and the belowground food web, i.e. from input to output, and with time resolved turnover rates (Pausch, et al., 2016b).

3.5 The idea behind and hypotheses

The present work systematically elaborates the effects of resource inputs on nematode communities across a soil depth transect and analyses the flow of carbon through biotic compartments within the nematode micro-food web. A field on the impact of **resource quality and availability** on food web dynamics and C flow was performed at an agricultural site in Holtensen near Göttingen. The arable land was grown with wheat as a C_3 source and a ^{13}C signal was introduced by cropping the C_4 plant *Zea mays*. Four treatments were established: wheat and wheat with maize litter, fodder maize and corn maize. The maize litter originated from corn maize plots, where only cobs were harvest and the remaining plant was shredded and applied to plots. The entire aboveground plant parts were harvest at fodder maize plots. Plant litter contains complex, recalcitrant carbon compounds (cellulose and lignin) whereas rhizodeposits comprise labile carbon substrates (sugars, carboxylic and amino acids). Thus treatments with corn maize supplied the soil fauna with above- and belowground plant carbon (i.e. labile and recalcitrant resources), whereas the carbon at fodder maize treatments was derived from root tissue and rhizodeposits (predomimantly labile resources). Corn maize and wheat with maize litter amendment support the fungal based soil food web and the carbon flow through the fungal energy channel.

The nematode community was studied at three sampling dates in two successive years: (i) summer- with highest root exudation, (ii) autumn- with maize harvest and plant litter input, and (iii) winter- with rain events and high migration of dissolved organic matter. Three different horizons were investigated: (1) top soil, (2) rooted zone below plough layer, and (3) root free soil. We hypothesize that the nematode density will decrease strongly with depth, and dependent on nutrients and abiotic soil factors, nematode assemblages form separate metacommunities residing at different depths. Furthermore, the impact of resource quality and availability will shape the nematode community. In particular the application of plant litter will induce a strong bottom-up effect and fosters the fungal decomposition pathway, whereas the influence of crop plant will be more distinct in plant-feeders and in the rooted-zone.
Additionally, a **^{13}C labelling** experiment was performed in the field to calculate the **plant carbon flow**, the major C pools and the C turnover rates within the soil food web. The aims of the labelling experiments were to quantify the C input by maize rhizodepositions in the trophic cascade, identify key biotas and to calculate the root derived C in organisms.

We hypothesize that rhizodeposit-C is predominantly decomposed by the bacterial community in the rhizosphere and thus fosters the bacterial energy channel. Further the ^{13}C incorporation depends on C pool size (i.e. organismic biomass).

Further, in a **laboratory experiment ^{14}C** was used to determine a **complete C budget** describing the dynamics of root-derived carbon from the model plant *Z. mays* to the nematode micro-food web. The mass flow ^{14}C pulse labelling experiment will further clarify, if leakage of plant metabolites caused by plant feeders supports rhizosphere bacteria and their consumers (i.e. bacterial-feeding nematodes). We hypothesize that a fast and high incorporation of ^{14}C in plant-feeding and bacterial-feeding nematodes takes place and, hence, besides the herbivore food chain, the bacterial energy channel of the detritus food chain is primarily sequestering recent plant photoassimilates.

In sum, the present research determines the effects of resource quality and availability on nematode density, biomass and community composition in an arable field across season and soil depth (Fig.4). Additionally the ^{13}C pulse-labelling experiment in the field investigates the flux of root- derived C into different compartments of the soil food web. Finally, to gather a complete budget for the root-derived carbon in the nematode micro-food web, a laboratory experiment with the radioactive ^{14}C isotope was performed.

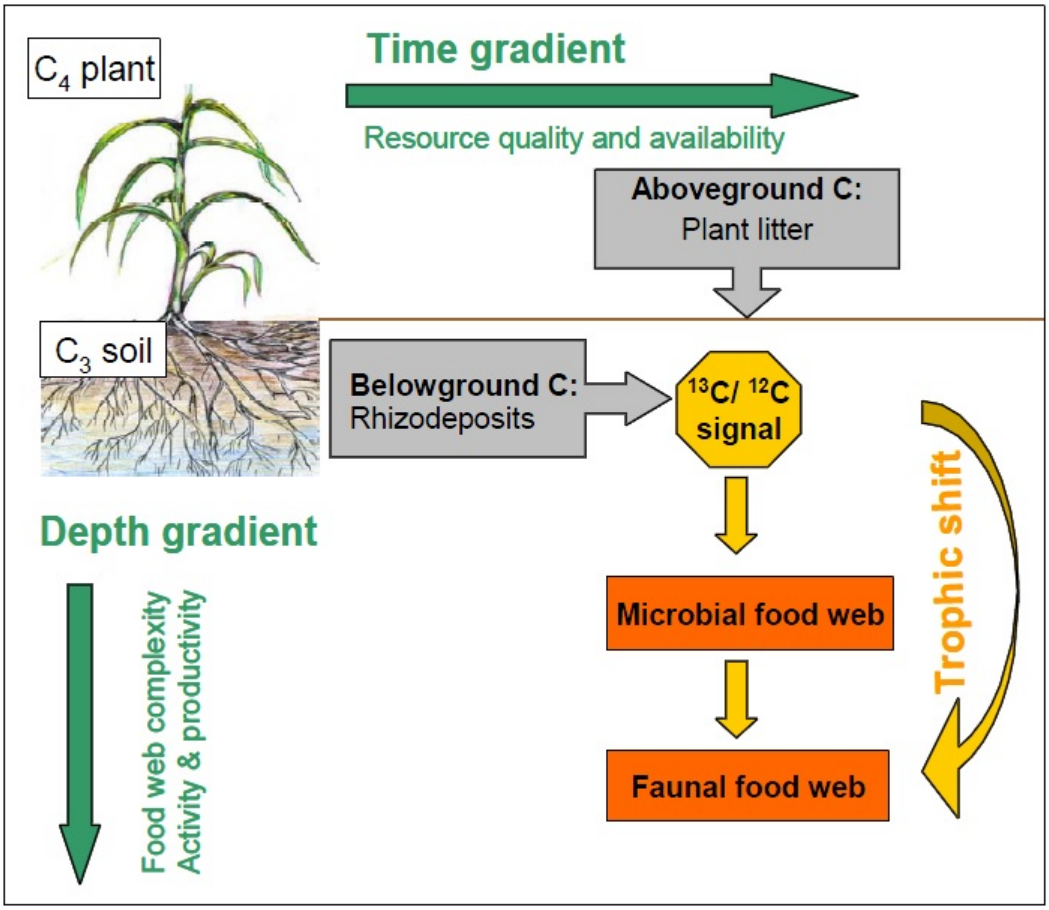


Figure 4: A schematic overview on the flux of plant carbon into the food web of an arable soil. The ^{13}C signal was introduced by growing the C_4 plant *Zea mays* or by adding maize litter to the soil. The different resources fuelled the major carbon pathways based on roots, bacteria and fungi. (Picture courtesy: Liliane Rueß)

4. Methods

4.1 Field experiment

4.1.1 Field site and agriculture management

The experimental field site is located on a terrace plain of the river Leine and was established in 2009 near Göttingen, Lower Saxony, Germany (51°33´N, 9°53´O; 158m NN). The area has a temperate climate with a mean annual precipitation of 720mm and air temperature of 7.9 °C, affected by both western maritime Atlantic climate and eastern continental climate. The field site is oriented in north- western direction with a mean base slope of approximately 2%. According to IUSS (2007) the dominant soil types at the site are Cambisols (Braunerden) and Luvisols (Parabraunerden) with the latter partly stagnic (Pseudogley). Depending on long-term agricultural management two plough layers (0.2m and 0.3m depth) were detected with strong soil compaction below the second plough layer. The mean depth of the A-horizon is 34±6.4cm.

Table 1: Selected soil properties. After Kramer et al., 2012, modified

Horizon[a]	**Depth**	**Texture**[b] **clay/silt/sand**	**pH (H_2O)**	**pH ($CaCl_2$)**	**Bd**
	[m]	% (w/w)			[g cm^{-3}]
Ap1	0-0.25	7.0/87.2/5.8	6.6	6.0	1.38
A(I)p2	0.25-0.37	7.1/87.8/5.0	6.9	6.2	1.61
Btv1	0.37	7.1/87.7/5.1	7.3	6.6	1.55
Btv2	>0.65	6.8/88.4/4.8	7.7	7.0	1.68

bd: bulk density

a: classification according to KA5

b: according to the German classification system

Ap: plough zone (1+2)

Btv: discoloration horizont with clay shift

In a stripe design of two rows the field was cropped with maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.). In the first vegetation period (2009) winter wheat ("Julius"; 224 kg ha^{-1}) and maize ("Ronaldinio"; 34 kg ha^{-1}) were grown, in the second season (2010) summer wheat ("Melon"; 224 kg ha^{-1}) and hybrid maize ("Fernandez"; 26 kg ha^{-1}). The fertilization practices at maize plots were N fertilizer (ammonium nitrate urea solution: in 2009:122.4kg N ha^{-1}; in 2010: 79kg N ha^{-1}) and NP fertilizer (diammonium phosphate: 2009/ 2010: 32 kg N ha^{-1}; 83 kg P ha^{-1}) added shortly before and after seeding.

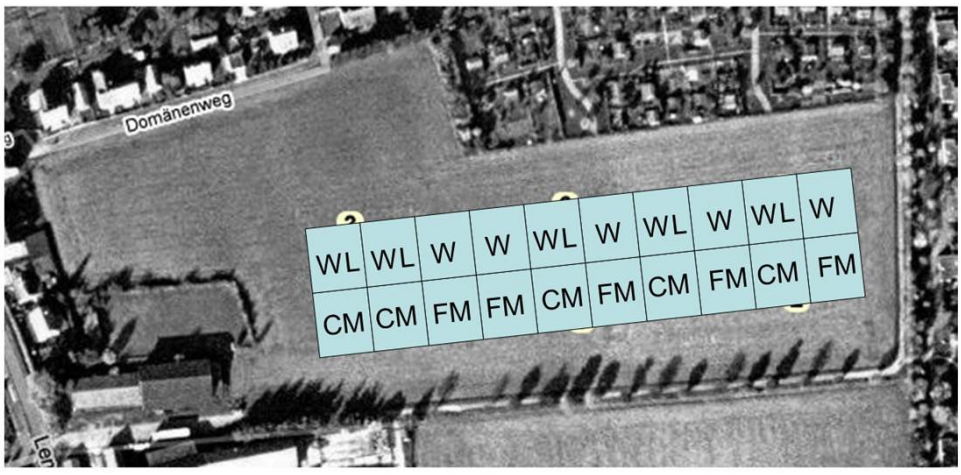
Fertilizer at wheat plots were applied as follows: in 2009 NS fertilizer (21kg N ha^{-1}, 24kg S ha^{-1}) in March, 50 kg N ha^{-1} ammonium nitrate urea solution two times in April and 40 kg N ha^{-1} in May and June each. In 2010 the summer wheat was fertilized with 61 kg N ha^{-1} ammonium nitrate urea solution in April and 40kg N ha^{-1} in June. The mean C and N contents were 11.6 and 1.2 mg g^{-1} dry weight soil of the Ap horizon.

The wheat plots received six times and maize plots twice different herbicide combinations in 2009 and 2010 wheat was treated once and maize plots twice with herbicide combinations during the growing season.

4.1.2 Treatments and sampling

The study was set up to manipulate resource availability and quality for the micro-food web under two different crop plants. Within the maize and wheat stripes 10 experimental plots of 24 x 24 m each were established and assigned to four treatments with five replicates each: corn maize (CM), fodder maize (FM), wheat (W) and wheat with litter (WL) (Fig.5). The CM and WL plots were amended with litter as hackled maize shoots (0.8 kg DW m^{-2}, C-content: 0.35 kg m^{-2}) in November 2009 and 2010 each, whereas the FM and W plots received no litter. No crop rotation took place during the experimental period.

Figure 5: Experimental field design with four different treatments (Source: Google, September 2009)



The nematode fauna was sampled in 23rd July 2009 and 22nd July 2010 (plant growth with highest root exudation), 29th September 2009 and 23rd September 2010 (harvest with plant residues input), and 11th December2009 and 13th January 2011(fallow with high migration of organic matter). Samples were taken at three different depths: plough layer (0-10 cm), rooted zone (30-40 cm in 2009; 40-50 cm in 2010) and root free zone (60-70 cm). From each plot eight samples were taken with a soil corer (diam. 2.5 cm), bulked and gently mixed by hand. Subsamples of ca. 50 g FW were taken for nematode faunal analysis and determination of soil moisture each. For every treatment and depth four replicates were taken, in total 288 samples within two years.

4.1.3 Nematode fauna

Nematodes were extracted with a modified Baermann method according to Ruess (1995). The extraction was at room temperature for 24 h (approx. 18°C) and afterwards a heating regime was applied with 5 °C steps for 6 h, starting with 20 °C and ending at 45 °C. Nematodes were fixed in 4% cold formaldehyde solution. For each sample total numbers of nematodes were counted under light microscope (Leitz DIAPLAN, Leitz, Germany) with a 630 x magnification. For the sampling in July 2009 and 2010 a proportion of 10% of the total individuals per sample were determined to family level. The nematodes were identified under a light microscope following Bongers (1987).

As a scale of soil ecosystem conditions the maturity index (*MI*) was calculated, excluding the plant parasites, as $MI = \sum_{i=1}^{n} v(i) * f(i)$, where $v(i)$ is the coloniser–persister (*c-p*) value assigned to taxon *i* and $f(i)$ is the frequency of taxon *i* in the sample (Bongers, 1990). Plant parasitic nematodes were separately considered by the calculation of the plant parasite index (*PPI*) using the same formula.

Nematode faunal analysis was performed without the dauer larvae (non-active stage) of Rhabditidae. The Enrichment (*EI*), Structure (*SI*) and Channel Index (*CI)* were calculated according to Ferris at al. (2001). Distinctive feature is the enrichment weighting of nematode functional guilds.

The following equations were used: $EI = 100 * e / (e + b)$; $SI = 100 * s / (s + b)$ and $CI = 100 * (0.8\ Fu_2 / (3.2Ba_1 + 0.8Fu_2)$, where *e* is the enrichment, *b* the basal, and *s* the structure component. Fu_2 represents fungal feeders with *c-p*-classification 2, Ba_1 bacterial feeders with *c-p*-classification 1.

To determine the major energy channel in the soil food web the ratio of fungal to bacterial feeder (*F/B*) was computed (Freckman & Ettema, 1993). Additionally, the trophic diversity (*T*) was calculated with $T = \frac{1}{\sum pi^2}$, in which p_i is the proportion of trophic group ***i*** in the community (Heip, et al., 1988).

The ratio *RD/R* of Rhabditidae dauer larvae (*RD*) to active forms (*R*) was assigned, which provides a measure for resource availability. If the proportion of dauer larvae is low, the resource supply is more or less stable. In contrast if the rate of dauer larvae is high, the decomposition channel is changing from bacterial to fungal domination (Ferris & Bongers, 2009).

The Shannon-Wiener diversity index *H´* (Pilou, 1971) was calculated for nematode families using the following equation: $H' = -\Sigma (p_i \ln p_i)$, where p_i is the proportion of *i*-th taxon in a sample.

To calculate the biomass (fresh weight) of nematodes Andrassy´s formula was used (Andrássy, 1954) as:

$$G = a^2 * b / 16*100.000 \ [\mu g]$$

with *a* as largest body width, *b* as body length. The correction factor 16 has been introduced by Andrássy and multiplication with 100.000 converts data to µg. Data of the length and body width were taken from Bongers (1987) as an average value for all species listed within a genus.

4.2 ^{13}C Pulse-labelling in the field

4.2.1 Treatment and sampling

The pulse-labelling experiment was conducted in 14th July 2010 at the arable field in Holtensen, near Göttingen, described in chapter 4.1.3. Four plots (1x1 m²) including nine maize plants each, were covered with a labelling chamber (2m high). A chamber was built up with aluminium frames coated with transparent LDPE foil with a total light transmission (~90%). An excess of 5 M H_2SO_4 was added to the tracer solution (16 g 99% ^{13}C-enriched Na_2CO_3 solved in 100 ml H_2O and 4 ml of 1 M NaOH) from outside the chamber with a syringe.

$$Na_2CO_3 + H_2SO_4 \rightarrow Na_2SO_4 + CO_2 + H_2O$$

The puncture whole was sealed with a tape. Air was pumped through the solution with an aquarium pump to guarantee the reaction of all added tracer with the acid.

After the plants were labelled for four hours (2pm-6pm) the chambers were removed and plants were allowed further growth under natural CO_2 conditions.

At each labelling plot in the depth of 5cm two steel collars (ID 13cm, height 15cm) with beakers (ID 5cm, height 5cm) for NaOH (80ml of 1M NaOH) were installed to catch CO_2 and analyse the $\delta^{13}C$ value of the soil CO_2 efflux.

$$2NaOH+C_2O \rightarrow Na_2CO_3+H_2O$$

At the no-labelled plot eight collars were set up randomly to take a $\delta^{13}C$ control value. At each sampling the NaOH solution was substituted. For ^{13}C natural abundances soil samples were taken shortly before labelling, labelled probes were taken after 2, 5, 10 and 25 days. Before sampling one plant per plot and each sampling date was harvest 1cm above the soil surface. The soil samples were retrieved by using a Riverside auger (ID 5 Eijkelkamp, Giesbeek, The Netherlands) at the plant position at the depth of 0-10cm, where 50% of the root system of maize plants are present (Pausch, et al., 2013).

4.2.2 Nematode fauna

The plot soil subsamples (50-80 g FW) from each replicate were extracted with a modified Baermann method appropriate to Ruess (1995), see chapter 4.1.3. For $\delta^{13}C$ analysis specimens each nematode sample were handpicked using an inverse light microscope and separated in trophic groups (bacterial feeders, fungal feeders, plant feeders, omnivores, predators). Nematodes were transferred in tin capsules (5 x 9 mm; HEKAtech GmbH, Wegberg, Germany) and dried for 2 days at 60°C.The tin capsules with the nematodes were weight before and after drying to get the water content of the nematodes. Subsequently the dry mass of each trophic group of nematodes was calculated. The C content of the nematodes was assigned as 50% C of dry mass (Schmidt, et al., 2000).

Nematode samples contained very low amounts of C (average of 1 to 24 µg per sample), and therefore were measured with an adapted method on an Eurovector EA (Eurovector EA3000, Eurovector S.p.A. Milano, Italy) coupled to a Delta V Plus IRMS (Thermo Fisher Scientific, Bremen, Germany). The EA was fitted with smaller oxidation and reduction reactor tubes (ID 7.8 mm, 450 mm length) to allow lower carrier gas flow and increased sensitivity (Langel & Dyckmans, 2014).

For all analysed material the standards (Australian National University sucrose and NBS 19) were calibrated with reference to the international standard (Vienna Pee Dee Belemnite).

Total C contents and $\delta^{13}C$ values of shoot, root and soil samples were measured using an elemental analyser (EA) NA 1500 (Carlo Erba Instruments, Milano, Italy) interfaced to a Delta plus isotope ratio mass spectrometer (IRMS) (Thermo Fisher Scientific, Bremen, Germany).

The ratio of $^{13}C/^{12}C$ [‰] was calculated according to Petersen & Fry (1987)

$$\delta X = [(R_{sample} - R_{standard})/(R_{standard})] \times 1000$$

Where X represents the heavier isotope (^{13}C) and R represents the ratio between the heavy and the light isotope ($^{13}C/^{12}C$).

4.2.3 Calculation of ^{13}C content

By multiplying the ^{13}C excess ($\chi^E(^{13}C)$, atom%) with the total C stock of the respective pool ($n(C_P)_F$, g C m^{-2}) the ^{13}C excess mass of the nematode C pool per square meter ($n(^{13}C_P)_F$, g ^{13}C m^{-2}) was calculated. To convert atom% to absolute values, results were divided by 100:

$$n(^{13}C_P)_F = \frac{\chi E(^{13}C)}{100} . n(C_P)_F$$

$$n(C_P)_F = z \cdot \rho \cdot n(C_P) \cdot 10$$

where F stands for the area at the arable field, z (cm) is the thickness of the respective soil layer, ρ (g cm^{-3}) is the soil bulk density (1.38 g cm^{-3} at the plough layer, 1.7 g cm^{-3} at rooted zone and 1.6 g cm^{-3} at root free zone) and n (C_P) is the C content (mg C g $soil^{-1}$) of the pool. Independently from a dilution of ^{13}C by unlabelled recently assimilated C the absolute tracer amounts showed the dynamics of ^{13}C allocation within nematode C pools. The measurement of tracer in- and out fluxes including ^{13}C respired to CO_2 resulted in the ^{13}C excess in all pools. But it was not possible to estimate the total amount of the tracer flowed through each pool, only the incorporation of the tracer at certain time can be quantified. During a sampling period the minimal tracer flux into the nematode C pool ($f\,(C_P)_F$, %) was estimated based on the ^{13}C excess mass of the respective pool ($n\,(^{13}C_P)_F$, g ^{13}C m^{-2}).

4.3 ^{14}C as tracer in the laboratory experiment

4.3.1 Treatment and labelling

In November 2010 at the arable field in Holtensen, near Göttingen intact soil cores were taken with a soil corer with an inner diameter 12 cm and height 30 cm, transferred into cylindrical Plexiglas pots (inner diameter 13 cm, height 30 cm) and then covered with a dark foil (Pausch, et al., 2013). Before labelling (day 0) and after labelling (day 2, 5, 10, 16) the ^{14}C incorporation into the nematode community were measured. For an undisturbed growth of soil microorganism the maize seeds ("Ronaldino") were cleaned from adhering fungicide, at which they were water-soaked for a night and afterwards washed with a brush in a sieve under constant water flow. After germination on wet filter paper for three days, three seedlings were transferred per pot and covered with a plastic lid, which had an opening for the shoots. The soil water content was adjusted to 70 % of the water holding capacity (WHC). No fertilizers were applied. At a temperature of 26 to 28°C during day and 22 to 23°C at night and a light intensity of ca. 400 µmol m^{-2} s^{-1} the maize plants grown in a climate chamber.

