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Carbon budgets of top- and subsoil food webs in an arable system

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ABSTRACT

This study assessed the carbon (C) budget and the C stocks in major compartments of the soil food web (bacteria, fungi, protists, nematodes, meso- and macrofauna) in an arable field with/without litter addition. The C stocks in the food web were more than three times higher in topsoil (0–10 cm) compared to subsoil (> 40 cm). Microorganisms contained over 95% of food web C, with similar contributions of bacteria and fungi in topsoil. Litter addition did not alter C pools of soil biota after one growing season, except for the increase of fungi and fungal feeding nematodes in the topsoil. However, the C budget for functional groups changed with depth, particularly in the microfauna. This suggests food web resilience to litter amendment in terms of C pool sizes after one growing season. In contrast, the distinct depth dependent pattern indicates specific metacommunities, likely shaped by dominant abiotic and biotic habitat properties.

1. Introduction

Plant C transfer by litter and roots into soils plays a vital role in regulating ecosystem responses to climate change (Bardgett, 2011). However, understanding the ecosystem functions of soil C storage requires knowledge of the linkages between plant C resources and belowground biota. While easily degradable substrates such as rhizodeposits are assumed to be metabolised quickly in the bacterial energy channel, recalcitrant litter likely fosters the fungal energy channel, working at slower rates (Moore et al., 2005; Holtkamp et al., 2011). Soil food webs therefore are crucial for the balance between C mineralization and sequestration (Bardgett and Wardle, 2010), yet empirical data on the C pools of functional groups are scarce. Only recently, root C incorporation into the soil food web of an arable soil was traced using a $^{13}CO_2$ pulse labelling of crop plants (Pausch et al., 2016).

Crop residues are important in the formation of soil organic matter, and for that reason often left on the field to maintain organic C stocks and to improve soil fertility. Agricultural practices that disturb soil C pools may increase greenhouse gas emissions and reduce soil quality (Turmel et al., 2015), which also applies to the management of food, fodder and bioenergy crops such as maize (Hudiburg et al., 2014). The aboveground inputs by maize to soil (to 1 m depth) were estimated between 70–81% of total plant C input, and indiscriminate removal of residues was shown to considerably diminish soil C stocks (Carvalho et al., 2017).

In contrast to the knowledge on the impact of crop management on soil C stocks, it is less clear how much C from above- ad belowground inputs is allocated to individual soil food web pools. Moreover, the availability and quality of plant C varies considerably with soil depth. Organic amendments are an important energy and nutrient source for soil communities predominantly in the plough layer (Navarro-Noya et al., 2013). In the rooted zone below the Ap horizon major resources are root residues and rhizodeposits, whereas organisms in the subsoil depend mainly on organic matter translocation from upper soil layers (Ferris and Bongers, 2006; Kautz et al., 2012).

The present study, for the first time, systematically elaborates the C stocks in all major groups of the soil food web up to 70 cm depth in an arable soil. The experimental field was cropped with *Zea mays* without and with application of maize shoot litter. The resulting two treatments were: fodder maize (FM), with the aboveground plant removed at

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harvest, mainly supplying belowground C sources, and corn maize (CM), which in addition adds aboveground litter to the soil. Food web assemblages investigated comprised microorganisms (bacteria, fungi), microfauna (protists, nematodes) and meso-/macrofauna. We hypothesized that (i) litter and root resources, and their distribution along the soil depth profile control C pools in organisms, and (ii) amendment with litter increases C incorporation into functional groups of the fungal channel, in particular in the top soil.

2. Materials & methods

2.1. Experimental field site

Fodder (FM) and corn maize (CM) plots (24 × 24 m, 4 replicates each) were established at an arable field north-west of Göttingen, Germany (51°33′N, 9°53′O; 158 m NN). The area has a temperate climate with a mean annual precipitation of 720 mm and air temperature of 7.9 °C. The dominant soil types at the site are loamy Cambisols and Luvisols with the latter partly stagnic.

