Contents lists available at ScienceDirect

# Geoderma

journal homepage: www.elsevier.com/locate/geoderma



Ziqi Guo<sup>a</sup>, Peng Li<sup>e</sup>, Lihui Ma<sup>a,b,\*</sup>, Xiaomei Yang<sup>c,d</sup>, Jinqiu Yang<sup>a</sup>, Yang Wu<sup>a</sup>, Guobin Liu<sup>a,b</sup>, Coen J. Ritsema<sup>d</sup>, Violette Geissen<sup>d</sup>

<sup>a</sup> State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University, Yangling 712100, China

<sup>b</sup> Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, China

<sup>c</sup> College of Natural Resources and Environment, Northwest A&F University, 712100 Yangling, China

<sup>d</sup> Wageningen University & Research, Soil Physics and Land Management, POB 47, NL-6700 AA Wageningen, Netherlands

<sup>e</sup> Chendu Engineering Corporation Limited, Power China, Chendu 610072, China

ARTICLE INFO

Handling Editor: Y. Capowiez

Keywords: Microplastics Crop growth Cascading effects Functional traits Soil health

### ABSTRACT

Microplastics (MPs) is a major threat to agroecosystems. Their accumulation and impacts should be evaluated to advance our understanding of soil function and health. Uncovering the role of cascade effects in regulating crop growth is crucial to understanding the link between MPs disturbance and environmental functions. Therefore, we aimed to assess how the cascade changes between (non-) biological factors and functional traits of maize regulate the response of maize growth to MPs in different nutrient soil environments. We found that soil dehydration induced by MPs may disrupt the balance of the physiological status of maize, negatively affect photosynthetic performance, and enhance competition among organisms for limited nutrients. However, root-responsive nutrient cues with a high degree of tectonic freedom allowed adaptive phenotypic plasticity to occur, masking the negative effects of MPs. In nutrient-rich soil environments, moderate and high intensity (>0.5 %) MPs disturbances initiated root nutrient foraging activities, and maize tended to decrease its cost of investing in root construction, i.e., increasing specific root length (SRL) to promote its own growth. The growth of maize was mainly characterized by increases in the belowground biomass (BGB, 7.11 to 20.81 g) and aboveground biomass (AGB, 61.11 to 118.26 g). Our study suggests that a cascade effect between environmental factors initiated by MPs and the functional architecture of the maize root system drives maize to regulate its growth by responding to nutrient cues. These findings will help to ensure food security, formulate environmental risk management policies and protect soil health, especially in the context of future agriculture.

### 1. Introduction

Microplastics (MPs, plastics that are <5 mm) are an emerging anthropogenic stressor widely distributed in terrestrial ecosystems. Thousands or even tens of thousands of MPs particles are estimated to be detected in 1 kg of terrestrial soil (Zhou et al., 2019). Basic soil processes and functions, such as biogeochemical cycling (Machado et al., 2018a), plant mineral nutrients (Machado et al., 2019), and hydrological properties (Guo et al., 2022) have been or will likely be affected by MPs. Generally, MPs have positive, negative, or no effect on the soil ecological processes (Machado et al., 2018b; Khalid et al., 2020; Gao et al., 2022). We lack a predictive understanding of MPs' ecological functions and characteristics, such as their environmental preferences, effect sizes, and potentials, in complex terrestrial environments. Terrestrial ecosystems contain more MPs than the ocean, and they exert greater pollution pressure (Yang and Gao, 2022). The ongoing accumulation of MPs in terrestrial ecosystems may have unpredictable ecological consequences, such as biased effects on soil water movement, nutrient cycling and plant growth (Rillig, 2012; Machado et al., 2018a). However, the interaction between MPs and soil processes is still being explored. Therefore, the accumulation and impacts of MPs should be expeditiously evaluated to advance our understanding of soil function and health.

E-mail address: gjzmlh@126.com (L. Ma).

https://doi.org/10.1016/j.geoderma.2023.116759

Received 7 June 2023; Received in revised form 25 November 2023; Accepted 15 December 2023

Available online 19 December 2023





<sup>\*</sup> Corresponding author at: State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University, Yangling 712100, China.

<sup>0016-7061/© 2023</sup> The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC license (http://creativecommons.org/licenses/by-nc/4.0/).

Uncovering the underlying mechanisms that support crop growth and the biophysical and other processes involved is essential to predict the link between environmental disturbances and ecological functioning. Environmental limitations are usually caused by (non-) biological factors, such as temperature, water, and nutrients, and their interactions with organisms (Strand and Weisner, 2004). However, crops have extraordinary environmental adaptations and growth homeostasis (Qiao et al., 2022), and their mechanisms to mitigate disturbances should be researched. Functional traits, a key link in ecosystem cascade effects, reflect crop behavior to increase nutrient acquisition mainly by adjusting the state of developmental and physiological responses (Giehl and von Wiren, 2014), including physiological traits (photosynthetic performance) and nutritional traits (root structure). Changes in the functional structure of the root system may indirectly respond to disturbances in MPs through changes in mean diameter and length that drive adjustments in crop nutrient acquisition strategies (Alimi et al., 2018). For example, Pehlivan and Gedik. (2021) showed that maize shortens its root system in response to disturbances in MPs, affecting the whole-plant metabolism and ultimately hampering its growth.

