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Body size induced changes in metabolic carbon of soil nematodes under N deposition and precipitation regime change in a temperate grassland

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Abstract

Background Global climate change has resulted in precipitation regimes exhibiting an increasing trend in rainfall intensity but a reduction in its frequency. Nitrogen (N) deposition is a crucial component of the global N cycling. Nematode body size is a trait that responds to climate change and is used as a standard trait-based indicator in soil community analysis. Variations in body size influence metabolic carbon (C). We examined the ways by which body size and metabolic C of nematodes respond to changing precipitation regimes and how N deposition regulates these responses by an 8-year manipulative experiment.

Methods Nematode body size was indicated by the community-weighted mean (CWM) mass. We quantified C metabolism components of soil nematodes including production C, respiration C, and corresponding C use efficiency (CUE) under different precipitation intensities and N addition in a semi-arid steppe on the Mongolian Plateau. The Mantel test was used to determine the correlations between CWM, CUE and environmental factors. The partial least squares path modeling (PLS-PM) was conducted to quantify direct or indirect contributions among latent variables.

Results We found that heavy precipitation intensity increased the CWM mass of total nematodes and omnivores-predators without N addition. N addition decreased CWM mass of bacterivores across all the precipitation intensity treatments. Stronger precipitation intensities might be favorable for nematode production and respiration C. Variations in the nematode CWM mass drove the CUE to change with N addition.

Conclusions Our findings provide new insights into the mechanisms underlying nematode body size and C metabolism, and highlight that explorative studies, such as manipulative experiments, are needed to identify traits underlying size-related effects and to investigate how they affect CUE of nematodes. These efforts may increase our understanding of how changes in precipitation regimes and N deposition may alter soil nematode communities in grassland ecosystems.

Keywords Community-weighted mean, Metabolic footprint, Nitrogen addition, Precipitation intensity

Introduction

Nematodes are one of the dominant components of soil communities and feature in all major trophic levels of soil food web (Bardgett et al. 1999). The functional role of nematodes in soils can be inferred by their trophic position and they are therefore classified into trophic groups based on feeding guilds, that is, bacterivores, fungivores,

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plant parasites and omnivores-predators (Neher 2010). Given their pivotal roles in processing organic nutrients and control of soil microorganisms, soil nematodes play critical parts in regulating carbon (C) and nutrient dynamics. Most knowledge on nematode community variations has focused on compositional data based on abundance of individual taxa or functional groups (Quist et al. 2016; Yang et al. 2021). However, data on species richness, abundance, and composition may have limitations for expressing the actual ecological roles of soil nematodes (Shade et al. 2017), as differences in body size can compensate for variations in nematode abundance easily (Norkko et al. 2013). Body size is a morphological trait with the broadest functional meaning, as the scaling of physiological and behavioral features by mass underpins the dynamics of population and food web (Ferris 2010; Schneider et al. 2012). Therefore, body size can be considered more suitable to quantify the effects of environmental change (e.g. climate change) on soil nematodes.

Precipitation is the main change driver of the soil nematode community structure in grassland ecosystems (Franco et al. 2019; Cui et al. 2022). Available soil moisture is often regulated by the precipitation regime (e.g. precipitation frequency) rather than by the total precipitation amount (Wu et al. 2011). Over the past few decades, grasslands in arid and semi-arid areas have been subjected to variations in precipitation regimes that have shifted toward more intense but fewer rainfall events (Galloway et al. 2008; Yu et al. 2018). Most studies have reported that variations in precipitation influenced nematode abundance and composition (Landesman et al. 2011; Guo et al. 2021); however, its effects on body size remain unclear.

Precipitation changes may control nematode body size by regulating resource availability, as it is skewed toward small body sizes when resources are limited (Mulder 2010; Andriuzzi and Wall 2018). In addition, soil nematodes are critical to soil C cycling as they can transfer C from primary producers to higher trophic levels (van den Hoogen et al. 2019; Wan et al. 2022), making them ideal models for investigating the consequences of body size changes on ecosystem functions. Ferris (2010) proposed nematode metabolic footprint based on the two components (respiration and production) of C metabolism. The respiration component is released as CO_2 through respiration and production component is the C allocated during growth lifetime, such as body growth and egg production. Carbon use efficiency (CUE) of metabolic processes is evaluated as the ratio of C production to the total C uptake, which is crucial for determining the fate of the soil organic carbon (SOC) (Geyer et al. 2016). Accumulating evidence has suggested that the metabolic footprint provides a metric of the magnitude of soil nematodes contributions to global C cycling (Kergunteuil et al. 2016; van den Hoogen et al. 2019). However, there is little evidence to confirm whether precipitation-induced changes in nematode body size affect metabolic C, especially CUE.

In addition to precipitation, changes in nitrogen (N) deposition are widespread factors affecting global climate change. Factorial manipulations of N addition and precipitation are commonly used to quantify their effects on nematode communities (Thakur et al. 2019). However, the effects of N addition and precipitation on nematode communities are frequently inconsistent across studies and are, therefore, difficult to predict. Two primary factors may account for the lack of consensus regarding the response of soil nematodes to N addition and precipitation change. First, N addition and precipitation change have different effects on the basal resources of the soil food web, such as bacteria, fungi, and root, which in turn may influence the nematode community structure (Wang et al. 2021). Second, the indices of nematode community selected to detect environmental effects may not be sufficiently sensitive. Therefore, a trait-based community-weighted mean (CWM) approach is required to determine the body size-related differences in nematode communities with multi-trophic levels. The CWM provides a measure of trait composition unbiased by differences in abundance; specified soil nematodes with the same taxa in the same proportion have identical CWM, irrespective of variations in the abundance of individuals (Andriuzzi et al. 2020). Hence, alterations in N addition and precipitation changes may affect the CWM of traits, even if taxonomic diversity indices (based on species richness and abundance) remain largely unaffected.