Twenty five days after planting whilst in the tillering phase, $^{14}CO_2$ labelling was applied to the maize. Before the labelling started the slashes in the plastic lid were proofed with a silicon paste (NG 3170, Thauer & Co., Germany). Eight maize plants were placed per chamber (Fig.6), which was connected with a bottle of 5 ml Na_2 $^{14}CO_3$ labelling solution (ARC Inc., USA) with a ^{14}C activity of 1.2 MBq per plant (Pausch et al., 2013). 10ml of 5 M H_2SO_4 were added to the labelling solution and dissolved $^{14}CO_2$ reached into the atmosphere of the chamber. After four hours of labelling the air was cleaned from unassimilated $^{14}CO_2$ by pumping it through 15 ml of 1 M NaOH solution for two hours. Finally the labelling chamber was opened and the CO_2 evolved from the soil of four pots each (the four replicates respectively) was trapped in 15ml solution of 1 M NaOH. The solution was regularly changed on first day after labelling every two hours, then twice daily and then once every 2 days until 16 days after labelling (Pausch, et al., 2013).

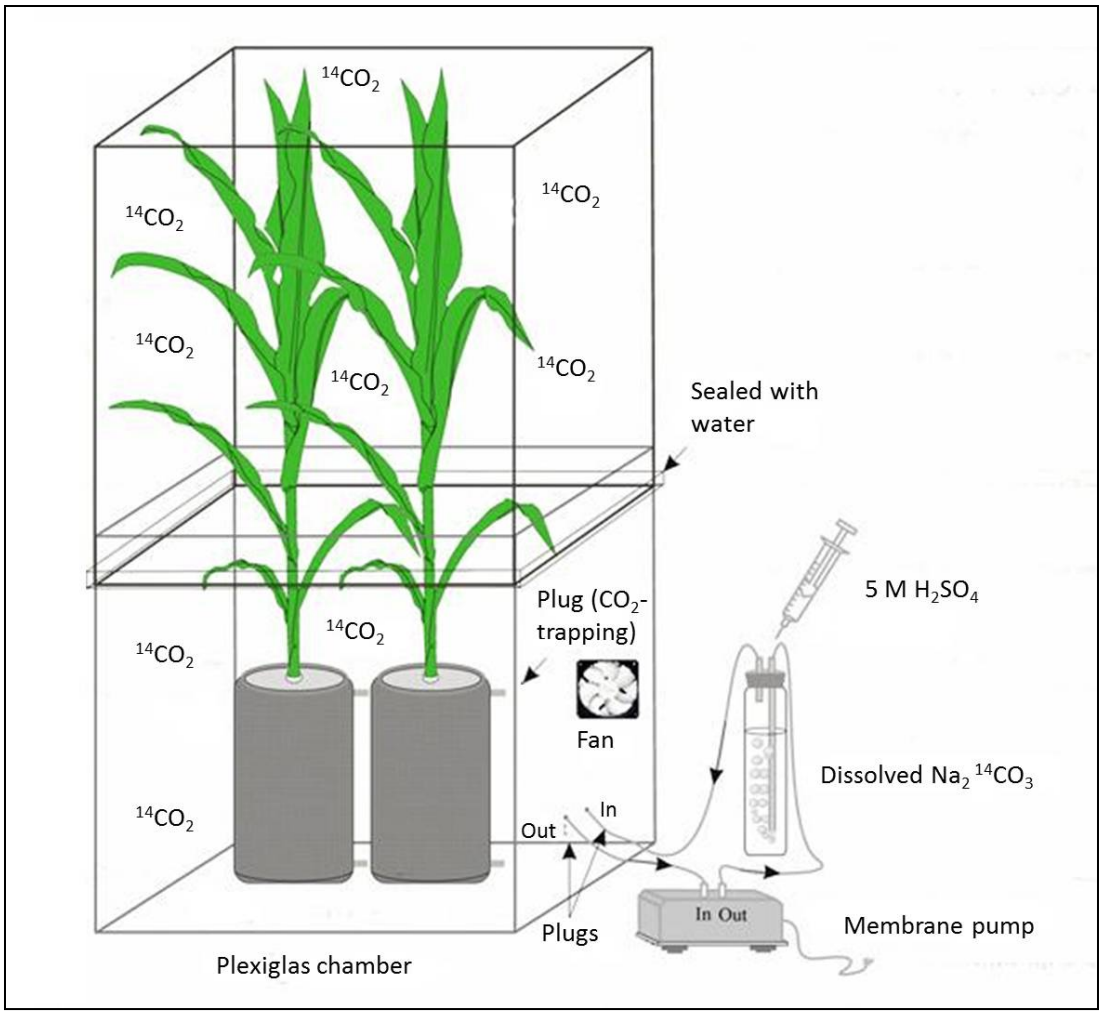


Figure 6: Labelling Chamber for $^{14}CO_2$ pulse-labelling experiments (Picture courtesy: Johanna Pausch)

4.3.2 Sampling and preparation of nematodes

At 2, 5, 10 and 16 days plants and soil were sampled after labelling with four replicates for each sampling day plus four unlabelled pots at day 0. For day 10 only three replicates were available due to the loss of one pot. Maize shoots were cut at their base and roots were separated from soil by hand. The soil cores in the pots were separated into two parts; one half was use for nematode extraction and the other half for measurement of the soil rhizodeposition. About 50 to 80 g FW from the upper soil core were taken for nematode extraction after the modified Bearman method described by Ruess (1995). Nematodes were fixed in a cold solution of 4% formaldehyde. The total number of individuals was counted under a light microscope (Leitz DIAPLAN, Leitz, Germany), whereas ten per cent (or a minimum of 100) individuals per samples were identified to genus level. Every nematode sample was carefully washed back into a vial for the later use of ^{14}C analyses.

The nematodes were separated into their trophic groups with the use of a fine pulled glass pipette (Roth, Germany) under an inverse microscope (Olympus CK2, Olympus, Germany) and individuals were sorted into a scintillation vial for each sample separately (Wheaton, USA). In assuming that the dauer larvae of Rhabditidae were inactive and had not participated in the uptake of ^{14}C, they were grouped into the bacterial feeders. According to Andrássy (1956) the biomass (fresh weight) was calculated for each genus, summed up for each trophic group per day and multiplied with the factor 100.000 converts data into µg. For the used formula see 4.1.3.

The C content of the nematodes was calculated as 12.5% C of the fresh weight, due to the assumption that the dry weight extinguished 25% of the fresh weight and has a carbon content of 50% (Schmidt, et al., 2000).

4.3.3 ^{14}C Measurement: Liquid Scintillation

The method of liquid scintillation was used to measure the ^{14}C content of the nematodes. Therefor each sample was evaporated from the formaldehyde solution first and then a 6 ml Rothiscint scintillation cocktail (Roth, Germany) was added. The radioactive carbon in the samples offered a beta-decay, whereas under beta-particle (β-) emission, a neutron decayed in a proton. The energy of the β- emission stimulated the scintillation cocktail, whereas photons set free. This kind of chemiluminescence can be detected and measured by a Liquid Scintillation Counter (LS 6500 Multi-Purpose Scintillation Counter, 217 Beckman, USA). A photomultiplier detects this emitted light energy as counts per minute (CPM). Each sample stayed for 180 minutes in the counter for a measurement. The efficiency of ^{14}C counting was about 92% with a ^{14}C activity measurement error less than 2% (Pausch, et al., 2013). The natural ^{14}C background signal, which was measured on day 0 before labelling, was subtracted from all labelling data, i.e. from the ^{14}C activity of each nematode trophic group or the total population, respectively. The following formula was used for the ^{14}C activity calculation per pot in kBq:

$$^{14}C \text{ activity} = \left(\frac{DPM}{n_{Sample} * n_{Total}}\right) / 6000 \qquad \text{[kBq/pot]}$$

Where DPM is: disintegration per minute, n_{Sample}: number of nematodes of trophic group in sample, n_{Total}: total number of nematodes in pot.

Assuming that the ^{14}C allocation between above- and belowground pools is completed after 16 days, the ^{14}C budget was calculated. The ^{14}C activity of the respective C pool ($a(^{14}C)_{pool}$; kBq pot^{-1}) was related to the total ^{14}C recovery at day 16 ($a(^{14}C)_{total}$; kBq pot^{-1}), i.e. to the sum of the ^{14}C activity in soil, shoot, root and CO_2 to calculate ^{14}C (%) recovered in a C pool ($r(^{14}C)_{pool}$; %):

$$r(^{14}C)_{pool} = a(^{14}C)_{pool}/a(^{14}C)_{total}*100 \qquad [\%]$$

4.4 Statistics

Statistical analyses were performed using Statistica 9.1 (StatSoft, Hamburg). The Kolmogorow-Smirnow-Test of Gaussian distribution was done prior to statistical tests. If data didn´t show normal distribution, there were transformed (e.g. square root) before further statistical analysis. ANOVA tests were applied to reveal treatment effects on nematode population density, biomass or community indices. Nematode data were the dependent variable, and time or treatment the independent variable. As soil depth was significant for almost all nematode taxa the factors litter and crop were set as fixed. If significant differences were detected, Tukey test was applied for pairwise comparison of means.

Multivariate statistics were conducted with PRIMER v6.1 (Clarke & Gorley, 2006). Biomass of nematode families were subjected to analysis of similarity (ANOSIM), followed by non-parametric multi-dimensional scaling (nMDS) and similarity percentages procedure (SIMPER) to determine the differences between crops and depths for 2009 and 2010. Prior to analyses, biomass of nematode families was standardized and transformed by square root. The Bray-Curtis similarity index and a scatter plot with a 33% similarity slice factor were applied to the data set.

Correlations between biomass of nematode (dependent variable) trophic groups and those of bacteria and fungi (independent variables) were performed using regression analysis ($P< 0.05$; CI =0.95) in Statistica 9.1.

To investigate significant differences ($P\leq0.05$) in ^{13}C excess between the sampling days ANOVA in combination with Tukey test was used. Differences in ^{13}C-incorporation in time between trophic groups of nematodes were analysed by repeated MANOVA and subsequent by Wilk's lambda tests. In case of significant differences (Wilk´s lambda) Tukey tests were used to further decide significant effects over time. Statistical analyses were performed with the Statistica 9.1.

To identify significant differences in ^{14}C activities statistical analysis was performed as an ANOVA for the factor time, followed by Tukey test using Statistica 9.1.

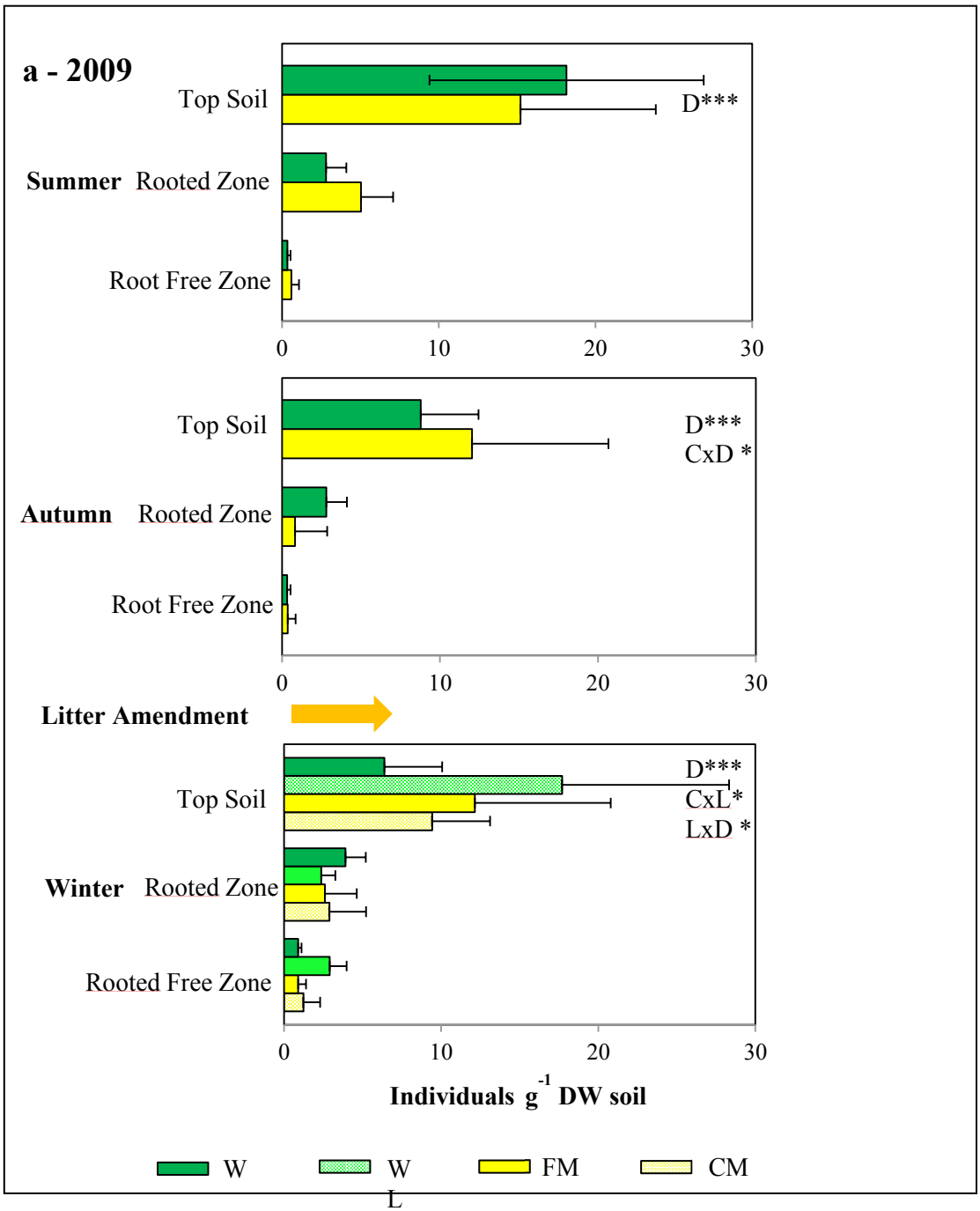
5. Results

5.1 Field experiment on the effects of resource quality and quantity on the nematode community

Parts of the following results are published at Scharroba et al. (2012; 2016).

5.1.1 Population density

In the two investigated vegetation periods the nematode population density ranged from 18.2 ± 8.8 Ind. g^{-1} DW (W: summer 2009, top soil) to only 0.09 ± 0.05 Ind. g^{-1} DW (FM: autumn 2010, root free zone) (Fig.7a+b).



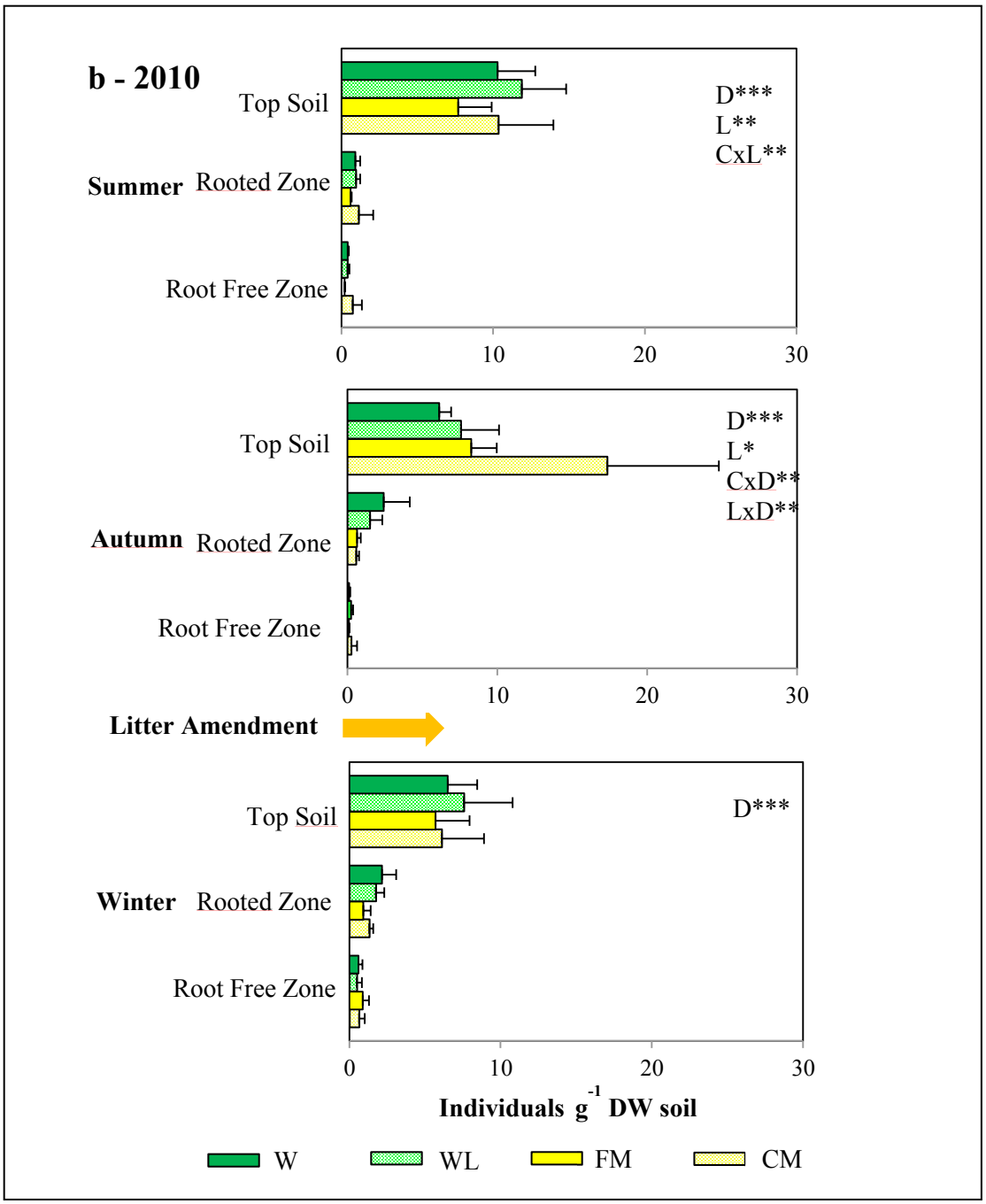


Figure 7a+b: Nematode population density (Individuals g^{-1} DW soil ± SD) is presented for the first (a-2009) and second (b-2010) vegetation period at plots cropped with wheat and maize and threatened with (W, FM) or without litter (WL, CM) in top soil, rooted zone and root free zone.; Statistical significances are based on two-way ANOVA correlated to depth (D), crop (C) and Litter (L) with *P<0.05; **P<0.01; ***P<0.001. (Scharroba, et al., 2016).

Nematode densities decreased significantly from top soil to root free zone at all sampling dates at wheat and maize plots, respectively (ANOVA depth: $P<0.001$, see Table S1). Neither in the first nor in the second vegetation period there was no main crop effect on population density. In 2009 and 2010 significant interactions were registered in autumn at the end of the growing period (2009: $F_{2,41}=3.6$, $P=0.04$; 2010: $F_{2,36}=6.7$, $P=0.003$, Table S1). Generally, the population density was higher under maize plots in top soil (average 10.4±3.8 Ind. g^{-1} DW) but lower in the rooted zone (average 1.05±1.5 Ind. g^{-1} DW) compared to wheat plots (top soil: 10.1±4.5 Ind. g^{-1} DW, rooted zone: 1.4±0.8 Ind. g^{-1} DW).

After the first litter amendment in October 2009 the nematode population density was significant affected by the interaction between crop and litter ($F_{1,36}=4.14$; $P=0.05$) and the interaction between litter and depth ($F_{2,36}=3.54$; $P=0.04$) in the winter (Fig. 7a). Especially at WL plots in top soil nematode density was almost three times higher (17.7 ± 10.6 Ind. g^{-1} DW) as in W plots without litter application (6.4 ± 2.5 Ind. g^{-1} DW). The impact of litter amendment was similar at the root free zone, where both WL and CM plots had distinctly higher nematode densities compared to W and FM plots. In summer 2010 the population density was still affected by litter addition ($F_{1,36}=8.19$; $P=0.007$), especially in the top soil. In autumn 2010 the nematode population was strongly supported under maize as crop, with numbers twice as high as for all other treatments (17.3±7.4 Ind g^{-1} DW; $F_{1,36}= 5.37$, $P=0.03$). These effects proceeded across depth (LxD: $F_{2,36}=3.89$, $P=0.03$). After the second litter application in November 2010 there was no changes in population density observed in the winter sampling (Fig. 7b).

5.1.2 Community composition

In total 27 different nematode families were observed in the soil across seasons, crops and treatments in the two investigated vegetation periods. The nematode community of the arable soil comprised in total 23 families for 2009 and 21 families for 2010 (Table S2+b in the Appendix). Generally more families were detected under wheat compared to maize with 8 to 19 and 7 to 16, respectively. In top soil 14 to 19 families at wheat plots and 14 to 16 families at maize plots were found in 2009 and 2010, respectively. In the rooted zone 11 to 16 families at wheat plots and 10 to 16 families at maize plots were observed in both vegetation periods. Only 8 to 12 families occurred at wheat plots and 7 to 12 families at maize plots in the root free zone in 2009 and 2010. For most nematode families a strong decline in density with soil depth was detected (ANOVA, $P<0.05$; Table S2a+b).

The following 11 families showed not a significant decrease in 2009: Monhysteridae, Panagrolaimidae, Plectidae, Prismatolaimidae, Aphelenchoididae, Dolichodoridae, Heterodoridae, Hoplolaimidae, Dorylaimidae, Qudsianematidae and Mononchidae. 9 families didn't decrease significantly with depth in 2010: Microlaimidae, Monhysteridae, Leptonchidae, Neontylenchidae, Meloidogyne, Psilenchidae, Rotylenchidae, Thornenematidae and Nygolaimidae.

As soil depth was significant for almost all nematode taxa the factors litter and crop were set as fixed in ANOVA, and the effects of resource availability on the most dominant families are presented in Table 2a + b). While in 2009 before litter amendment the nematodes showed a scattered crop effect, in 2010 both crop plant and litter amendment distinctly altered nematode community across depth. Briefly in 2009, the dauer larvae of bacterial-feeding nematodes Rhabditidae presented a positive crop effect in rooted zone (30-40cm: F1, 14=6.3, P=0.03) as well as the fungal-feeding nematodes Aphelenchidae (30-40cm: F1, 14=5.9, P=0.03). Likewise Paratylenchidae (0-10cm: F1,14=5.3, P=0.04) and Pratylenchidae (0-10cm: F1,14=5.5, P=0.04) as plant feeders and the fungal feeding nematode Anguinidae (0-10cm: F1,14=5.6, P=0.03) showed a significant crop effect in top soil. Whereas wheat as crop had a positive impact on these nematode families expect of Rhabditidae dauer larvae, which was supported by maize plants.