With increasing MPs residues, they may greatly threaten the functions and services of cultivated soil (Zhao et al., 2022). Cultivated soil is often improved by fertilization to obtain stable and high-yield crops, so MPs may be exposed to multi-nutrient cultivated soil (Liu et al., 2022a). The strong correlation between fertilization treatments and soil physical structure, nutrient content, and (micro) biological processes suggests that these changes may regulate the effects of MPs on soil ecosystem functions (Zhao et al., 2019). Crop functional traits and soil ecosystem functions are closely related (Valencia et al., 2018), but the response of functional traits to poor or fertile soil environments with comparative limiting factors, especially in the soil environment where MPs interference exists, remains unknown (Zhang et al., 2023). In addition, MPs diversity also provides additional evidence to explore stressors affecting soil function and services. The relative contribution of different particle sizes and concentration combinations, and the difference of MPs types can explain the different effects of MPs on crop growth. For example, Ingraffia et al. (2022) showed that disturbance of MPs combinations in a controlled pot experiment impacted maize growth. However, Gao et al. (2022) found that combinatorial disturbances positively affected maize plant performance and morphological characteristics. Increasing evidence shows that MPs affect plant growth and production, but the plant response also greatly depends on the type of MPs (Yang and Gao, 2022). Polypropylene is a common residual plastic type in agricultural soil, which decomposes slowly in soil. It may give priority to microorganisms by increasing the ratio of carbon to nitrogen in soil, and finally affect plant growth (Zhang et al., 2022a). However, a recent study gives evidence to the contrary, reporting the positive effects of high density polyethylene and biodegradable polylactic acid on plant growth (Yang et al., 2021). Numerous knowledge gaps limit our understanding of the effects of nutrient changes and MPs disturbances on agroecosystems, thus limiting our ability to accurately predict the ecological consequences of MPs.

Therefore, we selected sandy soils for a pot incubation experiment to clarify whether the combined effects of MPs and soil nutrients on plant growth are mediated by cascading effects between (non-) biotic factors and crop functional traits, including photosynthetic and nutritional traits. We expected that (1) improvements in soil quality and environment, by multi-nutrient environments, are expected to reduce the negative interference of MPs and ultimately regulate maize nutritional traits; (2) changes in the functional structure of the root system associated with multi-nutrient soil environments explain most of the variation in maize growth parameters when MPs are present.

### 2. Materials and methods

### 2.1. Study site and soil collection

In April 2019, soil samples were collected from Ansai County, Shaanxi Province (107.8–108.3°E and 34.1–34.5°N) (soil properties are detailed in Table 1). The area is at an elevation of about 1068–1309 m asl and has a temperate semi-arid climate with an average annual temperature of 8.8 °C (Sun et al., 2017). After on-site observation and consultation with local farmers, the 0–20-cm layer of clean plow soil (Deng et al., 2018; Liu et al., 2022b), which was vulnerable to natural and human interference and not covered with plastic film, was collected. Specifically, 12 plots of  $5 \times 5$  m were randomly selected in the study area and a buffer zone of 1 m was set between each plot. Soil samples were collected in quadruplicate from 9 ( $1 \times 1$  m) subplots along the diagonal of each plot using soil drills (5 cm in diameter) after removing surface debris and rocks. The collected soil samples were transported to the laboratory, dried at room temperature (25 °C ± 1), screened (2-mm sieve), and stored for subsequent determination and analysis.

### 2.2. MPs and its characteristics

Polypropylene particles (Beijing Youngling-TECH Company, China), which are widely distributed in agricultural soil with high amounts of residue, were selected as the test materials (see Table S1 for details) (Yang and Gao, 2022). In this study, we considered two MPs factors, i.e., concentration and particle size. First, we screened MPs into three particle size grades through 500- (P500), 200- (P200), and 20-µm (P20) sieves (Fig. S1). Then, the three MPs particle sizes were applied to the tested soil at concentrations of 0.5 % (C0.5), 1 % (C1), and 2 % (C2). Previous studies have shown that MPs residues may be as high as approximately 7 %, therefore, the MPs concentrations selected for this study can be considered relevant to anthropogenically disturbed soil environments (Fuller and Gautam, 2016). The MPs were washed twice with hydrochloric acid before the start of the test. We then washed the MPs three times with deionized water. Then, they were placed on an ultrasonic instrument and washed with deionized water for 10 min. After thorough washing, they were dried in an oven at 45 °C, without exposing them to the melting point temperatures of the MPs. After spraying with gold, a scanning electron microscope (SEM) (Nova Nano SEM-450, FEI) operating at an accelerating voltage of 5 kV was used to observe the MPs' morphologies (see Fig. S1A for details).

