Soil Nematode Communities in Grasslands

Effects of Plant Species Identity and Diversity

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Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2007

Acta Universitatis Agriculturae Sueciae

2007: 48

Abstract

Viketoft, M. *Soil nematode communities in grasslands – effects of plant species identity and diversity*. Doctor's dissertation.
ISSN: 1652-6880, ISBN: 978-91-576-7347-3

This thesis summarizes the results of five studies investigating the effect of plant species on soil nematode communities in grasslands. Nematodes (roundworms) are ubiquitous members of the soil fauna and have been much used as indicators of soil conditions. Plants have the ability to affect soil organisms through structural modification of the soil habitat and through the quantity and quality of organic matter that is returned to soil, in the form of plant litter and root exudates.

The influence of grassland plant species on the soil nematode fauna was investigated in an experimental grassland, a glasshouse experiment and in a semi-natural grassland. Monocultures of 12 grassland plant species belonging to three plant functional groups, viz. grasses, legumes and non-leguminous forbs, were investigated in the field experiment and a subset of these in the other two systems. Plant species effects were common, for example, plant feeding and bacterial feeding nematodes responded positively to legumes and grasses, while forbs enhanced fungal feeding nematodes. Plant species identity appeared to be much more important than plant functional group for the nematode fauna. The effects of plants were quite consistent between field and glasshouse experiments.

The influence of plant species diversity and functional diversity on the nematode fauna was investigated in the experimental grassland. Plant species composition proved to be more important for soil nematode communities than any of the plant diversity measures, but the hypothesis that species or functional diversity of plants affect nematode diversity or composition could not be rejected. My results also suggest that plant species identity may be an important determinant of spatial structure in natural grasslands.

There was a succession of the nematode fauna during the eight years after establishment of the experimental grassland, especially indicated by the increase in maturity index of the nematode fauna. The results highlight the need for long-term experiments to reveal successional trends in soil nematode communities after cessation of agriculture. The increase of plant feeders with time, the slow colonization rate and the enhanced abundance of fungal feeders in soil under forbs have implications for nature restoration of former agricultural land.

Keywords: Nematoda, plant diversity, plant-soil relations, plant monoculture, nematode feeding groups, nematode community structure, plant species identity, rotifers, tardigrades

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Nematoder i gräsmarker
Effekter av växtart och växtdiversitet

Nematoder (rundmaskar) är sannolikt den individrikaste gruppen av flercelliga djur. På varje kvadratmeter mark kan det finnas miljontals nematoder. Dessa är viktiga för markprocesser som mineralisering och är en av de viktigaste djurgrupperna i markens näringsväv. I denna avhandling har jag undersökt hur växter påverkar nematoder. Jag har undersökt både effekten av växtart och av växtdiversitet i ett fältförsök, ett växthusförsök och i en naturlig betesmark.

Växter kan påverka markdjur genom att påverka mikroklimat, förändra strukturen i jorden och genom det organiska material som de tillför marken i form av förna och rotexudat. I mina studier, där jag som mest undersökt 12 olika växtarter, har jag funnit att det är vanligt med växtartseffekter på nematoder i gräsmarker. Typen av växtart påverkar nematodsamhällets sammansättning mer än diversiteten (antalet växtarter). Generellt fann jag att växt- och bakterieätande nematoder gynnades av förekomst av klöver och gräs, medan svampätande nematoder fanns i större antal under örter.

Innan fältförsöket anlades användes fältet för odling av främst korn. Efter etableringen av gräsmarken provtogs fältet vartannat år för att studera successionen i nematodfaunan. Efter åtta år hade de nematodarter som är beroende av mer stabila miljöer ökat i antal men endast någon enstaka nematodart hade tillkommit. Jag har sett att växtätande nematoder ökar i antal med tiden, att svampätare gynnas av örter och att koloniseringshastigheten är låg. Detta är av praktisk betydelse bland annat vid restaurering av före detta jordbruksmark till gräsmark. Mina resultat har bidragit till en ökad förståelse om hur olika organismgrupper ovan och i mark interagerar med varandra, att både diversitet och arttillhörighet av växter är av betydelse för markfauna och att rumsliga och tidsmässiga aspekter är viktiga för vår förståelse av de processer som styr organismsamhällens sammansättning.

Contents

Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Viketoft, M., Palmborg, C., Sohlenius, B., Huss-Danell, K. & Bengtsson, J. 2005. Plant species effects on soil nematode communities in experimental grasslands. *Applied Soil Ecology* 30, 90-103.

II. Viketoft, M., Bengtsson, J., Sohlenius, B., Berg, M.P., Petchey, O., Palmborg, C. & Huss-Danell, K. Long-term effects of plant diversity and composition on soil nematode communities in grasslands. (Manuscript)

III. Viketoft, M., Sohlenius, B., Boström, S., Palmborg, C., Bengtsson, J., Berg, M.P. & Huss-Danell, K. Temporal dynamics of soil nematode communities in a grassland plant diversity experiment. (Manuscript)

IV. Viketoft, M. Effects of six grassland plant species on soil nematodes: A glasshouse experiment. (Submitted manuscript)

V. Viketoft, M. 2007. Plant induced spatial distribution of nematodes in a semi-natural grassland. *Nematology* 9, 131-142.

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Introduction

There is an intimate link between soil organisms and the plant community (Bardgett, 2005). Plants affect the physical soil environment, provide carbon and other nutrients to the decomposer community and act as hosts for many soil organisms, such as herbivores, pathogens and symbionts. The most important way in which plants affect soil organisms is through their influence on the quantity and quality of organic matter that is returned to soil, in form of plant litter and root exudates. A framework for explaining how individual plant species affect soil food webs on the basis of plant ecophysiological traits has been suggested (Wardle, 2002, 2005). Plant species adapted to more fertile soils invest more in rapid growth than in secondary defence compounds, in comparison with plant species adapted to infertile conditions, and this may influence the relative importance of bacterial- vs. fungal-based channels in soil food webs. In addition to plant species identity, plant diversity may influence soil biota by creating a more heterogeneous set of substrates and also providing more microhabitats (Wardle & Van der Putten, 2002; Wardle, 2005).

Grasslands contain an abundant and diverse fauna above and below ground, and nematodes are among the most abundant organisms in grassland soils (Bardgett & Cook, 1998). Nematodes perform important functions in the soil, *e.g.* feeding on and dispersing both saprophytic, beneficial and pathogenic bacteria and fungi, as well as regulating the amount of inorganic nitrogen available to plants (Freckman & Caswell, 1985). They are one of the most important faunal components in soil food webs (De Ruiter, Griffiths & Moore, 2002). Very little is known about the specific effects of individual plant species in grasslands on the entire nematode fauna. Traditionally, most studies have focused on the plant feeding nematodes (Yeates, 1987; Verschoor, 2001). Therefore, I focused on the effect of plant species on the free-living nematodes in the soil in an ecosystem, grasslands, that has not been well studied in Sweden. I have used a combination of field and glasshouse experiments, and studies of a natural grassland. The nematode fauna has been investigated in soils that have been cultured by single grassland species for substantially longer time than other experimental studies on the effects of plants on soil biota.

Aims of the thesis

The aim of this thesis was to investigate the effect of grassland plant species and plant diversity on soil nematode communities. Firstly, the effect of individual grassland plant species on the nematode fauna was examined. This was done in an experimental grassland (Paper I), in a glasshouse experiment (Paper IV) and in a semi-natural grassland (Paper V). Most experimental studies focusing on effects of plants on soil nematode communities have been rather short term (1-3 years), but when I started my samplings the experimental grassland had been established for 7 growing seasons. Therefore, this already existing experiment provided a unique

opportunity to study nematode communities that had been under the influence of the same plant species for several years.

Secondly, the effect of plant diversity and species composition on total nematode abundance and the nematode community composition was also investigated (Papers II and III). Thirdly, the development of the nematode community over time from the 2nd to the end of the 8th growing season was examined in the experimental grassland (Paper III). This study could indicate the successional trends in the nematode fauna after cessation of agriculture, and also whether plant effects on soil fauna are more likely to be manifested in long-term studies than in short-term ones.