In 2010 the major effect wheat crop supported plant-feeding Pratylenchidae (40-50 cm: F1,12=21.7, P=0.0006, 60-70cm: F1,12=8.79, P=0.01) and Paratylenchidae (0-10 cm: F1,12=8.2, P=0.01) too. The bacterial-feeding Rhabditidae preferred litter amendment under maize (0-10 cm: F1, 12=4.85, P=0.05, 40-50 cm: F1, 12=15.34, P=0.02). The response of fungal- feeding nematodes varied and limited to the plough layer; Aphelenchoididae reached highest densities at W and WL (F1,12=8.8, P=0.01), but Aphelenchidae showed highest densities at maize plots with 39 ±14 (Ind. 100 g^{-1}DW ± SD) at FM and 109 ±61 (Ind. 100 g^{-1}DW ± SD) at CM plots with a positive litter effect (F1,12=8.4, P=0.01).

Table 2a. July 2009: Predominant nematode families (individuals 100 g^{-1}DW ± SD) presented at maize (FM) and wheat (W) plots in three different depths: Top Soil (0–10cm), Rooted Zone (30-40cm), and Root Free Zone (60-70cm). DL – dauer larvae. ANOVA with *, **, *** at $P < 0.05$, 0.01, 0,001. Values within a soil depth with the same or no letters are not significantly different according to Tukey at $P < 0.05$. C –crop. Families with spread amounts are not showed, but measured in the total sum. (Scharroba, et al., 2012)

	c-p	TOP SOIL			ROOTED ZONE			ROOT FREE ZONE		
	value	W	FM	ANOVA	W	FM	ANOVA	W	FM	ANOVA
Bacterial feeders										
Cephalobidae	2	416±261	373±135		58±43	116±73		8±0.8	13±5	
Monhysteridae	1	8±9	4±5		1±1	7±11			0.8±1	
Plectidae	2	20±20	4±5		8±6	2±3			1.3±2	
Rhabditidae(without DL)	1	202±115	315±354		58±36	99±62		5±4	7±4	
Rhabditidae (DL)	-	341±242	555±382		60±37	110±47	C*	5±5	5±4	
Fungal feeders										
Anguinidae	2	135±163**a**	4±2**b**	C*	15±12	7±8		0.3±1	0.5±1	
Aphelenchidae	2	127±91	67±97		14±7	25±12	C*	3±2	7±11	
Aphelenchoididae	2	40±44	30±34		27±22	36±23		13±18	25±28	
Plant feeders										
Dolichodoridae	3	19±28			4±5	1±3			0.4±1	
Paratylenchidae	2	173±181**a**	4±5**b**	C*	13±6	13±18		3±3	3±4	
Pratylenchidae	3	225±167**a**	17±5**b**	C*	6±8	4±3		4±5	2±4	
Tylenchidae	2	122±100	82±50		29±21	79±77		5±5	6±7	
Omnivores										
Qudsianematidae	4	7±11	13±14		0.7±2	4±4			0.4±1	
Thornenematidae	5	7±11	2±4		1±2					
Predators										
Anatonchidae	4	11±1	5±0.3			1±3				
Mononchidae	4	12±13				4±7				
Nygolaimidae	5	7±8								
Total number of families		19	16		16	16		8	12	

Table 2b. July 2010: Predominant nematode families (individuals 100 g^{-1}DW ± SD) presented at maize plots with litter (CM) or without (FM) and wheat plots with litter (WL) or without (W) in three different depths: Top Soil (0–10cm), Rooted Zone (30-40cm), and Root Free Zone (60-70cm). DL – dauer larvae. ANOVA with *, **, *** at $P < 0.05$, 0.01, 0,001. Values within a soil depth with the same or no letters are not significantly different according to Tukey at $P < 0.05$. C –crop. Families with spread amounts are not showed, but measured in the total sum. (Scharroba, et al., 2012)

	c-p value	TOP SOIL					ROOTED ZONE					ROOT FREE ZONE				
		W	WL	FM	CM	ANOVA	W	WL	FM	CM	ANOVA	W	WL	FM	CM	ANOVA
Bacterial feeders																
Cephalobidae	2	177±96	201±95	156±66	251±70		17±13	29±33	14±4	21±5		7±1	6±4	3±1	10±8	
Monhysteridae	1	2±4	20±19	-	2±4		1±2	1±0.3	0.4±1	1±1		0.2±0.4	0.3±0.4	0.3±0.4	1±1	
Panagrolaimidae	1	7±8	21±17	5±9	-	C*	-	-	-	-		-	-	-	-	
Plectidae	2	8±12	26±21	2±5	2±4	C*	0.4±1	0.2±0.5	1±1	0.3±0.4		0.3±0.5	1±1			
Rhabditidae(without DL)	1	206±40	139±46	165±100	257±107	L*	1±1**b**	4±3**b**	5±2**ab**	44±7**a**	C**	5±5	4±2	1±2	10±9	
Rhabditidae DL	-	161±133	273±214	229±150	559±275		3±2	4±3	16±13	21±11		3±1	9±9	3±3	25±42	CxL*
Fungal feeders																
Anguinidae	2	13±19	23±18	2±5	10±13		0.3±1	1±1	0.3±0.4	-		0.3±0.4	0.3±1	-	0.3±1	
Aphelenchidae	2	24±12**b**	31±7**b**	39±14**b**	109±61**a**	C*,L*	13±5	12±6	6±2	11±5		6±4	4±2	3±2	2±1	
Aphelenchoididae	2	227±43**a**	229±96**a**	65±60**b**	190±60**ab**	C*	3±1	4±4	6±5	3±2		6±3	7±5	1±1	13±13	
Plant feeders																
Paratylenchidae	2	66±69	80±61	2±5	8±9	C*	1.8±3	0.2±0.5	1±1	0.4±1		-	0.2±0.3	-	-	
Pratylenchidae	3	10±9	6±12	5±1	6±7		40.1±19**a**	26.8±1.2**ab**	4±3**b**	7±9**b**	C***	10±4**a**	4±4**ab**	4±4**ab**	0.3±1**b**	C*, L**
Tylenchidae	2	110±61	111±58	85±45	101±47		11±6	11±4	4±4	4±3	C*	2±1	3±2	2±2	12±17	
Omnivores																
Qudsianematidae	4	2±4	3±6	4±5	2±4		0.1±0.3	0.3±1	-	0.2±0.4		0.4±1	0.3±0.4	-	1±1	
Thornenematidae	5	2±3	5±6	-	-		-	-	-	-		-	-	-	-	
Predators																
Anatonchidae	4	15±6	7±8	5±7	6±8		-	-	-	-		-	-	-	-	
Total number of families		14	17	14	14		11	11	10	10		10	12	7	9	

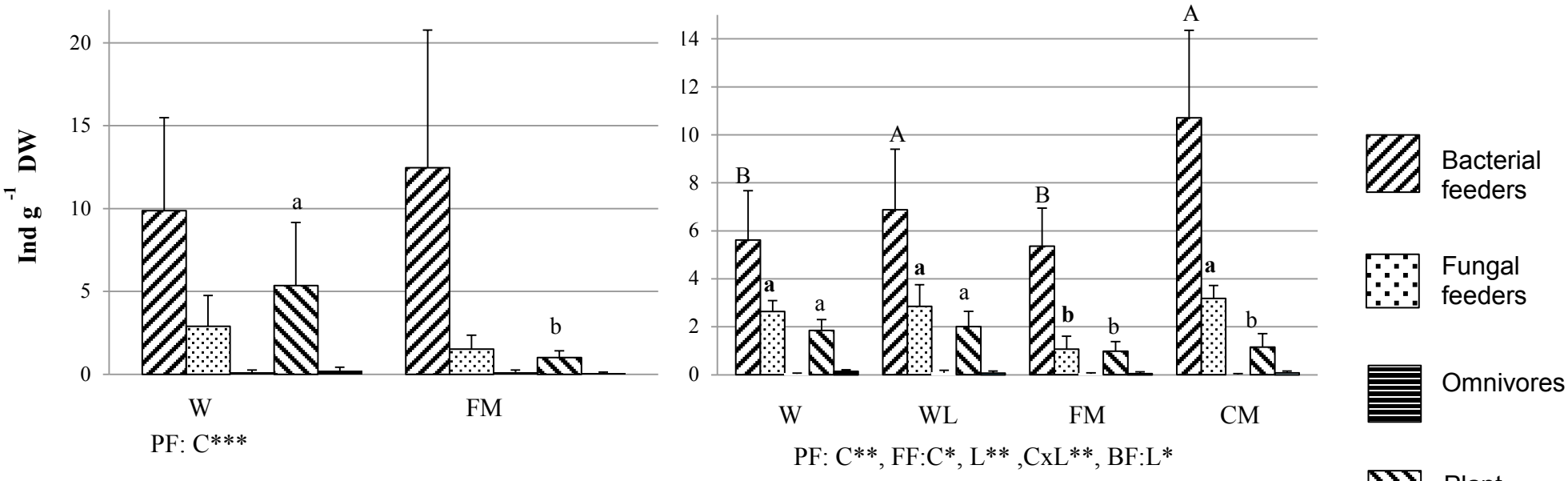
5.1.3 Trophic composition

The major trophic groups of nematodes across treatments were bacterial, fungal and plant feeders in both investigated vegetation periods (Fig.8a-c). In top soil the numbers ranged from 5.4±1.6 to 12.5±8.3, 1.1±0.5 to 3.2±0.6 and 0.9±0.4 to 5.4±3.8 g^{-1} DW, for bacterial, fungal and plant feeders, respectively. The densities of omnivores and predators were low, with highest numbers in the top soil. Here omnivores made up 0.12±0.13 g^{-1} DW at wheat plots as well as 0.13±0.13 g^{-1} DW at maize plots and predators made up 0.19±0.23 g^{-1} DW at wheat plots as well as in maize plots 0.05±0.08 g^{-1} DW. In 2009, the first year of the experiment, the plant-feeding nematodes showed a significant effect, here wheat as crop fostered them in the top soil (*F1,12*=22.3, *P*=0.0005, Fig 8a). The bacterial-feeding nematodes preferred significantly maize as crop in the rooted zone (*F1,12*=8.3, *P*=0.014, Fig. 8b).

In contrast in the second year 2010 much more litter and crop influences were detected. The different treatments most strongly affected fungal feeders, with maize as crop, litter amendment and both in combination had a positive impact (Crop: *F1,12*=5.93; *P*=0.03;Litter: *F1,12*=12.09, *P*=0.005; CxL: *F1,12*=10.31, *P*=0.007; Fig 8a). Wheat as crop had a positive impact on plant feeders *(F1,12*=10.03, *P*=0.008), and litter addition on bacterial feeders (*F1,12*=5.14, *P*=0.04). In the rooted zone the plant-feeding nematodes distinctly increased in plots cropped with wheat (*F1,12*=25.53, *P*=0.0005, Fig 8b). At the root-free soil in 60-70cm the bacterial feeders dominated the nematode community at litter amended plots with densities of 0.2±0.1 and 0.46±0.5 Ind/g DW at WL and CM, respectively (*F1,12*=5.07, *P*=0.04, Fig 8b).

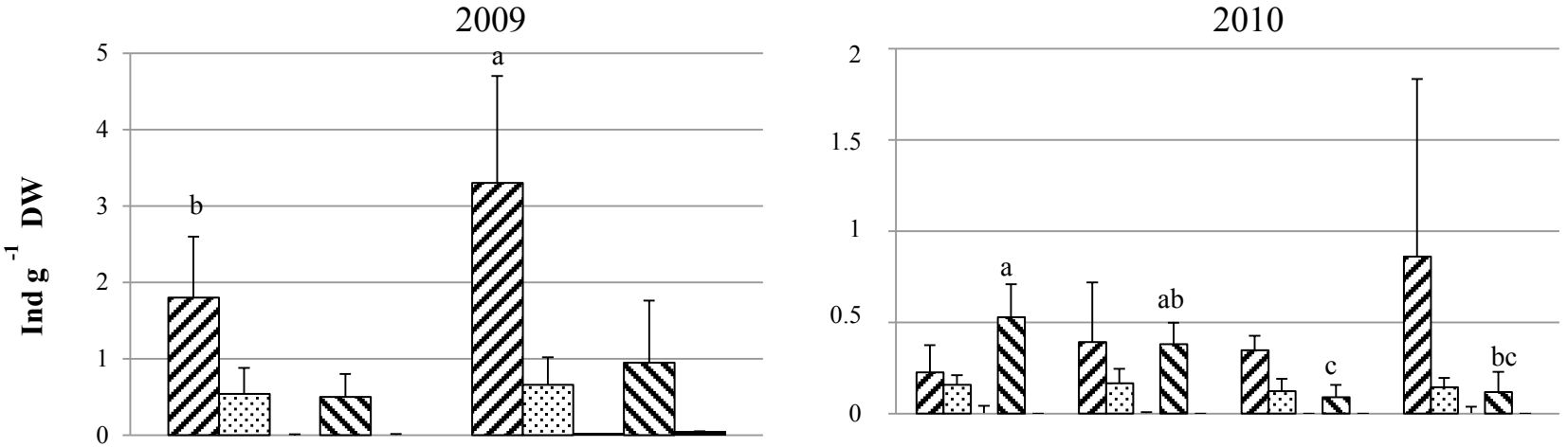
8a

TOP SOIL



8b

ROOTED ZONE



FM W WL FM CM

PF:C***

8c

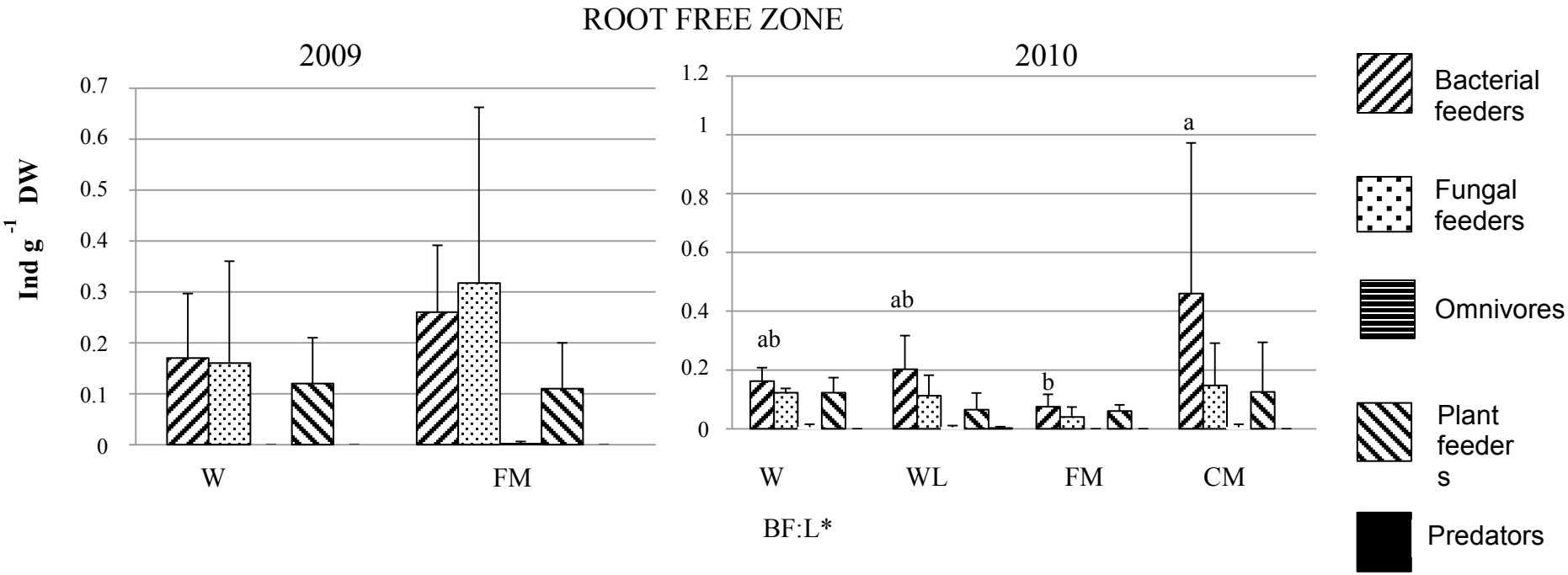


Figure 8: Nematode trophic structure (Ind g^{-1} DW±SD) at plots cropped with either fodder or corn maize and wheat with and without maize litter in TOP SOIL, ROOTED ZONE, ROOT FREE ZONE in 2009 and 2010. PF - plant feeders, BF - bacterial feeders, FF - Fungal feeders. C - crop, L - litter; ANOVA with *, **, *** at $P < 0.05, 0.01, 0.001$. Columns within depth and year with the same or no letters are not significantly

different according to TUKEY at $P< 0.05$.

5.1.4 Nematode faunal indices

Several indices were calculated to identify potential effects of crop plant and litter amendment on the nematode community, with a major focus on disturbance, trophic structure, resource availability and nutrient flow (Tab.3). Both, the Maturity Index (*MI*: 1.6 to 2.0) and the Plant Parasite Index (*PPI*: 2.0 to 2.7) were low in the investigated vegetation period. Neither crop nor litter application had an impact on the *MI*. In 2010 for the *PPI* a crop ($F_{1,12}$=12.6; P=0.004) and litter effect ($F_{1,12}$=16.5; P=0.002) in the root free zone was observed with lowest values under CM compared to all other treatments. The Enrichment Index, with values mostly above 50, points to a good nutrient availability in the soil in both vegetation periods (Table 3). In 2010 in the rooted zone the nutrient input to the food web was higher under maize, especially at CM plots ($F_{1,12}$=8.8, P=0.01). The Structure Index was very low (*SI*: 0 to 18.5) across treatments and depths, assigning an overall basal food web of low complexity for 2009 and 2010.

Table 3: Nematode faunal indices and ratios at maize or wheat plots threatened with (CM, WL) or without (FM,W) litter in three different depths for 2009 and 2010: a- top soil, b - rooted zone, c - root free zone. ANOVA with *, **, *** at $P < 0.05$, 0.01, 0,001. Values within a soil depth with the same or no letters are not significantly different

2009	TOP SOIL			ROOTED ZONE			ROOT FREE ZONE		
	W	FM	ANOVA	W	FM	ANOVA	W	FM	ANOVA
MI	1.8±0.2	1.8±0.2		1.6±0.2	1.7±0.2		1.8±0.2	1.9±0.1	
PPI	2.5±0.3	2.2±0.2		2.2±0.1	2.1±0.1		2.3±0.2	2.0±0.6	
EI	60.6±1.8	64.3±7.2		63.8±8.9	65.2±7.6		57.6±6.6	56.7±2.8	
SI	15.8±14.5	12.7±8.2		2.8±4.7	10.1±11.4		0.9±1.5	0.7±1.3	
CI	25.6±8.6	17.1±11.7		25.4±15.5	19.0±14.6		47.8±36.3	46.7±20.4	
F/B	0.3±0.4	0.2±0.1		0.4±0.4	0.2±0.3	C**	0.9±1.8	1.3±2.7	
RD/R	1.7±1.9	1.9±1.1		1.2±1.3	1.2±1.5		1.3±4.3	0.8±1.3	
H`	2.3±0.3	1.9±0.2	C*	2.2±0.2	2.04±0.2		1.7±0.5	1.9±0.3	
T	4.0±1.7**b**	11.2±4.8**a**	C***	7.2±0.5	2.1±0.01		0.003±0.005**b**	1.6±0.3**a**	C*

2010	TOP SOIL					ROOTED ZONE					ROOT FREE ZONE				
	W	WL	FM	CM	ANOVA	W	WL	FM	CM	ANOVA	W	WL	FM	CM	ANOVA
MI	1.7±0.02	1.8±0.1	1.7±0.2	1.7±0.1		2.0±0.1	1.7±0.3	1.8±0.1	1.9±0.5		1.8±0.3	1.8±0.1	1.8±0.2	1.8±0.2	
PPI	2.1±0.1	2.1±0.1	2.1±0.2	2.1±0.1		2.7±0.2	2.7±0.1	2.6±0.3	2.5±0.3		2.8±0.1**a**	2.5±0.2**a**	2.6±0.3**a**	2.1±0.1**b**	C**,L**
EI	71.8±2.5	66.3±3.4	71.7±11.8	69.2±7.3		31.8±15**b**	46.7±20.3**ab**	55.7±9.1**ab**	68.7±15.2**a**	C*	58.7±16.5	62.7±7.3	53.1±18.7	68.5±6.7	
SI	15.2±7.7	14.2±7.5	11.4±12.2	7.6±5.6		2.9±5.9	1.5±3	0±0	2.3±4.7		5.6±11.1	7.8±9.7	25.9±5.6	4.0±8	
CI	20.7±4.5	27.9±2.7	22.3±21.8	23.4±15.9		77.6±22.8**a**	42.9±9.5**ab**	35.2±12.6**b**	27.3±18.4**b**	C**,L*	51.8±36.5	37.9±18.4	56.6±36.6	25.9±5.6	
F/B	0.7±0.3	0.7±0.7	0.3±0.4	0.6±0.3		0.8±0.4	0.5±0.3	0.6±1.3	0.2±0.1		0.9±0.3	1.0±1.4	0.9±1.1	0.7±1.0	
RD/R	0.8±3.3	2.0±4.7	1.4±1.5	2.2±2.6		4.4±2.1	1.1±1.1	3.0±7.0	0.5±0.2		0.6±0.3	2.0±5.0	2.1±2.1	2.4±5.0	
H`	1.8±0.1	2.0±0.1	1.6±0.1	1.7±0.1	C***, CxL*	1.5±0.3	1.6±0.4	1.7±0.1	1.5±0.3		1.7±0.1	1.8±0.2	1.5±0.2	1.5±0.1	C*
T	2.8±0.4	2.8±0.2	2.3±0.5	2.4±0.2	C*	2.2±0.3	2.6±0.4	2.5±0.4	2.3±0.7		2.9±0.4	2.6±0.3	2.6±0.2	2.5±0.5	

according to Tukey at $P < 0.05$. C – crop, L – litter. (Scharroba, et al., 2016), modified.

In Figure 9 values of *EI* were plotted against *SI* and with two exceptions all data were arranged in quadrat A of the fauna profile from Ferris & Bongers (2009). Only data pairs from plots cropped with wheat in 2010 at rooted zone showed a lower *EI* and are located in quadrat D. Here the soil is poor in nutrients and the decomposition takes place by fungal and not bacterial feeders.