Maize was sown in spring 2009 ("Ronaldinio"; 34 kg ha^{-1}) and 2010 ("Fernandez"; 26 kg ha^{-1}). CM plots received hackled maize shoots at an amount of 0.8 kg dry weight m^{-2} (C-content 0.35 kg m^{-2}, C:N 18.5), resembling the shoot biomass of maize. Litter was applied on the soil surface of CM plots after maize harvest on the 27th of October 2009, whereas FM plots received no litter. Details on management and soil properties are given in Kramer et al. (2012) and Pausch and Kuzyakov (2012).

2.2. Sampling and processing

Maize root biomass sampled in July 2009 was used for the calculations. The applied design covered the entire spatial variability of roots in the field (Pausch et al., 2013). In July 2010, representative samples were taken to ensure that biomass was not significantly different compared to 2009. Only the portion of the maize root system below the soil surface was considered as root biomass and thus, the aboveground crown root was not included.

On 22nd of July 2010, soil was sampled at 0–10 (top soil), 40–50 (rooted zone beneath plough layer) and 60–70 cm depth (root free zone). From each plot, ten samples were taken with a soil corer (diam. 2.5 cm), bulked and gently mixed by hand. Sieved (< 2 mm) subsamples were either dried at 60 °C and analyzed for total C using an elemental analyzer NA 1500 (Carlo Elba Instruments, Milano, Italy), stored at −20 °C until analysis of phospholipid fatty acids (PLFA) or at 8 °C until extraction of total microbial biomass, protists, and nematodes at the next day.

Total soil microbial biomass C (C_{mic}) was determined by chloroform fumigation-extraction method (Vance et al., 1987), with the modification that fumigated (24 h) and non-fumigated soil samples (10 g of moist soil) were extracted with 40 ml of 0.025 M K_2SO_4 solution (Kramer et al., 2012). For estimation of the total C_{mic} a k_{EC} factor of 0.45 was used (Wu et al., 1990). PLFAs were extracted from 6 g soil according to Frostegård et al. (1993). To calculate C contents, fungal PLFA concentration was multiplied with the conversion factor 85 (Klamer and Bååth, 2004). Since the microbial biomass C consists mainly of fungal and bacterial C, the bacterial C was calculated by subtracting fungal C values from C_{mic} values of the soil.

Potential abundance of morphotypes of cultivable protist groups were determined according to Finlay et al. (2000) and biomass estimated using an average cell size of 50, 400, 3000 µm^3 for flagellates, amoebae, and ciliates, respectively (Stout and Heal, 1967), and a dry weight conversion factor of 0.212 pg µm^{-3} (Griffiths and Ritz, 1988). The C content was accepted as 50% of fresh weight (Griffiths and Bardgett, 1997).

A modified Baermann method (Ruess, 1995) was used to extract nematodes from soil. Nematode biomass (fresh weigh) was determined according to Andrássy (1954) as $V = \frac{a^{"} * b}{1.7}$ [µg], with a as largest body width, b as body length and *1.7* as conversion factor. The C in nematodes was calculated as 12.5% C of the fresh weight, following Schmidt et al. (2000), assuming that dry weight is 25% of fresh weight and has a C content of 50%.

For soil arthropod extraction, two additional soil samples of 20 cm diameter and 10 cm depth were taken in July 2010 at each plot using a stainless steel corer. Animals were determined from 0 to 10 cm soil depth as their densities deeper in soil were very low; macrofauna virtually was absent at deeper layers (N. Scheunemann, unpubl. data). Soil arthropods were extracted from the soil cores by heat (Kempson et al., 1963) and identified to species level using a dissecting microscope for macrofauna and a light microscope (1000× magnification) for mesofauna. The two pseudoreplicates per plot were pooled and their arithmetic mean was used for further analysis, resulting in four replicates (n = 4) per treatment. Using body width, specimens were assigned to mesofauna (< 2 mm) and macrofauna (> 2 mm). Taxa were separated into decomposers and predators according to Pausch et al. (2016). The biomass was calculated from measured body lengths, and C content determined in dried specimens using an elemental analyzer (Eurovector, Milano, Italy).

