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Belowground plant inputs exert higher metabolic activities and carbon use efficiency of soil nematodes than aboveground inputs

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ABSTRACT

Soil nematodes are key components of soil food web and, through their metabolic activities, play a crucial role in soil carbon (C) cycling. Aboveground and belowground plant C inputs can directly, or indirectly via soil microbes, modify nematode abundance and community composition. Aboveground and belowground C inputs differ in chemical composition, amounts, and frequency, so we hypothesized that the two input pathways affect nematode communities differently. To assess the relative contributions of aboveground versus belowground inputs to nematode community composition and activity, we subjected grassland soils to four plant input pathways over two consecutive years: no input, only aboveground input (+A), only belowground input (+B), and both aboveground and belowground inputs (+A + B). Nematode metabolic footprints, as estimates of C used in growth/reproduction and C lost by respiration, and C use efficiency (C used/(C used + C lost)) were calculated. We predicted that soils with belowground inputs, which are more directly linked to the soil biota, and which contain a more labile blend of molecules, would support richer and more complex nematode communities, and also favor a bacterial-driven decomposition channel. Accordingly, we showed that + B soils supported higher nematode numbers than + A soils, and that the bacterial decomposition channel was dominant in + B soils, while the fungal decomposition channel dominated in + A soils. Compared with + A soils, +B input system increased nematode structure footprints (the metabolic footprints of nematodes in upper functional guilds) rather than enrichment footprints (the metabolic footprints of enrichment opportunistic nematodes). Moreover, we observed that, compared to + A soils, +B soils had higher growth and respiration rates of bacterivores, omnivores-predators, and total nematodes. Finally, we found higher C use efficiency values for omnivores-predators and total nematodes in + B than in + A soils. We thus conclude that belowground plant-derived resources, by changing the ratio between fungivores and bacterivores, induce a faster carbon turnover rate, and higher metabolic activity of soil nematodes within soil food web, ultimately spurring richer and more efficient soil food web than aboveground inputs.

1. Introduction

Plants influence soil community composition by providing resources to soil organisms, and in turn, soil communities affect plant communities through the regulation of soil nutrient cycling, as well as through direct impacts on plant performance (Bardgett and Wardle, 2010; Eisenhauer et al., 2013). However, while soil food web largely depends on plant-derived resources, the relative importance of plant aboveground versus belowground inputs for soil organisms is not yet fully understood (Eisenhauer and Reich, 2012). Aboveground residues have often been

Abbreviations: NI, no input; +A, only aboveground input; +B, only belowground input; +A+B, both aboveground and belowground inputs; CUE, carbon use efficiency; NCR, nematode channel ratio.

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assumed to be the dominant carbon (C) source for soil food web (Clemmensen et al., 2013; Freschet et al., 2013). However, there is increasing evidence that the influences of belowground inputs have been underestimated (Sauvadet et al., 2016; Sokol and Bradford, 2019). Therefore, identifying how aboveground and belowground plant resources affect the metabolic dynamics of soil organisms will constitute an important step forward in understanding the structuring forces of soil food web, and plant-soil feedback dynamics (Wardle et al., 2004; Bardgett and Wardle, 2010).

Plant-derived resources such as aboveground leaf litter and belowground root litter as well as exudates supply the primary resources for belowground communities (Keith et al., 2009). However, the different pathways and characteristics of aboveground and belowground inputs are critical in determining the compositional characteristics of soil communities (Fujii and Takeda, 2012; Eissfeller et al., 2013). Firstly, the decomposition of aboveground resources starts at the soil surface, whereas the decomposition of belowground resources starts directly in the soil (Fujii and Takeda, 2017). Secondly, resource quantity and quality generally differ between aboveground and belowground inputs (Mueller et al., 2013; Wang et al., 2017), with important consequences for soil community structure (Wardle, 2002; Keith et al., 2009). Moreover, the utilization of C from different substrates relies on different functional groups of microorganisms and, consequently, succession of microbial communities occurs as decomposition proceeds (Sun et al., 2013; Zhou et al., 2016). There is increasing evidence that root-derived resources (i.e., root exudates) play a larger role in fueling soil communities than root biomass, and therefore are an important driver of soil food web dynamics (Pausch et al., 2016; Zieger et al., 2017). Root exudate production especially stimulates soil bacterial communities, as bacteria prefer labile C sources (Phillips et al., 2011). Contrastingly, fungal communities are partly specialized on the decomposition of recalcitrant C sources, and therefore play a predominant role in the decomposition of aboveground resources (Bray et al., 2012; Kraft et al., 2015). As such, aboveground inputs likely stimulate fungal communities relatively more than belowground resources if root exudates dominate the soil belowground inputs.

Nematodes, as the most abundant soil invertebrates, form an important group of soil organisms that contribute to belowground C cycling (Pausch et al., 2016; van den Hoogen et al., 2019), as they affect the decomposition of organic matter through their trophic interactions with bacteria and fungi (Zhang et al., 2021). As such, the relative abundance of bacterivores (B) and fungivores (F) can be used as indicator of the strength of bacterial and fungal decomposition pathways, respectively (Kondratow et al., 2019; Huo et al., 2021). Moreover, the relative importance of the two decomposition pathways can be determined by means of the ratio between bacterivores and fungivores (B/F) or the nematode channel ratio (NCR = B/(B + F)) (Yeates, 2003; Hánël, 2010). Accordingly, nematodes can be used as indicators for determining the main carbon cycling pathways in response to aboveground and belowground plant inputs.

