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Original article

Effects of crop species richness on the community of soil nematodes in an experimental agro-ecosystem

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ABSTRACT

Biodiversity losses in terrestrial ecosystems may negatively affect the functioning of underground ecosystems, especially in trophic interaction networks. These effects have mainly been found in grassland ecosystems. The responses of underground agro-ecosystems to biodiversity loss are largely unknown. Here, the relationships between crop species diversity and the abundance, diversity and functional indices of soil nematodes were examined in a 4-yr field experiment across five crop species richness levels (1, 2, 4, 8, and 16). The relationships between crop biomass and nematode abundance or ecological indices were also tested. Crop species richness had no significant effects on either total abundance nematode, nematode abundance within each trophic group, or nematode ecological indices. However, the plant parasitic nematodes, *Psilenchus* and *Partylenchus*, significantly differed among crop species diversity. Crop biomass significantly increased the abundances of total nematodes, plant parasites and omnivores/predators, and decreased that of fungivores. Furthermore, the responses of PPI (Maturity index of plant-parasitic nematode), EI (Enrichment index), and SI (Structure index) to crop biomass were positive, although CI (Channel index) was negatively affected. Redundancy analysis (RDA) further showed that crop species diversity and crop biomass account for 0.7% and 1.9% of the variation in nematode abundance, respectively. Our results clearly indicate that soil nematode abundance and community composition was more affected by crop biomass than by crop species diversity in agricultural systems.

1. Introduction

A positive relationship between biodiversity and ecosystem functioning has been reported in many studies [1–3]. Generally, a higher plant biodiversity in terrestrial ecosystems has positive effects on ecosystem properties, such as productivity [4,5], nutrient cycling [6], and multi-trophic interaction networks [7–9]. However, most studies addressing the influence of plant species diversity on higher trophic level organisms have focused on aboveground invertebrates [7,8,10,11]. Belowground and aboveground systems are intimately linked, and thus a combined above- and belowground approach should be used to enhance our understanding of the regulation and functioning of biodiversity [12,13]. Studies from grassland systems that examined both above- and belowground higher organisms reported that plant diversity had strong bottom-up effects on the multi-trophic interaction network, and belowground responses to plant diversity were relatively weaker than aboveground responses [9]. Given that there is high diversity of organisms belowground, the response of soil micro-organisms to plant diversity may be species-specific [14,15].

Nematodes are abundant and diverse invertebrates in belowground systems [16]. They play multiple roles in nitrogen mineralization and organic matter decomposition within the soil food web [17,18] and comprise a wide range of trophic groups including

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bacteria, fungi, and plant feeders, as well as predators and omnivores [19]. Nematode community structure can serve as an indicator for other soil biota and the soil food web as a whole [20]. Given the ease of recovering nematodes from soil and the ability to identify them to meaningful taxa or 'functional groups', soil nematodes offer great potential for their use as indicators of plant biodiversity in grasslands [9,14,15,21–25] and for assessing the impact of changing land use on soil conditions [26,27]. Plant diversity in grasslands has been shown to affect the relative abundance of soil nematode functional groups and changes in plant diversity can influence nematode community structure [9,14,15].

In contrast to grasslands, agricultural systems typically have much greater nutrient losses, partly due to removal of agricultural products from the landscape, and a higher frequency of disturbances due to farming practices such as tillage, fertilizer addition and pesticide treatment [27–29]. Agricultural production also commonly uses plant varieties selected for higher yield, which can generate a tradeoff in root-to-shoot ratios that affects the quantity and quality of nutrients and energy flow through soil food webs in both space and time [30]. As such, these key differences between grasslands and agro-ecosystem attributes may ultimately affect soil nematode abundance and community composition [26,27,31]. In multi-cropping production systems in which more than one plant variety or species is grown, soil biotic communities can be affected by crop diversity, with increases observed in the abundance, diversity, and activity of several functional groups [32]. However, these studies examined relatively low levels of crop species diversity ($\leq$3 species). The effects of higher levels of crop diversity (>5 species) on soil nematode communities remains to be considered. Therefore, a 4-yr field trial was carried out to explore the impacts of five crop species richness levels (1, 2, 4, 8, and 16) on abundance and community structure of soil nematodes. The goal of this study was to ascertain whether community structure of soil nematodes differed among different levels of crop species diversity, and to broadly compare the response of soil nematodes to plant species diversity between agricultural and grassland systems.

2. Materials and methods

2.1. Study region and experimental design

This study was conducted at the Experimental Farmland of Shandong Academy of Agricultural Sciences, located in Yishui, China. The region has a temperate maritime monsoon climate with cold winters and warm summers. The mean annual temperature and precipitation are 14.1 °C and 849 mm, respectively. The soils are Podzol E soil type.