The different plant communities were expected to affect the nematode fauna and cause differences in community composition. The hypotheses were:

- Individual plant species differ in their effects on the total nematode abundance, the nematode community composition and the presence of individual nematode taxa.
- Plant species belonging to the same plant functional group (grasses, legumes, non-leguminous forbs) will have similar effects on the nematode fauna.
- An increased species or functional diversity of plants will affect nematode diversity positively, as well as influence nematode community composition.
- There will be a succession after cessation of agriculture towards a nematode fauna characteristic of natural grasslands, indicated by an increase in the maturity index and diversity, as well as in nematode taxa sensitive to disturbance.

Background

Nematodes

Nematodes (roundworms) are multicellular animals, which are found everywhere in the world, both in marine, freshwater and terrestrial habitats. In the soil, nematodes constitute a large part of the soil fauna and their numbers often reach several millions per m^2 of surface soil. Temperate grasslands and deciduous forests are ecosystems where high abundances of nematodes have been found (Sohlenius, 1980). Free-living nematodes in the soil have an average length of 1mm, and they move between soil particles or aggregates. Nematodes are essentially aquatic organisms and depend on waterfilms around particles for active movement. Plant parasitic nematodes frequently move more than 15 cm and sometimes up to 1 m in less than a month (reviewed by Robinson, 2004). The majority of nematodes are found within the top 10 cm of the soil, although some may be found much deeper (Yeates, Stannard & Barker, 1984). Because nematodes are so abundant and relatively easy to sample they have been much used as indicators of soil conditions (Ritz & Trudgill, 1999; Yeates, 1999; Ferris, Bongers & De Goede, 2001; Neher, 2001).

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Nematodes have a widely differing diet and therefore occupy several trophic levels in soil food webs. They can be grouped according to the type of food that they consume, based on the morphology of their mouthparts (Fig. 1). The most common groups are plant feeders, fungal feeders, bacterial feeders, omnivores and predatory nematodes (Yeates *et al.*, 1993). Plant feeders are characterised by a protrusible, hollow stylet that they use to penetrate the cell wall of plant cells to ingest the cell contents (Fig. 1a). Some of the plant-feeding nematodes cause great economic losses in agriculture.

Fungal-feeding nematodes also possess a stylet, but it is not as robust as in most plant feeders. These nematodes have the ability to control plant-pathogenic fungi but may also suppress mycorrhizal fungi, a disadvantage to the plants (Freckman & Caswell, 1985). Bacterial feeders have a tube-formed stoma (Fig. 1b) and draw bacterial suspensions into the alimentary canal by the sucking action of the esophagus. These nematodes may be beneficial as they stimulate mineralization by consuming and dispersing microorganisms (Ingham *et al.*, 1985). Bacterial-feeding nematodes may also have a beneficial effect on plant growth through consumption of plant-pathogenic bacteria but a negative effect through feeding on symbiotic rhizobia and benefical bacteria (Freckman & Caswell, 1985).
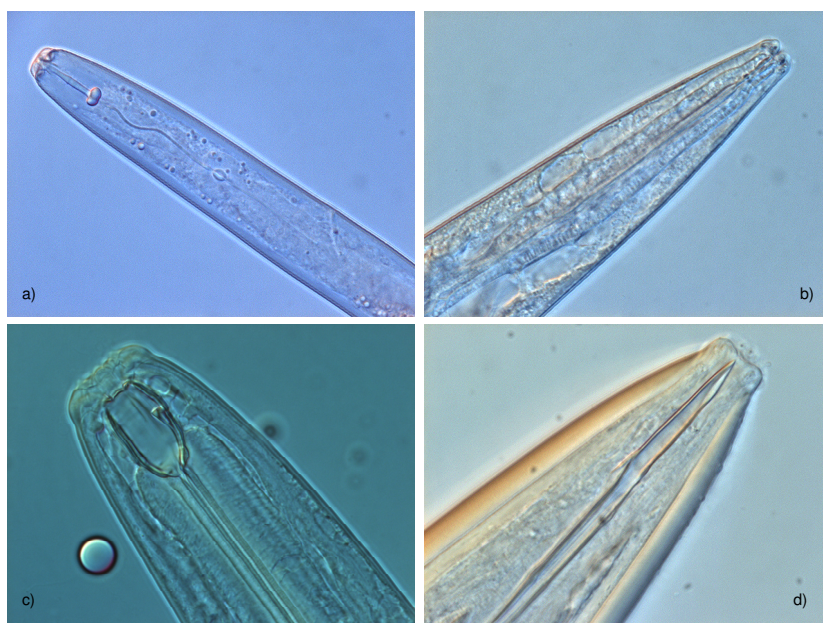

Fig. 1. Head region of a) a plant feeding nematode (*Pratylenchus*), b) a bacterial feeding nematode (*Acrobeloides*), c) a predatory nematode (*Coomansus parvus*) and d) an omnivore (*Dorylaimus stagnalis*). Photo: Hanny van Megen, Wageningen University.

Predaceous nematodes often possess a stylet, teeth, denticles (minute teeth) or various combinations of these. They feed on *e.g.* protozoa, rotifers, tardigrades and other nematodes. Predators that have one or several teeth (Fig. 1c) ingest their prey whole and use the teeth to tear the cuticula open. Predaceous nematodes that have a stylet feed much like the plant- and fungal feeders, piercing their prey and sucking out the contents. Omnivores can feed on a wide range of food sources, like algae, bacteria, fungi and other animals. They are characterised by a protrusible, hollow spear (Fig. 1d).

In addition to competing with other organisms in the soil, nematodes are attacked by both parasites and predators. Mites, tardigrades and oligochaetes predate on nematodes, but there are also nematode-trapping fungi and bacteria that produce toxins (Dindal, 1990).

Rotifers

Rotifers, as well as tardigrades (below), are also part of the soil microfauna and are obtained when extracting nematodes. Therefore these faunal groups were also examined in this thesis. Rotifers are predominantly freshwater inhabitants, and to occur in the soil they require a significant proportion of water film. However, they may be very abundant reaching densities up to 2 millions m^{-2}. Rotifers are about 200-500 μm and have a ciliated corona ("wheel organ") that functions both in locomotion and food gathering. Rotifers are primarily omnivorous, feeding on *e.g.* dead or decomposing organic material, bacteria and unicellular algae. In this thesis, rotifers were studied in Papers I and V, where the effect of plant species on their total abundance was investigated.

Tardigrades

Tardigrades occur in marine, freshwater and terrestrial habitats. They have four pairs of legs that all end in a set of claws, which make them look like teddy bears and hence their other name water bears. Tardigrades occur in the surface 1-2 cm of many soils and are particularly associated with mosses, lichens, liverworts and rosette angiosperms (Dindal, 1990). Tardigrades possess stylets that allow them to pierce plant cells or animal body cells, and they have an exceptional ability to survive extended periods of dehydration in a stage called anhydrobiosis, even if such conditions last for several years or decades. Tardigrades were studied in paper V, where the effect of plant species identity on their total abundance was examined.

Effects of plants on soil biota

Plants have the ability to affect the physical soil environment and thereby influence the microenvironment experienced by the soil organisms. Plant roots contribute to pore formation, in particular enlargement of existing pores (Angers & Caron, 1998). Larger nematode species that often are predators or omnivores and nematode species with head-ornaments both require larger pore spaces for their movement (Yeates, 1980; De Goede & Bongers, 1994; Ritz & Trudgill, 1999). Roots also play an important part in development of water-stable aggregates, *e.g.*

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through accumulation of inorganic chemicals at the root surface that act as cementing agents and through the structural support in aggregates of undecayed, senescent roots (Gregory, 2006). The uptake of water by plant roots makes the soil drier closer to the root (Young, 1998). Nematodes are living in the waterfilm in the soil and move actively in water films 2-5 µm thick (Anderson, 1988), but different nematode species react differently to soil moisture (Sohlenius, 1985; Bakonyi & Nagy, 2000).