To further characterize the carbon and energy flows within soil food web, nematode metabolic footprints can be examined (Bhusal et al., 2015; Kergunteuil et al., 2016). Nematodes' metabolic footprint, i.e., the amount of C used throughout their life cycle, can be separated into two main components: production and respiration (Ferris, 2010). The production component assesses the amount of C conserved to support growth and reproduction, while the respiration component is the C released during their metabolic activity (mainly by respiration) (Ferris et al., 2012). The ratio of respiration C to production C may evaluate the partitioning efficiency of nematode metabolic C (Ferris et al., 1997), and can facilitate a better understanding of soil biological C sequestration (Zhang et al., 2019). Recently, the carbon use efficiency (CUE) of nematodes, calculated as the ratio between C used for production and the sum of C used for both production and respiration, has been proposed as a novel, more integrative parameter (Luo et al., 2021). A greater CUE indicates that more C has been utilized for growth and reproduction rather than for respiration, and therefore it should represent soils that facilitate an increase of the soil C stock (Liu et al., 2020; Oliver et al., 2021).

Moreover, it has been well documented that substrates consisting of more degradable compounds can trigger a higher microbial CUE than those containing more recalcitrant compounds (Cepakova and Frouz, 2015; Qiao et al., 2019). Manzoni et al. (2008) also suggested that decomposers lowered their CUE to exploit residues with low initial nitrogen concentration and high C:N ratio (recalcitrant compounds), a strategy used broadly by bacteria and consumers across trophic levels. The activity of soil nematodes, at least the bacterivores and fungivores, can generally be assimilated to microbial activity (Jiang et al., 2018; Thakur and Geisen, 2019). In copiotrophic environments, bacterivores can increase the turnover rate of bacterial communities (Jiang et al., 2017). However, oligotrophic environments may sustain the development of fungal community with potential benefits to fungivores (Thakur and Geisen, 2019). Despite the importance that nematode CUE might have in soil biological C sequestration, the concept has rarely been applied, and how plant aboveground and belowground inputs differentially affect soil nematode metabolic footprints and CUE remains scarcely explored.

The objectives of this study were to examine the relative contributions of plant aboveground and belowground inputs to soil nematode community composition and nematode metabolic footprints in a two-year grassland experiment. We predicted that (1) since bacteria use preferably labile C sources present in root exudates, then belowground inputs would favor the development of bacterivore assemblages and contribute to the C flow into soil nematode food web through the bacterial decomposition channel. On the contrary, aboveground inputs would then facilitate fungivores and carbon cycling, which would be driven by the fungal-mediated decomposition channel. We also predicted that (2) if labile carbon within root exudates would be more easily assimilated by soil nematodes than recalcitrant carbon forms from aboveground inputs, belowground inputs should induce higher CUE of nematodes than aboveground inputs. The results of our study will contribute to the understanding of the mechanism by which aboveground and belowground inputs drive soil carbon cycling and the role of nematodes in such process.

2. Materials and methods

2.1. Study site

Our study was conducted in Haicheng county (40°58′N, 122°43′E), Liaoning Province, China. The region is characterized by a humid continental climate with a mean annual temperature of 10.4 °C, a mean annual precipitation of 721 mm, and non-frost period of 166 days. The soil is classified as Hapic-Udic Alfisols based on the US Soil Taxonomy, with basic properties as follows: soil pH (H_2O) 5.10, 11.30 g kg^{-1} soil organic carbon, 1.14 g cm^{-3} bulk density at 0–20 cm depth (Wang et al., 2021). Prior to 2018, the experimental site was an agricultural field with continuous maize (*Zea mays* L.) cropping for more than 100 years. In 2018, the site was abandoned and converted into grassland.

2.2. Experimental design and soil sampling

A grassland experiment was initiated in the spring of 2018, and was set up according to a randomized block design with three replicated blocks, and each block contained the four treated plots: no input (NI), only belowground input (+B), only aboveground input (+A), both aboveground and belowground inputs (+A + B) (Fig. S1). The experiment started from bare soil for all treatments. No seeds were applied and seedling emergence was due to the natural seed bank in the experimental grassland patches. Each plot was 4 m × 4 m in size and individual plots were separated from each other by 1-meter broad strips. During the growing season (from May to October), plant shoots and roots were

manually removed from the NI and + A plots every two weeks when the seedlings sprouted, while plants in + B and + A + B plots naturally grew. When the leaves turned yellow in fall (at the end of October), the aboveground plant biomass in + B plot was mowed, then transferred to the + A plot in the corresponding block, and spread evenly on the soil surface. The aboveground plant parts of + A + B plot were also mowed and evenly overlaid on the soil surface to guarantee the experimental consistency with + A. Both + A and + A + B plots were covered with fixed nets to prevent leaf litter from being blown away or accidentally displaced. The same experimental manipulations were applied for a second year in 2019. The dominant plant species within all experimental plots were the grasses *Setaria viridis* (L.) Beauv., *Echinochloa crusgalli* (L.) Beauv. and the forb *Conyza canadensis* (L.) Cronq.

At the end of October 2019, five soil cores in each plot were randomly sampled from the top 0–20 cm soil layers using a soil auger (2.5 cm internal diameter) and mixed uniformly to obtain one composite sample per plot. The collected fresh samples were kept at 4 °C until further nematode analysis. Soil water holding capacity was measured according to the method proposed by Lowery et al. (1996). Aboveground biomass was cut from a 50 cm × 50 cm quadrat and root biomass was sampled using a stainless-steel auger (6 cm-diameter) with 80 cm depth at the + B plots, and then dried at 60 °C and weighed. The shoot–root biomass ratio was about 9:1 based on dry weight (Fig. S2). Soil temperature was monitored using a temperature probe of an EGM-4 portable CO_2 analyzer (PP Systems, US). Soil organic carbon and total nitrogen concentrations and ^{13}C and ^{15}N abundance were determined by an elemental analyzer (Elementar vario PYRO cube, Germany) coupled to an isotope ratio mass spectrometer (IsoPrime 100 Isotope Ratio Mass Spectrometer, Germany). The data for soil temperature and water holding capacity are shown in Fig. S3.