2.3. Data analysis

All data were converted to mg C per m^2 using the formula:

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

where 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 0–10 cm; 1.6 g cm^{-3} at 40–50 cm; 1.7 g cm^{-3} at 60–70 cm) and $n(C_P)$ is the C content (mg C g soil^{-1}) of the pool (for details see Pausch et al., 2016).

Additionally to the C content, the C pool size of major food web groups was expressed as percentage of (1) complete food web, (2) faunal food web, (3) micro-food web, and (4) nematodes. The data were log-transformed to meet the requirement of homogeneity of variance (Levene test). One-way ANOVAs followed by post-hoc Tukey's HSD test were used to identify significant differences ($P < 0.05$) between soil depths in C stocks and in % C for each organism group within a treatment. Differences between CM and FM were inspected using t-tests.

3. Results

Soil organic matter contained more than 97% of total belowground C (on average 1550 g C m^{-2} at 0–10 cm and 600 g C m^{-2} at 60–70 cm), whereas up to 1.5% of the C (24 g C m^{-2}) was held in microbial biomass (bacteria and fungi) and only a minor C pool in the soil fauna (Table 1). Considering the entire food web, bacteria and fungi contained more than 95% of all C (Fig. 1A). A shift in C pools occurred with depth. While bacteria and fungi had equal C pools in the topsoil (0–10 cm), fungal C was lower at 40–50 cm and higher at 60–70 cm for both treatments (CM, FM). Litter addition resulted in higher contribution of fungal C to total C in the CM as compared to FM plots in the topsoil (Table 1), yet the difference was not significant ($P = 0.1$; Fig. 1A).

The animal food web was dominated by macro- and mesofauna, with the largest C stock of 0.29–0.67 g C m^2 in macrofauna decomposers (Table 1, Fig. 1B). Within the micro-food web, cultivable protists accounted for the highest C pool, except in the top soil where nematodes and ciliates had equal proportions (Fig. 1C). The dominant protists across treatments and depth were ciliates with much larger C stocks (ranging from 0.10 to 0.25 g C m^{-2}) as compared to flagellates and amoebae (< 0.03 g C m^{-2}), but the latter increased with depth. Litter addition did not significantly affect any of the protist groups. Among nematode trophic groups, bacterial feeders accounted for the largest C pool with 0.09–0.13 g C m^{-2} in the upper 0–10 cm soil (Table 1,

Table 1
C stocks in soil, roots and food web components (g C m^{-2} ± SEM). Upper case letters indicate significant differences (P ≤ 0.05) between soil depths for individual food web components within the same treatment. If no letters are shown, there is no significant depth effect. Asterisks indicate differences in C stocks of single organisms between the corn maize (CM) and the fodder maize (FM) treatments.