Plants affect the amount and quality of resources that enter the soil system. The rhizosphere is the soil volume under the influence by roots. The plant can stimulate microbial growth in the rhizosphere because it releases organic material through sloughing-off of border cells, secretion of mucilage, root exudation and senescence of root epidermis (Nguyen, 2003). Different plant species promote different microbial communities, both in terms of microbial biomass and activity (Wheatley, Ritz & Griffiths, 1990; Bardgett *et al.*, 1999; Wardle *et al.*, 2003; Innes, Hobbs & Bardgett, 2004) as well as community composition (Grayston *et al.*, 1998; Marschner *et al.*, 2001; Smalla *et al.*, 2001; Kowalchuk *et al.*, 2002). Plants enhance different parts of the microbial community through chemotactic responses of some bacteria and antimicrobial exudates against others (Bais *et al.*, 2004). In addition, plant roots interact with microorganisms through competition for inorganic nutrients (Kaye & Hart, 1997). Therefore, plants can stimulate microbial activity through the supply of organic substrates, but at the same time limit microbially mediated processes through their depletion of nutrients (Van Veen, Merckx & Van de Geijn, 1989). However, the nitrogen fixation of atmospheric N_2 in legumes (Carlsson & Huss-Danell, 2003) leads to higher levels of inorganic nitrogen in the soil (Scherer-Lorenzen *et al.*, 2003; Palmborg *et al.*, 2005). This nitrogen is taken up by neighbouring plants (Mulder *et al.*, 2002; Paynel & Cliquet, 2003) and affects the bacterial community (Stephan, Meyer & Schmid, 2000).

Because plants affect the microbial community they should also be able to affect the bacterial-feeding fauna. Bacterivorous nematodes are affected by the rhizosphere with higher abundances than in the bulk soil (Griffiths, 1990; McSorley & Frederick, 1996). There are also differences in nematode numbers in soil under different plant species (Sohlenius, Boström & Sandor, 1987; Sohlenius & Sandor, 1987; Griffiths, 1990). Furthermore, different nematode species with the same feeding behaviour may react in different ways (Griffiths, Young & Boag, 1991; Yeates, 1999).

Plants may also differ in the quantity and quality of resources returned to soil by plant litter and especially plant quality is a major driver of decomposer invertebrate communities (Wardle *et al.*, 2006). Plants vary in chemical composition leading to their litter decomposing at different rates, and the nitrogen concentration is an important factor (Wardle, Bonner & Nicholson, 1997; Wardle *et al.*, 1998; Scherer-Lorenzen *et al.*, 2003). For example, early successional plants produce high-quality litter while plants that dominate late in the succession produce low-quality, phenolic-rich litter, resulting in a switch from dominance of bacteria to fungi as primary decomposers (Wardle, 2002; Bardgett, 2005).

The quality of plants as a food resource is naturally also important for plant-feeding nematodes (Verschoor *et al.*, 2001b). Among the nematodes, the plant feeders are the ones that are in the closest contact with plants and therefore they are directly affected by the plant and its roots (Cohn *et al.*, 1996; Yeates, 1999). Plant-feeding nematodes are attracted to roots (Prot, 1980) and they have a root-dependent vertical distribution in the soil (Verschoor *et al.*, 2001a). Some plant-feeding nematodes are highly specialised on a few host plants while others are more generalistic (Thies, Petersen & Barnes, 1995; Bell & Watson, 2001). In agricultural crops, susceptible plants may lead to nematodes increasing to high numbers while resistant plants lead to a reduction in nematode abundance (Yeates, 1987). Some plants have also been found to exert nematicidal effects (Khan, 1990; Akhtar, 1998; Oka *et al.*, 2000; Aballay, Flores & Insunza, 2001). Plant species also differ in their ability to support growth of nematophagous fungi that can be important for the control of *e.g.* root-knot nematodes (Bourne, Kerry & De Leij, 1996; Bourne & Kerry, 1999).

An effect of plant species on the soil nematode fauna has been found in natural ecosystems. For example, the type of ground cover vegetation affected the abundances of different nematode trophic groups in a Scots pine stand (Magnusson, 1983) and heather (*Calluna vulgaris*) was of great importance for the recovery of the nematode fauna after clear-cutting of a pine forest (Sohlenius, 1996). In grassland ecosystems some studies have investigated the effect of plant species on soil nematodes. Both glasshouse (Wardle *et al.*, 2003) and field experiments (Wardle *et al.*, 1999; Korthals *et al.*, 2001; De Deyn *et al.*, 2004) have been used in addition to sampling in natural grassland ecosystems (Porazinska *et al.*, 2003). In general, plant-feeding nematodes were the group most often and strongest affected by plant species, followed by bacterial-feeding nematodes.

Plant-soil feedbacks

Feedbacks describe a sequence of interactions in which the result of a process affects the conditions that initially generated the process (Ehrenfeld, Ravit & Elgersma, 2005). In the case of positive feedback, the soil community favours the plant species that produced the community, and in the case of negative feedback, the plant species that produced the soil conditions are disfavoured until it no longer has an effect on the soil community, causing it to increase and once again being disfavoured (Ehrenfeld, Ravit & Elgersma, 2005). Hence positive feedback is directional, whereas negative feedback is stabilizing. While there is substantial evidence that plants can affect microbial as well as faunal community composition (see above), there is less evidence for the following strong feedback links from soil to plants. However, in a pot experiment with four old-field perennial plants, Bever (1994) found that plants can culture a soil community that has strong negative effects specific to that plant type.

Most evidence for reciprocal plant-soil feedbacks comes from interactions between plants and their pathogens, parasites or herbivores. For example, in a set of pot experiments, Klironomos (2002) found that rare plants exhibited a relative

decrease in growth on 'home' soil in which pathogens had had a chance to accumulate, whereas invasive plants benefited from interactions with mycorrhizal fungi. In an experiment with two plants from a coastal foredune system, Van der Putten & Peters (1997) found that soil-borne pathogens of marram grass (*Ammophila arenaria*) may reduce the competitive ability of their host when grown in mixture with the immediate successor, *Festuca rubra*, and thereby enhance succession. In a grazed grassland with a mosaic of alternating dominance of *Festuca rubra* and *Carex arenaria*, Olff *et al.* (2000) found that soil-borne pathogens, *i.e.* plant-feeding nematodes, were responsible for the pattern, because *Carex* growth was strongly reduced at higher densities of plant feeders and *Festuca* may enhance nematode densities, while not being harmed by them. In the same ecosystem, Blomqvist *et al.* (2000) found that mounds created by yellow ants differed in physical and chemical conditions from the surroundings, and that these mounds affected the distribution of *Carex* and *Festuca* in the grassland. The mounds also affected the nematode community and this could contribute to the distribution of the two plant species. De Deyn *et al.* (2003) showed that the invertebrate soil fauna may enhance secondary succession and local plant species diversity through selective feeding on roots of dominant plants, thereby enhancing the relative abundance of subordinate plant species and also species from later successional stages.

The effects of plants on nematodes and the existence of plant-soil feedbacks suggests that plants may be a major determinant of spatial structure in soil communities by favouring or suppressing different species or groups (Olff *et al.*, 2000; Saetre & Bååth, 2000; Ettema & Wardle, 2002).

Effects of plant diversity

The effect of biodiversity on ecosystem processes, in particular plant productivity, in grassland ecosystems has been a much debated area of research for the last 15 years. The pioneering experiment was conducted in a system of controlled-environment chambers (the Ecotron) by Naeem *et al.* (1994), and after that others have followed (*e.g.* Tilman, Wedin & Knops, 1996; Tilman *et al.*, 1997). All these studies varied species richness by random draws from a pool of species, and their results have been criticized as being explained by the sampling effect, *i.e.* increased probability of including a species with dominant effect in larger groups of randomly selected species (Aarssen, 1997; Huston, 1997).

A later major international collaboration, the BIODEPTH project (BIODiversity and Ecological Processes in Terrestrial Herbaceous ecosystems) (Hector *et al.*, 1999; Minns *et al.*, 2001), included constrained random draws and all monoculture treatments to overcome some of the previous problems. However, the relative importance of overyielding (through resource use complementarity) versus sampling (selection) effect for the results remains uncertain (Huston *et al.*, 2000; Loreau & Hector, 2001; Hector *et al.*, 2002). Several, but not all, experiments using randomly assembled communities have found that primary production exhibits a positive relationship with plant species and functional-group diversity (Loreau *et al.*, 2001), but community composition is at least as important as species

or functional richness alone as predictors of ecosystem properties (Hector *et al.*, 1999; Hooper *et al.*, 2005).