2.3. Soil nematode extraction and identification

Soil nematodes were extracted from 100 g of fresh soil using a modified cotton-wool filter method (Townshend, 1963). Total nematode abundance and abundances of the different trophic groups were expressed as number of individuals per 100 g dry soil. In each sample, 100 nematode individuals were selected and identified to genus level using an inverted compound microscope (Bongers, 1994). Next, nematodes were classified into the following four trophic groups characterized by feeding habits: bacterivores, fungivores, plant-parasites and omnivores-predators (Yeates et al., 1993). We then calculated the nematode channel ratio (NCR), which reflects the relative importance of the bacterial decomposition channel versus the fungal decomposition channel in the decomposition process (Yeates, 2003), using the formula NCR = B/(B + F), where B and F are the numbers of bacterivores and fungivores, respectively. A value of NCR higher than 0.5 indicates that substrates are mainly utilized by bacteria and the bacterial decomposition channel dominates the decomposition of organic matter. An NCR value lower than 0.5 indicates a system dominated by the fungal decomposition pathway (Yeates, 2003).

2.4. Data calculations and analysis

Nematode metabolic footprint (NMF), by integrating both a C production component and a C respiration component, evaluates the amount of C flowing in and out of the soil food web (Ferris, 2010; Ferris et al., 2012). NMF is calculated as: NMF = Σ (N*t* (0.1(W_t/m_t) + 0.273 ($W_t^{0.75}$))), where Nt, W_t, and m_t refer to the abundance, the body mass and the colonizer-persister (cp) values of the genus t of each nematode in the community, respectively (Ferris, 2010). The average fresh body mass of nematodes of each nematode genus can be obtained from the online database: http://nemaplex.ucdavis.edu/Uppermnus/topmnu.htm. The metabolic footprints of bacterivores, fungivores and plant-parasites can also be calculated separately to assess through which channels C and energy enter the soil nematode food web (Ferris et al., 2012).

In addition, the NMF provides estimates of ecosystem services performed by different nematode functional guilds (cp 1–5) (Ferris, 2010). The enrichment footprint (Fe) represents the metabolic footprints of those nematode guilds (enrichment opportunistic nematodes; cp-1 bacterivores and cp-2 fungivores) that respond most rapidly to resource enrichment, while the structure footprint (Fs) represents the contribution of higher trophic guilds (cp 3–5) to soil functions (e.g., the potential suppression of pest and invasive organisms) (Sánchez-Moreno et al., 2009; Ferris, 2010; Maina et al., 2020). The functional metabolic footprint was calculated as the total area of the two functional footprints (Fe and Fs), which was equal to (Fs × Fe)/2, as illustrated in Fig. 4. Larger functional footprint values indicate higher amounts of C flowing within the soil food web. The graphical representation of the Fe and Fs is obtained by plotting metabolic footprints values in the EI/SI biplot (Ferris, 2010): (SI-0.5Fs/k, EI); (SI, EI + 0.5Fe/k); (SI + 0.5Fs/k, EI); (SI, EI-0.5Fe/k). SI and EI represent the structure and the enrichment indices, respectively (Ferris et al., 2001). If the shape of the nematode functional metabolic footprint is rhomboid, it indicates that the productivity and turnover of preys are not sufficiently big for supporting the development of large-sized predatory nematodes (Ferris, 2010). On the other hand, if the shape is close to a square, it indicates that the number of preys is enough to allow the presence of large-sized predatory nematodes in the soil community (Ferris, 2010).

Nematode production C was estimated based on nematode biomass C and calculated as follows:

$$\text{Nematode production C} = \sum_{t=1}^{n} 20\% \times 52\% \times \text{Wt} \times \text{Nt} \times 1000$$

where the unit of nematode production C was expressed as ng g^{-1}. 20% is the conversion from fresh mass to dry mass (Persson et al. 1980), while 52% is the ratio of C in the dry mass (Persson et al., 1983). W is the individual fresh body mass (μg), t represents the nematode genus t, N represents the number of individuals per 1 g dry soil, and 1000 is the conversion factor from μg to ng.

Nematode respiration C was firstly estimated according to the oxygen consumption (C_1), then corrected by soil temperature (C_2) and finally adjusted by soil moisture (Ekschmitt et al., 1999), since environmental temperature and moisture act as key determinants of nematode respiration (Bhusal et al., 2015; Zhang et al., 2019).

According to the Ideal Gas Equation, the following equation was applied to transfer the volumetric amount of consumed O_2 to the respired C (C_1) presented on a mass basis:

$$C_1 = \text{Rt} \times 12/(0.0831 \times (\text{Tc} + 273)) \times 720$$

$$\text{Rt} = 1.4 \times \text{Wt}^{0.72}$$

where Rt is the amount of O_2 consumed by the genus t (nL O_2 per g dry soil per hour) (Klekowski et al., 1972) and calculated on the basis of nematode fresh body mass, 12 represents the molecular weight of C, 0.0831 implies the general gas constant (0.0831 L bar mol^{-1} °K^{-1}), Tc is the constant temperature (20 °C), 273 is the conversion from °C to °K and 720 is the conversion factor for up-scaling ng C per g dry soil per hour into ng C per g dry soil per month (Zhang et al., 2019).

Then, C_1 was corrected to C_2 by soil temperature (T) as:

$$C_2 = C_1 \times Q_{10}^{(T-20)/10}$$

where Q_{10} is assumed to be 3 (Didden et al., 1994). Finally, nematode respiration C was obtained from the adjustment of C_2 by soil water holding capacity (WHC) as:

$$\text{Nematode respiration C} = C_2 \times \left(0.190 + 0.0174 \times \text{WHC} - 5.87 \times 10^{-6} \times \text{WHC}^2 - 9.25 \times 10^{-7} \times \text{WHC}^3\right)$$

The calculation of nematode production C and respiration C were firstly calculated for each individual genus, then for all different trophic

groups, and then for complete nematode community. Moreover, nematode carbon use efficiency (CUE) was calculated by the following equation (Luo et al., 2021): CUE = Production C/(Production C + Respiration C).