In this study, we conducted an 8-year field experiment to evaluate the effects of changes in precipitation intensity and N addition on the soil nematode community in a typical semi-arid steppe on the Mongolian Plateau. We determined CWM mass, C metabolism components (production and respiration C), and corresponding CUE. We proposed the following hypothesis: (1) larger precipitation events (large in amount but low in frequency) increase soil moisture content, which in turn increases nematode CWM mass by promoting large-bodied nematodes; (2) a smaller body size may cause reduced metabolic C and CUE; and (3) N addition would exacerbate the positive effects of higher precipitation events on the nematode CWM mass and/or metabolic C by changing plant properties and carbon availability (Fig. 1).

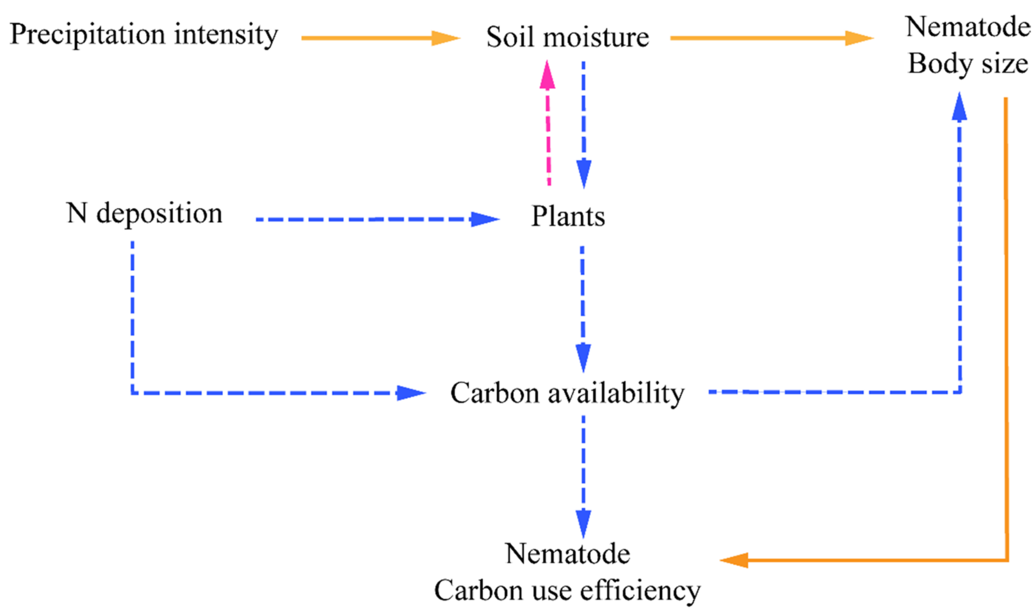


Fig. 1 The assumed effects of altered precipitation intensity and N addition on nematode body size and carbon use efficiency. The possible mechanisms underlying the changes in nematode body size and carbon use efficiency and involving different drivers are presented. The blue and pink arrows indicate assumed positive and negative effects, respectively. The orange arrows indicate the possibility of both positive and negative effects. The solid and dashed lines indicate the mechanisms that can directly and indirectly drive the responses in nematode body size and carbon use efficiency to treatments, respectively

Methods

Study site and experimental design

This study was conducted at Duolun Restoration Ecology Research Station of the Institute of Botany, Chinese Academy of Sciences, located in a typical steppe in Inner Mongolia, China (42°02′ N and 116°17′ E, 1324 m a.s.l.). The mean annual temperature in the region is 2.1 °C, and the mean annual precipitation is 379 mm (Hao et al. 2019). According to the Food and Agricultural Organization (FAO), the soil was classified as Haplic Calcisols. The soil organic carbon content (SOC) is 16.1 g kg^{-1} (Niu et al. 2011), while the contents of N and phosphorus are 1.7 g kg^{-1} and 0.28 g kg^{-1}, respectively (Niu et al. 2010). Two perennial grasses (*Stipa krylovii* and *Agropyron cristatum*) and one perennial forb (*Artemisia frigida*) were the dominant plant species in the studied grassland.

The field experiment was established in 2012 using a randomized block design with four replicates to simulate changes in N deposition and precipitation patterns. Each block consisted of 12 plots (3 m × 4 m), including five precipitation intensity levels with (N10) and without N addition (N0), as well as two control plots. Urea ($CO(NH_2)_2$) was added as a N source, and the rate approached the critical threshold for an N-induced increase in the aboveground biomass (N10: 10 g N m^{-2} yr^{-1}) (Bai et al. 2010). The addition of water started in June and July, the maximum period of primary productivity on grassland every year. The water used for irrigation was obtained from a reverse osmosis system. The total amount of precipitation added was 80 mm (20% of MAP) but varied the size and frequency of the applied precipitation events (Cui et al. 2022). Water was added at five intensities, i.e. 2 mm (low precipitation intensity), 5 mm (low precipitation intensity), 10 mm (moderate precipitation intensity), 20 mm (heavy precipitation intensity), and 40 mm (extreme precipitation intensity) in 40, 16, 8, 4, and 2 events, correspondingly.