A few studies with experimentally manipulated plant species diversity have found positive effects of plant diversity on soil microbial biomass (Spehn *et al.*, 2000; Zak *et al.*, 2003), microbial diversity (Stephan, Meyer & Schmid, 2000; Kowalchuk *et al.*, 2002) and fungal abundance (Zak *et al.*, 2003) but not fungal diversity (Waldrop *et al.*, 2006). However, in some cases the effects were attributed to the increases in plant production with increased plant diversity (Zak *et al.*, 2003).

Few effects of plant diversity have been found for soil fauna. The density and the biomass of earthworms has been shown to increase with increasing plant species diversity (Spehn *et al.*, 2000; Milcu *et al.*, 2006), soil mite diversity to increase as plant species number increased from 1 to 2 (St John, Wall & Behan-Pelletier, 2006), while different Collembola species have showed differing responses to plant and plant functional group diversity (Salamon *et al.*, 2004; Milcu *et al.*, 2006). For nematodes, De Deyn *et al.* (2004) showed that nematode taxonomic diversity was enhanced by plant species diversity. In addition, there was a positive relationship between the abundance of the dominant plant parasitic nematode, *Paratylenchus*, in the root zone of *Cirsium arvense* and the number of plant species per m^2 (Bezemer *et al.*, 2004). Nematode taxonomic richness and the Shannon diversity index were higher in a mixed species grass culture than in a cocksfoot grass monoculture (Wasilewska, 1995).

In the light of these conflicting studies of effects of plants species and diversity, I wanted to use an already existing long-term field experiment, semi-natural grasslands and glasshouse experiments to study the relationship between plants and soil organisms in more detail.

Materials and methods

Sites and treatments

Röbäcksdalen

Röbäcksdalen is an experimental grassland that is located at the experimental fields of the Swedish University of Agricultural Sciences in Umeå, northern Sweden (63º45'N, 20º17'E, 12 m above sea level) (Fig. 2a). This grassland was established in 1996 as part of the pan-European BIODEPTH-project (Hector *et al.*, 1999). Before establishment of the grassland, the field was mainly used for barley cultivation. The soil is classified as silt loam (4.1% clay, 57.9% silt, 38.0% fine sand). The experimental grassland consists of 72 plots, 2.2 m by 5.0 m, of which 60 is part of the diversity experiment and the rest are herbivory plots (not considered further in this thesis) (Fig. 2b). Two blocks were created because of the presence of a small height gradient. The diversity plots were planted with different

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a)

b)

Fig. 2. a) The BIODEPTH field-site in Röbäcksdalen, Umeå, Northern Sweden and b) the design of the field experiment. Numbers indicate the number of plant species in the diversity treatments and plots shaded in grey were included in the time-series. Plots without numbers were not sampled.

combinations of plant species, viz. 0, 1, 2, 4, 8 and 12 of the following twelve species: four grasses, *Dactylis glomerata* L., *Festuca ovina* L., *Phalaris arundinacea* L., *Phleum pratense* L., four legumes, *Lotus corniculatus* L., *Trifolium pratense* L., *Trifolium hybridum* L., *Trifolium repens* L., and four non-leguminous forbs, *Achillea millefolium* L., *Leucanthemum vulgare* Lam., *Ranunculus acris* L. and *Rumex acetosa* L.. These species were chosen because they are common in leys and semi-natural grasslands in Sweden. Between the plots, 1.5 m wide walkways were sown with *P. pratense* and cut regularly.

   In 2002, I sampled all of the monoculture plots (24 plots) (Paper I), and in 2003 all of the 60 diversity plots were sampled (Paper II). A subset of the plots in diversity treatment 1, 4 and 12 had previously been sampled by Jan Bengtsson and Matty Berg (in 1997), by Jan Bengtsson and Björn Sohlenius (in 1999) and by Björn Sohlenius (in 2001), and in combination with the 2003 sampling they constitute the time-series (Paper III).

Pustnäs

Pustnäs is part of a semi-natural grassland located along river Fyrisån south of Uppsala, in the middle of Sweden (59°48'N, 17°40'E) (Fig. 3). The soil is a silty clay loam and the vegetation is dominated by various types of grasses, *e.g. Agrostis* and *Festuca*, and flowering plants such as *Trifolium* spp., *Ranunculus* spp. and *Filipendula vulgaris*. Scattered in the grassland are bushes, *Juniperus communis* and *Rosa* sp. The site is grazed continuously by cattle throughout the growing season every year. In 2003, I took samples from patches of *Festuca ovina* and *Trifolium repens*, as well as random samples from the mixed vegetation (Paper V).

Fig. 3. The Pustnäs field site outside Uppsala in the middle of Sweden.

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Glasshouse

In 2005, I established a glasshouse experiment with 6 of the plant species grown in Röbäcksdalen, viz. *F. ovina*, *P. pratense*, *T. hybridum*, *T. repens*, *A. millefolium* and *R. acetosa* (Paper IV). These were the same plant species that were sampled as monocultures in the time series.

Sampling and identification

In the experimental and in the semi-natural grassland, soil samples were taken with a soil auger (diam. 2.3 cm) to a depth of 10 cm. In Röbäcksdalen six samples were taken in each plot while in Pustnäs two samples were taken at each sampling spot. In the experimental grassland, the samples were mainly taken during late summer (August to beginning of September). However, the monoculture plots were sampled an additional time in June and the semi-natural grassland was only sampled in June.

   In the glasshouse, soil samples were taken with a cork drill (diam. 1.5 cm) down to the sand in the bottom of the pots. The pots were sampled four times during the experiment (once every fourth week) and one sample from each pot was taken each time.

   The animals were extracted from a subsample of each core, with a modified Baermann method and treated as described in Sohlenius (1979). The total numbers of nematodes, rotifers and tardigrades in each sample were determined under low magnification (50x). For identification of nematode species or genera, the suspensions were examined under higher magnification (200x). A subset of the nematodes (100-400 depending on the study) was identified. The nematodes were placed into different feeding groups according to Yeates *et al.* (1993) and Sohlenius (2002). Nematodes feeding on epidermal cells or root-hairs were represented as plant-associated nematodes (Yeates, Wardle & Watson, 1993), giving the groups plant feeders, plant-associated nematodes, fungal feeders, bacterial feeders (further divided into Rhabditida r-selected, Rhabditida K-selected and Adenophorea in Papers II and III), omnivores and predators.

   In this thesis I have used the term nematode communities for the collection of nematode taxa found in my samples. I chose this definition although nematodes belong to different groups that interact rather than act as a functional unit.

Nematode community measures

Community parameters such as abundances of the different nematode feeding groups, abundances of individual species or genera, number of nematode taxa (S) and diversity indices were estimated. I used both Shannon's diversity index (H') and Simpson's diversity index (1-D), as well as Shannon's evenness measure (J') (Magurran, 2004).

Nematode indices were also calculated, *e.g.* the maturity index (MI) and the plant parasite index (PPI) (Bongers, 1990). MI is an ecological measure of disturbance that is based on placing non-plantfeeding nematode families into a colonizer-persister (c-p) scale, ranging from 1 to 5 (Bongers, 1990). Low c-p values are assigned to nematode families that have a short life-cycle, a high colonization ability and are tolerant to disturbances, and hence a high MI indicates a nematode fauna that is dependent on more stable environmental conditions. PPI is a maturity index exclusively for plant parasites and has been shown to be positively correlated with primary production (Bongers, 1990).

I also calculated the ratio of bacterial feeders to fungal feeders (B/F) (Paper V), another version of this ratio (B/(F+R) where R is the abundance of plant-associated nematodes) (Wasilewska, 1997) (Paper I) and the nematode channel ratio (NCR=B/(B+F)) (Yeates, 2003) (Papers II, III and IV). All these ratios are an evaluation of which decomposition pathway, fungal or bacterial, that is dominating. The second ratio (B/(F+R)) takes into account that plant-associated nematodes are partially fungivorous. In addition, the channel index (CI), enrichment index (EI) and structure index (SI) were also calculated (Ferris, Bongers & De Goede, 2001) (Paper V). The CI indicates the predominant decomposition pathway, like the indices above, the EI assesses food web response to available resources and the SI suggests the complexity of the food web.