#### 2.3. Experimental design

Ten MPs combinations, including a control (CK, 0 %), were established to carry out (non-) fertilization treatment (see Table S2 for details). In June 2019, according to the conventional soil improvement measures in the study area, we selected three fertilizers for fertilization treatment, including urea ( $0.15 \text{ g} \cdot \text{kg}^{-1}$ ), Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub> ( $0.1 \text{ g} \cdot \text{kg}^{-1}$ ), and K<sub>2</sub>SO<sub>4</sub> ( $0.2 \text{ g} \cdot \text{kg}^{-1}$ ). Place the manually mixed MPs and soil mixture on a multifunctional oscillator (HY-2A, Guohua, China) and continue to shake for 10 min (Guo et al., 2022). All treatments including control were equivalent. Then, we manually transferred the mixture of each

Table 1				
Basic physical	and chemica	l properties of soil	in the study	area.

1 0								
Soil texture	Clay (%)	Silt (%)	Sand (%)	SOC g/ kg	TN g/ kg	TP g/ kg	TP pH g/ kg	
Sand	2.55	2.73	94.72	2.68	0.13	0.47	8.65	

Clay represents the < 0.002 mm size class; Silt represents the 0.002–0.02 mm size class; Sand represents 0.02–2 mm size class; SOC represents soil organic carbon; TN represents soil total nitrogen; TP represents soil total phosphorus; pH represents soil pH.

combination (15 kg) into pots (bottom diameter: 22 cm; top diameter: 30 cm; height: 30 cm), and planted three maize seeds (Huanong 887, Yangling Seed Company, China) in the center of the pots. After seedling emergence, the two weaker seedlings were removed and one seedling per pot was left for subsequent determination and analysis.

The pots were placed in the climate chamber of the Institute of Soil and Water Conservation, Chinese Academy of Sciences, Yangling, Shaanxi Province, China (AGC-Doo3N, Hangzhou, China) (Fig. S1B). The position of pots were alternated every two weeks. The day and nighttime temperatures were maintained at 28 °C and 25 °C, respectively. The photoperiod (day: night) was 14:10 h, the light intensity was maintained 300  $\mu$ mol·m<sup>-2</sup>·s<sup>-1</sup>, and the relative humidity was kept at 80 %. During the growing period of maize, the soil water content was controlled at (65  $\pm$  5) % of the field water capacity by gravimetric method. Maize was harvested in October 2019 (114 days after planting). During harvest, maize was divided into stems and roots for preservation, which were used to determine root functional traits and growth characteristics. After maize harvest, the soil samples in the flowerpot were passed through a 2-mm sieve and divided into two parts: (1) one part was air-dried naturally and passed through 1-mm and 0.25-mm sieves to analyze soil properties; (2) The other part was stored at 4 °C for subsequent soil microbial characteristics. This study included 20 treatments with 6 replicates in each treatment, with a total of 120 pot samples.

Photosynthetic parameters include net photosynthetic rate (Pn,  $\mu$ mol·m<sup>-2</sup>·s<sup>-1</sup>), intercellular carbon concentration (Ci,  $\mu$ mol·mol<sup>-1</sup>), stomatal conductance (Gs, mol·m<sup>-2</sup>·s<sup>-1</sup>), and transpiration rate (Tr, mmol·m<sup>-2</sup>·s<sup>-1</sup>). These photosynthetic performance parameters were measured according to the method provided by Gao et al. (2016). Specifically, the middle of the fully unfolded second (or third) functional leaf of maize (counted from top to bottom) was measured using a portable infrared gas analyzer (Li-6400, Li-COR, Lincoln, NE, USA) between 10:00 a.m. and 11:30 a.m., one day before sample harvesting.

Here, we measured four related maize growth parameters, including plant height (PH), root-shoot ratio (R:S), belowground biomass (BGB), and aboveground biomass (AGB). In addition, the root functions of three related functional traits were measured, including root length (RL), root diameter (RD), and specific root length (SRL). The change in RL reflected different response strategies of maize to nutrient concentration (Giehl and von Wiren, 2014). RD is a sensitive index reflecting the root foraging strategy (Kong et al., 2019). SRL reflects the relationship between the "investment" and "income" of roots, and is usually used to indicate the availability of external resources (Kramer-Walter et al., 2016; Xia et al., 2021). PH was determined by measuring the height of the soil in the pots to the highest point of the maize leaves at natural extension using a tape measure prior to the sampling. For sampling, the maize root system was carefully removed from the soil and rinsed with deionized water. The root system was cleaned of all residue, placed in a sieve (410 µm) and continued to be rinsed with deionized water. Root systems from the same treatment were homogenized in steel containers and three subsamples were randomly selected to detect root traits. The samples were placed flat on transparencies (210 mm  $\times$  297 mm) and scanned using an Epson 4490 scanner (EPSON Inc). RL and RD were determined using a CIA 2.0 image analysis system (CID. