



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



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ABSTRACT

The assemblages of organisms residing at different soil horizons are important drivers for carbon and nutrient cycle in arable systems, yet knowledge on food web dynamics below the plough zone is sparse. The present study investigated the effects of 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. Resource quality was manipulated by crop plant (maize and wheat) and organic amendment (with/without maize litter), to differently fuel the major soil carbon pathways based on roots, bacteria and fungi. Nematode assemblages were used as model to determine changes in the structure, function and carbon allocation of the soil micro-food web.

The biomass of nematode families as well as the fungal to bacterial feeder ratio $F/(F+B)$ assigned a predominance of the bacterial carbon channel in the arable soil. The differences in spatial and temporal availability of major plant resources, i.e. litter (recalcitrant substrate) and rhizodeposits (labile carbon), separated the nematode fauna into meta-communities along the depth profile. The seasonal pattern in population density, and the positive effects of litter amendment predominantly in the top soil, indicated low migration between these patches during crop growth. However, mass-flow as resource subsidy for communities at depth takes place under fallow during winter. Crop type was most important for carbon allocation, with wheat generally resulting in a greater biomass build-up of nematodes. The biomass distribution of trophic groups differed with depth, pointing to a strong bottom-up effect in the root channel, whereas predation likely was the primary regulating force in the fungal channel. Overall, combining nematode community composition with biomass revealed spatially separated micro-food web assemblages, differing in structure and carbon allocation. Thereby transport processes cross community boundaries, linking top soil and subsoil, notably in periods without a crop.

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1. Introduction

Soil food webs rely on the organic carbon input provided by plants, and the related variations in chemical composition and physical structure are highly relevant for both microbial and faunal decomposers (Ruess and Ferris, 2004; Ruf et al., 2006; Kramer et al., 2012). The two main plant resources in belowground systems are litter, slowly decomposable plant material, and rhizodeposits, readily available carbon sources. While bacteria predominantly degrade labile, and fungi recalcitrant compounds (Strickland and Rousk, 2010), soil nematodes and their interactions with

microorganisms stimulate these decomposition processes (Freckman 1988; Neher, 2010). Moreover, nematodes hold a central position in the soil food web, with highest density among multicellular taxa and functional groups at all trophic levels (Yeates, 2010). Due to their diverse trophic interactions, the composition of the nematode fauna reflects changes in plant resources related to species, season or management practice (e.g. De Goede and Bongers, 1994; Ferris and Matute, 2003; Leroy et al., 2009; Ugarte et al., 2013). Despite this key role in food web dynamics, the effects of resource quality and availability on nematode community structure have rarely been assigned across soil depth (Liang et al., 2005; Scharroba et al., 2012).

In arable soils the aboveground litter input, either by crop or by organic amendment, plays a dominant role in nutrient availability

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for the soil community inhabiting the plough layer. Due to removal of crop plants at harvest as well as fertilization practice, these plant resources fuel the soil food web only temporarily (Ferris et al., 2001; Navarro-Noya et al., 2013). The resources in the rooted zone are dominated by plant root residues and rhizodeposition, with the highest exudate release taking place in spring and summer (Aulakh et al., 2001). Referring to rhizodeposition, annual crop plants again represent an ephemeral carbon and nutrient supply for soil biota. In contrast, organisms inhabiting root free deeper soil layers depend on nutrient translocation from above, predominantly occurring on heavy rainfall and after snowmelt under fallows after harvest (Totsche et al., 2007; Dibbern et al., 2012). This distinct vertical stratification in resource quality and availability affects the composition of soil organism assemblages across the depth profile, with highest diversity and biomass generally located in the uppermost soil layer. However, as half of the global organic carbon pools are present below 30 cm depth (Jobbagy and Jackson 2000), studies on the soil fauna in relation to nutrient and carbon cycling should also consider subsoil.

The spatial pattern of resources along the soil profile is postulated to be accompanied by unique assemblages of taxa associated with organic material (top soil), plant roots (rooted zone) or oligotrophic environments (root free zone) (Ferris and Bongers 2006; Ferris 2010). This view adopts the concept of metacommunities described by Wilson (1992), where spatial heterogeneity fragments ecological systems into a mosaic of patches. In soils, separation into metacommunities is driven by both, the abiotic environmental heterogeneity (e.g. texture, moisture, O₂, CO₂) as well as the quality and availability of plant resources (e.g. litter, root exudates) within the depth transect. As the latter has a major impact on food web dynamics, trophic assemblages differing in diversity, composition and linkage establish across depth.

