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RESEARCH ARTICLE

Considerable impacts of litter inputs on soil nematode community composition in a young *Acacia crassicapa* plantation

Cancan Zhao[1], Yin Li[1], Chenlu Zhang[2,3,*], Yuan Miao[1], Mengzhou Liu[2,3], Wanlin Zhuang[1], Yuanhu Shao[2,3], Weixin Zhang[2,3], Shenglei Fu[2,3,*]

1 *International Joint Research Laboratory for Global Change Ecology, Laboratory of Biodiversity Conservation and Ecological Restoration, School of Life Sciences, Henan University, Kaifeng 475004, China*
2 *Key Laboratory of Geospatial Technology for the Middle and Lower Yellow River Regions, Ministry of Education, College of Environment and Planning, Henan University, Kaifeng 475004, China*
3 *Henan Key Laboratory of Integrated Air Pollution Control and Ecological Security, Kaifeng 475004, China*

HIGHLIGHTS

• Nematodes was investigated in a young *Acacia crassicapa* plantation in southern China
• Both litter addition and root presence enhanced soil nematode abundance.
• Litter addition significantly altered soil nematode community composition.
• Root presence had a limited impact on nematode trophic group composition.

ARTICLE INFO

GRAPHICAL ABSTRACT
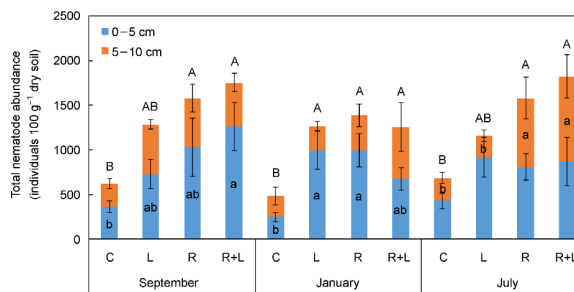
ABSTRACT

Aboveground litter inputs and root exudates provide basal resources for soil communities, however, their relative contributions to soil food web are still not well understood. Here, we conducted a field manipulative experiment to differentiate the effects of litter inputs and living root on nematode community composition of surface and subsoils in a young *Acacia crassicapa* plantation in southern China. Our results showed that both litter addition and root presence significantly enhanced soil nematode abundance by 17.3% and 35.3%, respectively. Litter addition altered nematode trophic group composition, decreased fungivore to bacterivore ratio, and enhanced maturity index and structure index, which led to a bacterial-based energy channel and a more complex food web structure. However, root presence had a limited impact on the nematode community composition and ecological indices. Despite nematodes surface assembly, soil depth did not affect nematode trophic group composition or ecological index. Our findings highlight the importance of litter inputs in shaping soil nematode community structure and regulating soil energy channel.

* Corresponding authors
E-mail address: zcl@vip.henu.edu.cn (C. Zhang);
              fsl@henu.edu.cn (S. Fu)

1 Introduction

There is little doubt that plants play a major role in structuring soil food web via creating their own habitat and regulating resource availability (Keith et al., 2009). In forest ecosystems, 80%–90% of the carbon fixed in tree tissue ultimately enters the decomposer food web (Bardgett et al., 2005). Tree-fixed carbon either reaches the soil via aboveground litter materials or via belowground root exudates, thereby fueling the soil food web (Pollierer et al., 2007).

In food web systems model, the litter based carbon channel seems to be the most important (Moore et al., 2004; Elfstrand et al., 2008; Freschet et al., 2013). Litter quantity and quality can impact soil biota directly as a resource or modify the habitat heterogeneity and soil properties, which indirectly affect the performance of soil biota (Kalinkat et al., 2013; Chen et al., 2020a; Zhao et al., 2021). Litter addition has been shown to increase, and conversely litter removal to decrease, the abundance of soil organisms and their diversity (Bastow, 2011; Sauvadet et al., 2016; Liu et al., 2019). In contrast, the negative and neutral effects of litter on soil biota were also found. Saj et al. (2009) have proposed that litter addition reduces the total number of bacterivorous and predatory nematodes. It has been reported that litter addition did not alter the abundance or diversity of soil nematodes or their carbon pool (Sayer, 2006; Pausch et al., 2018). The effects of litter on soil biota may vary with ecosystem type, litter quality and quantity, and experimental method.

Root exudates, as another important carbon input to the soil, can be decomposed within a few hours (Jones et al., 2005). The rapid use coupled with high local concentration of exudates around the roots leads to the rhizosphere effect (Ruf et al., 2006). A growing number of studies suggest that belowground rather than aboveground tree inputs have strong impacts on soil food web structure, especially in the short-term (Ruf et al., 2006; Kudrin, 2017). Using a ^{13}C-labeling experiment, Pollierer et al. (2007) demonstrated that the majority of soil invertebrates obtain their carbon from roots. Similarly, root presence rather than shoot litter addition influenced nematode trophic group composition in a mesocosm experiment (Keith et al., 2009). However, the relative importance of aboveground and belowground resources to soil community composition remains less well understood.