Differences in community composition of nematodes between plant species and plant communities were analysed by ordination, using Principal Component Analysis (PCA) (Papers I, II, III and V). Renkonen's percentage similarity index (Paper I) was used to analyse community similarity between treatments.

Statistical analyses

The statistical procedure in Paper II follows the original BIODEPTH model (Spehn *et al.*, 2005) but for a single site. However, in Paper III I did not use this model because in the time-series only a subset of the diversity levels were sampled and it was not meaningful to test for linear effects when there were only three diversity levels. Hence I could use a simpler repeated mixed model (in SAS) that investigated the effect of plant diversity by comparing 1 vs. 4 vs. 12 plant species plots with estimate statements. For the other statistical methods, see the individual papers (I-V).

Results and discussion

Plant species effects

Effects of plant species on nematodes were common in the investigated grassland ecosystems (Table 1). The different nematode community measures are discussed more thoroughly in the following sections. The investigated plant species belonged

to three plant functional groups: grasses, legumes and non-leguminous forbs. My series of studies point towards the conclusion that it is better to use plant species identity rather than broadly defined plant functional groups when investigating the effect on the nematode fauna. For example, the two legumes, *T. repens* and *T. hybridum*, and the two forbs, *A. millefolium* and *R. acetosa*, had very different effects on the nematode communities where *T. repens* and *R. acetosa* supported high numbers of plant feeders while *T. hybridum* and *A. millefolium* did not. In paper III, we also used a new continuous measure of plant functional diversity, but the conclusion that plant species effects dominate still holds (see also below).

My results suggest that plant species identity may be an important determinant of spatial structure in nematode communities in natural grasslands (Paper V). In addition, accounting for differences in nematode species pool, the effects of plant species appear quite consistent between field and glasshouse experiments (Paper IV). This implicates that future results found in the glasshouse may be relevant for field conditions.

Table 1. *Plant species effects found on nematodes in the papers included in this thesis. n.d.=not determined*

| | Plant species effects | | | | |
	I	II [a]	III [a]	IV	V
Total nematode abundance	√	√	√	√	
No. nematode taxa				√	
Diversity indices	√	√		√	√
Evenness	√	√		√	
MI		n.d.	√		
PPI		n.d.	√		
Feeding groups	n.d.	√	√	√	√
B/F, NCR	√	√	√	√	√
Individual nematode taxa	√	n.d.	√	√	√
Species composition (Principal components)	√	√	√	n.d.	√

[a] Effect of plant community

Total abundances

The total abundance of nematodes was affected by plant species in the field (Paper I) and the glasshouse experiment (Paper IV) but not in the semi-natural grassland (Paper V). In both the former studies of plant monocultures, *T. repens*, *P. pratense* and *R. acetosa* had high abundances of nematodes (Fig. 4). In addition, *D. glomerata* and *L. corniculatus* in the experimental grassland and *F. ovina* in the glasshouse had high abundances of nematodes. Both in the field and the glasshouse experiment, the plant-feeding genus *Paratylenchus* (Fig. 5) dominated the nematode communities with the highest total abundance. In the semi-natural grassland, this genus did not dominate and no difference between the two plant species in total nematode abundance was found. Also, when *Paratylenchus* was excluded from the analysis the difference in total nematode abundance was no longer significant (Paper I). To conclude, the total abundance of nematodes alone

is not a useful measure for the effect of plant species on nematode communities. You also need to know which nematode species are present.
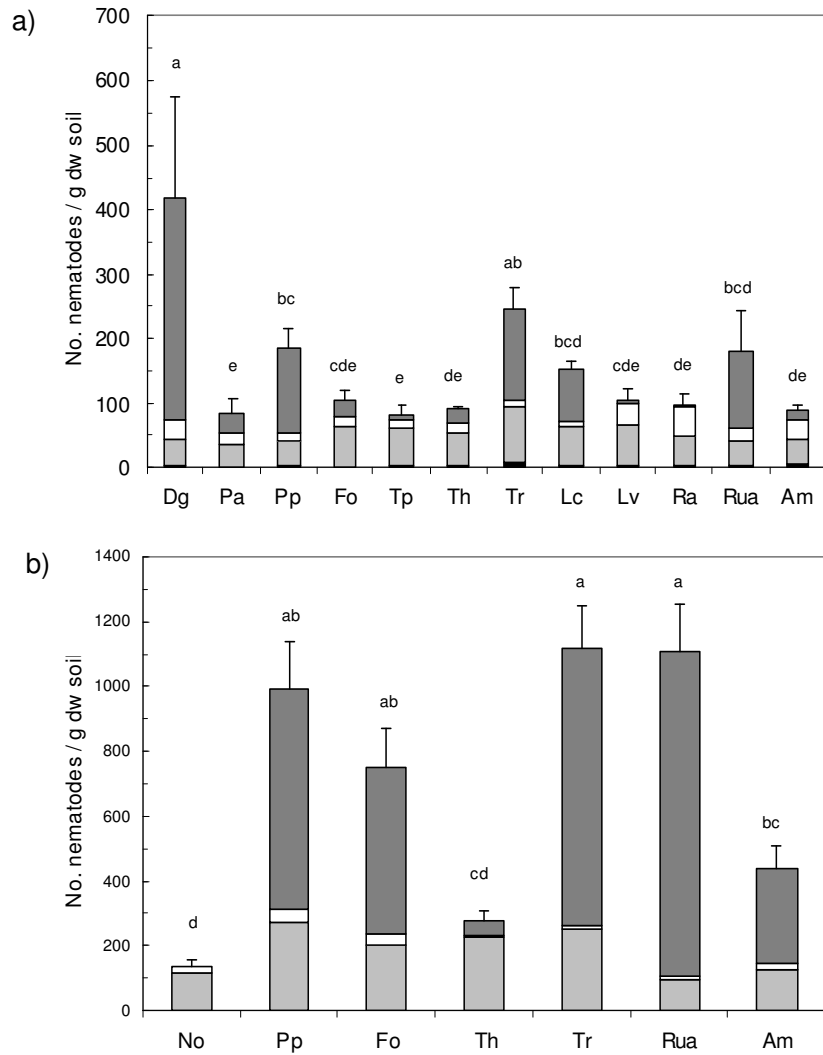

Fig. 4. Mean abundance (SE) of nematodes, divided into different nematode feeding groups (black, omnivores; light grey, bacterial feeders; white, fungal feeders/plant-associated nematodes; dark grey, plant feeders) in the experimental grassland (n=4, 2 in June and 2 in September) a) and in the final sampling in the glasshouse experiment (n=10) b). Different letters indicate significant differences in mean abundance among plant species. Dg, *Dactylis glomerata*; Pa, *Phalaris arundinacea*; Pp, *Phleum pratense*; Fo, *Festuca ovina*; Tp, *Trifolium pratense*; Th, *Trifolium hybridum*; Tr, *Trifolium repens*; Lc, *Lotus corniculatus*; Lv, *Leucanthemum vulgare*; Ra, *Ranunculus acris*; Rua, *Rumex acetosa*, Am, *Achillea millefolium*, No, no plants.
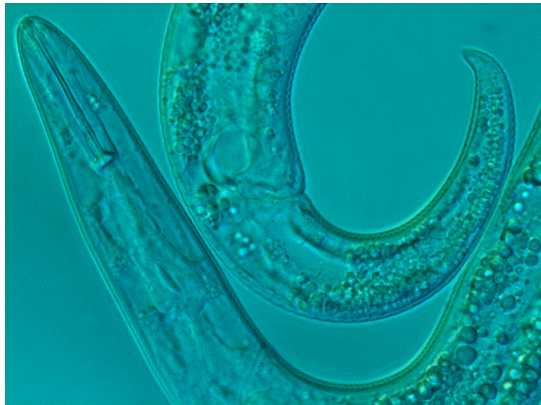
20

Fig. 5. Paratylenchus, the dominating nematode genus in the studies in this thesis. Photo: Hanny van Megen, Wageningen University.