For statistical analyses, nematode abundances, metabolic footprints (including Fe, Fs and functional metabolic footprint) and production C as well as respiration C of nematodes were all ln(x + 1)-transformed to improve normality of the residuals. Soil properties, the abundances of nematodes, metabolic footprints, production as well as respiration C and CUEs of nematodes were analyzed using a linear model with 'input treatment' as fixed factor and 'replicate block' as random factor. Tukey's honest significant difference tests were used as post hoc comparisons of means among treatments and differences at $P < 0.05$ level were considered as statistically significant. All statistical analyses were performed using the software package SPSS 16.0 for Windows (SPSS Inc., Chicago, IL, USA). The effect of plant inputs on nematode community composition was examined using a redundancy analysis (RDA) and performed by CANOCO software 4.5 version (ter Braak, 1988). A Monte Carlo permutation test (999 permutations) was used to test the significance of treatments.

3. Results

3.1. Nematode abundance and community composition

The total abundance of soil nematodes varied among the four input treatments, with greater numbers observed in + B and + A + B plots than in NI and + A plots (Fig. 1, $F_{(3,6)} = 16.12$, $P < 0.01$). This was also the case for omnivores-predators ($F_{(3,6)} = 23.40$, $P < 0.01$) and plant-parasites ($F_{(3,6)} = 15.81$, $P < 0.01$). The abundance of fungivores was higher in + A + B plots than in NI plots ($F_{(3,6)} = 4.93$, $P < 0.05$), but was similar between + A and + B plots (Fig. 1). The abundance of bacterivores did not significantly differ among the four input treatments ($F_{(3,6)} = 4.71$, $P = 0.051$).

In total, 39 nematode genera were recorded in this study (Supplementary Table S1). The first principal component (PC1) of the nematode community ordination accounted for 72.4% of the total variation, and separated NI from the other three treatments (Fig. 2), which was verified by the significance test in the RDA ($F = 2.87$, $P < 0.05$). The nematode compositions in + A and + B treatments were separated by the axis of PC2, which accounted for 17.6% of the total variation. Notably, there

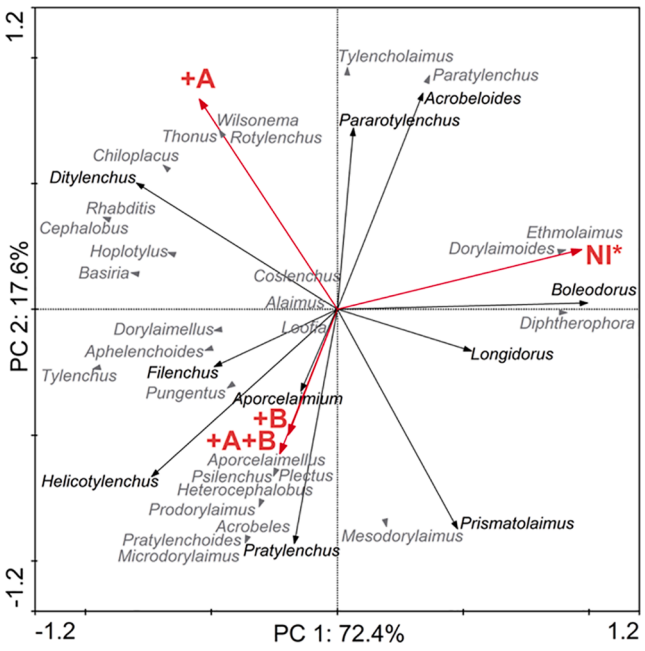

Fig. 2. Redundancy analysis of soil nematode genera under different pathways of plant input. NI, no input; +A, only aboveground input; +B, only belowground input; +A + B, both aboveground and belowground inputs. Arrows represent nematode genera with relative abundances over 3% (10 genera).

was a positive correlation between the genus *Boleodorus* and NI treatment, while the genus *Ditylenchus* was positively correlated with + A treatment (Fig. 2).

The nematode channel ratio, calculated by bacterivores/(bacterivores + fungivores), was higher in NI and + B plots (greater than 0.5) than in + A plot (lower than 0.5) (Fig. 3, $F_{(3,6)} = 7.60$, $P < 0.05$), indicating that the bacterial decomposition channel dominated in NI and + B plots but that the fungal decomposition channel dominated in + A plots.