It has been established that soil biota exhibits a typical depth differences, which often associates with variations in biotic factor of tree root and abiotic factors, such as organic matter content, oxidation-reduction potential, and soil pH (Lazarova et al., 2004; Stone et al., 2014; Moradi et al., 2020). Reductions of soil biota abundance and diversity and changes in the distribution of trophic group composition with increasing soil depth have been observed in several studies (Allison et al., 2007; Eilers et al., 2012; Tian et al., 2017). The role of the root-derived carbon seems to be even more important for soil biota in subsoil horizons (Potapov et al., 2017). Thus, study on depth differences of soil biota is needed for understanding the relative contribution of plant root.

Soil nematodes are the most abundant multi-cellular animal and play an important role in regulating microbial community and driving soil nutrient (De Long et al., 2016). Nematodes are effective indicators of soil community structure since they respond to disturbance rapidly, occupy several trophic levels in soil food webs, and can be divided into five ecologically trophic groups (Bongers and Ferris, 1999). The processes of bottom-up control in soil food web can be examined entirely within the soil nematode community. In addition, nematode ecological indices such as maturity index, structure index, and enrichment index, have been proved to be useful tools to assess ecosystem function (Neher and Darby, 2009; Zhao et al., 2016).

In the last few decades, intensively anthropogenic disturbances such as excessive deforestation and floor litter removal have greatly affected ecosystem function. A series of environmental problems of forest degradation and biodiversity loss continue to emerge. Artificial forests are established enormously in degraded habitats for ecological restoration during the past 40 years (Yang et al., 2009). *Acacia crassicapa* is an exotic species, and has high growth rates. *Acacia crassicapa* is commonly used as pioneer species for afforestation in southern China due to its tolerance to barren and acidic soils, and substantial nitrogen fixation ability (Zhao et al., 2018). In this study, we conducted a field manipulative experiment to differentiate the effects of leaf litter and living root on soil nematode community composition in a young *Acacia crassicapa* plantation. Given that root exudates are more labile and easily degradable than litter, we tested the first hypothesis that living root input is more important for shaping soil nematode community composition than litter. We proposed the second hypothesis that nematode community composition would change with soil depth due to the variation of resources. Fungivore and plant parasite nematodes may be decline with soil depth due to their dependence on plant roots.

2 Material and methods

2.1 Site description and experimental design

The experiment was carried out at Heshan National Field Observation and Research Station of Forest Ecosystem (112°50′ E, 22°34′ N), which is located in Heshan city, Guangdong Province in southern China. The average altitude is 80 m. The climate in this region is typical subtropical monsoon climate with a distinct wet and dry season. The mean annual precipitation is 1688 mm during 2005–2012 (Chen et al., 2019), with the rainy season from April to September. The mean annual evaporation is 1600 mm. The mean annual temperature is 22.3°C, ranged from 12.6°C in January to 29.2°C in July. The soil is classified as Ultisol developed from sandstone (Wan et al., 2015). The climax vegetation of the study area is monsoon evergreen broad-leaved forest. However, most natural forests have degraded

into abandoned hilly land due to long-term human disturbance.

The experiment was initiated in 2005 and used a complete randomized block design with four treatments, including: (1) no tree planted and no litter addition – abandoned hilly land as control (C); (2) no tree planted but with addition of *A. crassicapa* litter (L); (3) planted *A. crassicapa* but with litter removed from soil surface – with the tree root system intact (R); (4) planted *A. crassicapa* with the root and litter intact (R + L). Each treatment was replicated six times with an area of 4 × 6 m² per plot. The distance between any two replicates was more than 1 km. For the L treatment, the *A. crassicapa* litters were collected from adjacent to the experimental area and added monthly as much as natural levels of litterfall. In the R and R + L treatments, *A. crassicapa* saplings were planted at a spacing of 2 m × 3 m. There were no significant difference in understory vegetation composition among all the treatments. To simulate shade of *A. crassicapa* tree and thus eliminate interference of light intensity under all treatments, artificially non-living trees were installed in the C and L treatments. No significant variation of photosynthetically active radiation was detected between *A. crassicapa* plantations and artificial trees conditions. When soil samples were taken in September 2007 (see the next section), *A. crassicapa* trees were three years old with an average height of 6.3 m and an average diameter at breast height of 64 mm.

2.2 Soil sampling and analysis

Soil samples were collected from all the 24 plots for three times of September 2007, January 2008, and July 2008. In each plot, a soil auger (5-cm diameter, 10-cm depth) was used to take samples at 0 – 5 cm and 5 –10 cm depth. Four soil cores of the same depth were randomly taken in each plot and pooled into a single composite sample. Litter was removed from soil surface before soil samples were taken. After visible plant roots and stones were removed and the soil was passed through a 2-mm sieve, the samples were placed in an icebox and transported to laboratory.

Nematodes were extracted from 50 g of moist soil using the Baermann funnel method for 48 h (Barker, 1985). After preservation in 4% formalin solution, nematodes were placed in a counting chamber and counted with a stereomicroscope. In each sample, the first 100 individuals encountered were identified to genus with a DIC microscope (400×), and classified into five trophic groups (bacterivore– Ba, fungivore– Fu, plant parasite– PP, predator– Pr, and omnivore– Om) and 16 functional guilds (Ba$_1$, Ba$_2$, Ba$_3$, Ba$_4$, Fu$_2$, Fu$_3$, Fu$_4$, PP$_2$, PP$_3$, PP$_4$, PP$_5$, Pr$_3$, Pr$_4$, Pr$_5$, Om$_4$, and Om$_5$; Ferris et al., 2001). All nematodes were identified when the sample contained fewer than 100 individuals.

Soil organic carbon was measured by the oxidation of H_2SO_4/K_2CrO_7 and titration with $FeSO_4$. Total nitrogen was measured using an ultraviolet spectrophotometer after Kjeldahl digestion. Gravimetric soil moisture was measured by the oven-drying method for 12 h at 105°C. Soil pH was determined in a soil water mixture of 1:2.5 ratio (w/v) using a digital pH meter.

2.3 Data analysis

Maturity index (MI) was calculated as follows:

$$MI = \Sigma[v(i) \times f(i)] \tag{1}$$

where $v(i)$ is the c-p value of free-living taxa i and $f(i)$ is the proportion of that taxa of the total number of free-living nematodes in a sample. Low and high values of maturity index represent highly disturbed and highly stable soil ecosystem, respectively (Bongers, 1990).

Nematode channel ratio (NCR) was calculated as follows:

$$NCR = Ba/(Ba + Fu) \tag{2}$$

where Ba is bacterivore nematode abundance, and Fu is fungivore nematode abundance. The NCR indicates the relative importance of bacterivore and fungivore channels in the soil decomposer food web.

Structure index (SI) and enrichment index (EI) were calculated as follows:

$$SI = 100 \times s/(s + b) \tag{3}$$

$$EI = 100 \times e/(e + b) \tag{4}$$

where b is the basal food web component (Ba$_2$, Fu$_2$), e is the enrichment component (Ba$_1$, Fu$_2$), and s is the structure component (Ba$_3$– Ba$_5$, Fu$_3$– Fu$_5$, Pr$_2$– Pr$_5$, Om$_4$–Om$_5$). High EI and SI indicate an enriched environment, and a complex or stable food web, respectively (Zhao et al., 2015a).

All the data were analyzed through a repeated measures ANOVA to determine the effects of litter addition, root presence, soil depth, sampling time, and their potential interaction on nematode and soil properties. The multiple comparisons based on one-way ANOVA were used to compare the differences of nematode abundance and trophic group percentage among treatments. General linear regressions were performed to assess the relationships between nematode ecological indices and soil properties. ANOVA and regressions were performed using SPSS 22.0 (SPSS Inc., Chicago, IL, USA). Redundancy analysis (RDA) were performed using Canoco 4.5 (Ithaca, NY, USA) to evaluate the associations of soil nematode community composition with soil properties.

3 Results

3.1 Nematode community composition

Litter addition increased the total nematode abundance by 17.3% than no litter addition, while root presence significantly increased the total nematode abundance by 35.3% than no root (Fig. 1, Table 1). Multiple comparison showed R and R + L treatments enhanced total nematode abundance than C

treatment at all sampling times. Mean nematode abundance at $0-5$ cm depth (776.5 individuals 100 g^{-1} dry soil) was higher than that at $5-10$ cm (462.3 individuals 100 g^{-1} dry soil). No effect of sampling time on nematode abundance was detected (Fig. 1, Table 1).