Soil sampling and property analysis

Soil was sampled in September 2020 (the end of the growing season). In each plot, seven soil cores (2.5 cm in diameter) were randomly collected from a depth of 0–10 cm and mixed together as one composite sample per plot. Soil samples were stored at 4 °C until soil properties and nematodes were analyzed. We characterized soil physicochemical properties including pH values, soil moisture (SM), the contents of soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), dissolved organic carbon (DOC), microbial biomass C (MBC) and N (MBN), NH_4^+-N and NO_3^--N. We determined vegetation properties including aboveground biomass (AGB), belowground biomass (BGB) and species richness. Details are shown in Additional file 1: Methods S1.

Nematode data

Nematode body size analysis

Soil nematodes were extracted from 50 g fresh soil using a modified cotton-wool filter method (Oostenbrink 1960). The extracted nematodes were stored in a 4% formalin solution. After counting the total number of nematodes in each sample, at least 100 individuals (if available) were randomly selected and identified to their genus level. Based on their feeding habits and colonizer-persister values (*cp* 1–5), nematodes were classified into four main trophic groups: bacterivores, fungivores, plant parasites, and omnivores-predators (Bongers 1990; Yeates et al. 1993). The mean fresh body mass (μg) of each nematode genus was taken from the publicly available database (http://nemaplex.ucdavis.edu). The CWMs of body size (μg) of the total nematode community and each trophic group were calculated as follows:

$$CWM = \sum_{i=1}^{N} p_i x_i,$$

where p_i is the relative abundance of individuals of genus i and x_i the mean fresh body mass (μg) of genus i (Andriuzzi et al. 2020; Garnier et al. 2004).

Nematode metabolic carbon analysis

Nematode production C and respiration C are the two components of soil nematode metabolic C (Ferris 2010). Production C (P_i) was calculated as below:

$$P_i = (N_i \times 20\% \times 52\% \times W_i \times 1000)/m_i,$$

where N_i is the abundance of genus i in 1 g dry soil; W_i is fresh body mean (μg) mass of genus i; m_i is the *cp*-class of genus i; 20% is the conversion coefficient from fresh body mass of nematodes to dry mass (Persson et al. 1980); 52% represents the proportion of carbon in the dry mass (Persson 1983), and 1000 is the conversion coefficient from μg to ng. Respiration C (R_i) was calculated as follows:

$$R_i = N_i \times (W_i \times 1000)^{0.75} \times 0.273,$$

where N_i is the abundance of genus i in 1 g dry soil; W_i the mean fresh body (μg) mass of genus i; 1000 the conversion coefficient from μg to ng; 0.75 a regression parameter (Atkinson 1980; Ferris 2010), and 0.273 the relative molecular weight of C in CO_2 (12/44 = 0.273).

The metabolic C of four trophic groups and total nematodes was determined by calculating and summing the production C and respiration C of each nematode genus, respectively.

CUE of nematodes was calculated as described by Luo et al. (2021) as shown below:

$$CUE = (\Sigma Production\text{-}C_{i)})/(\Sigma Production\text{-}C_i + \Sigma Respiration\text{-}C_i),$$

where the Σ *Production-C*$_i$ is the sum of production C of genus i in respective trophic groups and Σ *Respiration-C*$_i$ the summary of respiration C of genus i in the respective trophic groups.

Statistical analysis

The effects of changes in precipitation intensity and N addition on environmental factors (including pH, SM, SOC, TN, TP, DOC, MBC, MBN, NH_4^+-N, NO_3^--N, AGB, BGB and species richness), nematode production C, nematode respiration C, CUE, and CWM mass were analyzed using mixed-effect models. The environmental factors, nematode production C, nematode respiration C, CUE, and CWM mass were the response variables. Precipitation intensity, N addition, and their interactions as fixed effects and blocks as random effects were used. The normality of the response variables was assessed using the Shapiro–Wilk test. The data for the response variables were transformed using natural logarithms before analysis to improve normality. Two-way analysis of variance (ANOVA) was used to analyze precipitation intensity, N addition, and their interactive effects on nematode production C, nematode respiration C, CUE, and CWM mass. Linear regression was used to reveal relationships between SM and CWM mass and relationships between CWM mass and CUE through trophic groups and total nematodes. The Mantel test was used to determine the correlations between CWM, CUE, and environmental factors. The "plspm" package in R was used to conduct partial least squares path modeling (PLS-PM) to quantify direct or indirect contributions among latent variables including soil moisture, soil pH, soil, and vegetation properties.

(See figure on next page.)

Fig. 2 The responses of community-weighted mean (CWM) mass of total nematodes and trophic groups to precipitation intensity with (N10) and without N addition (N0) (**A**–**E**). Relationships between CWM mass and soil moisture are shown from **F**–**J**. Error bar means standard error (S.E.)