		Treatment					
Soil Depth [cm]		CM 0–10 cm	FM	CM 40–50 cm	FM	CM 60–70 cm	FM
	Soil (including organisms)	1602.9 ± 26.8	1487.2 ± 17.9	855.9[a]	788.1[a]	621.0 ± 60.0	586.6 ± 48.6
	Roots	–	20.4 ± 5.2	–	2.1 ± 0.8	–	0.3[b]
Microorganisms							
	Bacteria	10.1 ± 3.1 A	12.5 ± 2.3A	5.5 ± 0.3A	4.5 ± 0.5B	1.2 ± 0.3B	1.0 ± 0.2C
	Fungi	14.2 ± 2.1 A*	8.8 ± 0.6A	2.7 ± 0.3B	2.7 ± 0.3B	2.2 ± 0.2B	1.8 ± 0.2C
Macrofauna ($x*10^{-3}$)	Decomposers	669.3	292.7	–	–	–	–
	Predators	157.6	93.9	–	–	–	–
Mesofauna ($x*10^{-3}$)	Decomposers	10.7	8.0	–	–	–	–
	Predators	8.0	5.4	–	–	–	–
Protozoa ($x*10^{-3}$)	Ciliates	184.3 ± 43.3	175.5 ± 53.2	162.2 ± 32.4	248.7 ± 92.4	101.8 ± 22.0	111.9 ± 59.6
	Amoebae	15.1 ± 3.0	17.1 ± 1.2	14.4 ± 1.8*	6.0 ± 2.3	28.3 ± 6.7	22.1 ± 6.8
	Flagellates	8.8 ± 1.6	9.8 ± 1.2	4.6 ± 1.4	4.1 ± 0.0	8.0 ± 1.4	8.2 ± 1.4
Nematodes ($x*10^{-3}$)	Bacterial feeders	131.5 ± 27.4A	92.5 ± 21.7A	24.8 ± 18.2B	4.7 ± 1.5B	9.6 ± 3.8B	1.45 ± 0.8B
	Fungal feeders	20.4 ± 7.4A*	3.6 ± 0.9	0.7 ± 0.1B	0.5 ± 0.1	0.5 ± 0.2B	0.2 ± 0.1
	Plant feeders	2.1 ± 0.4A	1.8 ± 0.4A	0.3 ± 0.1B	0.2 ± 0.1B	0.26 ± 0.18B	0.2 ± 0.1B
	Omnivores	0.5 ± 0.5	1.9 ± 1.2	0.1 ± 0.1	–	0.17 ± 0.17	–
	Predators	7.5 ± 4.5	5.3 ± 3.8	–	–	–	–

[a] Soil C stocks at 40–50 cm were extrapolated from fitted functions.
[b] Root C stocks at 60–70 cm depth were extrapolated from fitted functions.

Fig. 1D). The C pool of fungal feeders and predators ranged from 0.004–0.02 g C m^{-2} and 0.005–0.007 g C m^{-2}, respectively. Omnivores and plant feeders showed C pool sizes below 0.002 g C m^{-2} in the upper 10 cm (Table 1, Fig. 1D). While the C pool size of nematodes strongly decreased with depth (Table 1), the contribution of bacterial feeders to total C in the nematodes fauna remained constant (Fig. 1D).

4. Discussion

Crop residue addition is a common arable practice to increase soil organic carbon content, thereby fostering the detritus based food-chain and subsequently generalist predators (Birkhofer et al., 2008; von Berg et al., 2010; Serada et al., 2015). However, in the present study crop management, that altered resource quality and availability in soil, did not impact food web C pools across functional groups and depths. This might have been due to experimental manipulations, i.e. low litter amendment or short application time. However, the applied litter quantity (similar to aboveground maize biomass) resembles agricultural practice and the incubation period (nine month) are common in agricultural practice and represent one cropping cycle. The established system was monitored over 5 years (Kramer et al., 2013, Müller et al., 2016), confirming positive litter effects on the amount of bacterial and fungal PLFAs in the top soil already after the first vegetation period, and few changes in PLFA ratios between CM and FM with time. This effect of litter amendment is reflected in the present data, yet not significantly, by the higher contribution of fungal C to total C at the CM as compared to FM plots.

Aside from this minor impact on fungi, litter addition did not alter C pools of soil biota after one growth period. This is surprising, as high availability of recalcitrant organic resources is considered to enhance C and energy flux through the fungal channel of the food web (Ruess and Ferris, 2004; Scheu et al., 2005). A positive litter effect was observed at CM plots for the abundance of fungi and fungal feeding nematodes, predominantly in the top soil (Scharroba et al., 2012; Moll et al., 2015). In contrast, data on the meso- and macrofauna suggest that root C rather than shoot residues drive soil arthropod communities (Scheunemann et al., 2015). Overall, the C pool sizes of functional groups were quite resilient to the addition of organic resources, yet this may not necessarily have been the case for food web C fluxes. Using a $^{13}CO_2$ pulse labelling of maize at the experimental field site, Pausch et al. (2016) revealed that C stocks of soil organisms and ^{13}C incorporation did not match closely. Fungi, with a C stock less than half of that of bacteria, had C flux rates by far exceeding those of bacteria, thereby transferring plant C to higher trophic levels. In sum these findings challenge the widely accepted bacterial-fungal energy channel concept and are in line with recent perspectives that a clear split in distinct channels at lower trophic food web levels is oversimplistic (Ballhausen and de Boer, 2016; Geisen, 2016). Evidence was raised for multiple reticulated channels through which litter C flows (Wolkovich, 2016), and organic C likely forms a continuous rather than two or three separated pools (de Vries and Caruso, 2016). Our study, revealing stable C pools across functional groups further indicates a considerable resilience of the food web C budget to increased availability of recalcitrant resources.

In contrast, C stocks in the food web showed distinct changes with soil depth, suggesting abiotic (soil properties) and biotic (rooting depth) factors to be much more important than surface litter amendment. This was predominantly evident for soil arthropods, where below 10 cm depth the abundance of the mesofauna was very low and the macrofauna was almost absent (N. Scheunemann, unpubl. data). This distinct vertical distribution, with densities disproportionately high in the top soil, is well known, e.g. for mites (0–5 cm, Perdue and Crossley, 1990) or Collembola (0–10 cm, Ponge, 2000), and is related to greater moisture content, pore space, root biomass and microbial activity. Correspondingly, major organic resources, e.g. extractable organic carbon, microbial biomass, and maize roots were highest in the 0–10 cm layer at both FM and CM plots (Kramer et al., 2013, Pausch et al., 2013). On the other hand, this suggests pronounced resource

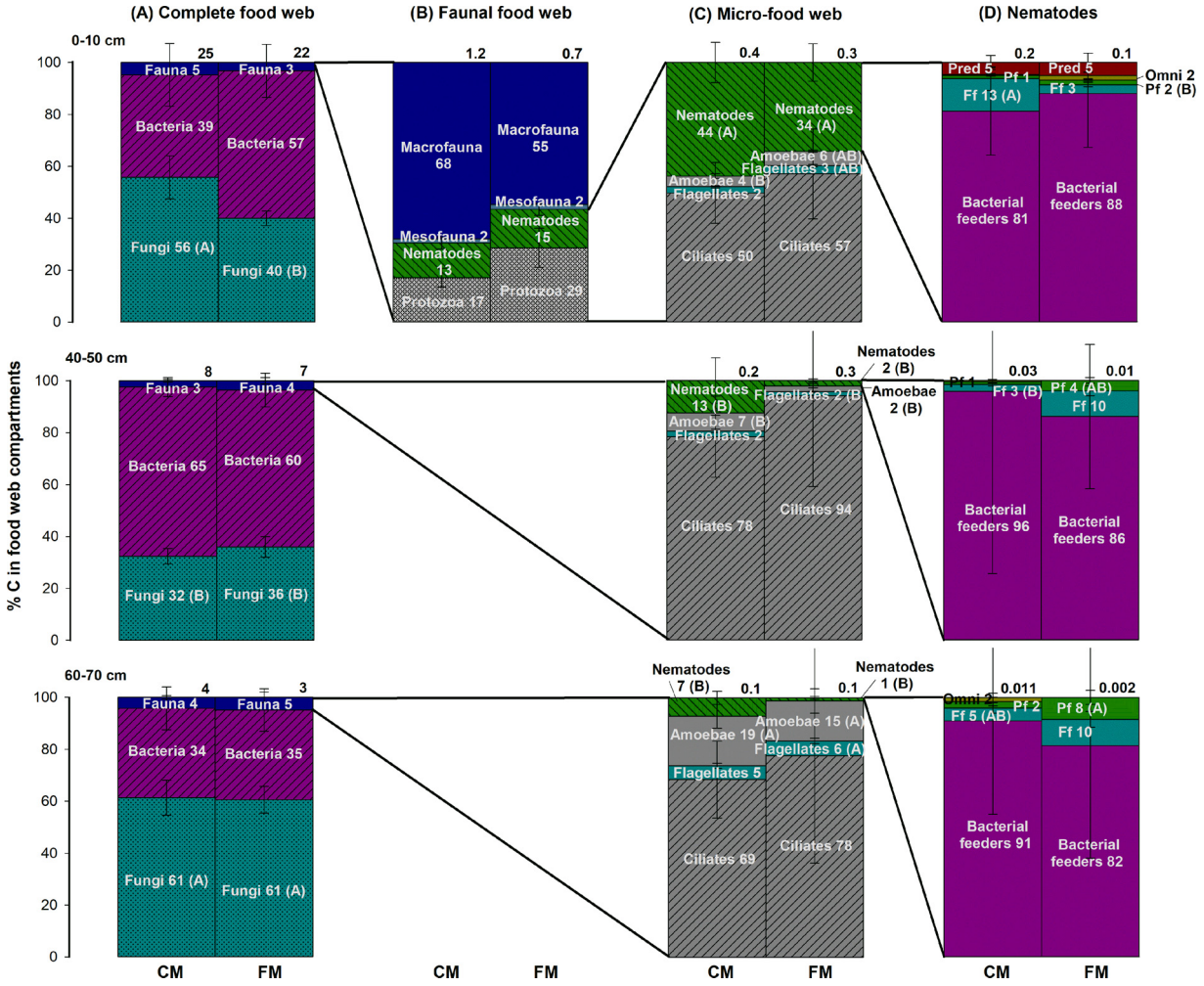

Fig. 1. Percentage of C in individual food web components of arable fields with corn maize (CM) and fodder maize (FM) at three soil depths (0–10, 40–50, 60–70 cm): (A) complete food web, (B) animal food web, (C) micro-food web, and (D) nematodes. Bold numbers above the bars are absolute C stocks in the respective food web component (g C m^{-2}). Upper case letters indicate significant differences ($P \leq 0.05$) between soil depths for individual food web components within the same treatment. If no letters are shown, there is no significant depth effect. No differences were detected when comparing % C in individual organism groups between CM and FM. Ff: Fungal feeding nematodes; Pf: Plant feeding nematodes; Pred: Predators; Omni: Omnivorous nematodes.

competition within the microfauna, dominating the faunal food web below the plough layer. The changes in microfaunal C pools across depth, among the different groups of protists as well as between protists and nematodes, indicate specific niche adaptations, likely a strategy to lessen competition. This is supported by the depth related changes in diversity and taxon composition of the micro-food web at the field site (Scharroba et al., 2012, 2016).