Litter addition significantly enhanced bacterivore, predator, and omnivore percentage by 7.9%, 123.9%, and 31.3%, whereas suppressed fungivore percentage by 26.6% than no litter addition. Root presence increased predator percentage

by 492.3% than no root (Fig. 2, Table 1). Treatment of L increased bacterivore but decreased fungivore percentage than C treatment at all sampling times. R and R + L treatments had little influence on bacterivore or fungivore percentage at the first two sampling times. Soil depth did not have obvious effect on the relative abundance of any trophic group. Fungivore and plant parasite percentage showed a temporal variation (Fig. 2, Table 1).
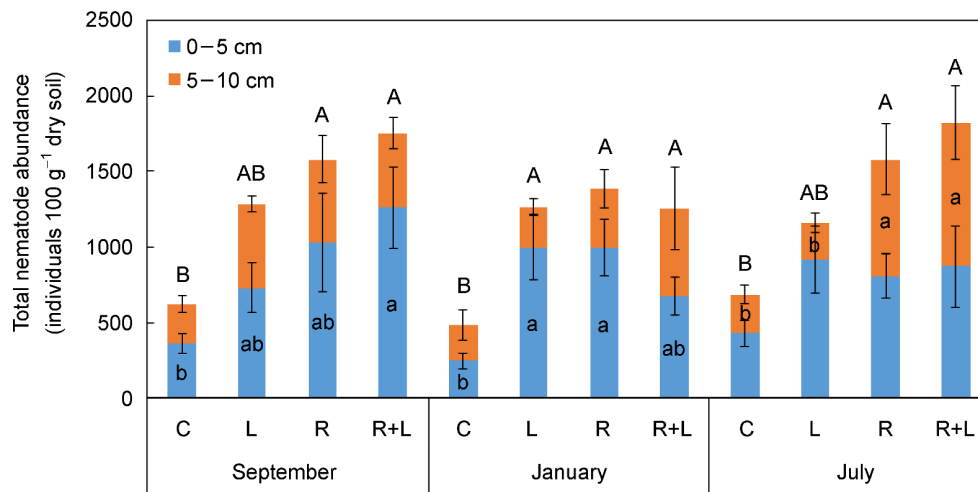

Fig. 1 Total nematode abundance under the four treatments at 0–5 cm and 5–10 cm depths in each sampling time (means±S.E., $n = 6$). C, L, R, and R + L represent control, litter addition, intact root, and intact root and litter, respectively.

Table 1 The results (P values) of repeated measures ANOVAs for the effects of litter addition (L), root presence (R), soil depth (D), sampling time (T), and their interactions on the soil nematode properties.

	NA	Ba%	Fu%	PP%	Pr%	Om%	MI	NCR	SI	EI
L	**0.026**	**< 0.001**	**< 0.001**	0.921	**0.017**	**0.017**	**< 0.001**	**< 0.001**	**< 0.001**	**0.001**
R	**< 0.001**	0.612	0.165	0.990	**< 0.001**	0.310	**0.005**	0.227	**0.010**	**0.023**
D	**< 0.001**	0.480	0.509	0.115	0.952	0.441	0.169	0.521	0.379	0.790
T	0.454	0.161	**0.012**	**0.030**	0.092	0.680	**< 0.001**	**0.013**	**< 0.001**	**0.002**
L × R	0.115	**< 0.001**	**< 0.001**	0.077	**0.021**	**0.003**	**0.008**	**< 0.001**	**< 0.001**	**0.004**
L × D	0.147	0.204	0.487	0.843	0.618	0.479	0.211	0.429	0.371	0.665
L × T	0.975	0.435	0.403	0.830	0.073	0.198	0.192	0.350	**0.017**	0.796
R × D	0.779	0.238	0.099	0.374	0.797	0.285	0.403	0.095	0.323	0.282
R × T	0.474	0.948	0.199	0.404	0.145	0.190	0.062	0.218	0.463	**0.005**
D × T	0.354	0.666	0.722	0.696	0.776	0.705	0.358	0.729	0.174	0.934
L × R × D	**0.027**	0.285	0.455	0.921	0.631	0.256	0.634	0.491	0.709	0.429
L × R × T	0.524	0.217	0.511	**0.025**	0.069	0.385	0.205	0.537	0.310	0.543
L × D × T	0.834	0.996	0.896	0.830	0.981	0.787	0.646	0.899	0.836	0.328
R × D × T	0.078	0.956	0.780	0.160	0.978	0.091	0.143	0.774	0.107	0.987
L × R × D × T	0.249	0.220	0.390	0.696	0.921	0.226	0.545	0.349	0.724	0.548