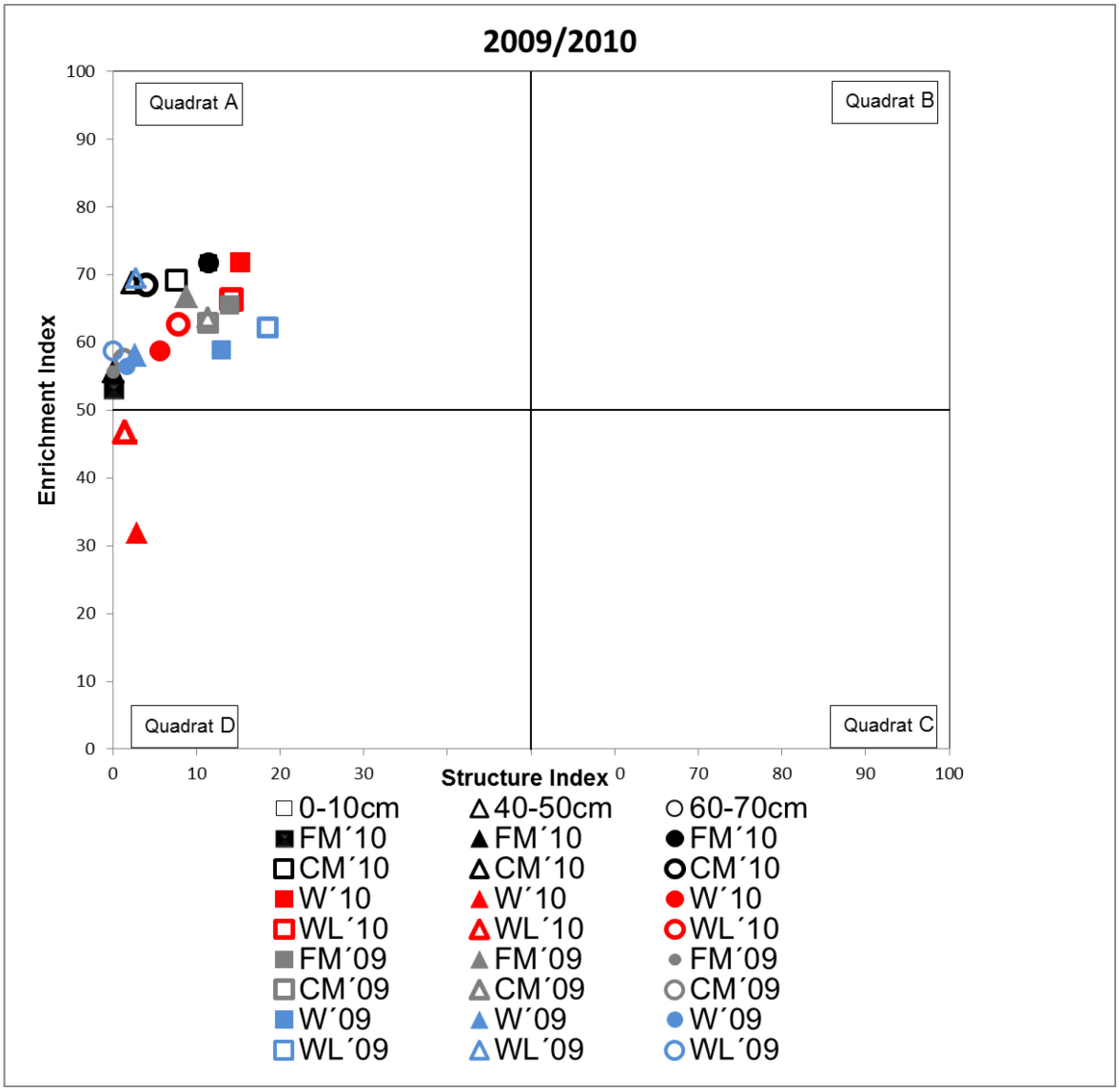


Figure 9: Fauna profile according to Ferris & Bongers (2009), For summer 2009 and 2010 values of EI were plotted against SI at the three depths: 0-10cm (TOP SOIL), 40-50cm (ROOTED ZONE) and 60-70cm (ROOT FREE ZONE)

In both years the Channel Index was mainly below 50 indicates carbon flow mainly through the bacterial channel (Table 3). In accordance with *EI* and *SI* in 2010 in the rooted zone the *CI* pointed to a fungal decomposition at W (CI=78), whereas the bacterial pathway

dominated at FM (CI=35) and CM (CI=27) plots (Crop: $F_{1,12}$=12.2, P=0.04; Litter: $F_{1,12}$=6.5, P=0.02).

The *F/B* ratios in top soil and rooted zone ranged from 0.2±0.1 (FM 2009, in top soil) to 0.8±0.4 (W 2010, rooted zone), indicating a bacteria dominated decomposition pathway (Table 3) with significant crop effect in rooted zone $F_{1,12}$=9.9, P=0.008) in 2009. On the opposite the *F/B* values in the root free zone in 2009 and 2010 ranged from 0.7±1.0 (CM 2010) to 1.3±2.7 (FM 2009), assigning a shift from bacterial- to fungal- dominated nutrient flow with depth.

Values of *RD/R* were fairly similar across plots and generally above 1 in the first vegetation period in 2009, pointing to a moderate nutrient reduction (Table 3). In 2010, after litter amendment, *RD/R* varied more strongly without a distinct pattern related to crop, litter or depth. The values at the rooted zone with up to 4.4 indicate shifts in the major decomposition pathways from bacterial to fungal domination.

The Shannon diversity index H' ranged between 1.5 and 2.3, with high diversity under wheat particularly in the plough layer (2009: Crop: $F_{1,12}$=6.8, P=0.02 and 2010: Crop: $F_{1,12}$=22.42, P=0.0005) and the root-free deep soil (2010: Crop: $F_{1,12}$=7.06, P=0.02; Table 3). Wheat in combination with litter revealed the highest nematode diversity (2010: 0-10 cm, Litter: $F_{1,12}$=5.85, P=0.03).

In both years the trophic diversity index *T* suggested a crop effect on nematode community- with high values under the maize rows at top soil ($F_{1,14}$=60.7; P=0.0001) and root free zone ($F_{1,13}$=6.4; P=0.03) in 2009 and in the opposite with high values under plots cropped with wheat ($F_{1,12}$=8.7; P=0.01) in 2010 (Tab.3)

Some of the evaluated indices additionally changed due to soil horizon the nematode community inhabited. In 2009 this were the *MI* ($F_{2,41}$=6.6; P=0.003), *T* ($F_{2,41}$=139.8; P<0.0001), and *F/B* ($F_{2,41}$=5.8; P=0.006), whereas in 2010 only the *PPI* ($F_{2,42}$=28.9; P<0.00001) was responsive to depth (Table 3, ANOVA not indicated).

5.1.5 Biomass as a measure for carbon allocation in nematodes

To assign the magnitude of C allocation in the nematode micro-food web, the biomass of nematode assemblages was determined using their distinct morphological metrics. The biomass of all families was significantly depend on soil horizons and decreased with depth ($F_{56,124}$=6.65; P<0.001). The highest biomass of the nematode community exhibited the bacterial feeders Rhabditidae (without DL) with 1203±1218 (mg FW m^{-2} soil) at FM plots in the top soil 2009. The Rhabditidae had almost the highest values across all depths at both vegetation periods. Within the fungal feeders Anguinidae (61.7±75.8 mg FW m^{-2} soil) showed in 2009 and Aphelenchoididae (50.2±9.7 mg FW m^{-2} soil) showed in 2010 the highest biomass at W plots in the top soil. At top soil Heteroderidae as root-knot parasite and the omnivorous Dorylaimidae offered the highest biomass within their trophic group with values 83.5±236 mg FW m^{-2} soil and 156±441 mg FW m^{-2} soil, respectively. Within the predators Anatonchidae showed with values of 117±51.4 mg FW m^{-2} soil the highest biomass at W plots in 2010.

The two different crops, maize and wheat crop affected the biomass build up in nematode families, with wheat imposing a strong positive effect. In 2009 higher biomass were achieved by Plectidae as bacterial feeders ($F_{1,14}$=5.3; P=0.04), Anguinidae as fungal feeders ($F_{1,14}$=4.7; P=0.05) and Pratylenchidae as plant-feeding nematodes ($F_{1,14}$=6.04; P=0.03) at wheat compared to maize plots in top soil. At the opposite the fungal feeders Aphelenchidae ($F_{1,14}$=6.08; P=0.03) and the plant feeders Tylenchidae ($F_{1,14}$=4.6; P=0.05) occurred in higher biomass in maize plots at the rooted zone.

In the second vegetation period, summer 2010, the bacterial-feeding nematodes Panagrolaimidae ($F_{1,12}$=7.6; P=0.02) and Plectidae ($F_{1,12}$=5.71; P=0.03), the fungal-feeding Aphelenchoididae ($F_{1,12}$=8.4; P=0.01), and the plant-feeding Paratylenchidae ($F_{1,12}$=8.8; P=0.01) showed a higher biomass at plots cropped with wheat compared to maize at the top soil (Table 4). Similarly, the biomass of the plant feeders Pratylenchidae (rooted zone: $F_{1,12}$=21.7; P=0.0006, root free zone: $F_{1,12}$=8.8; P=0.01) and Tylenchidae (rooted zone: $F_{1,12}$=8.9; P=0.01) were supported at wheat plots (Table 4b, c).

In 2010, eight months after litter amendment and establishing of the four different treatments (W, WL, FM, CM) the single litter effect apparent across treatments and depth was observed in the root free zone, where the plant-feeding Pratylenchidae had the lowest biomass at the litter amended plots ($F_{1,12}$=10.9; P=0.006).

Table 4 At three depths (a- Top Soil, b- Rooted Zone, c- Root Free Zone) the biomass of nematode families are presented at plots cropped with maize and wheat and treated with (CM,WL) or without maize litter (FM,W). ANOVA with *, **, *** at $P < 0.05$, 0.01, 0,001. Values within a soil depth with the same or no letters are not significantly different according to Tukey at $P < 0.05$. C – crop, L – litter.

(Scharroba, et al., 2016)

a - TOP	**2009**		**ANOVA**	**2010**				**ANOVA**
SOIL	W	FM		W	WL	FM	CM	
Bacterial feeders								
Cephalobidae	179±13	16±62		67±28	87±56	49±37	106±30	
Microlaimidae	-	-		-	1.3±1.7	-	-	
Monhysteridae	3.5±5.5	1±1.4		0.7±1.4	6.9±6.6	-	0.6±1.2	
Panagrolaimidae	-	-		6.9±8**b**	21.4±17.2**a**	2.3±4.6**b**	-	C*
Plectidae	17.8±17.5**a**	3.1±4.6**b**	C*	7.5±10.7	23.8±18.9	2.3±4.5	2±4.1	C*
Prismatolaimidae	1.8±5.1	0.5±1.3		-	-	-	-	
Rhabditidae	895±641	1203±1218		693±113	508±51	686±346	943±437	
Fungal feeders								
Anguinidae	61.7±75.8**a**	3.2±5.6**b**	C*	6.7±9.7	11.8±9.5	1.2±2.3	21.4±34.5	
Aphelenchidae	53.5±41	58±54.7		7.8±4.1	10.3±2.4	13.2±4.7	94.3±112.4	
Aphelenchoididae	8.7±9.8	6.6±7.8		50.2±9.7**a**	49.9±21.4**a**	14.3±13.3**b**	42.1±13.3**ab**	C*
Leptonchidae	-	-		-	3.3±6.7	-	-	
Neotylenchidae	-	-		-	-	-	5.5±11	
Plant feeders								
Dolichodoridae	3.6±7.6	-		-	-	-	-	
Heteroderidae	-	83.5±236		-	-	-	-	
Hoplolaimidae	0.9±2.7	-		-	-	-	-	
Meloidogyne	-	-		0.0±0.0	0.0±0.0	0.3±0.6	-	
Paratylenchidae	17±24.2	0.2±0.4		6.5±6.7	7.8±6	0.2±0.4	0.8±0.9	C*

a - TOP	**2009**		**ANOVA**	**2010**				**ANOVA**
SOIL	**W**	**FM**		**W**	**WL**	**FM**	**CM**	
Pratylenchidae	41.4±44.1**a**	2.9±3.5**b**	C*	1.8±1.8	1.1±2.2	0.9±1.8	1.1±1.3	
Psilenchidae	-	0.6±1.8		-	-	1±1.9	-	
Rotylenchidae	-	-		-	2.2±4.5	-	-	
Tylenchidae	38.5±53.7	10±6.1		15.9±8.8	16±8.4	12.3±6.4	14.6±6.7	
Omnivores								
Dorylaimidae	156±441	-		-	-	-	-	
Qudsianematidae	23.2±34.6	36±37		5.3±10.5	7.9±15.8	15±20.7	4±8.2	
Thornenematidae	16.8±23.9	5.2±14.7		7±14	19.2±22.2	-	-	
Predators								
Anatonchidae	83±119	42.1±67.6		117±51.4	56.7±66.8	42.2±60.5	50.6±68.8	
Mononchidae	29.5±66	-		-	-	-	-	
Nygolaimidae	12.7±23.4	-		-	-	-	9±18.1	
b - ROOTED	**2009**		**ANOVA**	**2010**				**ANOVA**
ZONE	**W**	**FM**		**W**	**WL**	**FM**	**CM**	
Bacterial feeders								
Cephalobidae	32.9±31.7	65.1±37.2		6.9±4.3	10.6±12.3	4±1.4	7±4.3	
Diplogasteridae	0.4±1.2	2.1±3.1		-	-	-	-	
Monhysteridae	0.2±0.5	2.8±5.5		0.4±0.6	0.5±0.2	0.2±0.3	0.3±0.6	
Panagrolaimidae	0.3±0.9	0.9±2.7		-	-	-	-	
Plectidae	5.2±9.2	2.1±4		0.6±0.6	0.3±0.6	0.6±1.1	0.3±0.6	
Rhabditidae	245±195	407±250		3.9±7.5	17.2±12.5	32.7±24.2	191±291	
Fungal feeders								
Anguinidae	9.6±10.6	4±5.4		0.2±0.3	0.3±0.6	0.2±0.3	-	
Aphelenchidae	5.4±3.3**a**	10.2±4.4**b**	C*	5.2±2.2	5±2.4	2.4±0.7	4.5±2.1	

b- ROOTED	2009		ANOVA	2010				ANOVA
ZONE	**W**	**FM**		**W**	**WL**	**FM**	**CM**	
Aphelenchoididae	7.2±6.6	9.7±6.6		0.7±0.2	1.2±1.2	1.8±1.4	1±0.5	
Plant feeders								
Dolichodoridae	1.7±2.9	0.4±1.1		-	-	-	-	
Hoplolaimidae	0.2±0.5	-		-	-	-	-	
Paratylenchidae	1.6±0.8	1.6±2.9		0.2±0.4	0.03±0.06	0.2±0.1	0.06±0.12	
Pratylenchidae	1.4±1.8	0.9±0.8		9.2±4.4**a**	6.2±2.7**a**	0.8±0.7**b**	1.6±2**b**	C***
Tylenchidae	3.7±2.7**a**	12.7±11.6**b**	C*	1.9±1	1.9±0.7	0.8±0.7	0.8±0.5	C*
Omnivores								
Qudsianematidae	-	2.4±6.9		0.8±1.6	0.8±1.6	-	0.9±1.7	
Thornenematidae	2.9±8.1	-		-	-	-	-	
Predators								
Anatonchidae	-	6.2±17.6		-	-	-	-	
Mononchidae	4±11.3	18±38		-	-	-	-	

c - ROOT FREE	2009		ANOVA	2010				ANOVA
ZONE	**W**	**FM**		**W**	**WL**	**FM**	**CM**	
Bacterial feeders								
Cephalobidae	3.9±3.4	7±4.4		2.3±0.6	2.1±1.4	0.9±0.4	3.4±2.8	
Monhysteridae	-	0.4±0.5		0.1±0.2	0.2±0.2	0.1±0.2	0.2±0.2	
Plectidae	-	1.3±2.2		26.3±52.6	0.8±1	-	-	
Rhabditidae	21.4±34.4	29.5±24.3		39.3±73.1	28.8±16.2	10.7±12.4	73.1±60.7	
Fungal feeders								
Anguinidae	0.09±0.2	0.1±0.4		0.1±0.3	0.1±0.3	-	0.1±0.3	
Aphelenchidae	1.2±0.9	2.4±3.5		2.3±1.5	1.6±0.7	0.8±0.8	0.8±0.5	

c- ROOT FREE	2009		ANOVA	2010				ANOVA
ZONE	**W**	**FM**		**W**	**WL**	**FM**	**CM**	
Aphelenchoididae	3±5	6.6±7.3		1.5±0.8	1.8±1.2	0.3±0.4	3.2±3.3	
Plant feeders								
Dolichodoridae	-	0.1±0.4		-	-	-	-	
Paratylenchidae	0.4±0.2	0.6±0.8		-	0.03±0.06	-	-	
Pratylenchidae	0.9±0.9	0.4±0.6		2.1±0.7**ab**	0.8±0.8**ab**	0.4±0.7**ab**	0.05±0.1**b**	C*, L**
Tylenchidae	0.7±0.8	1±1		0.3±0.2	0.5±0.3	0.3±0.3	2±2.8	
Omnivores								
Qudsianematidae	-	0.7±1.9		1.5±3.1	1.5±1.8	-	1.4±2.7	
Predators								
Nygolaimidae	-	-		-	1.3±2.6	-	-	

5.1.4 Biomass distribution

Subject to nutrient availability, humidity, depth and further parameter the soil fauna can be assemblage. Within the nematode fauna the depth gradient and crop were used as parameters to identify such metacommunities. To assign nematode biomass distribution in different soil horizons, non-parametric multidimensional scaling (nMDS) was applied followed by an analysis of similarity percentages (SIMPER). Using the two-way crossed ANOSIM ("depth" across "crop") the multivariate fitting of biomass pattern in nematode families resulted in a separation of soil depths (2009: Global R=0.46; P<0.001; 2010: Global R=0.69; P<0.001) and a less strong splitting of crops (2009: Global R=0.096; P<0.001; 2010: Global R=0.25; P<0.001). Figures 10 and 11 give the nMDS scatterplot for the years 2009 and 2010.

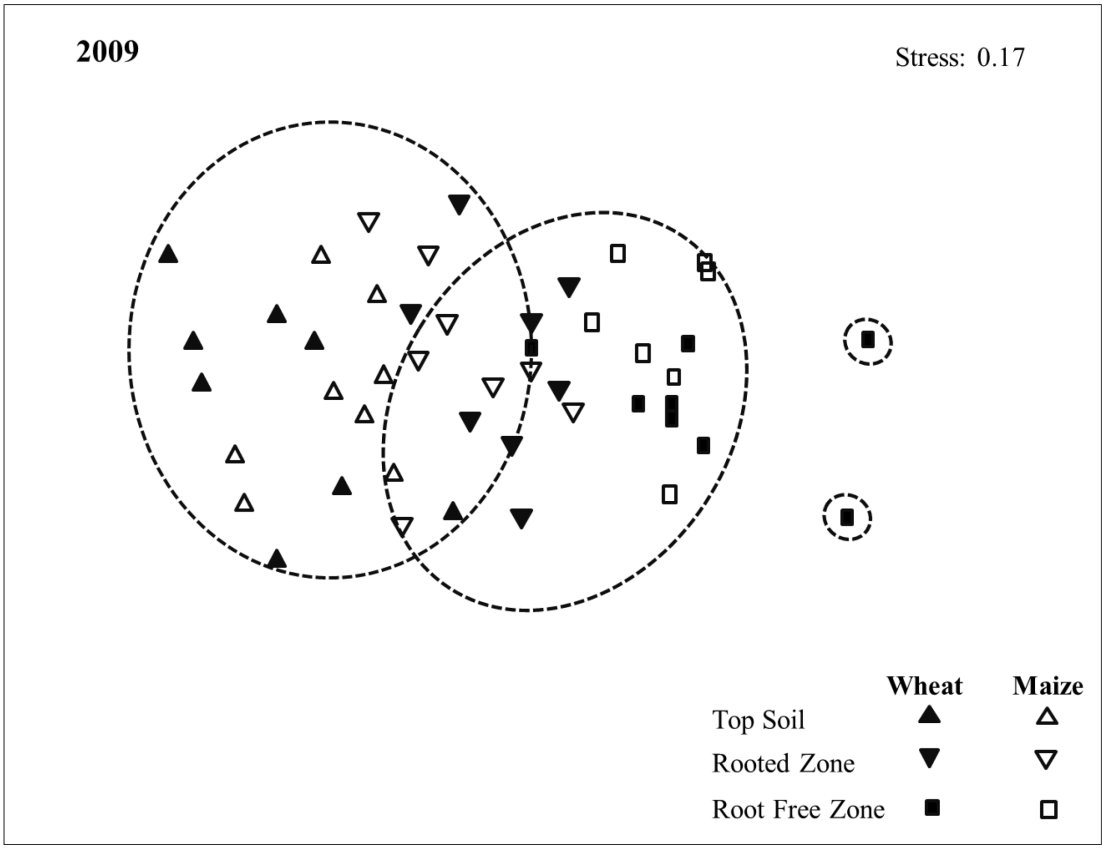


Figure 10 Allocation of nematode metacommunities along three different depths (top soil, rooted zone, root free zone) at plots cropped with wheat (W) or maize (M) by using non-parametric multi-dimensional scaling (nMDS) of nematode biomass Dashed line – Bray Curtis similarity level of 33%. After Scharroba et al. (2016), modified.

In 2009 two big groups (except to outliners for wheat in root free zone) were distinguished by applying a similarity level of 33% (Stress: 0.17). The highest similarity in biomass was amongst nematode communities at wheat and maize plots in the top soil. On the opposite, family biomass pattern of nematode assemblages in root free and rooted zone clustered together, with the latter partly overlapping with the top soil. Table 5 illustrates the impact of different nematode families to this separation according to SIMPER analysis.

Table 5 Contribution (%) of the biomass of nematode families to the dissimilarity between top soil, rooted zone, and root free zone in July 2009 analysed by similarity percentage analysis (SIMPER). Presented are the average dissimilarities between different soil depths and the contribution of the seven families with the highest influence on separation. DL – dauer larvae. After Scharroba et al. (2016), modified.