The experiment was established in 2007. The crop species used were selected from a pool of 20 crop species commonly grown in North China [10] that included cotton (*Gossypium* spp.), maize (*Zea mays* L.), soybean (*Glycine max* (L.) Merr.), tomato (*Solanum lycopersicum* L.), wild cabbage (*Brassica oleracea* L.), millet (*Setaria italica* (L.) Beauv), sweet sorghum (*Sorghum bicolor* (L.) Moench), ryegrass (*Lolium perenne* L.), adzuki bean (*Vigna angularis* (Willd.) Ohwi et Ohashi), peanut (*Arachis gypogaea* L.), mungbeans (*Vigna radiate* (L.) R. Wilczek), alfalfa (*Medicago sativa* L.), eggplant (*Solanum melongena* L.), celery (*Apium graveolens* L.), clover (*Trifolium repens* L.), wheat (*Triticum aestivum* L.), rape (*Brassica campestris* L.), sunflower (*Helianthus annuus* L.), kidney bean (*Phaseolus vulgaris* L.), sesame (*Sesamum indicum* L.). Five crop richness levels (1, 2, 4, 8, and 16) were designed by randomly selecting the species to be grown in each plot from the species pool listed above. Detailed species composition information for each plot is provided in Supplementary Table S1. There were 10 replications for each crop richness level. The field contained 50 plots (each 9 m × 9 m), with a 5-m walkway between any two plots. Each plot contained 22 rows and 22 columns of crop plants, with the same crop species within each row but potentially different crop species in adjacent rows. The same experiment designs continued four years until 2010, although crops were harvested in each year. No pesticides and chemical fertilizers were used during the course of study. Weed species in the plots were removed by hand and herbicide application was used to control weeds in the walkway.

2.2. Nematode sampling

Soil samples were collected from each plot at 0–20 cm depth at the early, middle, and late stages of crops in 2010, which was in accord with seeding stage, blooming stage, and maturing stage of crop. Five soil samples were taken from each plot along the diagonal and pooled. Pooled samples were stored at 4 °C until extraction. Nematodes were extracted from 100 g of fresh soil from each pooled sample by the method of centrifugal flotation in sucrose solutions [33–35]. Nematode abundance was measured as individuals per 100 g dry soil, and at least 100 nematodes from each sample were identified to genus according to Bongers [36] using an inverted compound microscope. The nematodes were ascribed to four trophic groups [19]: plant parasites (Pp_x), bacterivores (Ba_x), fungivores (Fu_x), and omnivores/predators (OP_x) (where $x = 1$–5) [20,37]. x represent the colonizer–persister (cp) scale according to their r and K characteristics [20]. Nematodes in cp-1 have short generation duration, high fecundity, and are regarded as "enrichment opportunists" and tolerant to disturbance and can be ascribed to r-strategists. In contrast, cp-5 nematodes produce few large eggs, have a long life cycle combined with a long generation time and are generally intolerant of disturbance and inhabit stable, mature ecosystems [20,38].

2.3. Nematode community index

To characterize community responses of soil nematode to crop species richness, the following community indices were calculated: (1) species richness S, the number of taxa; (2) Shannon–Wiener diversity index (H'), $H' = -\sum p_i \times \ln p_i$, where p_i is the proportion of the i th taxon [39]; (3) Maturity index of free-living nematode (MI), $MI = \sum v_i \times f_i$, where v_i = c–p value of the i th taxon, f_i = frequency of that taxon in a sample [37]; (4) Maturity index of plant-parasitic nematode (PPI), $PPI = \sum v_i \times f_i'$, f_i' = frequency of that taxon i in a sample [37]; (5) Channel index (CI), $CI = 100 \times (0.8 \times Fu_2)/(3.2 \times Ba_1 + 0.8 \times Fu_2)$ [20]; (6) Enrichment Index (EI), $EI = 100 \times e/(e + b)$, where $e = (Ba_1 \times W_1) + (Fu_2 \times W_2)$, $b = (Ba_2 + Fu_2) \times W_2$, $W_1 = 3.2$ and $W_2 = 0.8$ [20]; (7) the structure index (SI), $SI = 100 \times s/(s + b)$, where $s = Ba_x \times W_x + Ca_x \times W_x + Fu_x \times W_x + OP_x \times W_x$, $x = 3$–5, $W_3 = 1.8$, $W_4 = 3.2$, $W_5 = 5.0$ [20].

2.4. Biomass determination

Three plants were randomly collected for each species in each plot at each sampling date, and the dry organic matter biomass of whole plant (both above- and belowground parts together) was determined for each species after drying at 60 °C for 72 h. Then, the total biomass of each plot was represented by summing these weights for 22 plants in the central row in each plot.

2.5. Data analysis

We used two-way ANOVA (SAS 9.13, SAS Institute Inc., Cary, NC, USA) to test for effects of crop species diversity, sampling date and their interaction on abundance and ecological indices of soil