In conclusion, despite different amounts of resource inputs, C pools of the soil food web remain stable across all organism groups and soil depths (topsoil, rooted zone, subsoil), at least after one growth period. This points to a considerable resilience and allows to generalize the detailed food web C flows measured by ^{13}C (Pausch et al., 2016). Although revealing no litter effects, the food web C budgets and their distinct spatial pattern assigned form a valuable empirical database for future modelling of belowground C stocks and fluxes.

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References

Andrássy, I., 1954. Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta Zool. 1–15.
Ballhausen, M.-B., de Boer, W., 2016. The sapro-rhizosphere: carbon flow from saprotrophic fungi into fungus-feeding bacteria. Soil Biol. Biochem. 102, 14–17.
Bardgett, R.D., 2011. Plant-soil interactions in a changing world. F1000 Biol. Rep. 3 (16). http://dx.doi.org/10.3410/B3-16.
Bardgett, R.D., Wardle, D.A., 2010. Aboveground-Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change. Oxford University Press, Oxford, UK.
Birkhofer, K., Wise, D.H., Scheu, S., 2008. Subsidy from the detrital food web, but not microhabitat complexity affects the role of generalist predators in an aboveground herbivore food web. Oikos 117, 494–500.
Carvalho, J.L.N., Hudiburg, T.W., Franco, H.C.J., DeLucia, E.H., 2017. Contribution of above- and belowground bioenergy crop residues to soil carbon. Global Change Biol. Bioenergy 9, 1333–1343.
de Vries, F.T., Caruso, T., 2016. Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web. Soil Biol. Biochem. 102, 4–9.
Ferris, H., Bongers, T., 2006. Nematode indicators of organic enchrichment. J. Nematol. 38, 3–12.
Finlay, B., Black, H., Brown, S., Clarke, K., Esteban, G., Hindle, R., Olmo, J., Rollett, A., Vickerman, K., 2000. Estimating the growth potential of the soil protozoan community. Protist 151, 69–80.
Frostegård, Å., Tunlid, A., Bååth, E., 1993. Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipids fatty acid analysis. Soil Biol. Biochem. 25, 723–730.
Geisen, S., 2016. The bacterial-fungal energy channel concept challenged by enormous functional versatility of soil protists. Soil Biol. Biochem. 102, 22–25.
Griffiths, B.S., Ritz, K., 1988. A technique to extract, enumerate and measure protozoa