Group	Group average dissimi-larity	Family	Average biomass		Average dissimilar-rity	Contribution to group dissimilarity (%)
Top Soil & Rooted Zone	64.23		TopSoil	Rooted Zone		
		Qudsianematidae	1.76	0.12	4.85	7.56
		Pratylenchidae	1.77	0.42	3.88	6.04
		Aphelenchidae	2.12	0.83	3.86	6.01
		Anatonchidae	1.45	0.14	3.70	5.75
		Plectidae	1.41	0.71	3.69	5.74
		Anguinidae	1.36	0.81	3.56	5.55
		Monhysteridae	1.18	0.74	3.44	5.35
Top Soil & Root Free Zone	80.52		TopSoil	Root Free Zone		
		Rhabditidae(DL)	2.02	0.28	7.67	9.52
		Cephalobidae	2.08	0.36	7.28	9.04
		Aphelenchidae	2.12	0.34	6.95	8.64
		Qudsianematidae	1.76	0.07	6.49	8.07
		Tylenchidae	1.74	0.35	5.7	7.08
		Pratylenchidae	1.77	0.3	5.28	6.55
		Anatonchidae	1.45	0	4.76	5.91
Rooted Zone & Root Free Zone	63.82		Rooted Zone	Root Free Zone		
		Aphelenchoididae	1.48	0.99	5.81	9.10
		Rhabditidae(DL)	1.12	0.28	5.49	8.61
		Tylenchidae	1.09	0.35	5.01	7.85
		Cephalobidae	1.09	0.36	4.8	7.51
		Monhysteridae	0.74	0.24	4.78	7.48
		Anguinidae	0.81	0.05	4.73	7.05
		Plectidae	0.71	0.24	4.5	7.05

The greatest average group dissimilarity was observed between families in top soil and root free zone (80%), whereas dissimilarity was similar between top soil and rooted zone, and between rooted and root free zone (64%). The following nematode families affected the dissimilarity between top soil and rooted zone (in descending order): Qudsianematidae, Pratylenchidae, Aphelenchidae, Anatonchidae, Plectidae, Anguinidae and Monhysteridae. The Qudsianematidae and Aphelenchidae were also accountable for the parting of top soil from the root free zone, yet less important than Rhabditidae dauer larvae and Cephalobidae. The biomasses of these two families and of Aphelenchoididae, Tylenchidae, Monhysteridae, Anguinidae and Plectidae had the highest effect on dissimilarity between rooted zone and root free zone.

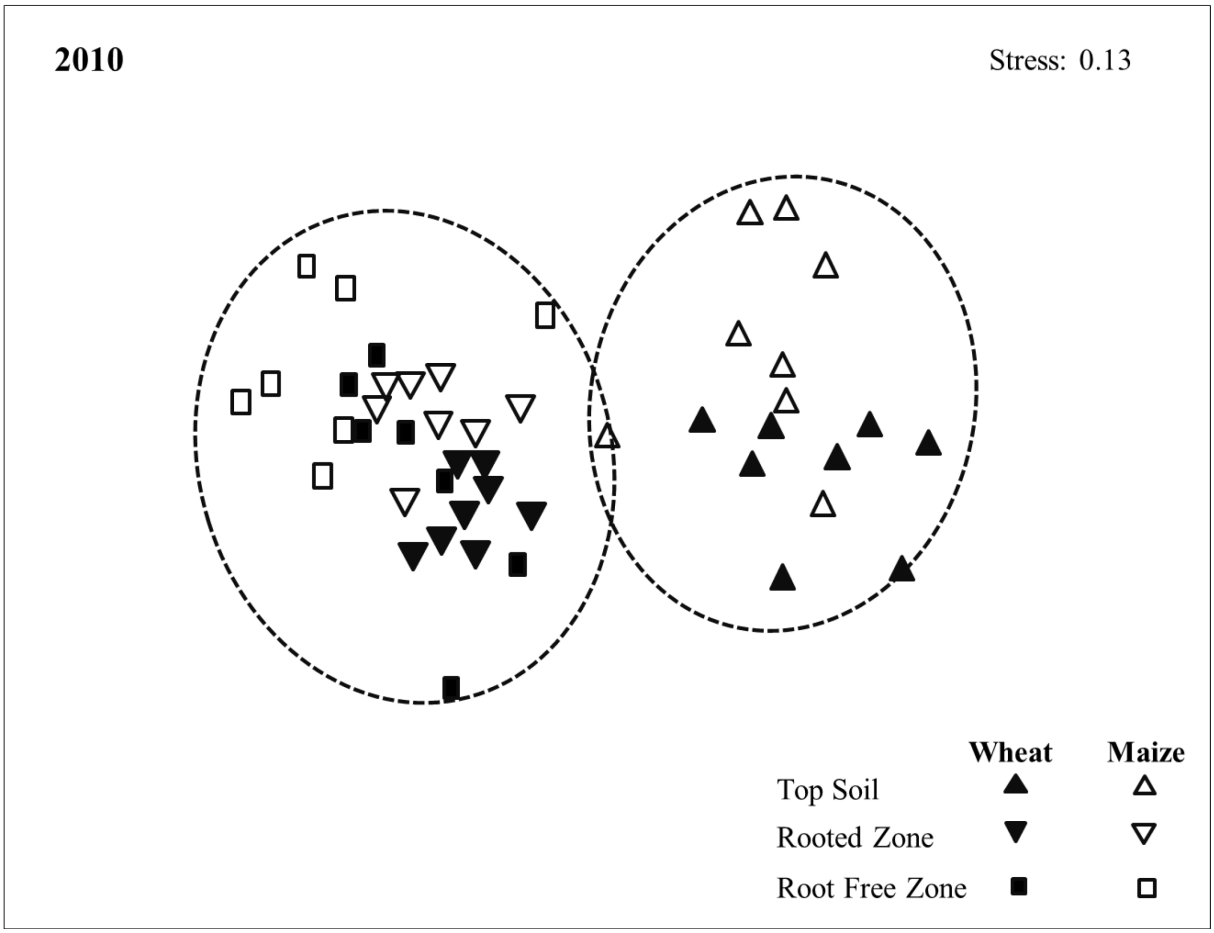


Figure 11: Allocation of nematode metacommunities along three different depths (top soil, rooted zone, root free zone) at plots cropped with wheat (W) or maize (M) by using non-parametric multi-dimensional scaling (nMDS) of nematode biomass Note that half of the plots were treated with maize litter for both crops. Dashed line – Bray Curtis similarity level of 33%. After Scharroba et al. (2016), modified**.**

In 2010 the top soil communities were separated from those in the rooted and root free zone (Fig. 11, stress: 0.13). Alike in 2009, greatest average group dissimilarity as between accumulations in top soil and root free zone (81%) and the top soil communities also varied considerably from those in the rooted zone (74%), whereas the assemblages, which located in the rooted and root free horizon, showed lower dissimilarity (49%, Table 6). Considering nematode families the biomass of Anatonchidae, Aphelenchoididae, Rhabditidae dauer larvae, Tylenchidae, Cephalobidae, Paratylenchidae and Pratylenchidae accounted most to the separation of top soil to rooted zone as well as to root free zone. In the opposite, Pratylenchidae, Monhysteridae, Plectidae, Qudsianematidae, Aphelenchidae, Rhabditidae dauer larvae and Tylenchidae were accountable for the dissimilarity of rooted and root free zone.

Table 6 Contribution (%) of the biomass of nematode families to the dissimilarity between top soil, rooted zone, and root free zone in July 2010 analysed by similarity percentage analysis (SIMPER). Presented are the average dissimilarities between different soil depths and the contribution of the seven families with the highest influence on separation. DL – dauer larvae. After Scharroba et al. (2016), modified.

Group	Group average dissimilarity	Family	Average biomass		Average dissimilarity	Contribution to group dissimilarity (%)
Top Soil & Rooted Zone	74.09		Top Soil	Rooted Zone		
		Anantonchidae	1.93	0	6.11	8.25
		Aphelenchoididae	2.28	0.38	5.94	8.01
		Rhabditidae(DL)	2.29	0.47	5.93	8.00
		Tylenchidae	2.27	0.65	5.04	6.80
		Cephalobidae	2.26	0.67	4.95	6.69
		Paratylenchidae	1.84	0.28	4.91	6.63
		Pratylenchidae	0.69	1.78	4.38	5.92
Top Soil & Root Free Zone	80.78		Top Soil	Root Free Zone		
		Anatonchidae	1.93	0	6.55	8.11
		Rhabditidae(DL)	2.29	0.05	6.32	7.82
		Cephalobidae	2.26	0.37	6.24	7.73
		Aphelenchoididae	2.28	0.43	6.24	7.72
		Tylenchidae	2.27	0.44	6.13	7.59
		Paratylenchidae	1.84	0.03	5.43	6.73
		Aphelenchidae	1.85	0.47	4.96	6.14
Rooted Zone & Root Free Zone	49.20		Rooted Zone	Root Free Zone		
		Pratylenchidae	1.78	0.78	11.29	22.94
		Monhysteridae	0.69	0.37	6.02	12.24
		Plectidae	0.22	0.50	4.89	9.94
		Qudsianematidae	0.27	0.41	4.60	9.35
		Aphelenchidae	0.82	0.47	3.84	7.80
		Rhabditidae (DL)	0.47	0.46	3.72	7.56
		Tylenchidae	0.65	0.44	3.63	7.37

Statistical differences of family biomass according to year, crop and the interactions are given in the appendix (Tab. S2).

5.1.5 Biomass of trophic groups

The biomass of trophic groups displayed a distinct depth pattern that reflected the environmental factors shaping biomass build-up of nematode assemblages. In Fig.12 the average relative biomass of trophic groups in the three major soil depths are displayed across treatments and in July of both years.

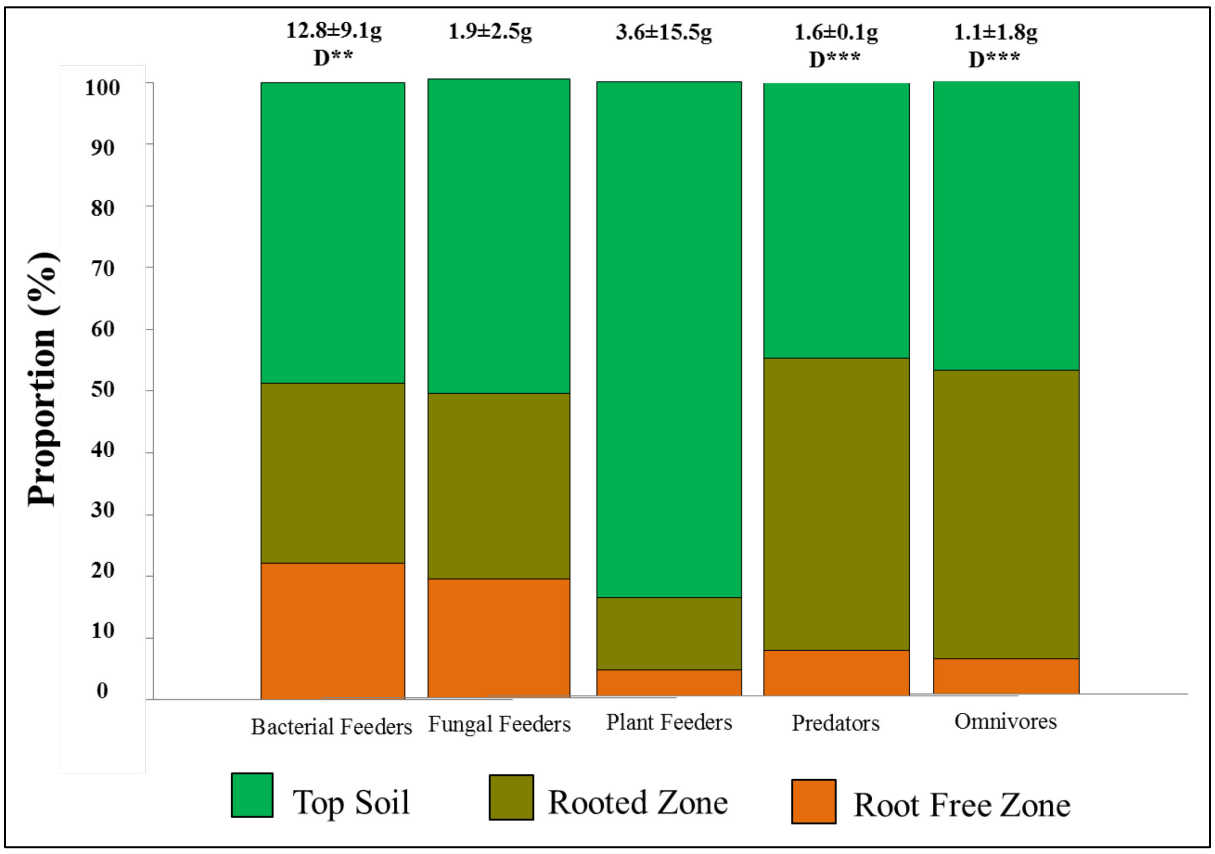


Figure 12 Relative biomass (% fresh weight) of each trophic nematode group is presented for all treatments in July 2009 and 2010 inhabiting the top soil, rooted zone and root free zone. After Scharroba et al. (2016), modified.

The biggest amount of biomass in the arable soil was observed in the bacterial-feeding nematodes with a total fresh weight of 12.8±9.1 g FW m^{-2} soil. These were followed by plant feeders with intermediate values of 3.6±15.5 g FW m^{-2} soil. In comparison the fungal feeders (1.9±2.5 g FW m^{-2} soil), predators (1.6 ±0.1 g FW m^{-2} soil) and omnivores (1.1±1.8 g FW m^{-2} soil) exhibited a much smaller biomass portion. About 50% of the biomass in bacterial- and fungal-feeding nematodes as well as predators and omnivores was detected in the top soil (Fig. 12). Especially in plant-feeding nematodes more than 80% of the biomass was accumulated in the uppermost soil layer. The biomass of bacterial and fungal feeders was

quite consistently dispersed in the communities located in the rooted zone (~ 30%) and root free zone (~ 20%).

In contrast, a decrease of biomass in the plant-feeding, omnivorous and predatory community was very low in the root free zone with 1, 5, and 8%, respectively and showed significant depth effects for bacterial feeders ($F_{2,92}$=10.9; P= 0.00009), predators ($F_{(4,164)}$=4.9; P= 0.00088) and omnivores ($F_{4,164}$=4.9; P= 0.00088).

The biomass pattern of nematode communities across depth and treatment were compared to the microbial biomass pattern at the investigated field site to detect correlations between nematodes and their food sources (data from Kramer et al., 2013). A regression analysis assigned correlations between the biomass of bacteria and bacterial-feeding (R^2=0.22, P<0.000002) as well as fungal-feeding (R^2=0.07, P<0.0078) nematodes. Further, a relation to bacterial biomass was detected for omnivores (R^2=0.0598, P<0.0169) and predators (R^2=0.2, P<0.000005). Equally, correlations were observed between fungal biomass and fungal-feeding (R^2=0.06, P<0.018), bacterial-feeding (R^2=0.23, P<0.000001) and predatory (R^2=0.25, P<0.0000001) nematodes.

5.2 Carbon flow into nematode food web

Together with co-workers a ^{13}C labelling experiment of maize plants was performed at the experimental site and data were published in Pausch et al. 2016a. At the arable field the following major carbon pools were assigned: maize as major C resource for the soil food web consisted of 317 g C m^{-2} in shoots and 28 g C m^{-2} in roots at the arable field (data from Pausch et al., 2016a). The bulk soil contained 1158 g C m^{-2}, whereas C in the total microbial biomass made up 29 g C m^{-2}, of which fungi comprised 9.8 and bacteria 19 g C m^{-2}. The rhizosphere soil had a smaller C stock then the bulk soil (453 g C m^{-2}), with corresponding smaller C pools of the microbial community (21g C m^{-2}), fungi (6.5 g C m^{-2}) and bacteria 14.5 g C m^{-2}; data from Pausch et al., 2016a).

Thus, regarding organismic C stocks, the bacterial community dominated the soil system. In comparison the nematode C pool was vanishing low and ranged from 0.004±0.002 to 0.068±0.013 g C m^{-2} in the biomass of nematodes. Predatory, omnivorous as well as plant feeding nematodes held less than 0.022 g C m^{-2}. Bacterial and fungal feeders accounted most to nematode biomass C with 0.051±0.007 and 0.068±0.013 g C m^{-2}, respectively. In the rhizosphere the bacterial feeding nematodes made up 0.4% of the bacterial C stock. In comparison to the fungal C stock the fungal feeding nematodes accounted 1.05%.

Table 7: The containing carbon of biomass in each trophic nematode group (g C m^{-2} ± SEM) as mean values within 25days. Data from Pausch et al. (2016a).

Trophic groups	**C stocks [g C m^{-2}]**
Bacterial feeders	0.051 ± 0.007
Fungal feeders	0.068 ± 0.013
Plant feeders	0.011 ± 0.002
Omnivores	0.007 ± 0.002
Predators	0.004 ± 0.002

To measure the incorporation of root- derived C into the nematode community, the ^{13}C excess mass was determined after 2, 5, 10 and 25 days after labelling. Already at day 2 after labelling all trophic groups of nematodes tracing a ^{13}C signal (Fig. 13). The fungal-feeding nematodes allocated the greatest amounts of plant derived C as indicated by their general high ^{13}C excess mass.

They significantly accumulated C within 25 days with 0.04±0.01 at day 2 to 0.13±0.06 g ^{13}C m^{-2} at day 25. This C accumulation in plant feeder tissue increased with time 0.01±0.01 at day 2 to 0.02±0.01 g ^{13}C m^{-2} at day 25. Also the ^{13}C signal in bacterial-feeding nematodes increased with time 0.04±0.01 at day 2 to 0.08±0.03 g ^{13}C m^{-2} at day 25.The higher trophic levels, the predators and omnivores showed a not-significant time-lag in ^{13}C accumulation compared to microbial feeding nematodes. The overall increase of ^{13}C excess in all trophic groups over the whole experimental time points to a steady flux of plant C into the nematode community.

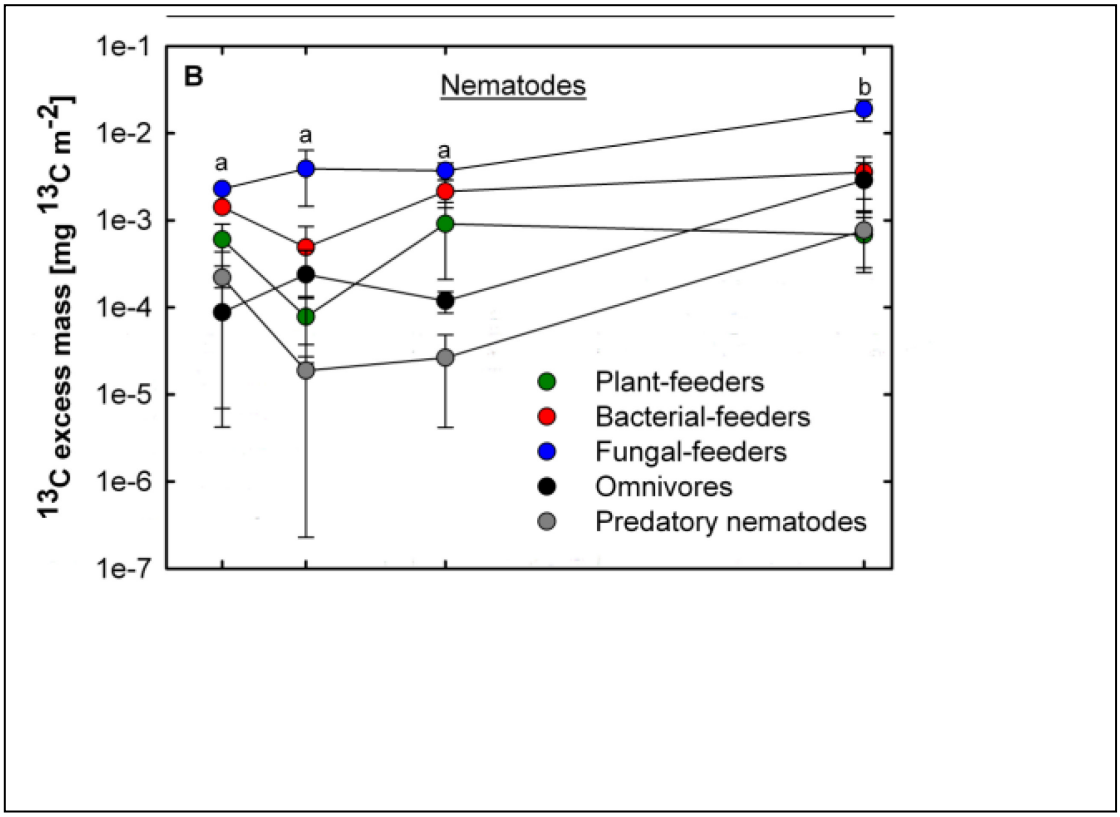


Figure 13: ^{13}C excess mass (mg ^{13}C m^{-2} ± SEM) at day 2, 5, 10 and 25 after $^{13}CO_2$ labelling of trophic groups of nematodes. Values of different sampling dates with the same or no letters are not significantly different according to Tukey test with $P \leq 0.05$. Note the logarithmic scale of the y-axis. Graph from (Pausch, et al., 2016a).

In the arable system the C pool of higher trophic levels was low with only 0.0072% C m^{-2} in nematodes. In Tab.8 there are represent relative turnover rates for the nematode C pool in food web, which were calculated with the assuming of steady state conditions (fixed values for pool size and flux rates). The highest turnover rates showed the fungal community with 4.34 in bulk soil and 15.6 in rhizosphere soil. The turnover rates of the bacterial community displayed values with 0.14 in bulk soil and 0.52 the rhizosphere. The whole microbial biomass in the soil presented turnover rates around 2.4. Depending on the amount of ^{13}C tracer, added during labelling, the values do not represent the absolute turnover rates. The high C turnover rate in the fungal energy channel suggests high ^{13}C incorporation in fungal feeding nematodes (Table 8; data from Pausch et al., 2016a). In contrast, the C flux into plant feeders, which are directly consuming plant material, was low with 0.0001% of total ^{13}C tracer incorporated at day 2 after labelling. Omnivores and predators as higher trophic levels gained comparable amounts of plant C. Thereby C pools differ clearly from C fluxes.

Table 8: By dividing the minimal tracer signal by the pool size (budget) the relative turnover rates of the nematode C pool of an arable soil are presented (Data from Pausch et al. (2016a).

Pool	Relative turnover rates
Nematodes	0.31
Bacterial feeders	0.11
Fungal feeders	0.45
Plant feeders	0.14
Omnivores	0.64
Predators	0.30

The mean turnover rate of nematodes (0.31) was half as much lower than that of omnivores, but higher than bacterial and plant feeding nematodes (Table 8). Because of these high turnover rates the omnivorous and fungal feeders were the main drivers of nematode micro-food web C flux.

In Figure 14 a detailed view of the carbon budget of the nematode food web is illustrated. The nematodes comprised 0.0072% of the total C per m², with the highest amounts in fungal feeders and bacterial feeders. The incorporation of root-derived ^{13}C into the nematode food web was about 0.0022% of tracer incorporation. With a proportion of 0.0016% the fungal feeding nematodes showed the highest ^{13}C incorporation within 25 days after $^{13}CO_2$ pulse labelling. The other trophic groups displayed a low level of tracer incorporation.