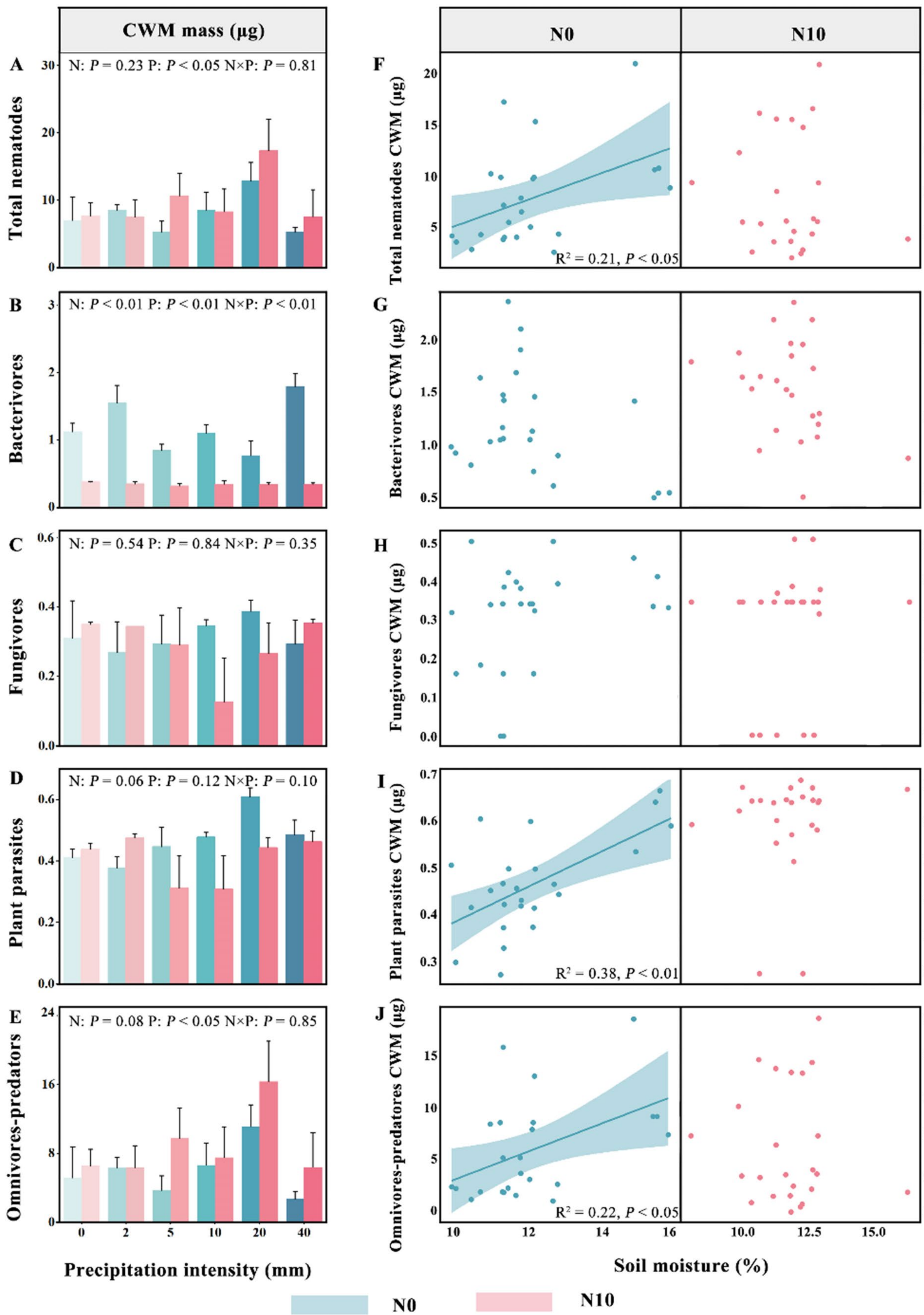


Fig. 2 (See legend on previous page.)

Table 1 Effects of altered precipitation intensity on production carbon of total nematodes and trophic groups with and without N addition

N addition	Precipitation intensity (mm)	Nematodes production carbon ng C per g dry soil Nem-C	BF-C	FF-C	PP-C	OP-C
N0	0	250.39 ± 29.94	207.38 ± 30.73	1.34 ± 0.74	3.56 ± 0.49	38.10 ± 4.13
	2	416.74 ± 47.28	317.82 ± 47.92	2.72 ± 1.80	6.00 ± 1.15	90.20 ± 5.41
	5	351.03 ± 32.80	241.11 ± 29.96	4.71 ± 1.49	21.50 ± 4.05	83.71 ± 35.06
	10	592.28 ± 65.57	333.28 ± 5.93	21.48 ± 1.26	54.93 ± 3.38	182.60 ± 58.84
	20	1013.34 ± 78.39	181.27 ± 22.18	24.00 ± 3.66	52.32 ± 9.22	755.74 ± 102.56
	40	1200.74 ± 97.59	1106.39 ± 82.25	23.21 ± 3.77	35.96 ± 5.85	35.19 ± 16.35
N10	0	79.76 ± 12.97	20.57 ± 3.01	2.33 ± 0.53	8.29 ± 2.05	48.57 ± 14.56
	2	76.67 ± 10.00	11.32 ± 1.00	1.57 ± 0.27	17.61 ± 2.30	46.17 ± 11.59
	5	180.69 ± 25.87	19.97 ± 4.72	4.91 ± 1.39	2.79 ± 0.99	153.00 ± 24.83
	10	77.97 ± 7.48	30.48 ± 3.84	0.14 ± 0.14	2.40 ± 1.47	44.95 ± 6.27
	20	717.97 ± 233.16	34.39 ± 6.11	3.02 ± 1.71	17.62 ± 4.05	662.93 ± 241.24
	40	154.63 ± 19.12	95.11 ± 6.53	3.65 ± 1.09	10.88 ± 3.11	44.98 ± 17.85
ANOVA	N addition (N)	80.09***	403.73***	87.93***	71.57***	0.47
	Precipitation (P)	23.34***	74.22***	16.55***	16.62***	22.56***
	N × P	8.17***	53.74***	17.75***	18.98***	0.48