To assess soil conditions and nutrient status, nematodes are widely used as bioindicators (Bongers 1990; Bongers and Ferris 1999; Neher 1998, 2001). The nematode micro-food web has basal, enriched and structural components, which can be used to assign the carbon and energy flow through root, bacterial and fungal energy channels. Thereby the composition of nematode functional guilds is a measure for structure and function of the entire soil food web (Ferris et al., 2001). Additionally, nematode biomass as attribute for carbon allocation, conveys valuable information on food web carbon flow (Ferris, 2010). Nematode biomass can be easily used as production component due to their vermiform, cylindrical shape and the standardized morphometric characteristics applied in their taxonomy. Described body weights (Andrassy, 1956) as well as conversion coefficients for dry weight and carbon content (Sohlenius et al., 1997) facilitate the estimation of taxon or trophic group biomass C. Thereby carbon flows through the different compartments of the nematode micro-food web can be quantified (Zhang et al., 2015b). Based on these features, nematode metabolic foot prints, either using biomass solely or in combination with respiration data, were successfully applied as measure for ecosystem services of functional guilds across ecosystem types (Ferris, 2010; Zhang et al., 2015a, 2015b).

The present study investigates the effects of resource quality and availability on nematode density, biomass and community composition in an arable field across season and soil depth. Resource quality was manipulated using two crop plants (maize and wheat) and management practices (with/without maize litter amendment), to differently fuel the major soil carbon pathways. Nematode communities were investigated along a depth gradient, i.e. along decreasing resource availability and food web complexity, comprising the compartments: (1) top soil within plough horizon (0–10 cm), (2) rooted zone beneath plough layer (30–50 cm), and (3) deeper root free soil (60–70 cm). Seasonal variation was

estimated in two successive years by sampling in summer (highest rhizodeposition), autumn (plant residue input), and winter (high migration of dissolved organic matter). Nematode trophic group biomass was related to the biomass of microbial and fungal food web resources at the respective sites.

Based on Ferris and Bongers (2006) we assumed that the differences in resource availability and abiotic environmental factors separate the nematode fauna into distinctly different assemblages along the depth gradient. For these metacommunities we hypothesised that: i) nematode assemblages differ in food web composition and function, and thus carbon allocation in biomass, ii) metacommunities in the root free zone are quite isolated from the processes above and translocation processes only occur in periods with sufficient mass-flow, iii) litter amendment fosters the fungal decomposition pathway in the top soil with a predominant biomass increase at lower trophic levels (i.e. bacterial and fungal feeders), whereas the impact of crop is most pronounced in the rooted zone and here in plant feeders.

2. Materials and methods

2.1. Field site and agriculture management

The experimental site was established in 2009 at an arable field (51°33'N, 9°53'O; 158 m NN) near Göttingen, Germany. The area has a temperate climate with a mean annual precipitation of 720 mm and air temperature of 7.9 °C. According to IUSS (2007) the dominant soil types at the site are Cambisols and Luvisols with the latter partly stagnic.

Previous to the set-up of the experiment the arable land was grown for 5 years with winter wheat, except for 2007, where the crop was sugar beet. Depending on long-term agricultural management two plough layers (0.2 m and 0.3 m depth) were detected with strong soil compaction below the second plough layer. The mean C and N contents of the Ap horizon were 11.6 and 1.2 mg g⁻¹ dry weight soil. More details on physical and chemical soil properties are given in Kramer et al. (2012).

In a strip-plot design of two rows the field was cropped with maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.). The strip-plot design is commonly used in agricultural field experiments to facilitate management practices such as tillage (Petersen, 1994). In the first vegetation period (2009) winter wheat ("Julius"; 224 kg ha⁻¹) and maize ("Ronaldino"; 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) in the respective rows, i.e. no crop rotation between maize and wheat was performed. During the sample period the C_{org} content ranged between 10.6 and 13.7 mg g⁻¹ dry weight soil across the different treatments. The fertilisation and herbicide practices are described in Kramer et al. (2012).

2.2. Treatments and sampling

Within the maize and wheat strips experimental plots of 24 × 24 m each were established and assigned to four treatments with four replicates each: corn maize (CM), fodder maize (FM), wheat (W) and wheat with maize litter (WL). The CM and WL plots were amended with litter by application of hackled maize shoots (0.8 kg DW m⁻², C-content: 0.35 kg m⁻², C:N 18.4) on the soil surface on 27th of October 2009 and 1st of November 2010 each, whereas the FM and W plots received no litter.

Soil sampling was performed in summer on 23rd of July 2009 and 22nd of July 2010 (plant growth with highest root exudation), in autumn on 29th of September 2009 and 22nd of September 2010 (harvest with plant residues input), and in winter on 8th of December 2009 and 6th of December 2010 (fallow with

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