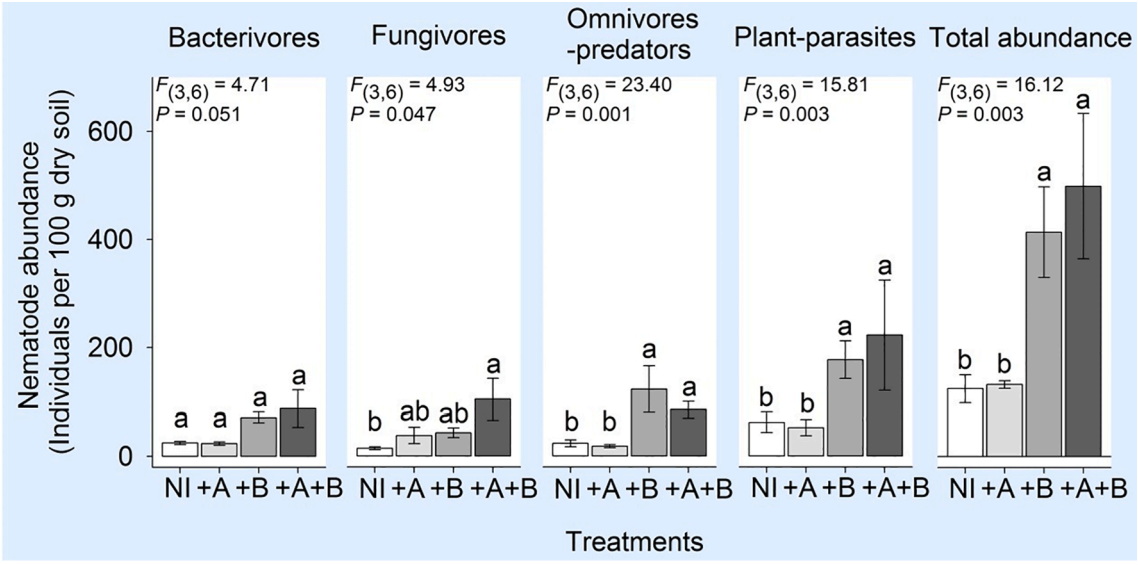

Fig. 1. Abundances of soil nematodes under different pathways of plant input (mean ± SE, $n = 3$). NI, no input; +A, only aboveground input; +B, only belowground input; +A + B, both aboveground and belowground inputs. Different lowercase letters represent significant differences among treatments, as determined by Tukey's honestly significant difference test, $P < 0.05$.

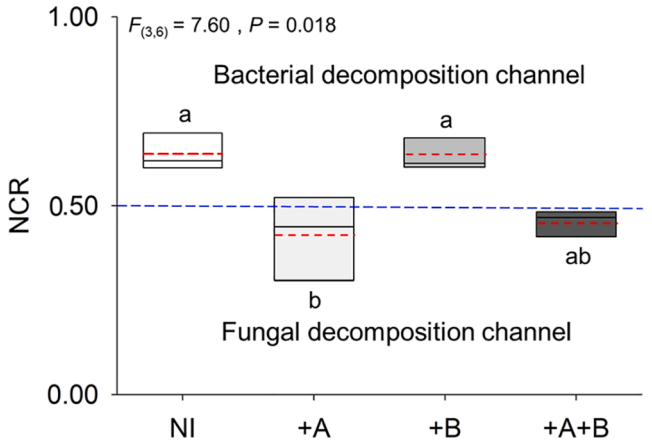

Fig. 3. Nematode channel ratio (NCR) under different pathways of plant input. NI, no input; +A, only aboveground input; +B, only belowground input; +A + B, both aboveground and belowground inputs. Different lowercase letters represent significant differences among treatments, as determined by Tukey's honestly significant difference test, $P < 0.05$.

3.2. Nematode metabolic footprints and carbon use efficiency

The metabolic footprints of bacterivores (Fig. 4a, $F_{(3,6)} = 23.27$, $P < 0.01$) and fungivores ($F_{(3,6)} = 8.40$, $P < 0.05$) were sensitive to different input treatments, but the footprint of plant-parasites was not ($F_{(3,6)} = 3.01$, $P = 0.116$). Compared with NI, a greater bacterivore footprint was observed in + B and a higher fungivore footprint in + A (Fig. 4a). The metabolic (enrichment and structure) footprint characteristics of soil nematodes varied among the input treatments (Fig. 4b). The enrichment footprint, the index for the metabolic footprint enrichment-opportunistic nematodes with low cp value, was highest in + A + B plots, intermediate in + A and + B plots, and lowest in NI plots ($F_{(3,6)} = 56.23$, $P < 0.001$). The nematode structure footprint, the index for the metabolic footprints of high trophic levels, was greater in + B and + A + B plots than in NI and + A plots ($F_{(3,6)} = 130.71$, $P < 0.001$). Nematode functional footprints, i.e., the total area of parallelogram for combination of enrichment and structure footprints, were used to indicate the amount of C flowing into soil nematode food web (Fig. 4c). The size of functional footprints ranked as + A + B > +B > +A > NI ($F_{(3,6)} = 114.14$, $P < 0.001$), indicating that belowground inputs caused a larger flow of C into the soil nematode food web than aboveground inputs. The shape of the functional metabolic footprint for + B plot was rhomboid, and that for + A + B plot was close to square (Fig. 4c), indicating that numbers of large-sized predatory nematodes are better sustained in + A