Mean and Standard Error values of four replicates are presented. Nem-C, BF-C, FF-C, PP-C, and OP-C represent the production carbon of total nematodes, bacterivores, fungivores, plant-parasites, and omnivores-predators, respectively. N0 and N10 represent control and N addition treatments (10 g N m^{-2} yr^{-1}). ***$P < 0.001$

Table 2 Effects of altered precipitation intensity on respiration carbon of total nematodes and trophic groups with and without N addition

N addition	Precipitation intensity (mm)	Nematodes respiration carbon ng C per g dry soil Nem-C_{CO2}	BF-C_{CO2}	FF-C_{CO2}	PP-C_{CO2}	OP-C_{CO2}
N0	0	167.00 ± 15.64	92.03 ± 12.52	3.02 ± 0.97	6.08 ± 0.72	65.87 ± 8.98
	2	282.70 ± 16.94	150.69 ± 4.73	3.38 ± 2.18	11.69 ± 1.98	116.94 ± 21.53
	5	228.88 ± 18.66	111.92 ± 14.15	7.69 ± 2.82	32.26 ± 7.22	77.02 ± 16.23
	10	476.38 ± 61.08	145.91 ± 2.09	35.70 ± 2.27	78.88 ± 5.66	215.89 ± 55.56
	20	1269.63 ± 61.57	140.53 ± 13.42	41.39 ± 4.85	84.79 ± 8.45	11,002.92 ± 50.63
	40	556.82 ± 41.02	412.26 ± 16.71	35.81 ± 6.38	54.40 ± 8.55	54.35 ± 24.65
N10	0	90.76 ± 11.84	24.42 ± 3.52	2.91 ± 0.67	11.16 ± 4.47	52.26 ± 13.45
	2	93.53 ± 12.09	13.44 ± 0.86	1.92 ± 0.33	24.88 ± 6.13	53.28 ± 12.33
	5	196.08 ± 29.44	25.56 ± 5.79	2.42 ± 0.86	5.53 ± 1.97	162.58 ± 30.32
	10	95.12 ± 6.52	36.08 ± 3.31	0.31 ± 0.31	4.54 ± 2.51	54.19 ± 4.21
	20	679.86 ± 197.63	44.21 ± 5.71	2.00 ± 1.07	33.04 ± 6.35	600.61 ± 204.14
	40	202.35 ± 17.05	119.04 ± 5.02	4.72 ± 1.48	18.63 ± 5.57	59.96 ± 16.44
ANOVA	N addition (N)	50.59***	621.18***	150.42***	80.60***	5.81*
	Precipitation (P)	44.99***	143.42***	23.60***	23.40***	39.24***
	N × P	5.11***	40.57***	23.91***	18.79***	3.44*

Mean and Standard Error values of four replicates are presented. Nem-C_{CO2}, BF-C_{CO2}, FF-C_{CO2}, PP-C_{CO2}, and OP-C_{CO2} represent the respiration carbon of total nematodes, bacterivores, fungivores, plant-parasites, and omnivores-predators, respectively. N0 and N10 represent control and N addition treatments (10 g N m^{-2} yr^{-1}). *represents $P < 0.05$, ***$P < 0.001$

Results

Nematode body size and metabolic carbon

Heavy precipitation intensity (20 mm) significantly increased the CWM mass of total nematodes and omnivores-predators (Fig. 2A, E, $P < 0.05$). N addition strongly decreased the CWM mass of bacterivores (Fig. 2B, $P < 0.01$), and this reduction was the lowest under the heavy precipitation intensity treatment (20 mm) (N addition × precipitation interaction, Fig. 2B, $P < 0.01$).

Precipitation intensity and N addition strongly affected the production and respiration C of total nematodes and different trophic groups. Higher precipitation intensities promoted the production and respiration C of total nematodes and different trophic groups. N addition significantly decreased the production and respiration C of total nematodes and bacterivores across all precipitation intensities. N addition significantly decreased the production and respiration C of fungivores and plant parasites under moderate (10 mm), heavy (20 mm), and extreme precipitation intensities (40 mm) (Tables 1 and 2).

Both precipitation intensity and N addition significantly influenced the CUE of total nematodes and bacterivores (Fig. 3A, B), and most of their lower values occurred with N addition. There were significant interactive effects between N addition and precipitation intensity on the CUEs of bacterivores and fungivores (Fig. 3B, C, $P < 0.01$).

Relationships between soil nematodes and environmental factors

Based on the results of the regression analysis, the CWM masses of total nematodes, plant parasites, and omnivores-predators were found to correlate with SM without N addition (Fig. 2F, I and J). The CWM mass of bacterivores was significantly correlated with pH ($P < 0.01$), AGB ($P < 0.01$), MBC ($P < 0.01$), and a relatively weak but significant correlation with TP and BGB ($P < 0.05$). There was a significant correlation between CWM mass of fungivores and BGB ($P < 0.01$). The CWM masses of omnivores-predators and total nematodes increased with an increasing DOC ($P < 0.01$). CUE of bacterivores was significantly correlated with pH ($P < 0.01$), MBC ($P < 0.01$), MBN ($P < 0.01$), AGB ($P < 0.01$), and BGB ($P < 0.01$), whereas a relatively weak but significant correlation existed with TP and NO_3^--N ($P < 0.05$). CUE of fungivores and omnivores-predators was positively correlated with BGB and DOC, respectively ($P < 0.05$). CUE of total nematodes correlated with pH ($P < 0.01$), MBC ($P < 0.05$), and AGB ($P < 0.05$).