from mineral soils. Soil Biol. Biochem. 20, 163–173.
Griffiths, B.S., Bardgett, R.D., 1997. Interactions between microbial feeding invertebrates and soil microorganisms. In: Van Elsas, J.D., Wellington, E.M.H., Trevors, J.D. (Eds.), Modern Soil Microbiology, pp. 165–182.
Holtkamp, R., van der Wal, A., Kardol, P., van der Putten, W.H., de Ruiter, P.C., Dekker, S.C., 2011. Modelling C and N mineralisation in soil food webs during secondary succession on ex-arable land. Soil Biol. Biochem. 43, 251–260.
Hudiburg, T.W., Davis, S.C., Parton, W., DeLucia, E.H., 2014. Bioenergy crop greenhouse gas mitigation potential under a range of management practices. Global Change Biol. Bioenergy 7, 366–374.
Kautz, T., Amelung, W., Ewert, F., Gaiser, T., Horn, R., Jahn, R., Javaux, M., Kemna, A., Kuzyakov, Y., Munch, J.-C., Pätzold, S., Peth, S., Scherer, H.W., Schloter, M., Schneider, H., Vanderborght, J., Vetterlein, D., Walter, A., Wiesenberg, G.L.B., Köpke, U., 2012. Nutrient acquisition from arable subsoils in temperate climates: a review. Soil Biol. Biochem. 57, 1003–1022.
Kempson, D., Lloyd, M., Ghelardi, R., 1963. A new extractor for woodland litter. Pedobiologia 3, 1–21.
Klamer, M., Bååth, E., 2004. Estimation of conversion factors for fungal biomass determination in compost using ergosterol and PLFA 18:2ω6,9. Soil Biol. Biochem. 36, 57–65.
Kramer, S., Marhan, S., Ruess, L., Armbruster, W., Butenschoen, O., Haslwimmer, H., Kuzyakov, Y., Pausch, J., Schoene, J., Scheunemann, N., Schmalwasser, A., Totsche, K.U., Walker, F., Scheu, S., Kandeler, E., 2012. Carbon flow into microbial and fungal biomass as a basis to understand the belowground food web in an agroecosystem. Pedobiologia 55, 111–119.
Kramer, S., Marhan, S., Haslwimmer, H., Ruess, L., Kandeler, E., 2013. Temporal variation in surface and subsoil abundance and function of the soil microbial community in an arable soil. Soil Biol. Biochem. 61, 76–85.
Moll, J., Goldmann, K., Kramer, S., Hempel, S., Kandeler, E., Marhan, S., Ruess, L., Krüger, D., Buscot, F., 2015. Resource type and availability regulate fungal communities along arable soil profiles. Microb. Ecol. 70, 390–399.
Moore, J.C., McCann, K., de Ruiter, P.C., 2005. Modeling trophic pathways, nutrient cycling, and dynamic stability in soils. Pedobiologia 49, 499–510.
Müller, K., Kramer, S., Haslwimmer, H., Marhan, S., Scheunemann, N., Butenschön, O., Scheu, S., Kandeler, E., 2016. Carbon transfer from maize roots and litter into bacteria and fungi depends on soil depth and time. Soil Biol. Biochem. 93, 79–89.
Navarro-Noya, Y.E., Gómez-Acata, S., Montoya-Ciriaco, N., Rojas-Valdez, A., Suárez-Arriaga, M., Valenzuela-Encinas, C., Jiménez-Bueno, N., Verhulst, N., Govaerts, B., Dendooven, L., 2013. Relative impacts of tillage, residue management and crop-rotation on soil bacterial communities in a semi-arid agroecosystem. Soil Biol. Biochem. 65, 86–95.