The rotifer abundance was affected by plant species both in the experimental (Paper I) (Fig. 6) and the semi-natural grassland (Paper V). However, it is difficult to draw any firm conclusions because only two plant species were investigated in the semi-natural grassland and *R. acetosa* that supported the greatest numbers in the field experiment was not one of them. In addition, it is possible that the results obtained in these studies merely reflect the rotifers' dependence on soil moisture (Moorhead *et al.*, 2003). Both studies that showed an effect of plant species on rotifer abundance were sampled in spring (June), when soil moisture generally is higher, and *T. repens* that had the greatest abundance of rotifers in the semi-natural grassland is intolerant to drought (Grime, Hodgson & Hunt, 1988). The abundance of tardigrades was only analysed in the semi-natural grassland (Paper V). It was in general low and not affected by plant species.
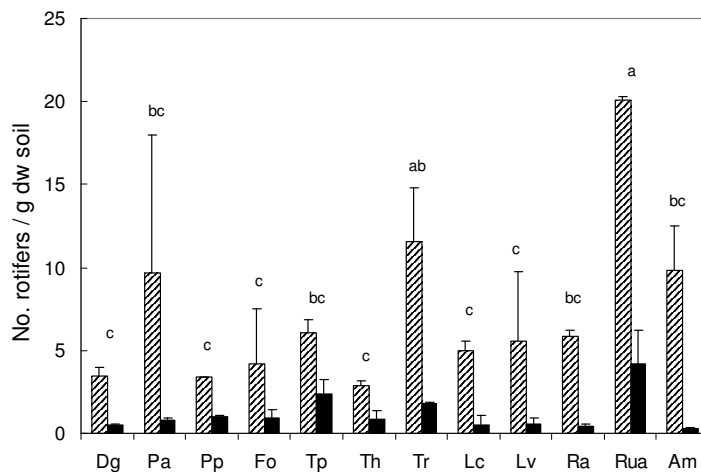

Fig. 6. Mean abundance (SE) of rotifers in the experimental grassland in June (striped bars) and September (black bars). Plant species abbreviations as in Fig. 4. Different letters indicate significant differences among plant species across season.

Diversity and community composition

The number of nematode taxa was in general not affected by plant species, except at one sampling in the glasshouse experiment (Paper IV). However, the different diversity indices were affected by plant species (Papers I, IV and V). Among the plant species investigated in more than one study, *A. millefolium* seems to support a diverse nematode fauna in comparison with the other plant species. However, the plant species with the most diverse communities in the field experiment, *T. pratense*, were not included in the other studies. The evenness index was affected by plant species in the field and the glasshouse experiment, but not in the semi-natural grassland. Again, it is probably the dominance of the genus *Paratylenchus* that is the reason for this result.

The maturity index (MI) and the plant parasite index (PPI) were only affected by plant species in the temporal study (Paper III). The MI was developed to be a measure for disturbance, and has been shown to be a sensitive indicator of decreasing human intervention in agroecosystems (Freckman & Ettema, 1993) and for measuring pollution-induced stress, especially by heavy metals (*e.g.* Korthals *et al.*, 1996; Yeates & Bongers, 1999). In the time-series (Paper III), the presence of forbs resulted in greater MI while presence of legumes lowered it. Legumes are often abundant early in succession, while forbs are favoured by long-term grazing or cutting. It is possible that the consecutive samplings were necessary to be able to reveal these effects of plant species on the MI, which are separate from and possibly confounding effects of time since disturbance events.

The different ratios between bacterial feeders and fungal feeders that were used were affected by plant species in all studies. In general, forbs seemed to increase the abundance of fungal feeders compared to bacterial feeders in the different studies. Also the abundances of the other feeding groups were affected by plant species. Rhabditida r-selected bacterial feeders were more common under legumes. This is also supported by the literature (*e.g.* Sohlenius, Boström & Sandor, 1987; Sohlenius, 1990). In addition, plant feeders seemed to be positively affected by the presence of grasses and legumes, and negatively by the presence of forbs.

Responses of individual nematode genera

The effect of plant species was also evident when examining individual nematode taxa (in most cases genera). Principal Component Analysis (PCA) based on the abundances of individual taxa was able to separate the different plant species in monoculture (Fig. 7). Plant- and bacterial-feeding genera responded most markedly to the investigated plant species. The three plant feeding genera preferred different plant species depending on which were included in respective study. Some plant species, *i.e. T. pratense, T. hybridum, L. vulgare, R. acris* and *A. millefolium*, had very low abundances of plant-feeding nematodes (especially *Paratylenchus*). It is possible that these plants species are of low plant quality for nematodes or that there are defence compounds in the roots (Van Der Putten, 2003).
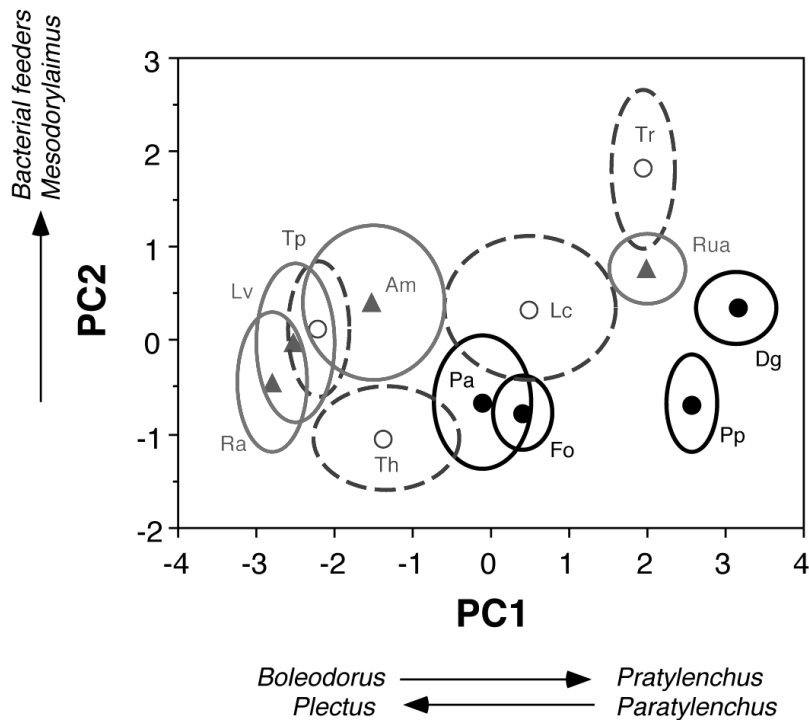
Fig. 7. A principal component analysis of nematode communities under monocultures of 12 different plant species, belonging to three plant functional groups (grasses, solid circles; legumes, open circles; forbs, triangles). Points represent means and the circle around each point represent standard error (n=4). PC1 and PC2 together explained 51% of the variation in the data. Plant species abbreviations as in Fig. 4.

The dominating bacterial feeder, *Acrobeloides*, reached high abundance under *F. ovina* in all the studies. Most other bacterial feeders preferred the legume *T. repens*, except *Acrobeles,* which tended to occur with greatest abundance under *R. acetosa*. A relative to this plant species, *Rumex acetosella*, exudes oxalic acid (Schöttelndreier *et al.*, 2001) and it is possible that this affects the composition of the microbial community (Johnson *et al.*, 2003; Marschner, Crowley & Yang, 2004).

Effects of plant diversity

There were few effects of plant diversity on the nematode fauna. The number of nematode taxa tended to be positively related to plant species richness in the field experiment (Paper II) (Fig. 8) and was correlated with the number of plant species in the random samples in the semi-natural grassland (Paper V). In addition, variation in nematode communities described by the third principal component was related to plant functional diversity, using a new and improved version of a continuous measure of functional diversity (Paper II). Total abundance of nematodes, and some of the feeding groups differed among the diversity treatments

in the time-series (Paper III). Plant feeders and plant-associated nematodes were more abundant in plots with 12 plant species, while omnivores/predators were less abundant in the 4 species plots. However, in the experimental grassland the effect of plant species richness could largely be explained by the presence of the legume *T. pratense* (Fig. 8). Because it is more likely that this plant species is present in plots with more plant species, one likely explanation for the relationship is the selection probability or sampling effect (Loreau & Hector, 2001; Wardle, 2002).