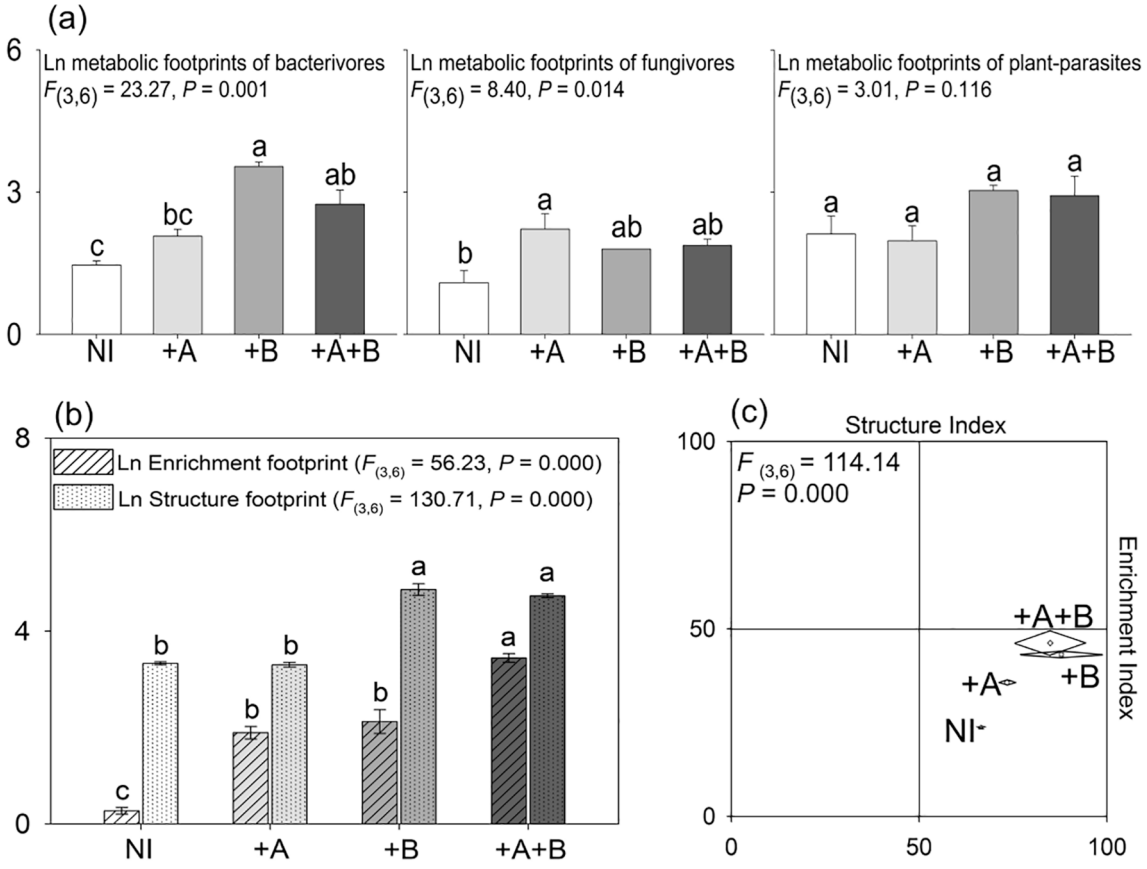

Fig. 4. Nematode metabolic footprints under different pathways of plant input. (a) Metabolic footprints of bacterivores, fungivores, and plant-parasites; (b) Nematode enrichment (Fe) and structure (Fs) footprints, which represent the metabolic footprints of enrichment opportunistic nematodes (cp-1 bacterivores and cp-2 fungivores) and the metabolic footprints of higher trophic guilds (cp 3–5); (c) Nematode functional metabolic footprints, in which the vertical and horizontal axis represent enrichment and structure footprints, respectively. The functional metabolic footprint is described by the sequentially joining points: (SI-0.5Fs/k, EI); (SI, EI + 0.5Fe/k); (SI + 0.5Fs/k, EI); (SI, EI-0.5Fe/k). Fs and Fe are structure and enrichment footprints, respectively. SI and EI are structure and enrichment indices, respectively, and the k value is 6. The nematode functional metabolic footprint is the total area ((Fs × Fe)/2) of the two functional (enrichment and structure) footprints (Ferris, 2010). NI, no input; +A, only aboveground input; +B, only belowground input; +A + B, both aboveground and belowground inputs. All the error bars showed standard error ($n = 3$). Different lowercase letters represent significant differences among treatments, as determined by Tukey's honestly significant difference test, $P < 0.05$.

+ B plots than in + B plots, due to higher prey numbers.

The pathway of plant input affected the production C and respiration C of bacterivores ($F_{(3,6)} = 70.20$, $P < 0.001$ and $F_{(3,6)} = 14.43$, $P < 0.01$, respectively), omnivores-predators ($F_{(3,6)} = 19.77$, $P < 0.01$, and $F_{(3,6)} = 12.47$, $P < 0.01$, respectively), and total nematodes ($F_{(3,6)} = 21.15$, $P < 0.01$, and $F_{(3,6)} = 12.61$, $P < 0.01$, respectively) (Fig. 5). + B Plots had greater production C and respiration C than NI and + A plots for bacterivores, omnivores-predators and the complete nematode community. The CUEs of omnivores-predators (Fig. 5, $F_{(3,6)} = 8.09$, $P < 0.05$), and the nematode community as a whole ($F_{(3,6)} = 5.71$, $P < 0.05$), were greater in + B than in + A input systems (Fig. 5). However, the CUEs of bacterivores ($F_{(3,6)} = 4.20$, $P = 0.064$), fungivores ($F_{(3,6)} = 1.38$, $P = 0.336$) and plant-parasites ($F_{(3,6)} = 1.62$, $P = 0.281$) did not vary among the plant input treatments (Fig. 5).

4. Discussion

We explored the impacts of aboveground and belowground inputs on soil nematode abundance, community composition, metabolic footprints and carbon use efficiency (CUE). Overall, our results show that belowground inputs supported higher nematode abundances and both functionally and taxonomically more complex nematode communities than aboveground inputs. As such, our study highlights the importance of plant input pathway as a driver of variation in soil nematode communities. Below, we discuss the effects of the implemented treatments on nematode community composition and metabolic activity, respectively.

4.1. Effects of aboveground vs. belowground inputs on soil nematode community

The abundances of omnivores-predators and plant-parasites were enhanced in plots with belowground inputs compared to plots without plant inputs, whereas aboveground inputs had a limited impact on nematode abundances (Fig. 1). Our findings are consistent with previous studies showing that higher root densities are associated with greater abundances of soil organisms (Pollierer et al., 2007; Keith et al., 2009). Omnivores-predators increased their abundance in soils in which roots were present. This result could be related to the associated increase in plant-parasites (i.e., greater availability of preys) in + B plots, which might have had a positive impact on the predator abundances (Keith et al., 2009). The reduction of plant-parasites in soils with limited plant growth (NI and + A) was expected (Wardle et al., 1999), although approximately 25% of plant-parasites persisted in these soils despite the continuous plant removal during two growing seasons (Fig. 1).