Pausch, J., Kuzyakov, Y., 2012. Soil organic carbon decomposition from recently added and older sources estimated by $\delta^{13}C$ values of CO_2 and organic matter. Soil Biol. Biochem. 55, 40–47.
Pausch, J., Tian, J., Riederer, M., Kuzyakov, Y., 2013. Estimation of rhizodeposition at field scale: upscaling of a ^{14}C labeling study. Plant Soil 364, 273–285.
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 pool size does not matter for carbon incorporation in below-ground food webs. Funct. Ecol. 30, 479–489.
Perdue, J.C., Crossley, D.A.Jr., 1990. Vertical distribution of soil mites (Acari) in conventional and no-tillage agricultural systems. Biol. Fertil. Soils 9, 135–138.
Ponge, J.-F., 2000. Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. Biol. Fertil. Soils 32, 508–522.
Ruess, L., 1995. Nematode fauna in spruce forest soils: a qualitative/quantitative comparison. Nematologica 41, 106–124.
Ruess, L., Ferris, H., 2004. Decomposition pathways and successional changes. Nematol. Monogr. Perspect. 2, 547–556.
Scharroba, A., Dibbern, D., Hünninghaus, M., Kramer, S., Moll, J., Butenschoen, O., Bonkowski, M., Buscot, F., Kandeler, E., Koller, R., Krüger, D., Lueders, T., Scheu, S., Ruess, L., 2012. Effects of resource availability and quality on the structure of the micro-food web of an arable soil across depth. Soil Biol. Biochem. 50, 1–11.
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.
Scheu, S., Ruess, L., Bonkowski, M., 2005. Interactions between microorganisms and soil micro- and mesofauna. In: Buscot, F., Varma, A. (Eds.), Microorganisms in Soils: Roles in Genesis and Functions. Springer Verlag, pp. 253–275.
Scheunemann, N., Digel, C., Scheu, S., Butenschoen, O., 2015. Roots rather than shoot residues drive soil arthropod communities of arable fields. Oecologia 179, 1135–1145.
Schmidt, I.K., Ruess, L., Bååth, E., Michelsen, A., Eklund, F., Jonasson, S., 2000. Long-term manipulation of the microbes and microfauna of two subartic heaths by addition of fungicide, bactericide, carbon and fertilizer. Soil Biol. Biochem. 32, 707–720.
Serada, E., Wolters, V., Birkhofer, K., 2015. Addition of crop residues affects a detritus-based food chain depending on litter type and farming system. Basic Appl. Ecol. 16, 746–754.
Stout, J., Heal, O., 1967. Protozoa. In: Burges, A., Raw, R. (Eds.), Soil Biology. Academic Press, London, pp. 149–211.
Turmel, M.-S., Speratti, A., Baudron, F., Verhulst, N., Govaerts, B., 2015. Crop residue management and soil health: a systems analysis. Agric. Syst. 134, 6–16.
Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707.
Von Berg, K., Thies, C., Tscharntke, T., Scheu, S., 2010. Changes in herbivore control in arable fields by detrital subsidies depend on predator species and vary in space. Oecologia 163, 1033–1042.
Wolkovich, E.M., 2016. Reticulated channels in the soil food web. Soil Biol. Biochem. 102, 18–21.
Wu, J., Joergensen, R.G., Pommerenign, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass-C by fumigation-extraction—an automated procedure. Soil Biol. Biochem. 22, 1167–1169.