NA, total nematode abundance; Ba%, bacterivores percentage; Fu%, fungivores percentage; PP%, plant parasites percentage; Pr%, predators percentage; Om%, omnivores percentage; MI, maturity index; NCR, nematode channel ratio; SI, structure index; EI, enrichment index.
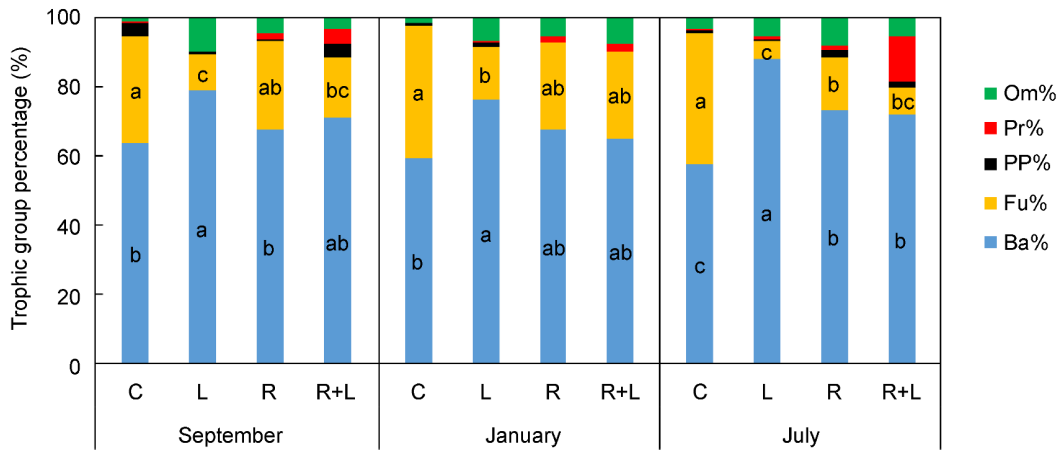
Fig. 2 Different nematode trophic groups percentage under the four treatments in each sampling time (*n* = 12). Average values of two soil layers were showed due to no significant soil depth effect on relative abundance of any trophic group. C, L, R, and R + L represent control, litter addition, intact root, and intact root and litter, respectively. Ba%, Fu%, PP%, Pr%, and Om% represent bacterivores percentage, fungivores percentage, plant parasites percentage, predators percentage, and omnivores percentage, respectively.

3.2 Nematode ecological indices

Litter addition significantly increased maturity index (Fig. 3A) and nematode channel ratio (Fig. 3B) than no litter addition.
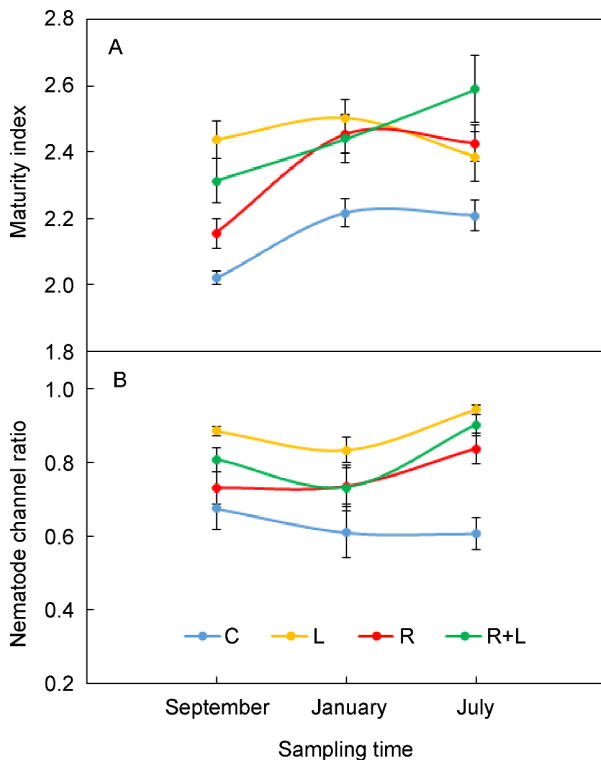
Root presence increased maturity index (Fig. 3A, Table 1). Faunal analysis revealed that the control plots were clustered in quadrat D, while most plots of other treatments appeared in quadrat C (Fig. 4), indicating more structured food web in the L, R, and R + L treatments. Both litter addition and root presence elevated structure index, but suppressed enrichment index (Fig. 4, Table 1). All nematode ecological indices showed strong temporal variation (Table 1).
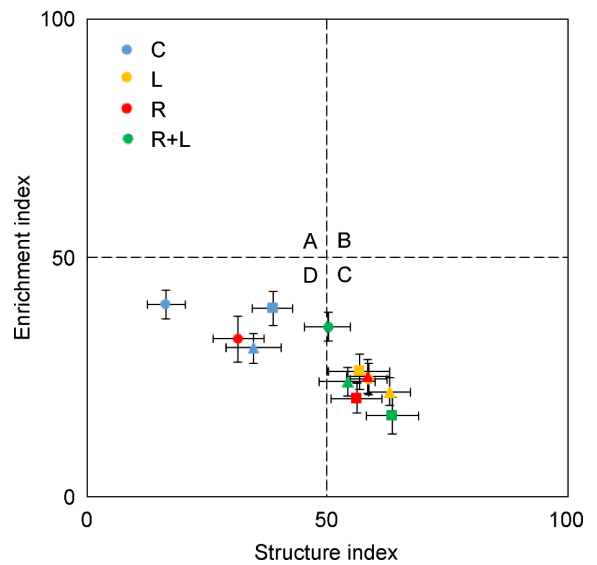