Nematode community composition varied among aboveground and belowground input treatments (Fig. 2), which was in line with the findings of Keith et al. (2009), Austin et al. (2014), and Palozzi and Lindo (2018). This was unlikely attributed to soil organic matter, as no differences in soil organic carbon and total nitrogen between aboveground and belowground inputs were found after two year of experimental manipulation (Supplementary Table S2). The variation in nematode community structure appears to be caused by different resource availabilities from the four input treatments (Zhang et al., 2015; Fujii and Takeda, 2017). Root exudates are less recalcitrant, and more continuously available than the resources provided by aboveground litter inputs, resulting in a more structurally complex and rich soil nematode community (Phillips et al., 2011), which included multiple predator and omnivore taxa such as *Aporcelaimium*, *Aporcelaimellus*, *Prodorylaimus* and *Microdorylaimus* (Fig. 2). Unexpectedly, *Boleodorus,* a relatively abundant plant-parasite was mostly associated with plots without plant inputs (Supplementary Table S1 and Fig. 2). Similarly, Pan et al. (2012) showed that *Boleodorus* was the dominant nematode genus in bare land. Generally, *Boleodorus* is classified as plant feeder and/or fungivore (Yeates et al., 1993); however, it is unlikely that there were sufficient plant-based resources available in the NI plots. Therefore, it

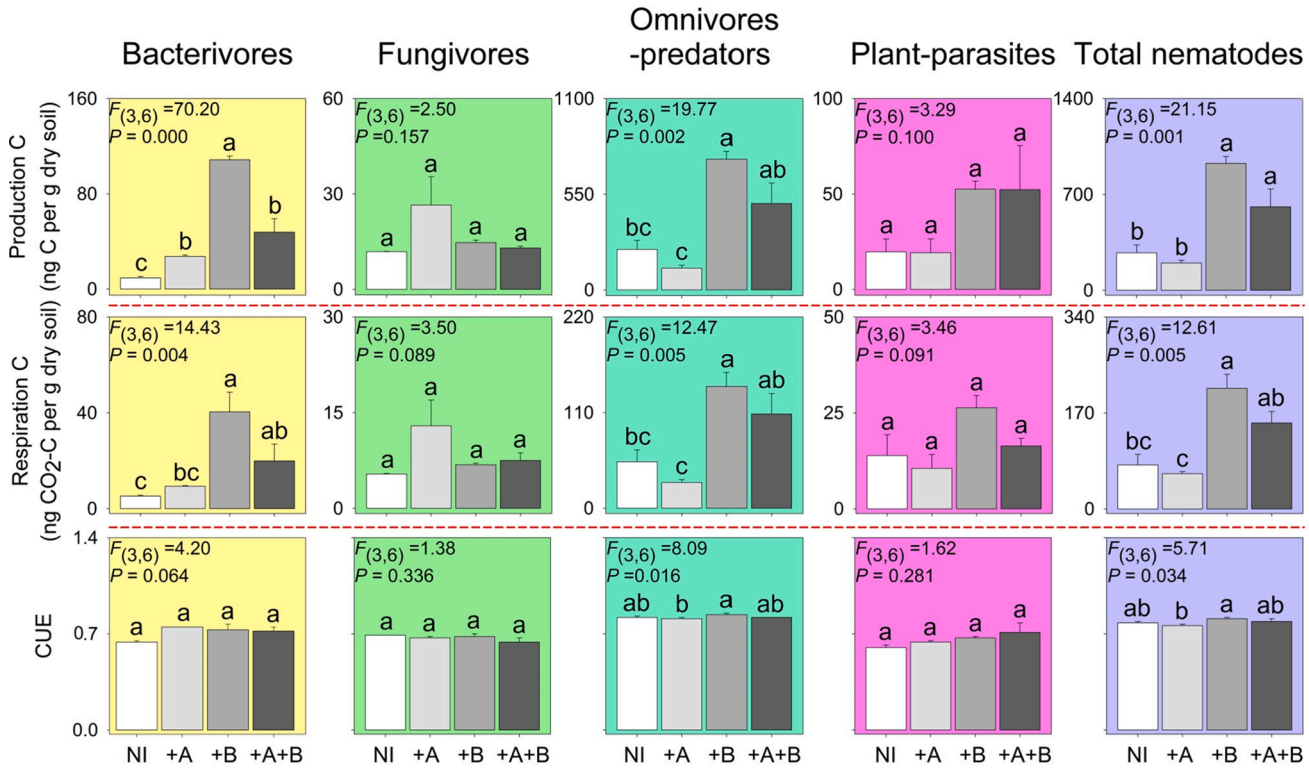

Fig. 5. Nematode production C, respiration C and C use efficiency (CUE) under different pathways of plant input (mean ± SE, $n = 3$). NI, no input; +A, only aboveground input; +B, only belowground input; +A + B, both aboveground and belowground inputs. Different lowercase letters represent significant differences among treatments, as determined by Tukey's honestly significant difference test, $P < 0.05$.

may be inferred that *Boleodorus* fed on algae, mosses and lichens rather than plant roots in the plots without plant inputs (Yeates et al., 1993).

Supporting our first hypothesis, the fungal decomposition channel dominated in plots with aboveground inputs, while the bacterial decomposition channel dominated in the belowground input plots (Fig. 3). Nematode communities of soils subjected to aboveground litter inputs were dominated by the fungivore *Ditylenchus* (Fig. 2). Aboveground litter inputs were generally more recalcitrant than belowground inputs, including root exudates (Berg and McClaugherty, 2003; Soong and Cotrufo, 2015). Soil fungi prefer to decompose the recalcitrant C sources, explaining the high relative abundance of fungivores in the soils to which aboveground litter inputs were added (De Vries et al., 2012; Soong et al., 2017; Kou et al., 2020). Contrastingly, root growth, through exudation of great amounts of labile C such as free sugars, likely stimulated bacterial growth (Phillips et al., 2011; Wang et al., 2017), resulting in larger numbers of bacterivores in soils with belowground inputs (Keith, 2007). Altogether, our results indicate that aboveground and belowground inputs affect the nematode community structure and thus alter the main decomposition channel through differences in resource quality (Scharroba et al., 2012).

