



Multiple species-specific controls of root-feeding nematodes in natural soils

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ABSTRACT

One of the major limitations to enhance sustainability of crop production systems is the inability to control root-feeding nematodes without using chemical biocides. In soils under wild vegetation, however, root-feeding nematodes affect plant performance and plant community composition varying from substantially to insignificantly. Previous studies in natural ecosystems have already shown that mutualistic symbionts, such as arbuscular mycorrhizal fungi and endophytes, may influence plant exposure to root-feeding nematodes. In order to learn more from natural systems, we examined nematode control in the root zone of a wild coastal foredune grass by microorganisms, other nematodes and microarthropods. We cultured all eight root-feeding nematode species that occur in the root zone of marram grass (*Ammophila arenaria*) in coastal foredunes of the Netherlands. Then, in an indoor growth experiment we exposed each nematode species to the potential natural antagonists collected from the same dune soil. Most of the eight dominant root-feeding nematode species could be controlled to some extent by more than one group of soil organisms added. The effectiveness of control varied among nematode species, which seemed to be controlled in a species-specific way. We conclude that in a natural soil the effectiveness of control by microorganisms, other nematodes or microarthropods varies among root-feeding nematode species. Most are controlled, at least to some extent, by soil microbes. However, some root-feeding nematode species are controlled only by microarthropods. Our results strongly suggest that sustainable agriculture will benefit from using a range of biological control mechanisms when controlling root-feeding nematodes, rather than relying on single control agents. Our suggestion also implies that conserving soil biodiversity is crucial in order to enhance the reliability of biological crop protection against soil-borne pests and diseases.

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1. Introduction

Belowground herbivores have a profound influence on the productivity and species composition of plant communities (Gange and Brown, 1989, 2002; de Deyn et al., 2003; Wäckers and Bezemer, 2003). The majority of belowground herbivores are root-feeding nematodes and insect larvae (Gange and Brown, 2002). Plant roots are a resource that a range of nematodes can utilize (Yeates, 1987). In some grassland ecosystems, nematodes are the dominant herbivores (Ingham and Detling, 1986). Most information on root-feeding nematodes, however, stems from agricultural systems, where root-feeding nematodes are notorious pests (Freckman and Caswell, 1985). Because chemical control of nematodes involves the use of persistent broad-activity chemicals, nematode control may disrupt complete soil food webs. Therefore, many efforts have been spent to improve biological control (Rodriguez Kabana, 1991; Kerry and Gowen, 1995). However, the results of biological control are notoriously unpredictable and most efforts have been dedicated to

a limited subset of nematodes, whereas solving one nematode problem often creates another one (Barker and Koening, 1998). Therefore, in order to enhance the sustainability of crop production methods, studying nematode control in nature may serve to ultimately enhance effectiveness of nematode control in agriculture (van der Putten et al., 2006).

Root-feeding nematodes have been estimated to take up as much as one quarter of the net primary production in prairie grasslands (Stanton, 1988). When present at low amounts, however, root-feeding nematodes may increase the allocation of assimilated carbon to roots, leading to increased root exudation and microbial activity in the rhizosphere (Bardgett et al., 1999). In that case, root-feeding nematodes may even enhance plant productivity through their positive feedback effects on plant nutrition. Opposite to prairie grasslands, the abundance of root-feeding nematodes in coastal foredunes appears too low to account for any plant growth reduction (de Rooij van der Goes, 1995). Some factors have been suggested as controlling root-feeding nematodes, such as competition (Brinkman et al., 2005b), arbuscular mycorrhizal fungi (de la Peña et al., 2006) endophytic fungi (Hol et al., 2007) and bottom-up control by the plant (van der Stoel et al., 2006). Whereas these

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processes are mainly driven by limitation of resource availability (so-called bottom-up and horizontal interactions), nematodes may also be controlled by predatory or parasitic soil organisms (Kerry and Hominick, 2002). These so-called top-down effects are caused by soil microorganisms, carnivorous nematodes, microarthropods and tardigrades. To date, no study has attempted to analyze a variety of potential factors involved in root herbivore control in a comparative way including a range of root-feeding nematode species.

Soil organisms play an important role in soil suppressiveness against plant diseases. What exactly makes soils suppressive to soil-borne pathogens has been an objective of many studies (Jaffee, 1993; Mazzola, 2002; Termorshuizen et al., 2006). Most studies conclude that soil suppressiveness is caused by the interactions between soil-borne pathogens and soil microorganisms (Alabouvette, 1999; Weller et al., 2002). The majority of studies have examined soil suppressiveness against fungal diseases (Alabouvette et al., 1993; Amir and Alabouvette, 1993; Postma et al., 2005; Heyman et al., 2007), whereas relatively few studies have examined suppressiveness against root-feeding nematodes. Nematode suppression may be caused, similarly as for fungi, by soil microorganisms (Dicklow et al., 1993; Kluepfel et al., 1993; Esnard et al., 1995; Kerry, 2000). All these studies are based on agricultural systems, whereas very few studies have examined pathogen or nematode suppression in natural soils (van der Putten et al., 2006). Natural coastal dune soil, which has become a model for studying plant-soil pathogen interactions, is suppressive to fungal pathogens due the anti-fungal compounds produced by the microorganisms (de Boer et al., 1998, 2003), as well as to root-feeding nematodes, although these mechanisms are less well known.