To conclude, plant species composition was more important for soil nematode communities than any of the plant diversity measures. This conclusion is also supported by other studies (De Deyn *et al.*, 2004; Wardle, 2005).
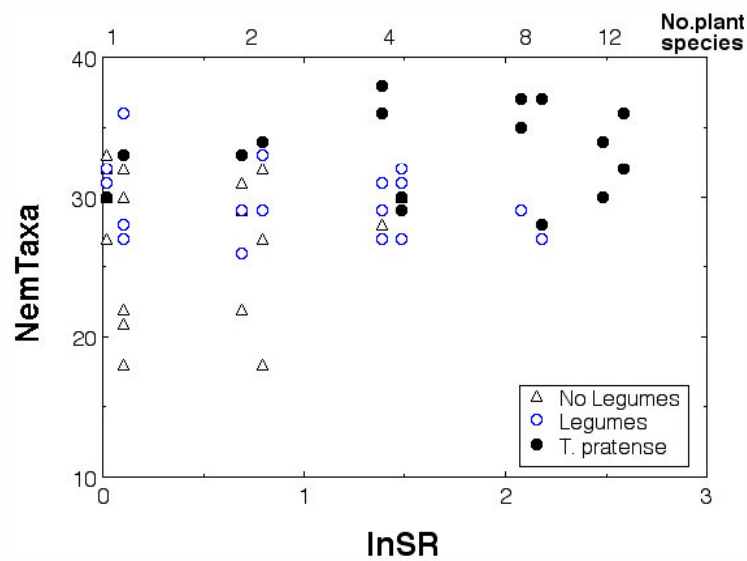

Fig. *8.* Plant diversity (ln SR) and nematode diversity (Nem Taxa) were positively related to each other (r=0.284, p=0.03, n=58). The effect was mainly driven by the presence of the legume *Trifolium pratense* in plots with high plant diversity (plots with and without *T. pratense* and legumes indicated; plots in block 2 have been displaced to the right).

Effects of time

Seasonal variation

The monoculture plots were sampled both in June and September and therefore give some information about seasonal variation in the nematode communities (Paper I). All diversity and community indices except total nematode abundance and PPI were affected by season, as well as a majority of the individual nematode genera. All indices and about two thirds of the individual genera abundances were higher in June than in September. The greater abundance of the bacterial feeder *Prismatolaimus* in June probably reflects the higher soil moisture in this month,

because this genus also occurs in fresh water (Bongers, 1988). On the other hand, the greater occurrence of plant feeders in September is probably a response to the presence and growth of plants during the growing season.

Succession

Prior to the establishment of the experimental grassland, the field site had been used for agriculture for at least 35 years. Therefore the time-series in Paper III reflects the successional trends after cessation of agriculture. The total nematode abundance increased significantly in 2003 (year 8) (Fig. 9) and plant feeders and Adenophorea bacterial feeders showed increasing trends with time, while Rhabditida r-selected bacterial feeders decreased. All in all, the nematode communities under almost all plant treatments moved in the same direction but they seemed to diverge with time (Fig. 10). Because the nematode communities were still changing between year 6 and 8, it would have been interesting to follow the plots further in time. The maturity index (MI) also increased with time, indicating the start of a development towards a nematode fauna characteristic of more stable environmental conditions.
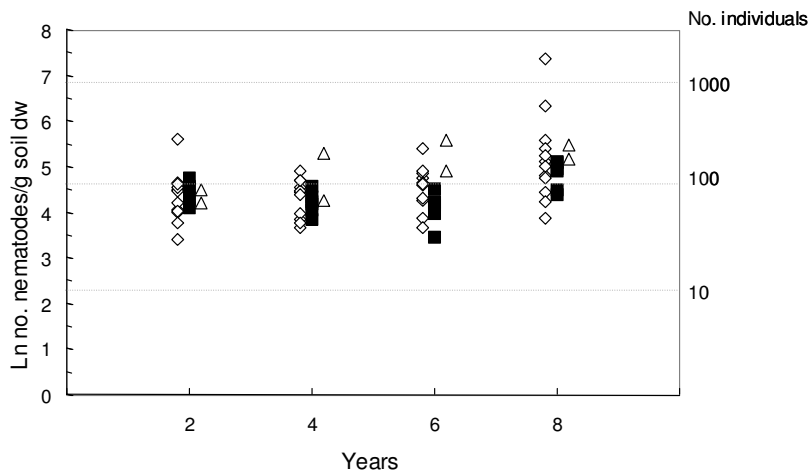

Fig. 9. Total abundance of nematodes (ln No./g soil dw) over time in soil under different plant diversity treatments: 1 (◊), 4 (■), and 12 (∆) plant species. Plots with monocultures have been displaced to the left, and plots with 12 plant species have been displaced to the right.
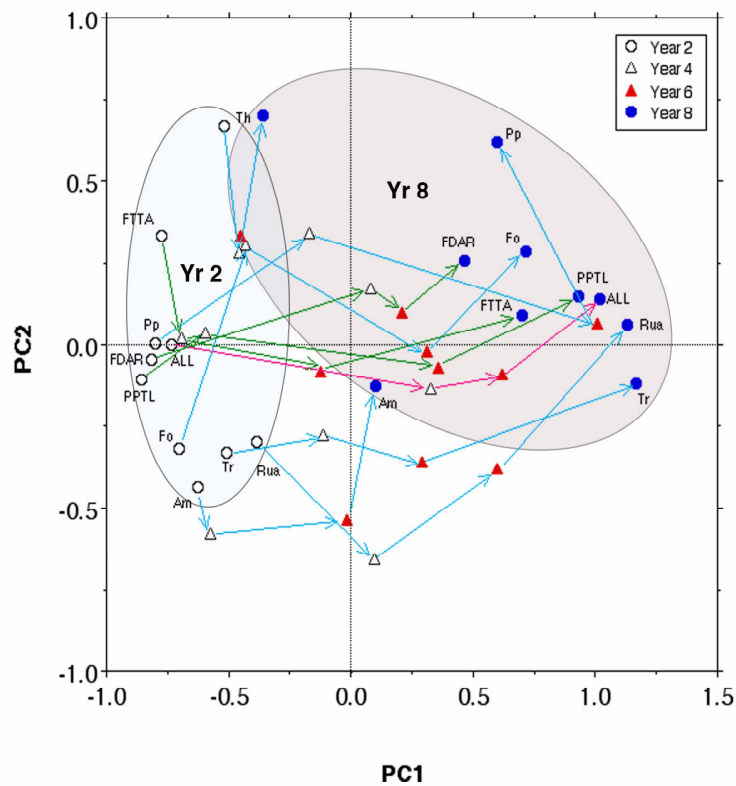
Fig. 10. PCA plot of the community composition of nematodes in different plant diversity treatments in 1997 (year 2), 1999 (year 4), 2001 (year 6) and 2003 (year 8). Means are given, n=2. Arrows have been drawn between consecutive years for each plant treatment. All treatments year 2 and year 8 are encircled. Abbreviations for monoculture plant treatment as in Fig. 4; DFAR, *D. glomerata*, *F. ovina*, *A. millefolium*, *R. acetosa*; FTTA, *F. ovina*, *T. hybridum*, *T. repens*, *A. millefolium*; PPLT, *P. arundinacea*, *P. pratense*, *L. corniculatus*, *T. pratense*; ALL, all 12 plant species.

A different way to look at the development of the nematode fauna over time is to compare the glasshouse experiment, the monoculture plots in Röbäcksdalen and the semi-natural grassland (Table 2). The glasshouse experiment is an artificial environment due to the defaunation at the start of the experiment, *i.e.* absence of other soil fauna and effects of the inoculate preparation and application on the nematodes, compared to the soil in the other two studies. The monoculture plots had been cultured by the plant species for seven years, while the semi-natural grassland has been a grassland for a much longer time period. With time the nematode abundance decreased, while the number of taxa as well as the diversity and maturity indices increased (Table 2). In addition, in Pustnäs, the semi-natural grassland, plant feeders were not as dominant as in the other studies and the proportions of the other feeding groups were higher. Strong dominance of plant

feeders, in particular *Paratylenchus*, in year 8 in the diversity experiment is probably the reason for the differing result between the time-series and this comparison. In the time-series, there was a decrease in diversity and an increase in total nematode abundance with time.