Fig. 3 Nematode maturity index (A) and nematode channel ratio (B) under the four treatments in each sampling time (means ±S.E., *n* = 12). Average values of two soil layers were showed due to no significant soil depth effect on any ecological index. C, L, R, and R + L represent control, litter addition, intact root, and intact root and litter, respectively.

Fig. 4 Faunal analysis of soil nematode community under the four treatments in each sampling time (means±S.E., *n* = 12). C, L, R, and R + L represent control, litter addition, intact root, and intact root t7799 and litter, respectively. Circle, triangle, and square represent September, January, and July, respectively.

3.3 Soil properties

Litter addition significantly increased soil organic carbon and total nitrogen by 23.1% and 19.3% than no litter addition, respectively, whereas root presence did not have obvious effect (Table 2). Soil organic carbon and total nitrogen at 0 – 5 cm depth were much higher than those at 5 – 10 cm. Litter addition increased soil moisture and decreased soil pH than no litter addition, conversely, root presence reduced soil moisture and increased soil pH than no root (Table 2). Soil pH at 0 – 5 cm depth was lower than that at 5 – 10 cm. The temporal variations in soil organic carbon, soil moisture, and soil pH were observed (Table 2).

3.4 Relationships of nematodes with soil properties

The result of redundancy analysis showed that the variation of soil nematode community structure was explained 36% and 13% by RDA1 and RDA2 axes, respectively. Data points for the L and R + L treatments were obviously separated from control (Fig. 5). RDA1 was highly related to soil moisture, total nitrogen, and soil organic carbon with correlation coefficient of 0.36, 0.23, and 0.20, respectively. Maturity index linearly increased with soil moisture, soil organic carbon, and total nitrogen (Table 3). Nematode channel ratio showed a positive correlation with soil moisture. Structure index showed positive correlations with soil moisture and total nitrogen, while

Table 2 Means (means±S.E.) of soil properties for three sampling time and repeated measures ANOVAs results (*F* values).

	Soil organic carbon (g kg^{-1})	Total nitrogen (g kg^{-1})	Soil moisture (%)	pH
0–5 cm				
C	18.73±2.16	0.67±0.08	17.04±1.19	3.96±0.04
L	25.90±3.14	0.83±0.08	24.63±1.29	3.84±0.02
R	19.00±1.31	0.61±0.03	16.57±1.51	3.97±0.02
R + L	24.74±2.97	0.81±0.08	19.17±1.90	3.97±0.02
5–10 cm				
C	13.26±1.29	0.49±0.05	18.69±0.96	4.05±0.03
L	15.00±1.36	0.54±0.06	22.90±1.25	3.97±0.02
R	15.06±1.50	0.51±0.04	19.52±1.37	4.00±0.02
R + L	15.66±1.31	0.55±0.04	18.52±1.24	4.02±0.01
ANOVA				
L	7.939**	6.353*	24.677***	7.805**
R	0.086	0.097	12.384***	5.150*
D	29.487***	22.351***	0.666	21.125***
T	6.542**	0.433	68.711***	10.888***
L × R	0.225	0.012	14.301***	9.846**
L × D	3.817	2.525	6.726*	0.827
L × T	2.386	1.433	0.293	1.241
R × D	0.383	0.317	0.791	3.964*
R × T	1.316	0.646	5.548**	3.006
D × T	1.917	0.690	1.440	1.223
L × R × D	0.003	0.102	0.006	0.005
L × R × T	0.089	0.031	0.289	2.210
L × D × T	3.259*	1.729	1.404	0.475
R × D × T	0.048	0.008	0.583	0.139
L × R × D × T	0.160	0.121	0.593	0.302

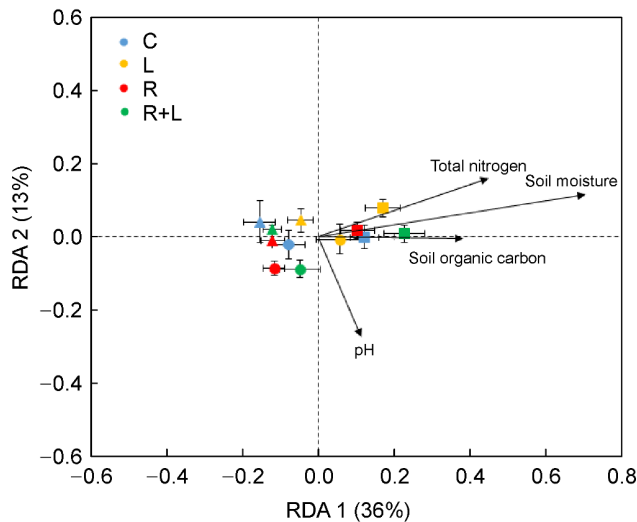Significance levels: *P < 0.05, **P < 0.01, ***P < 0.001.