The root zone of the wild coastal foredune grass *Ammophila arenaria* contains a wide range of different nematode feeding types, including ectoparasites that feed on the outer cortical cell layers and root hairs, semi-endoparasites, migratory endoparasites, as well as sedentary endoparasites that establish a feeding site to which females get attached in order to complete their life cycle (van der Putten and van der Stoel, 1998). In the present study, we explore the potential contribution of soil microorganisms, the whole nematode community and microarthropods to top-down control of all eight major root-feeding nematodes that co-occur on *A. arenaria* roots in the central part of its native range (van der Putten et al., 2005). The aim of our study was to determine to what extent different nematode species are potentially controlled by various groups of soil organisms (microorganisms, nematodes and microarthropods).

Six of the root-feeding nematode species were ectoparasites, which feed on outer cortical cell layers from the outside of the roots. These ectoparasitic root-feeding nematodes are considered to be feeding generalists (Yeates et al., 1993; van der Putten et al., 2005). Two other species were endoparasitic nematodes, which are feeding specialists. One of the endoparasites is a migratory endoparasite, which is less specialized than the other one, which is sedentary during the reproductive part of its life cycle. We extracted microorganisms, nematodes and microarthropods from non-sterile dune soil by wet sieving and elutriation. Subsequently we inoculated the microorganisms, nematodes and microarthropods into the root zone of *A. arenaria* plants that were obtained from seeds and grown in previously sterilized dune soil to which the different root-feeding nematode species had been added, species by species. The effects of adding the various soil organisms on nematode abundance and plant biomass were determined at the end of the experiment.

Our null hypotheses was that there were (a) no differences in top-down control among the root-feeding nematode species and (b) no differences in nematode control between the microorganisms, the full community of nematodes and the microarthropods.

These hypotheses would be rejected when (a) finding differences between nematode species and (b) between microorganisms, the full nematode community and the microarthropods in reducing nematode abundance when compared to controls with root-feeding nematodes only. Alternatively, we hypothesized that root-feeding nematode species are controlled in a species-specific way. This alternative hypothesis would be supported when control effects of microorganisms, the full nematode community and the microarthropods differ among the nematode species. We studied effects of root-feeding nematodes and their controls on biomass production of *A. arenaria* by comparing biomass between the various inoculation treatments and a non-inoculated control. Finally, we produced an overview of all knowledge on nematode control factors in the root zone of the grass *A. arenaria* to discuss our results and those of previous studies in relation to the question how root-feeding nematodes are controlled in the root zone of a non-cultivated grass. We also discuss our results in relation to the potential importance of soil biodiversity in agricultural soils for sustainable crop protection against root-feeding nematodes and other soil-borne pests and diseases.

2. Materials and methods

2.1. Soil, plants, nematodes and potential control organisms

Soil was collected from the mobile foredunes of Voorne, the Netherlands (51°55' N, 04°05' E) at peak growing season. The samples were collected from ten points parallel to the beach and 50 m apart from each other. At each sampling point, 50 kg of soil was collected from the youngest root zone of *A. arenaria*, which is situated on top of older root zones from previous growth seasons (van der Stoel et al., 2002). The soil was sieved (0.5 cm mesh size) to remove plant parts and debris and after that homogenized and stored in plastic bags at 4 °C until usage (van der Stoel et al., 2002). One half of the collected soil was sterilized by gamma irradiation with an average dose of 25 kGray, which is effective to eliminate all living soil organisms from dune soil (de Rooij van der Goes et al., 1998).

Seeds of *A. arenaria* were collected from random plants at the same field site and stored dry until usage. The seeds were germinated for 2 weeks on moist glass beads at 16/8 h light/dark regime at 25/15 °C. Seedlings with the first leaf of 2–3 cm long were transplanted to plastic 1.5 l pots filled with 1500 g sterilized dune soil (4 seedlings of *A. arenaria* per pot) with 10% w w⁻¹ soil moisture. Subsequently, the soil surface was covered with aluminum foil to protect the surface from desiccation. The soil moisture was maintained during the whole experiment by weighing the pots twice a week and re-setting the initial weight by adding demineralized water. Once a week full-strength Hoagland nutrient solution was added; first 3 weeks 12.5 ml pot⁻¹ and later 25 ml pot⁻¹ (Brinkman et al., 2004). The experiment was carried out in a greenhouse at a day temperature of 21 °C ± 2 °C and the day length was minimally 16 h by providing additional light to ensure minimally 225 μmol m⁻² s⁻¹ PAR with SON-T Agro lamps. The night temperature was 16 ± 2 °C.

Eight different most common in the coastal dunes root-feeding nematode species were used. Among those species six were ectoparasitic: *Criconema* sp., *Helicotylenchus pseudorobustus* (Steiner 1914) Golden, 1956, *Hemicycliophora* sp., *Rotylenchus* sp., *Tylenchorhynchus ventralis* (Loof, 1963) Fortuner and Luc, 1987 and *Tylenchorhynchus microphasmis* (Loof 1960) Jairajpuri and Hunt, 1983. Two other species were endoparasitic: sedentary *Heterodera arenaria* (Cooper, 1955) Robinson, Stone, Hooper and Rowe and migratory *Pratylenchus* sp. All those species originated from Dutch coastal foredunes and the cultures were from the NIOO at Heteren,

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