Relationships between body size and metabolic C of soil nematodes

There were significant positive responses of the CUEs of total nematodes, bacterivores, fungivores, and omnivores-predators to their corresponding CWM masses with N addition (Fig. 3F, G, H and J). The partial least squares path modeling (PLS-PM) could explain 72% of the variance in the nematode CUE ($R^2 = 0.72$, Fig. 4B). N addition was negatively and indirectly associated with the nematode CWM via negatively associating with pH and plant properties. Moreover, N addition had a negative and indirect effect on nematode CUE through its adverse effect on pH values. Precipitation intensity was positively and indirectly associated with nematode CWM by positively correlating with DOC and soil moisture. In addition, nematode CWM had a direct and positive effect on nematode CUE.

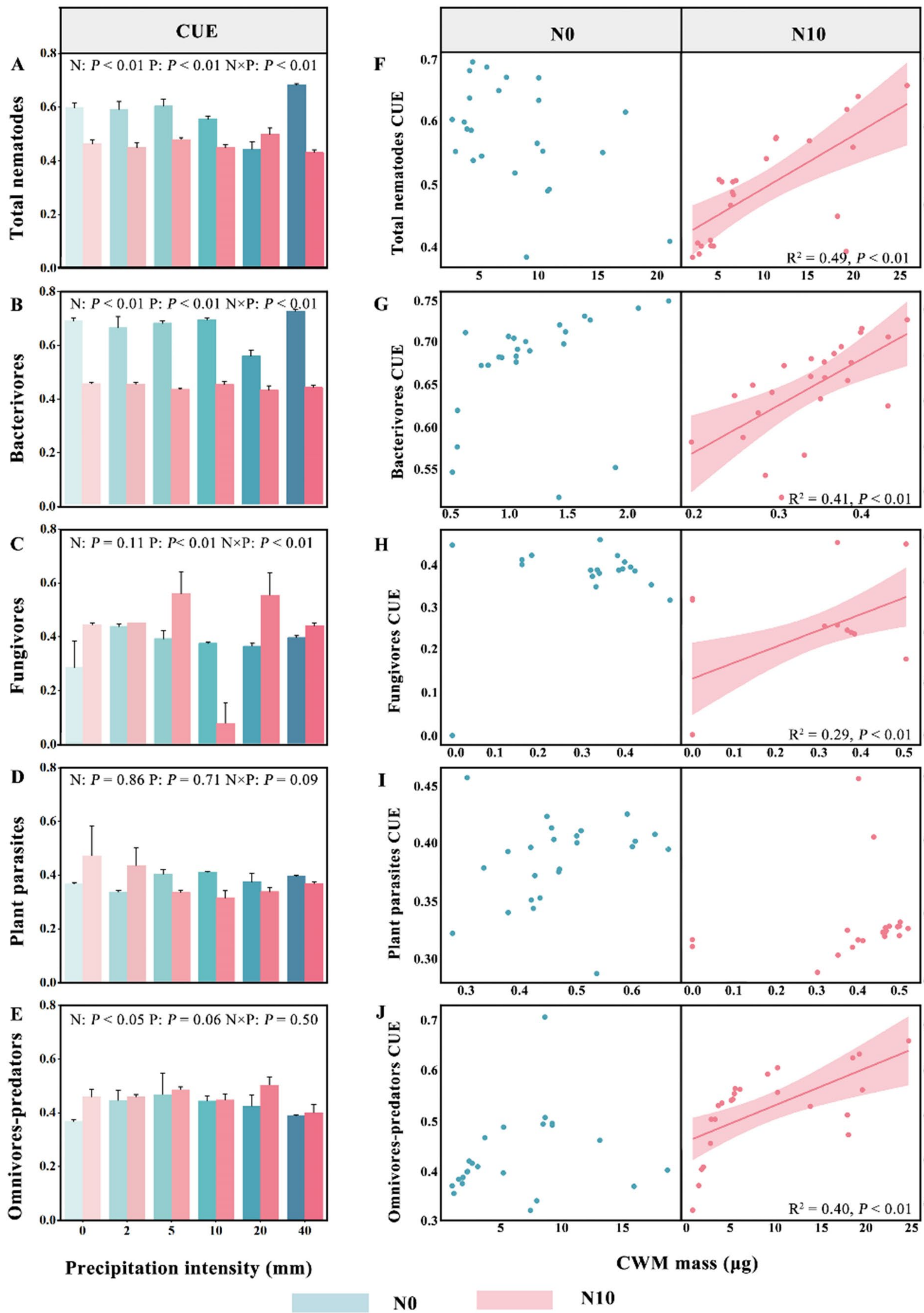
Discussion

Although aboveground animals often show trophic group- and size-based sensitivities to environmental changes, it remains unknown whether the same pattern applied to belowground fauna communities remains unknown. In this study, we used the CWM approach to investigate the responses of total and trophic group nematodes to altered precipitation intensity and N addition. Precipitation intensity-induced increase in soil moisture (SM) was a direct physical effect that improved nematode body size at the community level without N addition. High trophic level nematodes and plant parasites exhibited more pronounced changes in body size in response to SM variation than micro-feeding nematodes. Notably, variations in nematode body size influenced metabolic C with N addition. Therefore, our results suggest that climate change may affect the body size within nematode trophic groups, potentially impacting ecosystem functions, such as carbon cycling and sequestration.