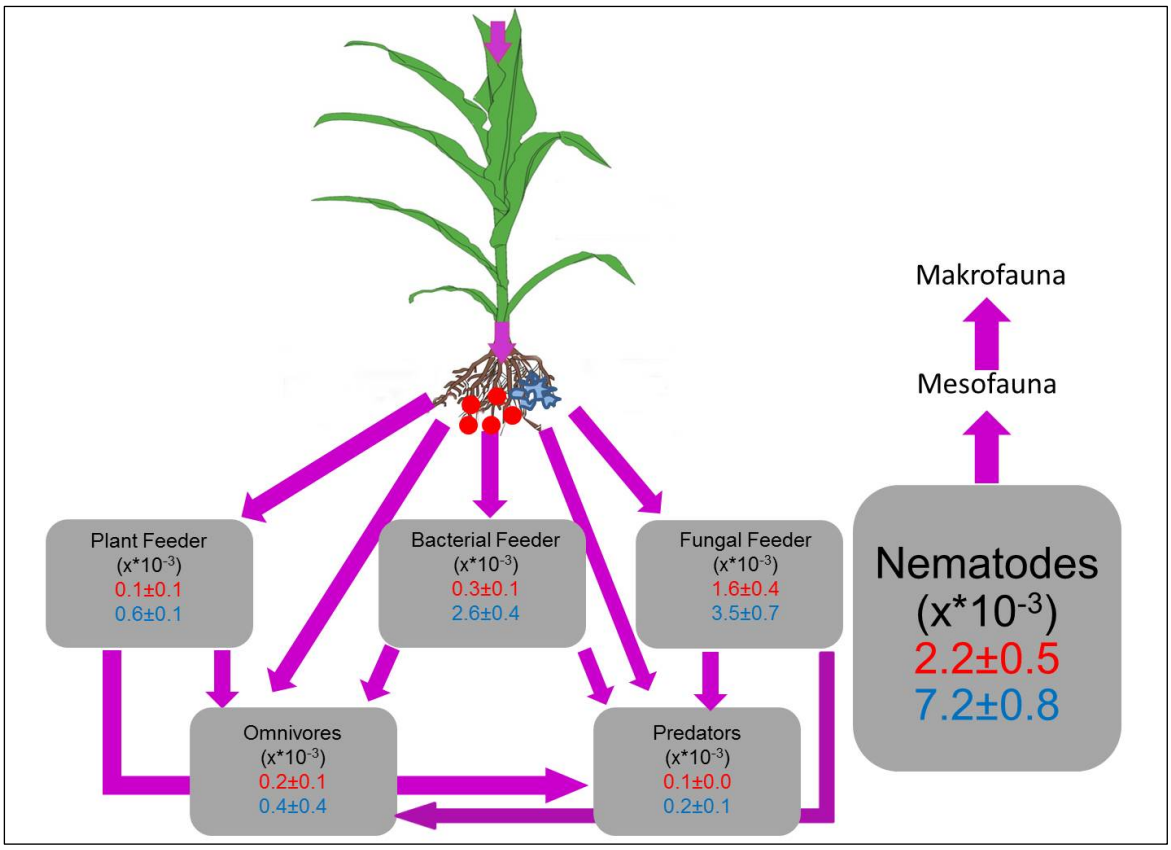


Figure 14: The carbon budget of the nematode food web of the upper 10cm of an arable soil. Values represented as % of total C per m² (blue values) and tracer incorporation (red value) within 25 days after $^{13}CO_2$ pulse labelling of maize. Data from (Pausch, et al., 2016a), modified.

5.3 ^{14}C as tracer for nematode trophic interaction

5.3.1 Development of the nematode community within experimental time

The $^{14}CO_2$ pulse labelling experiment was used to quantify the flux and dynamics of root-derived carbon from the model plant *Z. mays* to the nematode micro-food web, whereby the ^{14}C activity of each trophic group was identified. Data from this experiment were published in Pausch et al. 2016b.

At day 0 before labelling the population density of nematodes amounted ~590 Ind. 100 g^{-1} DW and increased significantly to ~1800 Ind. 100 g^{-1} DW until the end of the experiment at day 16. With a mean of ~43% (468 Ind. 100 g^{-1} DW) the plant feeders were the most abundant trophic group of all nematodes across the time. Bacterial- and fungal feeders represented ~33% (323 Ind. 100 g^{-1} DW) and ~18% (200 Ind. 100 g^{-1} DW) of the nematode community, respectively.

Table 9: Trophic groups of nematodes (individuals 100 g^{-1} DW ± SD) at day 0, and 2, 5, 10 and 16 days after $^{14}CO_2$ pulse labelling. Data from (Pausch, et al., 2016b)

	Time after labelling [days]				
	0	**2**	**5**	**10**	**16**
Trophic group	**[Ind 100 g^{-1} DW]**				
Plant-feeders	340±325	484±416	501±229	229±151	785±495
Bacterial-feeders	163±144	192±79	410±309	410±161	507±126
Fungal-feeder	78±29	94±39	163±99	161±41	503±147
Predators	2±3	1±3	4±5	2±3	5±7
Omnivores	8±3	5±4	7±4	15±9	2±2

The density of bacterial and fungal feeders increased slightly but not statistically significant over the experimental time. With an average of 1% (7 Ind. 100g^{-1} DW) and 0.3% (3 Ind. 100g^{-1} DW) omnivorous and predatory nematodes were scarce in the pot soil.

5.3.2 ^{14}C incorporation into trophic groups of nematodes

Already after 2 days all trophic groups of nematodes showed a ^{14}C signal, which is significant higher compared to the natural background signal from unlabelled control (data not shown). The values ranged from 0.09±0.05 Bq 100 g^{-1} DW at day 5 to 0.25±0.2 Bq 100 g^{-1} DW at day 16 (Fig. 15) for the whole nematode community. In accordance with the increasing population density the ^{14}C activity gained (not significant) with time (Fig. 15).

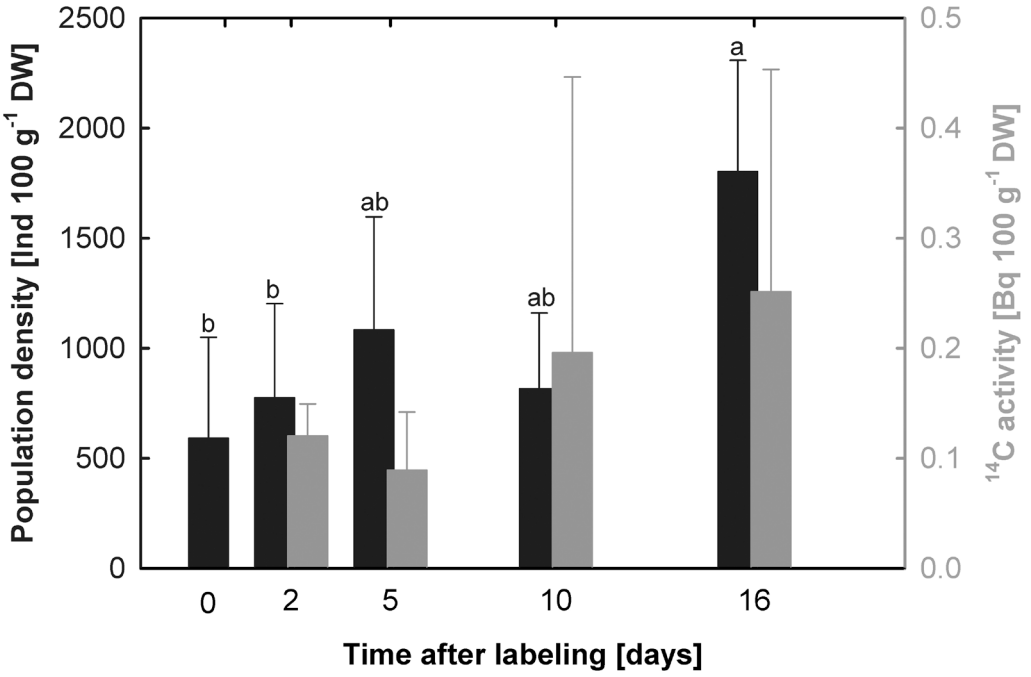


Figure 15 Nematode density in pot soil (individuals 100 g^{-1} DW ± SD, black bars) and ^{14}C activity (Bq 100 g^{-1} DW ± SD, grey bars) at day 0, 2, 5, 10, and 16 after $^{14}CO_2$ pulse labelling. Bars with the same or no letters are not significantly different over time according Tukey´s HSD tests at $P < 0.05$. Graph from (Pausch, et al., 2016b), modified.

In Figure 16 the trophic group ^{14}C activity is given as percentage of total belowground ^{14}C over time. Here the plant-feeding nematodes offered the highest ^{14}C activity across the whole experimental period, in which the ^{14}C activity increased at day 2 from about $0.7x10^{-3}$ % of total belowground ^{14}C to a maximum of $1.2x10^{-3}$ % at day 16 after labelling (Fig. 16). At day 5 and 16 after labelling the incorporation of root C into plant-feeders was significantly higher compared to the other trophic groups of nematodes. The ^{14}C transferred to bacterial-feeders varied between $0.3x10^{-3}$ % at day 5 to $0.7x10^{-3}$ % at day 10, whereas that of fungal-feeders only ranged between $0.04x10^{-3}$ % at day 5 and $0.1x10^{-3}$ % at day 16 after labelling. The ^{14}C activity from omnivores and predators as higher trophic groups was steady below $0.2x10^{-3}$%.

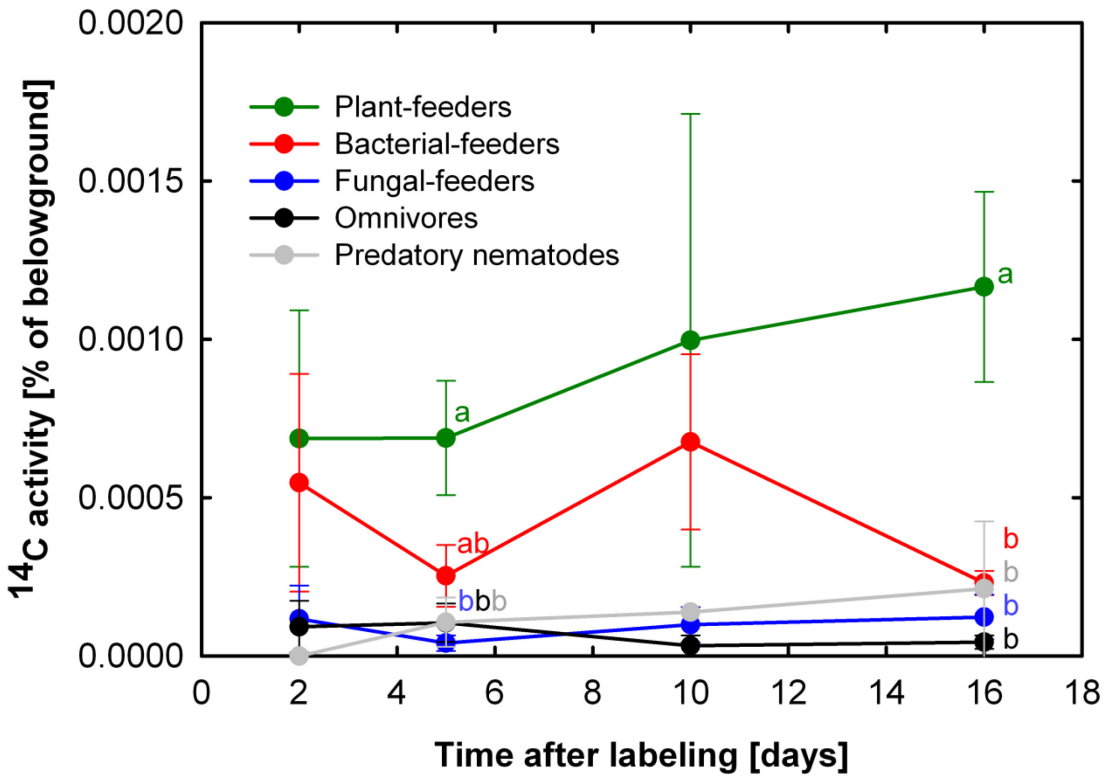


Figure 16: As percentage of total belowground the ^{14}C activities of nematode trophic groups were measured at day 2, 5, 10, and 16 after $^{14}CO_2$ pulse labelling. Significant differences ($P<0.05$) between the trophic groups at one sampling date are marked by different letters. Values with the same or no letters are not significantly different according Tukey Test at $P < 0.05$. Graph from (Pausch, et al., 2016b).

At the end of the experiment the root-derived C flux through the nematode micro-food web was observed. While ~79% of the ^{14}C tracer was detected in plant parts and ~23% in other soil pools only 0.96±0.57 x10^{-3}% ^{14}C tracer was incorporated in nematodes after 16 days (Pausch, et al., 2016b). In accordance with the highest density the plant-feeding nematodes incorporated the highest amount of ^{14}C (0.68x10^{-3}%, Table 10). In the opposite the bacterial- and fungal-feeders had approximately the same population densities at day 16 after labelling, but different ^{14}C content. The total recovery of ^{14}C from bacterial-feeders with 0.12x10^{-3}% was about twice as high as that of fungal-feeding nematodes. The omnivorous and predators incorporated 0.02x10^{-3} and 0.07x10^{-3}% ^{14}C, respectively.

Table 10: ^{14}C budget calculated as % of ^{14}C recovered in different nematode trophic groups 16 days after labelling (±SD). Data from (Pausch, et al., 2016b)

Trophic groups	**^{14}C [% recovery] x 10^{-3}**
Plant-feeders	0.68±0.55
Bacterial-feeders	0.12±0.07
Fungal-feeders	0.07±0.1
Omnivores	0.02±0.01
Predatory nematodes	0.07±0.1
Total nematodes	**0.96±0.57**

6. Discussion

6.1 Nematode communities at the arable field – general pattern

6.1.1. Density and community structure

Spatial environmental heterogeneity separates habitats into different patches, resulting in unique conglomerates of nematode taxa associated with specific soil horizons (Ferris & Bongers, 2006; Ferris, 2010). These so called metacommunities were described by Wilson (1992) as assemblages, which depend on resource availability and abiotic environmental factors. In line with this concept of metacommunities, the different soil layers at the investigated arable field were characterized by specific nematode assemblages, associated with organic material (top soil), plant roots (rooted zone) or oligotrophic environments (root free zone). The diversity of these metacommunities decreased along the depth profile, likely reflecting a decline in resource niches with depth.

In sum 27 nematode families were detected, which is nearly half the number reported from other arable fields (Neher & Olsen, 1999; Neher, et al., 2005). In the upper soil layers nematode numbers with 8 to 18 Ind. g^{-1} dry weight at the experimental site were quite similar to those reported from other farmlands (barley, wheat, soybean) with 8 to 10 Ind. g^{-1} dry weight (Sohlenius & Sandor, 1987; Neher, et al., 2005). Nematode diversity and density decreased significantly with depth, which are influenced by resource availability as well as in differences of soil abiotic factors such as pH, oxygen content, temperature and texture (Yeates, 1999; Griffiths, et al., 2002; Liang, et al., 2005; Sánchez-Moreno, et al., 2006). However, besides the continuous impact of soil properties, the nematode density pattern was also shaped by dynamic seasonal pattern. The decrease in population density due to depth gradient was small during summer and autumn with less than 3.8%, whereas in winter with up to 13.1% of top soil individuals were detected the root free zone. Thus, in the crop season, when plants need most of soil water, the seasonal pattern in depth distribution points to a low migration of nematodes between the different soil horizons (i.e. metacommunities). During the vegetation period only 9% (maize) and 3% (wheat) of the total precipitation left the main rooting zone in a depth of 65 cm (Schmalwasser, personal communication). However, in winter under the fallow, a vertical mass-flow occurs as a result of heavy rainfall or snowmelt events, which connects different soil compartments along the depth gradient. This is supported by studies on the bacterial community at the field site, which observed a transport of top soil bacteria to 35 and 65 cm depth directly after snowmelt (Dibbern, et al., 2014).

Among nematode trophic groups the bacterial-feeding *r*-strategists were most dominant, followed by fungal feeders, both common in intensively managed arable soils (Ferris, 2010). The micro-food web was depleted in trophic structure with depth, as higher trophic levels such omnivores and predators were manly restricted to the top soil. Omnivorous and predatory nematodes represented lowest densities over all trophic groups with an average proportion of only 1%, which indicated a bottom-heavy food web with no "long" food chains, and a low biomass allocation at higher trophic levels. As in any agroecosystem plant-feeding nematodes were detected predominantly in the rooted zone and made up a great proportion of the nematode community (Sohlenius & Sandor, 1987; Neher, 2010). In the root free zone plant-feeding nematodes belonged almost exclusively to the Tylenchidae, which are facultative root or fungal feeders (Yeates, et al., 1993), indicated a shift from roots to fungi resource as an adaption to changes in major resources. Further, in some cases the trophic classification of nematode families (Tylenchidae, Dorylaimidae) remains unclear (Yeates, et al., 1993), for instance within the Tylenchidae, normally classified as plant feeding nematodes, the genus *Filenchus* should be considered as a fungal feeder or root and fungal feeder (Okada, et al., 2005).

In line with other studies at intensively managed arable soil the *MI* and *PPI* pointed to a disturbed soil ecosystem with high numbers of *r*-strategists (Bongers, et al., 1997; Neher, et al., 2005; Brmez, et al., 2006). The low trophic diversity index (*T*) indicated mainly an absence of higher trophic groups. The *EI* and *SI* indicated a nutrient enriched soil system with a basal structure of nematode guilds, mostly with a *c-p* 1 or 2 classification. The *RD/R* index with high values of Rhabditidae dauer larvae indicated massive disturbance as a result of regular tilling and manuring. This is in line with the high Enrichment and low Structure Index. The *C/N* ratio was low and the nutrient reduction was provided by the bacterial community (Ferris & Bongers, 2009). This is underlined by *CI*, which values were mainly lower than 50 at all plots across depth and seasons.

The nematode faunal indices varied slightly from top soil to deeper soil layers. Significant depth effects were assigned by the *MI, T* and *F/B* in the first and by the *PPI* in the second vegetation period, pointing to changes in structure and function of the nematode metacommunities. While the *EI* decreased slightly the *SI* decreased strong along the depth profile, with an overall mean across 2009 and 2010 of 62 and 8, respectively. Thus, the metacommunities were depleted in higher trophic levels in adaption to fewer nutrients. Effects like strong rain events can translocate microorganisms as well as nutrients into the deeper soil layers, which supports or connects metacommunities across the depth profile. For example in

2010 in the root free zone the dauer larvae of Rhabditidae showed an increase at plots amended with litter.

Here the soil organic matter (SOM) at litter plots were transferred into the deeper soil layers during rain- or snowmelt events in winter and supported the increase of Rhabditidae. In summer, when water is needed by plants in the rooted zone, no SOMs transfer occurred into the root free zone and Rhabditidae formed dauer larvae in cause of nutrient lack.

In line with our hypothesis, the analysis of the nematode community indicate a nutrient enrichment as well as disturbance in the soil ecosystem at the field site with decreasing density with depth, which has been previously reported in soil ecosystems (Leroy, et al., 2009; Sánchez-Moreno, et al., 2006; Ugarte, et al., 2013). Furthermore, nematode assemblages composed a series of open communities along the depth gradient, with migration of organisms and resources predominantly in the fallow period in the arable soil. However, based on interspecific functional similarity of taxa in the same nematode family, indices may have a redundancy as suggested by other studies (Ettema, 1998; Ruess, et al., 2001; Yeates, 2003). Moreover, similar index values can be obtained with an abundance of nematodes or with only few individuals (Ferris & Bongers, 2009). Thus, the combination of density based indices with data on carbon allocation (i.e. nematode biomass) is needed to get more information about carbon and energy flow in the micro-food web.

6.1.2. Biomass of families as measure for food web carbon allocation

The nematode biomass in trophic groups can be used as a tool for carbon allocation and C flow in the food web with decomposition pathways in bacterial or fungal channels (Ferris, 2010). With their unique morphology nematode biomass can be easily calculated based on nematode body weights (Andrássy, 1954). The C content of the nematodes is then assigned as 50% C of dry biomass according to Schmidt et al. (2000). However, a drawback occurs as individuals are generally not separated in juveniles or adults, nor in female or male, although nematodes have been reported to vary in size and biomass with age or sex (Bongers, 1987). Nevertheless, the present biomass data can be considered as a good estimation of the C allocation and dynamics in the micro-food web. For a quantitative carbon analysing in an ecosystem the biomass data can further be combined with respiration data of nematodes to create a metabolic footprint, which was successfully applied by Ferris (2010) and Zhang (2015). Here the metabolic footprint of nematodes provided a method for observing the

available resources and assessed the effect of nematodes on ecosystem dynamics (Zhang, et al., 2015).

In the present study the overall mean of nematode biomass was ~21 g m^{-2} across treatments and soil depth for the entire population, which resembles values reported by Freckman & Zak (1991) for desert soil communities ranging between 1-20 g m^{-2}. Much lower biomasses were overserved at Danish beech forest with 0.25 g m^{-2} by Yeates (1988) and 0.7 g m^{-2} in afforested dune soil by Dunger (2008). The biomass pattern of nematode families showed a distinct depth profile similar to the nematode population density. The nMDS analysis with a Bray Curtis similarity level of 33% separated top soil and root free zone, with the rooted zone joined in between in the first vegetation period, whereas in the second year the top soil layer clearly splitted from the two bulked deeper horizons. Especially the omnivorous family Qudsianematidae and the predatory Anatonchidae caused this, pointing to longer energy channels with higher trophic levels in the top soil layer. This explicit separation indicated that the nematode community below the top soil was isolated from the carbon flux above, and that transport processes were unimportant for connecting metacommunities, at least after harvest in autumn. Similar dynamics were observed for extractable organic carbon (EOC) and microbial biomass (PLFAs) at the investigated field site, which were generally highest in the top soil (Kramer, et al., 2013). The translocation of microbes and carbon took place in autumn (harvest) and winter (fallow), which pointed to a restriction by plant growth. Nutrient transport was likely fostered by the significantly higher soil water content in winter (Kramer et al., 2013).

Previous research work on forest soils reported a homogenous distribution of nematode trophic groups within the first 25 cm of the soil gradient (Dunger, 2008; Zhang et al., 2015). In this study, all nematode trophic groups obtained their highest biomass in the top soil layer, of which plant feeders showed the highest proportion of 80% within their trophic group (Fig. 12). The biomass of plant feeding nematodes at the investigated arable field site reflects their resource with highest root biomass of maize and wheat apparent in the plough layer (Kramer et al., 2013). This correlation indicates a high impact of bottom-up effects in the root energy channel. In contrast, omnivores and predators showed a distinct vertical distribution with very small biomass below the top soil. Comparing the much lower nematode density in the rooted zone to the top soil, this points to a stronger predation pressure, i.e. top-down control, within the nematode community.