Fig. 5 Redundancy analysis (RDA) of the associations of soil nematode community composition (as indicated by functional guild) with soil properties (means±S.E., n = 12). C, L, R, and R + L represent control, litter addition, intact root, and intact root and litter, respectively. Circle, triangle, and square represent September, January, and July, respectively.

enrichment index showed negative correlations with soil moisture and total nitrogen (Table 3).

4 Discussion

We have demonstrated that both litter addition and root presence dramatically enhanced soil nematode abundance, suggesting the important roles of both aboveground and belowground resources input on soil nematodes. Litter addition but not root presence significantly altered nematode trophic group composition, which indicates litter input rather than root exudates would play more important role in shaping nematode composition in soil food webs.

4.1 Effects of litter addition on soil nematode

In the present study, litter addition significantly increased total nematode abundance, bacterivore, predator, omnivore percentage, soil organic carbon, and total nitrogen (Figs. 1, 2, Tables 1, 2, 3), suggesting a strong bottom-up effect of litter on soil nematode food web. This is consistent with findings of

some previous studies (Elfstrand et al., 2008; Eisenhauer and Reich, 2012; Zhao et al., 2021). The positive effect of litter on soil nematode abundance may involve both direct and indirect ways. First, *A. crassicapa* tree which has lower leaf C:N ratio, could produce a great quantity of litterfall and support more decomposers, including microorganisms and microbivores (Zhao et al., 2018). Secondly, in our study, earthworms as ecosystem engineers play a vital role in accelerating litter decomposition. Chen et al. (2020a) have reported that there are 145 earthworm individuals per m^2 in our experimental site. Litter removal could decrease the density of earthworm by 58% (Chen et al., 2020a). Such a large number of earthworms could burrow, mix litter and soil, consume soil materials, excrete feces, and subsequently accelerate nutrient cycling and support soil nematodes (Shao et al., 2017; Eisenhauer et al., 2019). Most inconsistent results, which suggest litter have limited impact, are derived from no earthworm microcosm or mesocosm experiment (Ruf et al., 2006; Keith et al., 2009), which could not veritably reflect the natural condition of ecosystem. Thirdly, litter not only directly provides a resource to soil nematodes, but also alters environmental conditions including habitat structure and microclimate, then indirectly influences soil nematodes (Zhang et al., 2018). Litter could form a protective layer on the soil surface and provide shelter for soil microfauna (Keith et al., 2009). In our study, litter addition improved soil moisture by 18.7% due to slower evaporation (Table 2), which facilitates nematode population growth (Zhang et al., 2019).

Litter addition decreased fungivore percentage, and increased bacterivore and omnivore-predator percentage (Figs. 2, 4, Table 1), indicating that litter may be central in shaping nematode trophic composition in soil food webs. Lower fungivore to bacterivore ratio in litter addition treatment is inconsistent with most previous studies (Wang et al., 2013; Malik et al., 2016). One possible explanation may be that the ecosystem in our study is seriously disturbed and degraded. Extensive deforestation have caused soil labile carbon depleted. Aboveground litter input could stimulate more bacteria and bacterivore nematodes growth at the initial stage of restoration. The higher soil moisture may be another reason for lower relative abundance of fungivores due to bacterial dependence on water and fungal drought resistance (Fig. 5, Tables 2, 3; Briar et al., 2012; Zhao et al., 2015b). In line with the changes in fungivore and bacterivore percentage, litter addition increased nematode channel ratio (Fig. 3B, Table 1), indicating that litter can cause a switch from the fungal-based to the bacterial-based energy channel, i.e.,

Table 3 Spearman correlation coefficients of the relationship between nematode ecological indices and soil properties.

	Maturity index	Nematode channel ratio	Structure index	Enrichment index
Soil moisture	0.242**	0.260**	0.226**	−0.176*
Soil organic carbon	0.168*	0.110	0.131	−0.041
Total nitrogen	0.233**	0.088	0.176*	−0.176*

Significance levels: *P < 0.05, **P < 0.01.

accelerate soil energy flow (Rooney et al., 2006; Zhao et al., 2019). Moreover, litter addition enhanced maturity index and structure index (Figs. 3, 4, Tables 1, 3), suggesting a more complex food web structure and trophic links (Ferris et al., 2001).