Heavy precipitation intensity increased the CWM mass of total nematodes and omnivores-predators without N addition. Body size shifts in nematode communities are partly or largely attributed to the responses of omnivores-predators (Niklaus et al. 2003; Zhao et al. 2015), which include large and sensitive taxa, resulting in an

(See figure on next page.)

Fig. 3 The responses of carbon use efficiency (CUE) of total nematodes and trophic groups to precipitation intensity with (N10) and without N addition (N0) (**A**–**E**). Relationships between CUE and community-weighted mean (CWM) mass are shown from **F** to **J**. Error bar means standard error (S.E.)



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increase in the total nematode CWM mass. SM content was higher under heavy precipitation intensity treatment than under the other treatments (Additional file 1: Fig. S1), which is partly consistent with the first hypothesis that larger precipitation events (larger precipitation intensity with low frequency) can increase the SM content. Increased precipitation intensity leads to deeper penetration of SM and less evaporation loss, contributing to greater soil water retention and further higher SM content (Papatheodorou et al. 2020). Nevertheless, a comparable increase was not observed under the extreme precipitation intensity treatment. This discrepancy can be attributed to the extended dry interval, leading to a higher overall SM content (Heisler-White et al. 2008).

CWM mass of omnivores-predators was positively associated with the SM content. This finding supports our first hypothesis and suggests that large-body nematodes benefit from higher water availability. Mechanistically, nematodes require water-filled habitat space in proportion to their size (Wallace 1968), and more water-filled soil space enables larger nematodes to survive. Although high-trophic-level predators may be particularly important in driving body size shifts in animal communities (O'Gorman et al. 2017), we found a stronger response in plant parasites to SM, suggesting that plant parasites have a stronger ecological association with water availability than soil microfeeding nematodes. Other morpho-functional traits (e.g. parasitic types: endo- or ectoparasites) can offset the positive relationships between the body size of plant parasites and resource availability (Verschoor et al. 2001). The DOC content was found to be positively correlated with the CWM of omnivores-predators (Fig. 4). This correlation can be explained by the fact that a high organic carbon content positively drives nematode CWM mass (Andriuzzi and Wall 2018; Andriuzzi et al. 2020). The increase in the CWM mass with increased DOC may originate from a more complex food web that supports a high proportion of larger and high-trophic-level nematodes (Verschoor et al. 2001).

Nematode activity is an important factor affecting the nematode metabolic C calculations (Sohlenius 1979; Ekschmitt et al. 1999; Verschoor 2002). In this study, we found that the C metabolism of the soil nematode community in the temperate grassland varied under different precipitation intensities. In specific, the production and respiration C of trophic groups and total nematodes were significantly higher under heavy precipitation and/or extreme precipitation intensity treatments (Tables 1 and 2), suggesting that stronger precipitation intensity (larger amount and less frequent) might be favorable for nematode production and respiration of C, and extreme precipitation intensity (40 mm) did not suppress nematode C metabolism (Table 2).

We assumed that a smaller body size would result in reduced CUE. This hypothesis was supported by the fact that body size, particularly when expressed by CWM mass, was strongly correlated with the CUEs of all nematodes and all trophic groups, except for plant parasites. As the metabolic C determination considers both body size and absolute abundance, body size may be an important driving factor for nematode metabolic C (Lu et al. 2023). However, significant positive relationships between body size and metabolic C were observed only with N addition. This is partially consistent with the third hypothesis, which states that N addition alters the response of nematodes to precipitation regime changes. This was also supported by the results that N addition decreased CWM mass of bacterivores across all the precipitation intensity treatments. The changes induced by N addition, including soil nutrients and the environment, may affect the C partitioning between production and respiration components (Ferris et al. 2012). In the present study, N addition significantly reduced the pH values for all precipitation intensities (Additional file 1: Fig. S1). A previous study demonstrated that N addition largely offsets the positive effects of increased precipitation intensity caused by soil acidification (Cui et al. 2022). These results together support the idea that body size variation is an adaptive strategy to cope with a period of resource shortage or environmental deterioration (e.g. soil acidification), which may further result in a decrease in energy expenditure and metabolic rate (Alonso-Alvarez and Tella 2001). These changes in nematode CUE are likely to have crucial implications for global C cycling and prediction of future climate scenarios.

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Fig. 4 The nematode CWM mass and CUE were related to environmental factors by partial Mantel tests (**A**). Partial least squares path modeling (PLS-PM) showing the effects of N addition and precipitation intensity on nematode CUE (**B**). Plant was indicated by AGB, BGB and species richness. Numbers adjoining the arrows indicate path coefficients, and the arrow width is proportional to the strength of the association. Red arrows represent significant positive relationships and blue arrows represent significant negative relationships ($P < 0.05$). R^2 values indicate the variance of variables accounted for by the model. Community-weighted mean = CWM, carbon use efficiency = CUE, soil moisture = SM, soil organic carbon = SOC, dissolved organic carbon = DOC, total soil nitrogen = TN, total soil phosphorus = TP, microbial biomass carbon = MBC, microbial biomass nitrogen = MBN, aboveground biomass = AGB, belowground biomass = BGB