4.2. Effects of aboveground vs. belowground inputs on soil nematode metabolic activity

Nematode metabolic footprint (NMF) can provide detailed knowledge about nematode community functioning and nematode contributions to the soil food web (Steel and Ferris, 2016; Sánchez-Moreno et al., 2018; Ewald et al., 2020). In the present study, belowground inputs increased the bacterivore footprint, while aboveground inputs increased the fungivore footprint, compared with the no-input treatment (Fig. 4a). This confirmed the flow of resources into the soil nematode food web through the bacterivorous channel under belowground inputs and through the fungivorous channel under aboveground inputs (Ferris, 2010; Zhang et al., 2015). The enrichment footprint is the metabolic footprint of nematodes from lower trophic levels that rapidly respond to resource enrichment, while the structure footprint indicates the metabolic footprint of higher trophic levels, which control the community composition of lower trophic levels (Ferris, 2010; Zhang et al., 2015). Compared to aboveground inputs, belowground inputs did not increase the nematode enrichment footprint, but enhanced the structure footprint (Fig. 4b). Possibly, high numbers of omnivores-predators under belowground inputs have constrained the development of lower trophic-level nematodes through top-down control (Cheng et al., 2012; Guan et al., 2018). This explained the absence of differences in the enrichment footprint between aboveground and belowground inputs (Fig. 4b). A greater functional metabolic footprint of nematodes was observed in the + A + B treatment than in other treatments (Fig. 4c). A higher functional footprint indicated that greater amounts of C were transited in the soil nematode food web (Zhang et al., 2016). Moreover, it should be noted that the shape of nematode functional metabolic footprint in the + A + B treatment tended to be a square (Fig. 4c). This supported the theory that prey numbers were sufficiently high to sustain predator communities, and that this system tended to be in metabolic balance (Ferris, 2010; Zhang et al., 2012). Consequently, increasing diverse plant-derived resource inputs could maintain the development of soil nematode community.

Carbon respiration is a widely used parameter for estimating the activity of soil organisms (Sohlenius et al., 1988). In this study, the respiration C of whole nematode communities ranged from 62.52 to 213.72 ng CO_2-C g^{-1} (Fig. 5), which was similar to the result of Zhang et al. (2019), but lower than the values reported for major European grassland soils (Ekschmitt et al., 1999). Our experimental site is dominated by fast-growing annual species and is situating in the stage of succession, as land abandonment lasted for only two years. When long-lived species with high root/shoot ratio become more dominant in our study system, root biomass may increase, resulting in higher nematode abundances and greater respiration C.

The production C and respiration C of bacterivores and omnivores-predators were greater in + B plots than in + A plots (Fig. 5). High production C and respiration C for bacterivores might be primarily attributed to bacterivores with low cp values having a high reproduction rate and going through a fast nutrient turnover process (Sieriebriennikov et al., 2014; Kou et al., 2020). Yu et al. (2015) suggested that higher CO_2 concentrations caused by the respiration of preys can attract more predators to the food source. In such a case, the increased CO_2 flux in the omnivores-predators of + B treatment likely reflects enhanced detritivore (e.g. bacterivore) activity (Sitvarin and Rypstra, 2014; Thakur and Geisen, 2019). During predation, bacterivores may have served as a conduit through which plant-derived C can be rapidly transferred omnivores-predators (Wardle and Yeates, 1993).

Supporting our second hypothesis, omnivores-predators, as well as whole nematode communities showed higher CUEs under belowground plant inputs than under aboveground inputs (Fig. 5). Possibly, the slow degradation of recalcitrant compounds, such as cellulose or lignin from aboveground inputs (Danger et al., 2016; Kou et al., 2020), resulted in a time lag in C transformation from fungivores to omnivores-predators, leading to a lower CUE of omnivores-predators under aboveground inputs. As *K*-strategists, omnivores-predators generally need a large amount of C to sustain their big size and biomass (Ferris, 2010). Higher CUEs of omnivores-predators and total nematodes under plant belowground inputs indicated a larger ratio of transformation from the plant-derived resource into the living bodies of soil nematodes (Luo et al., 2020), which would be helpful for soil C sequestration. It may be ascribed to the fact that omnivores-predators with high cp values can promote C conservation in their biomass and secondary products at low metabolic rates (Bongers and Bongers, 1998; Ferris, 2010). In addition, they can favor C conservation from the bottom to the high level of the soil food web by increasing the relationships among soil organisms (Morriën et al., 2017). Jiang et al. (2018) also suggested that the increased predator abundance had a positive influence on soil microbial community especially on keystone species, which could promote microbial-derived soil organic C retention. Future studies should elucidate how the impacts of aboveground and belowground inputs on metabolic activities of nematodes in soil C cycling vary across ecosystems.

5. Conclusion

Plant belowground inputs contributed more strongly to the development of soil nematode communities than aboveground inputs. However, plant aboveground inputs generated a fungal-based soil nematode community. The bacterial decomposition pathway was strengthened in the belowground input system, in which also the abundance of omnivores-predators was stimulated. As such, belowground inputs stimulated soil nematode metabolic activities by increasing the metabolic carbon of bacterivores and omnivores-predators. The greater carbon use efficiency of soil nematodes in the belowground input system suggested that the belowground plant-derived resources increased the capacity for conserving carbon in soils. Overall, our findings reveal how aboveground and belowground plant inputs generate different nematode communities, which in turn generate variation in carbon use efficiency and carbon sequestration within the soil system.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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