The number of taxa was clearly higher in the semi-natural grassland (Table 2). The number of nematode taxa in the experimental grassland is dependent on the species pool at the time of establishment of the experiment and dispersal into the field from the surroundings. Nematodes can be passively dispersed by wind and insect phoresis, but transport by other organisms such as earthworms, birds and humans are also important (Ettema, 1998). However, colonization may take decades (Wasilewska, 1997; Hedlund *et al.*, 2004). In addition, the distribution of nematodes may be restricted by climate. In a soil transplantation experiment, Sohlenius & Boström (1999a) found indications that some nematodes are sensitive to cold conditions, and that there was a tendency for more taxa migrating into the transplanted blocks at the more southern sites (Sohlenius & Boström, 1999b). The question therefore is if it actually is relevant to compare the field experiment with the results from Pustnäs. Ideally I should have investigated a natural grassland in Umeå, to really know the available species pool.

Table 2. *Comparison between the glasshouse experiment (the final sampling, n=70) (Paper IV), the monoculture plots in Röbäcksdalen (n=48) (Paper III) and the semi-natural grassland, Pustnäs (n=40) (Paper V). Means (SE) and percent of total abundance are given. The abundances are expressed as No. g^{-1} dw soil*

	Glasshouse	%	Röbäcksdalen	%	Pustnäs	%
Nematode abundance	689.0 (59.4)		152.5 (19.0)		82.5 (4.1)	
Total no. nematode taxa	17		40		97	
Shannon diversity index (H')	0.62 (0.03)		1.79 (0.07)		2.61 (0.04)	
MI	2.01 (0.004)		2.29 (0.03)		2.47 (0.04)	
Plant-feeding	483.2 (57.1)	70	77.0 (18.7)	50	20.6 (2.5)	25
Plant-associated	1.4 (0.9)	0.2	13.8 (1.6)	9	11.8 (1.3)	14
Fungal-feeding	19.6 (3.4)	3	6.5 (1.0)	4	10.8 (1.2)	13
Bacterial-feeding	184.7 (11.0)	27	51.9 (3.8)	34	34.4 (1.9)	42
Omnivores/predators	-	-	3.1 (0.4)	2	4.9 (0.3)	6

The studies in this thesis have focused on the effects of plants on soil nematodes, which is the first part of the plant-soil feedback loop (Ehrenfeld, Ravit & Elgersma, 2005). Although the other part of the loop was not directly studied, the observed results may have some implications. Increases of plant pathogens under particular plant species over time, is an example of negative feedback (Ehrenfeld, Ravit & Elgersma, 2005; Van der Putten, 2005). Because plant feeders became dominant some years after cessation of agriculture, the coming development and succession of the vegetation might be affected (*e.g.* De Deyn *et al.*, 2003). In addition,

organisms in the fungal pathway are considered to be less resistant to disturbance (Hedlund *et al.*, 2004) and my results suggests that planting of forbs may enhance these organisms. This thesis also demonstrates that colonization of grassland nematodes after cessation of agricultural management is rather slow. These results are important when considering the restoration of former agricultural land into grasslands.

Conclusions

My thesis demonstrates that plant species do indeed influence the nematode fauna in grassland ecosystems. In relation to the initial hypotheses it can be concluded that:

- Plant species effects on the soil nematode fauna were commonly found in the investigated grasslands. Effects were found on total nematode abundance, nematode community composition as well as on abundances of individual nematode taxa. The results indicate a need to identify nematodes at least to the genus level to be able to find plant species specific effects, and to be able to explain the effects found, as shown by the correlation between total nematode abundance and the abundance of the plant feeder *Paratylenchus* in some of these studies. However, some effects are observed when using feeding groups, but others are masked by the diverging behaviour of genera allocated to the same feeding group, *e.g.* among the bacterial feeders.

- In several cases, plant species belonging to the same plant functional group did not affect the nematode communities in similar ways. Therefore, plant species identity is much more relevant than plant functional group when investigating the effect on the nematode fauna.

- Plant species composition is more important for soil nematode communities than any of the plant diversity measures. However, the hypothesis that species or functional diversity of plants will affect nematode diversity or composition could not be rejected. My results also suggest that plant species identity may be an important determinant of spatial structure in nematode communities.

- There was a development of the nematode fauna with time in the field experiment, *i.e.* a succession, especially indicated by the increase in the maturity index. However, a comparison with the semi-natural grassland suggests that the impoverished species pool at the experimental site, because of a long period of agricultural practices, might result in a slow rate of successional change towards a nematode community characteristic of natural grasslands. Our results highlight the need for long-term

experiments to reveal successional trends in soil nematode communities after cessation of agriculture.

As this thesis shows, plant species affect the nematode fauna. However, it is more difficult to say what the causes are for the observed differences in nematode communities among the plant species. Several different possible mechanisms are at work simultaneously. For example, effects on pathogenic nematodes are a result of specific host-pathogen relationships, while effects on other groups, like bacterial feeders, are due to exudate and litter effects mediated by less specific food web interactions. Future studies may be able to elucidate the reasons for the plant species specific effects among plant species and find the explanations for the high species richness of nematodes in grasslands.

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Acknowledgements/Tack

Först och främst vill jag tacka min huvudhandledare Janne Bengtsson. Utan dig hade jag aldrig intresserad mig för dessa djur. Tack för din vägledning, din uppmuntran, för att du alltid har tagit dig tid för en ibland förvirrad doktorand och för att du trott på mig!

Jag vill också tacka mina biträdande handledare, Björn Sohlenius och Cissi Palmborg för all hjälp och stöd. Björn, för att du har lärt upp mig om nematoder och alltid tagit dig tid att svara på mina frågor, vare sig det handlar om nematoder, manuskript eller annat. Cissi, tack för idéer, konstruktiv kritik och för trevligt sällskap vid mina besök i Umeå.

Ett speciellt tack till Bengt Eriksson för din uppmuntran, ditt stöd och för din tro på mig.

Tack till alla på avd. för evertebratzoologi på Naturhistoriska riksmuseet för intressanta diskussioner och trevlig gemenskap i en inspirerande miljö.

Tack till alla som har hjälpt mig med fältprovtagningar, nematodutdrivningar, nematodräkning mm. Utan er hade det varit både jobbigare och betydligt tråkigare. Speciellt tack till Stina, Jan-Olof P, Calle Å, Per N, Lena, Anna-Karin W och Berit som har hjälpt till med praktiska detaljer och fått allt att fungera. Tack till Dietrich von Rosen, Birgitta Vegerfors-Persson och Ulf Olsson för statistisk hjälp. I would like to thanks Andy Hector, Bernhard Schmid and Luca Walker for statistical advice on the BIODEPTH model, and Hanny van Megen for the pictures of the nematodes.

Jag vill tacka alla kollegor, både gamla och nya, för trevlig samvaro vid fika- och lunchborden. Särskilt vill jag tacka Odlingslandskapets ekologi för gemenskap och inspiration. Extra mycket tack till alla markekologer för trevliga kurser, intressanta diskussioner och trevlig samvaro.

Tack till alla doktorandkollegor som har förgyllt min vardag. Ett speciellt varmt tack till Hanna för all hjälp med stort som smått, Kalle P för trevligt rumssällskap de första åren, Johan för trevligt rumssällskap de sista åren och för att du ser till att alla trivs, Erik för ditt glada humör och ditt uppmuntrande sätt och Eva B. för din optimism. Many thanks to all PhD students for fellowship and company.

Ett stort tack till min familj som alltid har stöttat mig. Speciellt tack till min egna lilla familj. Till Arvid för att du har gett mig ett nytt perspektiv på livet sedan du kom. En kram från dig när man kommer hem gör att alla bekymmer försvinner! Jakob, för att du alltid funnits där och trott mer på mig än vad jag har gjort själv. Du betyder allt för mig!