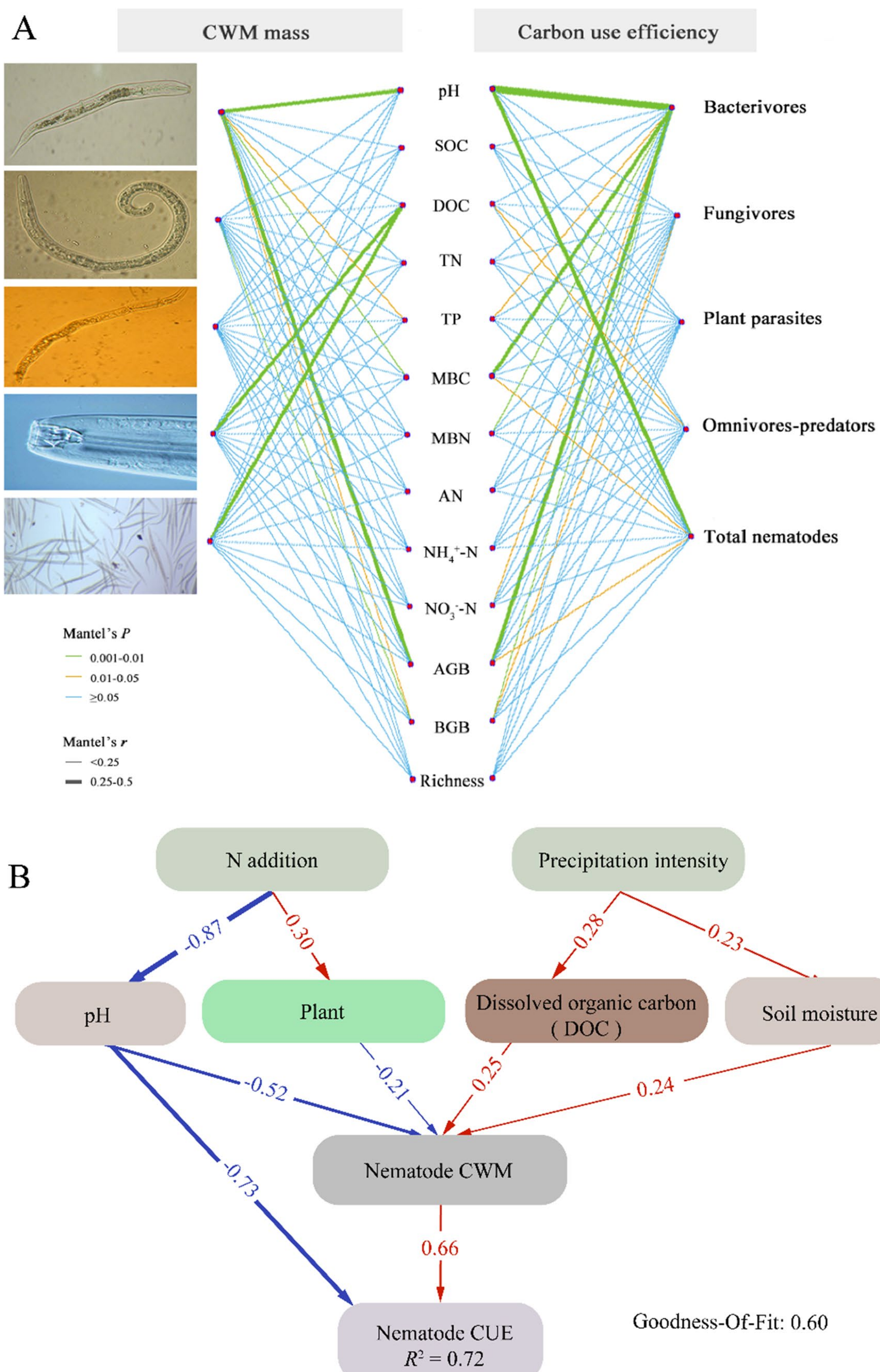

Fig. 4 (See legend on previous page.)

Conclusions

Our findings suggest that heavy precipitation improves soil moisture content, and soil water availability may shape omnivores-predators and plant-parasite body size structures without N addition. Large-bodied soil fauna and plant feeders in the soil food web may be more sensitive to altered precipitation regimes, such as drought or extreme rainfall. The production and respiration components of nematode trophic groups provide a quantitative metric to analyze the metabolic C of soil nematodes. Variations in the nematode CWM mass drove the CUE to change with N addition. Our study demonstrated that the interactive effects of altered precipitation regimes and N deposition changed the metabolic C content of soil nematodes by affecting body size. Explorative studies, such as manipulative experiments, are needed to identify traits underlying size-related effects and to investigate how they affect the CUE of nematodes. These efforts may increase our understanding of how future changes in precipitation regimes and N deposition may alter soil nematode communities in grassland ecosystems.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-024-00484-x.

Additional file 1: Fig. S1. Responses of soil environment (**A**), soil nutrients (**B**) and vegetation properties (**C**) to precipitation intensity with (N10) and without N addition (N0). Soil organic carbon = SOC, total soil nitrogen = TN, total soil phosphorus = TP, dissolved organic carbon = DOC, microbial biomass carbon = MBC, microbial biomass nitrogen = MBN, AN = Alkali-hydro nitrogen, aboveground biomass = AGB, belowground biomass = BGB.

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Author contributions

SC: conceptualization, methodology, writing—review & editing, investigation. XM: formal analysis, data curation, writing—review & editing. GZ: review & editing, project administration, funding acquisition.

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Availability of data and materials

The datasets analyzed in the study can be obtained via the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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