Analysis of the entire biomasses of trophic groups over all depths showed a strong carbon allocation in the bacterial-feeding nematodes, which was 3 times higher than in plant feeders and 10 times higher compared to predatory and omnivorous nematodes. The dominance of the bacterial energy pathway is a typical feature of intensively managed agroecosystems with regular fertilization due to readily available nutrients (e.g. Leroy et al., 2009; Neher, 2010, Ugarte, et al. 2013). The regression analysis indicated a dependence of bacterial and fungal feeders as well as predators to both bacterial and fungal biomass, whereas omnivores were only linked to bacteria.

The significant connection of biomass between predators and fungi was much stronger than those among other trophic groups, suggesting a carbon flux mainly from fungi to higher trophic levels. This is in line with the monitoring of Zhang et al. (2015), where predatory nematodes in a forest soil primarily fed on fungi. Accordingly, Pausch, et al. (2016b) reported that the carbon transfer from fungi into higher trophic levels via the fungal energy pathway was much faster than that of the bacterial channel at the experimental field site. Scheunemann et al. (2016) observed that most soil arthropods fed on fungi than on bacteria, with channeling the energy pathway into higher trophic levels of meso- and macrofauna.

In summary, in the nematode micro-food web the predation is the primary regulation in the fungal channel, as described for food web assemblages including meso- and macrofauna (Scheu, et al., 2005).

6.2 Impact of resource quality and availability

6.2.1 Amendment with maize litter

The soil food web dynamic depends on inputs from plants in form of litter (slowly decomposable) and rhizodeposits (readily available C), which differ in their quantity, quality and seasonal accessibility (Scheu, et al., 2005; Moore, et al., 2005; Ruf, et al., 2006; Kramer, et al., 2013; Moll, et al., 2015). Additionally, these substrates are not homogeneously dispersed in soil. Aboveground plant litter dominates in the upper soil horizons, while in the rooted zone rhizodeposits are the dominant nutrient source for organisms. The quantity of resources (e.g. carbon content) decreases along the depth profile and can be shaped and translocated by transport (heavy rain, snowmelt) or seasonality (drying, wetting, freeze, thaw) (Luo, et al., 2010; Yan, et al., 2012; Kalbitz, et al., 2000; Rumpel & Kögel-Knabner, 2011). In the present study nematodes with their functional groups at each trophic level of the food web were used to analyse the impact of such nutrient input via rhizodeposits and maize litter or their combination. Compared to the average soil *C/N* ratio of 9.7 at the Ap horizon the maize litter showed a considerable higher value of 18.4 (Kramer, et al., 2012).

Generally, after litter amendment the nematode density increased under both crops, wheat and maize, and the impact was still present in the second vegetation period in 2010, especially in the top soil layer. Significant effects by litter applications, which support nematode density, were already reported (Ferris & Bongers, 2006; Duncan, et al., 2007; Neher, 2010). The recalcitrant maize litter is slow decomposable thereby providing a long lasting resource, supporting the soil food web (saprophytic fungi, fungal-feeding nematodes) over more than one vegetation period (Ruess, et al., 2000; Albers, et al., 2006). Fungal-feeding nematodes, especially Aphelenchidae, were positively linked to litter amendment, as these recalcitrant compounds are predominantly degraded by fungi (Ruess, et al., 2000). Comparably, Kramer et al. (2013) observed a consistent increase of the microbial biomass at the litter plots of the experimental site with time. As major decomposers of recalcitrant organic matter, fungi were positively responsive in the top soil at the arable field (Moll, et al., 2015). However, this did not significantly foster the fungal-feeding nematodes, which is also reflected in the low *F/B* ratios independent of litter application. These results pointed to a strong top-down control in the fungal carbon and energy pathway as discussed above.

Among bacterial feeders the density as well as the biomass of Rhabditidae increased at plots cropped with maize especially at CM, indicating that litter amendment boosted the resource availability. With a short life cycle and high reproduction rate they are classified as strong *r*-strategists, and indicate high bacterial density (Ferris & Bongers, 2006). The positive

impact of litter amendment was apparent across all depths, which is in line with Leroy et al. (2009) who reported increased nematode numbers after organic amendments down to 70 cm depth.

In the opposite the plant-feeding Pratylenchidae were negatively affected by litter amendment in the root free zone, especially in CM plots, which was also mirrored in a lower *PPI*. Pratylenchidae were more attracted by wheat as maize, pointing to an adaption to their local host plant (wheat) or a better nutrient source due to higher root biomass of wheat.

As already described nematodes occupy a central position in the soil food web and interact in diverse biological processes, whereby they used for analysis of general soil food web conditions (Ferris, 2010; Yeates, 2010). The addition of soil organic matter results in enriched food webs and was indicated by a high Enrichment Index (*EI*), where the bacteria and fungi community increases and in turn the nematode community was supported. This is in line with long-term studies investigating organic amendments with nitrogen or manure (Liang, et al., 2009).

In line with our hypothesis the litter amendment with high *C/N* ratio supported higher biomass in the basal trophic level of the soil food web and represented a bottom-up effect on the size and activity of the micro-food web, but did not sustain a larger biomass at higher trophic levels. Bacterial and fungal feeders of the nematode micro-food web were supported by the organic matter application (litter) as well as by the availability of soluble organic compounds (rhizodeposits).

6.2.2 Maize *vs* wheat as crop plant

In central Europe wheat and maize are the most dominant crops, differing in growth rate, root structure, soil humidity or plant cover in the field (Stat., 2014; Lal, 1978; Filser, 1995). Moreover, within the annual crop cycle the root exudation is high in spring and summer, decreasing at plant senescense in autumn and lacking after harvest in winter (Aulakh, et al., 2001). In the present study, wheat had more root biomass (0.47±0.17 mg C g^{-1} soil) than maize (0.15±0.04 mg C g^{-1} soil) with higher nutrient availability in form of rhizodeposits at wheat plots (Kramer, et al., 2012). Additionally Kramer et al. (2013) observed higher water contents at wheat compared to maize plots. Thus, both crops can affect the nematode community differently due to their differences in root biomass and distribution, exudates and impact on soil conditions.

At the investigated arable field site the nematode fauna, particularly the density and biomass, were influenced by the availability of major plant carbon resources (rhizodeposits, plant litter), in different ways. In comparison to litter, the crop plant had less influence on the nematode population density, but was an important factor for biomass allocation. The crop plant had an evident impact on nematode family biomasses in the top soil, likely as a result of the higher microbial biomass under wheat compared to maize as reported by Kramer et al. (2013). Under wheat nematodes generally had more biomass, with significant effects for families including all basal trophic groups, i.e. the bacterial, fungal and plant feeders.

Meanwhile, the nematode family biomass pattern in the rooted zone varied. Maize had a positive impact on the nematode family biomass during the first and wheat during the second vegetation period. Surprisingly, the crop had a higher impact (herbivore food chain) than litter amendment (detrital food chain) on the nutrient pathway evidenced by Pratylenchidae and Paratylenchidae abundance in the rooted zone likely a result of higher root biomass associated with wheat compared to maize (Kramer et al., 2012). Interestingly, crop as well as litter impacts were still measurable in the deep root free horizon. Similarly, Liang et al. (2005) observed a vertical distribution of bacterial-feeding taxa differing along a depth gradient down to 150 cm depending on management practice (e.g. crop, fallow). Therefore, arable management practice influences the plant parasites not only in the rooted zone, but also in deeper horizons.

In the food chain the root, bacterial and fungal energy channels join together at higher trophic levels and thereby provide the development of omnivores and predators (Wardle, et al., 1995; Ferris, 2010). Generally, the higher trophic levels are fostered by the basal groups, which accumulate carbon in the form of higher biomass and higher diversities of predatory

and omnivores nematode fauna were observed at plots cropped with wheat. However, an nMDS showed that soil layer was the dominant factor influencing higher trophic levels with regards to enhanced carbon translocation in the top soil.

At the investigated field site, the trophic diversity was higher under maize during the first and under wheat in the second vegetation period, respectively. The trophic diversity is rather depended on season and management practice as on crop or litter amendment (Porazinska & Coleman, 1995; Neher & Olsen, 1999), this is in line with the very low Structure Index (*SI*), pointing to a disturbed basal food web typical for intensively managed agriculture sites (Neher, et al., 2005; Thoden, et al., 2011). Contrary, the Shannon diversity index *H´,* which is based on the proportion of family, indicated high diversity under wheat particularly in the plough layer in first vegetation period. Meanwhile, during the second vegetation period both indices pointed to a high diversity at family and trophic level in top soil and root free zone under wheat plots. The nutrient and carbon flow occurred mainly through the bacterial channel, which is mirrored in a low Channel Index (*CI*) and common in agroecosystems (Joergensen & Wichern, 2008). But with increasing soil depth the fungal energy pathway became more prominence in soil food web. Moll, et al. (2015) observed fungal communities along the depth profile till the root free zone, suggesting that plant resources still determined. Similar to the nematode the fungal community in deeper soil layers were supported by resource transfer during rain- or snowmelt events (Moll, et al., 2015).

In sum the nematode community showed higher biomass allocation under wheat than under maize, which is connected to higher root biomass and higher nutrient availability (rhizodeposits) at wheat plots. The nutrient flux occurred mostly via bacteria and their grazers, but with increasing soil depth the fungal energy pathway became more important. Furthermore, the diversity and structure of the nematode community was low under both crops due to the intensively agricultural management. In line with our hypotheses the plant-feeding nematodes (Pratylenchidae, Paratylenchidae) showed highest densities in the rooted zone, yet more under wheat than under maize, likely an adaption to the different host plants.

6.3. Carbon pools and turnover rates in the nematode micro-food web

The ^{13}C-pulse labelling experiment was established to measure the incorporation of maize

root-derived C into major soil compartments in the present study especially into nematodes in an arable field for 25 days. Nematode communities comprise functional groups at each trophic level and therefore are ideal models to disentangle the uptake and transfer of plant carbon into different food web compartments. Briefly about 20% of the ^{13}C assimilated by maize crop was transported to belowground, where the labelled carbon was predominantly incorporated into rhizosphere microorganisms rather than in those of the bulk soil (Pausch, et al., 2013). Within 2 days there was a quickly incorporation mainly into bacteria and saprotrophic fungi, only small amounts of ^{13}C were transferred into higher trophic levels, predominantly into fungal-feeding nematodes.

Assuming that 50% of the nematode biomass consists of carbon (Sohlenius, et al., 1997) the C pool of nematode communities in arable soils ranged from 0.1 to 0.57 g m^{-2} (Hendrix, et al., 1986; Sohlenius, et al., 1988; Hanel, 1995). Thus the 0.141 g C m^{-2} in the nematode fauna at the investigated arable field is fairly low, likely due to farming practice or crop plant. In particularly conventional tillage and annual crop cycles are known to reduce nematode biomass (Hendrix, et al., 1986; Sohlenius, et al., 1988). As already described above maize did not supported higher microbial and nematode biomass due to lower root biomass and exudates compared to wheat. In line with that, Scheunemann (2015) observed a higher abundance and diversity of soil arthropods at wheat than at maize plots. Compared to the macrofauna the nematode community showed similar and to the mesofauna higher C stock values. The mesofauna decomposers and predators accounted for only 0.004 ± 0.0006 g C m^{-2} and 0.007 ± 0.001 g C m^{-2}, respectively, and the macrofauna decomposers and predators for 0.146 ± 0.03 g C m^{-2} and 0.14 ± 0.09 g C m^{-2}, respectively (Scheunemann, et al., 2015). This underpins the importance of soil nematodes for carbon flux in arable systems. However, disturbance by agricultural management predominantly hampers omnivorous and predatory nematodes, typical *K*-strategists with low reproduction rates and long lifecycles, resulting in the detected low densities and corresponding low biomass C. This is in line with studies from Hanel (1995) and Sohlenius et *al.* (1988) where the C contents were twice as high in natural (forest) or no-tillage ecosystems.

Plant parasites directly consume plant tissue and therefore were expected to show the fastest and strongest allocation of labelled photo assimilates (Yeates, 1999). In contrast, carbon uptake was consistently higher in bacterial and fungal feeders compared to plant feeders over a period of 25 days after pulse labelling. Although bacterial-and fungal-feeding nematodes display very small C contents in single individuals (average 0.1 to 5.7 µg per specimen), with their high density, they accounted for a five to six time higher biomass C compared to omnivores and predators, and – as assigned by the ^{13}C signal, a strong carbon allocation at lower trophic levels of the micro-food web. Likely, bacterial and fungal feeders were fostered by rhizosphere microorganisms and not roots serving as main carbon resource as well as faster carbon turnover rates in rhizosphere communities. The latter is supported by the high ^{13}C excess mass in fungal feeding nematodes that corresponds to highest nematode densities and also to the fast turnover rate of the fungal community. The turnover rate was 49, and C incorporation 34, times higher than that of bacteria in bulk and rhizosphere soil, respectively. This indicates a distinct flux of recent photoassimilates through the fungal channel, which is in contrast with the low fungal biomass. The mean turnover rates of meso- and macrofauna were similar high to the values of fungal feeding nematodes (Pausch, et al., 2016a). However, Pausch et al. (2016a) observed high 13C incorporation and turnover rates in saprotrophic fungi, suggesting a major flow of plant-assimilated plant carbon via arbuscular mycorrhizal fungi to the soil food web as postulated by Drigo, et al.(2010) for arable systems. This is in line with carbon incorporation 4.3 and turnover rates 4.9 times lower in bacterial feeders compared to fungal feeders in the present study. Moreover the rapid carbon transfer by arbuscular mycorrhiza fungi shortly after labelling can be followed by a slower release from fungal mycelium to bacterial and fungal populations in the
(myco-) rhizosphere (Drigo, et al., 2010). These processes likely supported the ^{13}C accumulation in the nematode fauna within this term.

During the experimental period no decrease of the ^{13}C signal (e.g. via respiration) was observed within the nematode community, pointing to a regular flux of root C into higher trophic level. Firstly, due to higher soil moisture at day 25 considerable amounts of dissolved carbon were available to the soil microbes. Additionally a bulk of labelled plant carbon was accessible by root respiration and exudation till day 25. Similarly, the meso- and macrofauna showed a continuously incorporation of ^{13}C signal during the experimental time. Only the mesofauna predators accumulated higher ^{13}C amounts at day 10, pointing to diet switch from

prey to root-derived C (Pausch, et al., 2016a). However, according to studies from Mikola & Setälä upper trophic levels respond much slower and in the present study omnivores and predatory nematodes showed a consistent accumulation of ^{13}C over the whole experimental period of 25 days (Mikola & Setälä, 1998).

On the other hand, omnivores and predators displayed a low C pool size with high C fluxes and turnover rates, which indicates top-down control and controverts Ferris (2010) assumption that food webs in agroecosystems are bottom heavy. Their indirect trophic interactions and the consumption of primarily plant C from via omnivorous nematodes seem to play a more important role in nutrient flow models than assumed until now.

In sum the performed pulse labelling experiment revealed that the C stock and the incorporation of plant C is not closely linked, which is assigned by the different turnover rates of each pool. Thereby the C flux occurred mainly through the fungal energy channel and with higher turnover rates of root-derived carbon in fungal-feeding than bacterial-feeding nematodes. The carbon flow of arable soils is mainly controlled by the fungal community and their consumers. This contrasts our hypothesis and previous studies, whereas agroecosystems with their labile organic compounds were suggested to be dominated by the bacterial pathway and ecosystems like forests with complex organic compounds to be driven by the fungal energy channel (Ruess & Ferris, 2004; Wardle, et al., 2004).

Incorporating the present results in the scheme from Ruess & Ferris (2004) the following picture can be created for the investigated arable field:

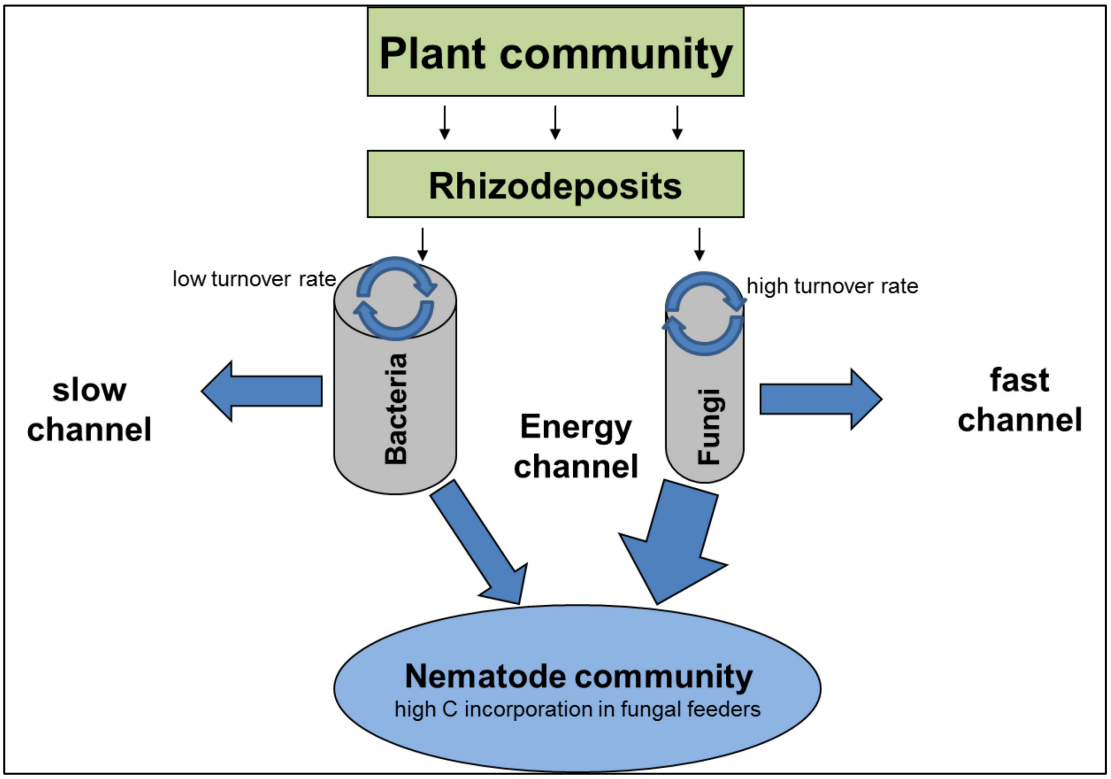


Figure 17: The carbon pathway through the bacteria and fungi energy channel with consideration of turnover rates in the investigated arable field (modified from Ruess& Ferris; 2004)

6.4. ^{14}C as tracer for nematode trophic interaction and C budget

To calculate a complete C budget, maize plants were pulse-labelled with ^{14}C in the laboratory. After labelling soil probes were taken after 2,5,10 and 16 days, which except for day 16, corresponds to the sampling scheme at the field labelling. The density of the endogenous nematode community in the undisturbed soil cores (0-30 cm depth) was 6.6 Ind. g^{-1}DW, which is similar to values (7.7 Ind. g^{-1} DW) at 0-10 cm depth under maize during the growing season (July) at the investigated field site. Likewise the nematode community composition and trophic diversity was comparable to the arable site, which points to a relatively undisturbed nematode community in the laboratory set-up.

In contrast to the field ^{13}C labelling of maize, the key drivers of carbon flow into the food web were the plant-feeding nematodes with highest densities over the entire experimental time. This plant parasites cause leakage of labile plant metabolites and open the carbon flow into the soil food web by supporting a higher microbial density (Yeates, et al., 1998; Poll, et al., 2007). Thus, the highest incorporation of root-derived ^{14}C occurred in plant-feeding nematodes due to direct feeding on plant roots, and not into fungal and bacterial feeders, which dominated the carbon pathway in the arable field.

In the undisturbed soil cores, high densities of plant parasites were observed, which were 5 times higher than in field soil, thereby increasing the importance of the root energy channel. In addition, at day 16 after labelling the root biomass in the 30 cm deep soil core was 8 times higher than in the investigated field site (Pausch, et al., 2013). This indicates that a C flux shift from detritivore to herbivore food chains can take place during the growing season, when increasing root biomasses supports plant parasites.

The constant increase of ^{14}C incorporation in plant-feeding nematodes within 16 experimental days points to a continuous flow of root-derived C into the herbivore food chain. Compared to the plant-feeding nematodes the uptake of plant C by bacterial- and fungal-feeders was lower over time and only 0.2% of the allocated ^{14}C of microbial biomass. Smith & Smith claimed that 10% energy allocation of the resource passed to next trophic level (Smith & Smith, 2006), but in the research work of Pausch et al. (2013) at our investigated field site only 1% of root-derived ^{14}C was incorporated in the microbial biomass at day 16 after labelling and about 62% was lost through respiration via CO_2. In the present laboratory study, at an experimental incubation temperature between 22 and 28°C, even more C might have been lost through respiration due to higher metabolic rates (10-20 ng CO_2 µg nematode^{-1} h^{-1}) of bacterial-feeders as reported by Ferris et al. (1995), at 25°C.

The carbon translocation into higher trophic levels was restricted, which is mirrored by low ^{14}C activity of omnivores and predators supporting findings by Ferris & Bongers (2006). In contrast, the omnivorous nematodes showed 10 to 30 times higher specific ^{14}C activity than bacterial- and fungal-feeders directly after labelling, which suggested that they feed direct on rhizosphere community (animals, microbes). The predatory nematodes accumulated the root-derived carbon very slow within 16 days, possibly they hunted mainly in the bulk soil.

About $0.96x10^{-3}$% of total recovery ^{14}C was assimilated by nematodes within 16 days after labelling, which is in line with results from the $^{13}CO_2$ pulse labelling experiment at the field site, were values differed between $0.1x10^{-3}$ and $1.6x10^{-3}$% (Pausch, et al., 2016b). The highest value ($0.68x10^{-3}$%) of recovery ^{14}C was observed in plant-feeding nematodes; however, Yeates et al. (1999) calculated even higher rates of ^{14}C recovery (0.02-0.09%). Tylenchidae, as external epidermal cell and root hair feeder, dominated the plant-feeding community with low influence of the carbon transfer from plant to soil fauna. Their low values of ^{14}C recovery are contrary to results from Yeates et al. (1999) with high ^{14}C activity of roots (28% ^{14}C recovery).

This indicates that the kind of plant parasites (endogen/exogen) and their host plants predominantly influence the speed and quantity of plant C flux into the nematode micro-food web.