4.2 Effects of root presence on soil nematode

Root presence profoundly enhanced total nematode abundance, however, had a limited impact on the nematode trophic group composition (Figs. 1, 2, 5, Table 1). These findings are inconsistent with our first hypothesis and the widespread assumption that root-derived resources serve as driver of soil food web dynamics (Keith et al., 2009; Zhang et al., 2018). In general, living root exudates mainly consist of easily degradable organic compounds including carbohydrates, N free carbonic acids, and amino acids (Gransee and Wittenmayer, 2000). These compounds could stimulate bacteria and bacterial-feeding nematodes growing (Rooney et al., 2006). Furthermore, roots of *A. crassicapa* (legume) could form symbioses with soil nitrogen-fixing bacteria, resulting in bacterial dominance and energy channel (Zhao et al., 2018). Our uncommon findings could be interpreted in four ways. First, planting *A. crassicapa* in abandoned land may increase plant diversity, then shift toward more fungal-dominated communities (Eisenhauer et al., 2011; Eisenhauer et al., 2017; Zhao et al., 2019). Secondly, root presence treatment have significantly decreased soil moisture, thereby suppress the relative bacterial energy channel to some extent (Table 2, Fig. 5; Kaneda and Kaneko, 2011; Sun et al., 2020a). Thirdly, roots provide carbon sources for soil communities, meanwhile compete for available and labile nutrients with bacteria and bacterivores to support the fast-growing of *A. crassicapa* (Bardgett et al., 2014). Finally, root presence have obviously enhanced relative abundance of predatory nematode, while their top-down effects on microbivores could result in stable bacterivore and fungivore percentage. Therefore, root presence can maintain the energy channel balance and do not change the nematode community composition in our study.

4.3 Different effects of litter and root

Soils comprise two major food chains, litter or detritus based and root based (Glavatska et al., 2017). In detritus-based food chain, litter as dead organic matter fuels the bacterial and fungal energy channel. While in root-based food chain, the predominant carbon sources are living plant tissue and root exudates (Ruess and Ferris, 2004). In our study, litter addition altered nematode community composition via changing relative bacterivore and fungivore abundance, i.e., through detritus-based food chain. However, in the root presence plots, the rhizosphere associated food web comprise both herbivore and detritivore food chain, which are more complex compared to detritus food web (Bais et al., 2006). Plant parasitic nematodes accounted for a small percentage of total nematode abundance in our study, and were not influenced by root presence (Table 1, Fig. 2). Lower root-based energy fluxes and complicated species interactions in the rhizosphere are the causes of limited impact of living root on soil nematodes community structure.

4.4 Effects of soil depth on soil nematode

Soil nematode abundance, soil organic carbon, and total nitrogen in the surface soils were higher than those in the subsoils (Fig. 1, Tables 1, 2). This surface assembly pattern has also been found in many previous studies (Zhang et al., 2010; Zhao et al., 2015a; Scharroba et al., 2016). Most of soil organic matter, which consist of leaf litter and root exudates, are accumulated at the surface layer as principal source for nematodes (De Long et al., 2016; Hsiao et al., 2018). In addition, oxygen is more favorable for microbial and nematode growth in the surface than in the subsoils (Sun et al., 2020b). Soil depth have no impact on nematode trophic group composition or any ecological index (Table 1), which is in contrast to our second hypothesis. A few studies have reported that soil microbial community shift with depth along with a decline in fungal/bacterial ratio, because fungi are often associated with plant roots and concentrated in the surface soils (Sradnick et al., 2014; Stone et al., 2014). No variation in nematode community composition in our study may be attributed to the homogenization of nutrients and living conditions among soil layers. The vertical distribution of soil communities depend on soil texture (Sradnick et al., 2014; Hsiao et al., 2018). Sandy soil in our experimental site may lead to little protected organic matter in soil aggregates, which facilitate nutrients of surface leaching into deeper (Chen et al., 2020b; Moradi et al., 2020). In addition, soil depth have not influenced soil moisture (Table 2), resulting in similar environmental condition.

5 Conclusion

Strong bottom-up effects of both aboveground litter and root exudates on soil food web are confirmed in the study. The results highlight that aboveground litter may be more important in shaping soil nematode community structure than belowground inputs in young *Acacia crassicapa* plantation. Therefore, future studies should not overlook the litter inputs, especially in degraded ecosystem. Floor litter should not be removed from artificial forests during early restoration. The study provides data and theoretical support for plantation management in southern China.

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