The present ^{14}C experiment demonstrated that $^{14}CO_2$ pulse labelling can be applied to disentangle the root-derived C fluxes through the soil micro fauna and their different trophic levels. The activity and recovery rates of ^{14}C made it possible to separate between herbivore and detritivore food chains and to disentangle their linkage at higher trophic levels. Shifts between these two major pathways are likely triggered by plant root growth within a crop season. Nematodes especially plant-feeders have a strong role as direct feeders on root C and hence influence C and energy translocations within soil food webs in agroecosystems.

7. Conclusions

The nematode community in the investigated arable field was dependent on resource availability and quality (litter, crop), as main drivers for food web dynamics. The impact of litter and, more importantly of crop type, was still present below the rooted zone, indicating that vertical distribution of nematodes should be considered, when investigating effects of agricultural management practice. Across the depth profile the nematode fauna was not homogenously distributed, but rather patched in different metacommunities. Near the soil surface these metacommunities exploited organic material from litter and roots, whereas in the rooted zone assemblages depended on plant roots, whilst in the oligotrophic root free horizon they were supported by organic resources, transferred by seepage water during fallow periods. The carbon flow through the soil micro-food web as indicated by nematode family biomass suggested diverse ecological niches along the soil profile. Further, the biomass distribution of trophic groups pointed to a stronger predation pressure in the rooted zone than in top soil. The root energy channel was mainly bottom-up controlled, whereas the fungal energy channel was top-down regulated. In sum, the combination of nematode community composition with biomass data it is a useful tool to describe the carbon flow in the soil micro-food web.

Generally, soil litter amendment induces a strong bottom-up effect on lower trophic levels (bacterial and fungal feeders) in the food web, which in turn supports higher trophic levels. Especially the fungal community and their nematode feeders is known to be supported by recalcitrant material like maize litter. However, in the present study only a slight increase in bacteria and fungal abundance was observed, while bacterial- and fungal-feeding nematodes responded stronger to litter amendment suggesting top-down control of microorganisms by nematodes. These results underline the various roles of microorganisms and nematodes in the soil carbon flux and point to complementary resource useage as well as facilitative interactions among decomposers.

The ^{13}C labelling experiment further disentangled the trophic relationships and showed that the fungal community and their nematode grazers controlled the flux of easily available root C with turnover rates of fungal feeders outweighed those of bacterial feeders. These findings are in contrast with the widely assumption that the fungal energy channel dominates in natural ecosystems soils (e.g. forest) based on input of recalcitrant resources, whereas agricultural systems are supported by labile root exudates with a C flux predominantly in the bacterial channel (Ruess & Ferris, 2004; Wardle, et al., 2004). Moreover, the C stock of nematode trophic groups was not closely linked to their root-derived C incorporation based on

different turnover rates, as stated by Pausch et al. 2016a: “Pool size does not matter”. The analysis of ^{14}C activity and recovery pointed to a shift between the herbivore and detritivore food chain during a crop cycle due to C resources released by plant root growth. Plant-feeding nematodes with highest ^{14}C activity facilitated the carbon transfer into the soil food web and to higher trophic levels.

Overall, the micro-food web in the investigated arable soil showed a high degree of disturbance and low complexity whereas the resource supply with recalcitrant maize litter did not support larger biomasses at higher trophic levels. The fungal energy pathway dominated the flux of root-derived C into the food web with highest turnover rates despite of small pool size. The root C flux into the food web was supported by plant-feeding nematodes.

They are small but powerful - THE NEMATODES. Within three experiments and with the help of thousands of little, tiny worms we disentangled the structure and function of the soil food web in an arable land.

8. References

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9. Appendix

Table S1

ANOVA *F* and *P* values for density of nematode families (Ind. g^{-1} DW soil ± SD) at plots cropped with wheat or maize (factor crop) with and without litter amendment (factor litter) during two successive years (2009 and 2010). Investigated were three soil depths: top soil, rooted zone, and root free zone (factor depth). Note that the litter treatment was established in October 2009. Significant differences are marked in bold, - not detected.

Sample Time	**Crop**		**Litter**		**Depth**		**Crop x Litter**		**Crop x Depth**		**Litter x Depth**	
	$F_{1,41}$	*P*	*F*	*P*	$F_{2,41}$	*P*	*F*	*P*	$F_{2,41}$	*P*	*F*	*P*
Summer 2009	3.76	0.06	-	-	**140.19**	**0.000**	-	-	2.03	0.14	-	-
Autumn 2009	0.49	0.48	-	-	**111.27**	**0.000**	-	-	**3.61**	**0.04**	-	-
	$F_{1,36}$	*P*	$F_{1,36}$	*P*	$F_{2,36}$	*P*	$F_{1,36}$	*P*	$F_{2,36}$	*P*	$F_{2,36}$	*P*
Winter 2009	2.65	0.11	2.0	0.16	**66.16**	**0.000**	**4.14**	**0.049**	1.1	0.35	**3.54**	**0.04**
Summer 2010	1.16	0.29	**8.19**	**0.007**	**250.54**	**0.000**	**6.29**	**0.02**	0.18	0.84	0.28	0.756
Autumn 2010	0.17	0.68	**5.37**	**0.03**	**172.39**	**0.000**	0.61	0.44	**6.7**	**0.003**	**3.89**	**0.03**
Winter 2010	1.68	0.29	0.17	0.68	**64.6**	**0.000**	0.39	0.53	0.8	0.45	0.39	0.67

Table S2a. July 2009: All nematode families (individuals 100 g^{-1}DW ± SD) at plots cropped with maize (FM) or wheat (W) or with in Top Soil (0–10cm), Rooted Zone (30-40cm), and Root Free Zone (60-70cm). DL – dauer larvae. ANOVA with *, **, *** at $P < 0.05$, 0.01, 0,001. Values within a soil depth with the same or no letters are not significantly different according to Tukey at $P < 0.05$. D –depth. (Scharroba, et al., 2012), completed

	c-p value	TOP SOIL		ROOTED ZONE		ROOT FREE ZONE		
		W	FM	W	FM	W	FM	ANOVA
Bacterial feeders								
Cephalobidae	2	416±261**a**	373±135**a**	58±43**b**	116±73**b**	8±0.8**c**	13±5**c**	D***
Diplogasteridae	1	-	-	1±1	1±3	-	-	
Monhysteridae	1	8±9	4±5	1±1	7±11	-	0.8±1	
Panagrolaimidae	1	-	-	1±1	2±3	-	-	
Plectidae	2	20±20	4±5	8±6	2±3	-	1.3±2	D*
Prismatolaimidae	3	9±18	-	-	-	-	-	
Rhabditidae(without DL)	1	202±115**a**	315±354**a**	58±36**b**	99±62**b**	5±4**c**	7±4**c**	D**
Rhabditidae (DL)	-	341±242**a**	555±382**a**	60±37**b**	110±47**b**	5±5**c**	5±4**c**	D***
Fungal feeders								
Anguinidae	2	135±163**a**	4±2**b**	15±12**b**	7±8**b**	0.3±1**c**	0.5±1**c**	D*
Aphelenchidae	2	127±91**a**	67±97**ab**	14±7**b**	25±12**b**	3±2**c**	7±11**c**	D***
Aphelenchoididae	2	40±44	30±34	27±22	36±23	13±18	25±28	
Plant feeders								
Dolichodoridae	3	19±28	-	4±5	1±3	-	0.4±1	
Heterodoridae	3	-	2±4	-	-	-	-	
Hoplolaimidae	3	3±6	-	1±1	-	-	-	
Paratylenchidae	2	173±181	4±5	13±6	13±18	3±3	3±4	D*
Pratylenchidae	3	225±167**a**	17±5**b**	6±8**b**	4±3**b**	4±5**b**	2±4**b**	D**
Psilenchidae	2	-	2±4	-	-	-	-	
Tylenchidae	2	122±100**a**	82±50**ab**	29±21**b**	79±77**ab**	5±5**c**	6±7**c**	D***
Omnivores								
Dorylaimidae	4	4±8	-	-	-	-	-	

	c-p-value	TOP SOIl		ROOTED ZONE		ROOT FREE ZONE		
		W	FM	W	FM	FM	W	ANOVA
Qudsianematidae	4	7±11	13±14	0.7±2	4±4	-	0.4±1	
Thornenematidae	5	7±11	2±4	1±2	-	-	-	D**
Predators								
Anatonchidae	4	11±1	5±0.3	-	1±3	-	-	D**
Mononchidae	4	12±13	-	-	4±7	-	-	
Nygolaimidae	5	7±8	-	-		-	-	D*
Total number of families		19	16	16	16	8	12	

Table S2b. July 2010: All nematode families (individuals 100 g^{-1}DW ± SD) at plots cropped with either fodder (FM) or corn (CM) maize and wheat without (W) or with maize litter (WL) in Top Soil (0–10cm), Rooted Zone (40-50cm), and Root Free Zone (60-70cm). DL – dauer larvae. ANOVA with *, **, *** at $P < 0.05$, 0.01, 0,001. Values within a soil depth with the same or no letters are not significantly different according to Tukey at $P < 0.05$. D –depth. (Scharroba, et al., 2012), completed.

	c-p value	TOP SOIL				ROOTED ZONE				ROOT FREE ZONE				
		W	WL	FM	CM	W	WL	FM	CM	W	WL	FM	CM	ANOVA
Bacterial feeders														
Cephalobidae	2	177±96**a**	201±95**a**	156±66**a**	251±70**a**	17±13**b**	29±33**b**	14±4**b**	21±5**b**	7±1**c**	6±4**c**	3±1**c**	10±8**bc**	D***
Microlaimidae	3	-	6±8	-	-	-	-	-	-	-	-	-	-	
Monhysteridae	1	2±4	20±19	-	2±4	1±2	1±0.3	0.4±1	1±1	0.2±0.4	0.3±0.4	0.3±0.4	1±1	
Panagrolaimidae	1	7±8	21±17	5±9	-	-	-	-	-	-	-	-	-	D**
Plectidae	2	8±12	26±21	2±5	2±4	0.4±1	0.2±0.5	1±1	0.3±0.4	0.3±0.5	1±1	-	-	D**
Rhabditidae(without DL)	1	206±40**a**	139±46**a**	165±100**a**	257±107**a**	1±1**c**	4±3**c**	5±2**c**	44±7**b**	5±5**c**	4±2**c**	1±2**c**	10±9**c**	D***
Rhabditidae DL	-	161±133**a**	273±214**a**	229±150**a**	559±275**a**	3±2**c**	4±3**c**	16±13**b**	21±11**b**	3±1**c**	9±9**b**	3±3**c**	25±42**b**	D***
Fungal feeders														
Anguinidae	2	13±19**a**	23±18**a**	2±5**bc**	10±13**ab**	0.3±1**c**	1±1**c**	0.3±0.4**c**	-	0.3±0.4**c**	0.3±1**c**	-	0.3±1**c**	D***
Aphelenchidae	2	24±12**b**	31±7**b**	39±14**b**	109±61**a**	13±5**bc**	12±6**bc**	6±2**c**	11±5**bc**	6±4**c**	4±2**c**	3±2**c**	2±1**c**	D***
Aphelenchoididae	2	227±43**a**	229±96**a**	65±60**b**	190±60**a**	3±1**c**	4±4**c**	6±5**c**	3±2**c**	6±3**c**	7±5**c**	1±1**c**	13±13**c**	D***
Leptonchidae	3	-	2±3	-	-	-	-	-	-	-	-	-	-	
Neotylenchidae	3	-	-	-	9±18	-	-	-	-	-	-	-	-	
Plant feeders														
Meloidogyne	3	-	-	4±8	-	-	-	-	-	-	-	-	-	
Paratylenchidae	2	66±69	80±61	2±5	8±9	1.8±3	0.2±0.5	1±1	0.4±1	-	0.2±0.3	-	-	D**
Pratylenchidae	3	10±9**b**	6±12**b**	5±1**b**	6±7**b**	40.1±19**a**	26.8±1.2**a**	4±3**b**	7±9**b**	10±4**b**	4±4**bc**	4±4**bc**	0.3±1**c**	D**
Psilenchidae	2	-	-	2±4	-	-	-	-	-	-	-	-	-	
Rotylenchidae	2	-	4±8	-	-	-	-	-	-	-	-	-	-	
Tylenchidae	2	110±61**a**	111±58**a**	85±45**a**	101±47**a**	11±6**b**	11±4**b**	4±4**c**	4±3**c**	2±1**c**	3±2**c**	2±2**c**	12±17**b**	D***
Omnivores														

	c-p-value	TOP SOIL				ROOT ZONE				ROOT FREE ZONE				
		W	**WL**	**FM**	**CM**	**W**	**WL**	**FM**	**CM**	**W**	**WL**	**FM**	**CM**	**ANOVA**
Qudsianematidae	4	2±4	3±6	4±5	2±4	0.1±0.3	0.3±1	-	0.2±0.4	0.4±1	0.3±0.4	-	1± 1	D*
Thornenematidae	5	2±3	5±6	-	-	-	-	-	-	-	-	-	-	
Predators														
Anatonchidae	4	15±6**a**	7±8**a**	5±7**a**	6±8**a**	**-b**	**-b**	**-b**	**-b**	**-b**	**-b**	**-b**	**- b**	D***
Nygolaimidae	5	-	-	-	2±4	**-**	-	-	-	**-**	**-**	**-**	**-**	
Total number of families		14	17	14	14	11	11	10	10	10	12	7	9	

Table S3

ANOVA *F* and *P* values for biomass of nematode families (µg FW g^{-1} DW soil**)** at plots cropped with either maize or wheat (factor crop) in July 2009 and 2010 (factor year). Presented are three soil depths: a- top soil, b - rooted zone, c - root free zone. Significant differences are marked in bold.

S3a

TOP SOIL	**Year**		**Crop**		**Year*Crop**	
	$F_{1,28}$	*P*	$F_{1,28}$	*P*	$F_{1,28}$	*P*
Bacterial feeders						
Cephalobidae	**10.94**	**0.003**	0.5	0.484	**0.00001**	0.981
Microlaimidae	2.333	0.138	2.333	0.138	2.333	0.138
Monhysteridae	0.502	0.484	2.213	0.148	0.510	0.481
Panagrolaimidae	**11.46**	**0.002**	**5.11**	**0.032**	**5.11**	**0.032**
Plectidae	0.0	0.989	**4.995**	**0.034**	0.477	0.495
Prismatolaimidae	1.995	0.169	0.005	0.942	0.005	0.942
Rhabditidae)	2.437	0.130	0.082	0.777	0.136	0.715
Fungal feeders						
Anguinidae	0.007	0.936	2.190	0.150	0.008	0.930
Aphelenchidae	**6.926**	**0.014**	3.263	0.082	1.526	0.227
Aphelenchoididae	4.473	0.043	0.927	0.344	0.008	0.931
Leptonchidae	1.0	0.326	1.0	0.326	1.0	0.326
Neotylenchidae	1.0	0.326	1.0	0.326	1.0	0.326
Plant feeders						
Dolichodoridae	4.193	0.05	4.193	0.05	4.193	0.05

Heteroderidae	1.0	0.326	1.0	0.326	1.0	0.326
Hoplolaimidae	1.0	0.326	1.0	0.326	1.0	0.326
Meloidogyne	1.0	0.326	1.0	0.326	1.0	0.326
Paratylenchidae	1.56	0.223	**16.56**	**0.00035**	0.16	0.696
Pratylenchidae	**6.607**	**0.016**	3.034	0.093	0.929	0.343
Psilenchidae	0.0	0.996	2.0	0.168	0.0	0.996
Rotylenchidae	1.0	0.326	1.0	0.326	1.0	0.326
Tylenchidae	1.097	0.304	0.654	0.425	0.793	0.381
Omnivores						
Dorylaimidae	1.0	0.326	1.0	0.326	1.0	0.326
Qudsianematidae	2.2	0.149	2.032	0.165	0.517	0.478
Thornenematidae	0.198	0.660	**4.722**	**0.038**	0.182	0.673
Predators						
Anatonchidae	1.831	0.187	0.521	0.476	0.459	0.504
Mononchidae	2.332	0.138	2.332	0.138	2.332	0.138
Nygolaimidae	0.354	0.557	0.354	0.557	3.311	0.08

S3b

ROOTED ZONE	Year		Crop		Year*Crop	
	$F_{1,28}$	P	$F_{1,28}$	P	$F_{1,28}$	P
Bacterial feeders						
Cephalobidae	**22.62**	**0.00005**	2.713	0.111	4.064	0.053
Monhysteridae	1.206	0.282	1.455	0.238	2.022	0.166
Panagrolaimidae	1.600	0.216	0.4	0.532	0.4	0.532
Plectidae	3.269	0.081	0.748	0.395	0.748	0.395
Rhabditidae	**15.502**	**0.0005**	3.849	0.06	0.206	0.653
Fungal feeders						
Anguinidae	**9.923**	**0.004**	1.8962	0.179	1.694	0.204
Aphelenchidae	**10.749**	**0.003**	2.079	0.160	**8.778**	**0.006**
Aphelenchoididae	**19.598**	**0.0001**	0.780	0.385	0.008	0.543
Plant feeders						
Dolichodoridae	3.619	0.067	1.359	0.253	1.359	0.253
Hoplolaimidae	1.0	0.326	1.0	0.326	1.0	0.326
Paratylenchidae	**7.357**	**0.01**	0.0008	0.977	0.0	1.0
Pratylenchidae	**17.308**	**0.0003**	**19.551**	**0.0001**	**14.446**	**0.0007**
Tylenchidae	**10.66**	**0.003**	3.498	0.072	**5.814**	**0.023**
Omnivores						
Qudsianematidae	0.220	0.642	0.662	0.423	1.234	0.276
Thornenematidae	1.000	0.326	1.000	0.326	1.000	0.326
Predators						
Anatonchidae	1.000	0.326	1.000	0.326	1.000	0.326
Mononchidae	2.482	0.126	1.004	0.325	1.004	0.325

S3c

ROOT FREE ZONE	Year		Crop		Year*Crop	
	$F_{1,27}$	P	$F_{1,27}$	P	$F_{1,27}$	P
Bacterial feeders						
Cephalobidae	**8.905**	**0.006**	1.929	0.176	2.224	0.148
Plectidae	0.809	0.376	0.809	0.376	1.194	0.284
Rhabditidae	0.909	0.349	0.374	0.546	0.00007	0.994
Fungal feeders						
Anguinidae	0.003	0.961	0.002	0.961	0.417	0.524
Aphelenchidae	0.207	0.653	0.032	0.858	2.363	0.136
Aphelenchoididae	3.573	0.069	1.214	0.280	1.130	0.297
Plant feeders						
Dolichodoridae	0.931	0.343	0.931	0.343	0.931	0.343
Paratylenchidae	**9.191**	**0.005**	0.239	0.628	0.339	0.565
Pratylenchidae	0.944	0.339	**6.255**	**0.019**	0.780	0.385
Tylenchidae	0.035	0.855	1.321	0.261	0.368	0.549
Omnivores						
Qudsianematidae	1.379	0.251	0.019	0.893	1.374	0.251
Predators						
Nygolaimidae	0.931	0.343	0.931	0.343	0.931	0.343

10. List of Publications

Scharroba, A., Dibbern, D., Hünninghaus, M., Kramer, S., Moll, S., Butenschoen, O., Bonkowski, M., Buscot, F., Kandeler, E., Koller, R., Krüger, D., Lueders, T., Scheu, S. & L. Ruess (2012). *Effects of resource availability and quality on the structure of the micro-food web of an arable soil across depth.* Soil Biology & Biochemistry, 50, 111-119.

Scharroba, A., Kramer, S., Kandeler, E., Ruess, L. (2016). *Spatial and temporal variation of resource allocation in an arable soil drives community structure and biomass of nematodes and their role in the micro-food web.* Pedobiologia, 59, 111-120.

Pausch, J., Kramer, S., **Scharroba, A**., Scheunemann, N., Butenschoen, O., Kandeler, E., Marhan, S., Riederer, M., Scheu, S., Kuzyakov, Y., Ruess, L (2016). *Small but active - the fungal channel drives carbon flow in the food web of an arable soil.* Functional Ecology 30, 479-489.

Scheunemann, N., Pausch, J., Digel, C., Kramer, S., **Scharroba, A**., Kuzyakov, Y., Ruess, L., Kandeler, E., Butenschoen, O., & Scheu, S. *Incorporation of root C and fertilizer N into the food web of an arable field: Variations with functional group and energy channel*. Food Webs, DOI:10.1016/j.foodweb2016.02.006

Pausch, J., Hofmann, S., **Scharroba, A**., Kuzyakov, Y., Ruess, L. *Fluxes of root-derived carbon into the nematode micro-food web of an arable soil.* Food Webs, doi:10.1016/j.foodweb.2016.05.001

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11. Thesis declarations

Declaration of the author's own contribution to manuscripts with multiple authors

Chapter 5.1 has been published in two papers (Scharroba, et al., 2012 ; Scharroba, et al., 2016); I have collected all data and did all statistics, graphs and tabs. In Detail Figures 7a+b,10, 11, 12, as well as Table 3 and 4 are published in Scharroba et al. 2016, whereas Table 3 has been completed in the present work. Tables 2a and b were already presented in Scharroba et al. 2012. Tables 5 and 6 are new and were not published.

Chapter 5.2 has been published and based on a dataset that was compiled by Johanna Pausch, Susanne Kramer, Nicole Scheunemann and me and are published together in (Pausch, et al., 2016a). Johanna Pausch supervised the experimental setup and provided stable isotope data on plant material and bulk soil, Susanne Kramer provided stable isotope data on microbial PLFAs and Nicole Scheunemann on meso- and macrofauna. All nematode data and calculations were done by me, Fig.3 was a co-work of all authors; created by Johanna Pausch for the publication (Pausch, et al., 2016a). Figure 13 and Figure 14 as well as Table 7 and 8 are modified or a specific section from Pausch et al. 2016a.

The experimental setup in Chapter 5.3. was supervised by Johanna Pausch, the plant and soil harvest in lab was done by Johanna Pausch and me for nematodes. Stable isotope data on plant material and bulk soil was provided by Johanna Pausch. Due to my pregnancy the master student Sylva Hofmann determined the ^{14}C-labeled nematode community in the framework of her master thesis and is actually submitted in a paper (Pausch, et al., 2016b). Based on my data Figure 15 and16 was created by Johanna Pausch for the paper. Table 9 and 10 are detailed sections or modifications from Pausch et al. 2016b.

The study design of each study was developed in the framework of the Research Unit "Carbon flow in belowground food webs assessed by isotope tracers" (FOR 918). All persons contributing to the manuscripts have been named so. All co-authors contributed to finalizing the manuscripts.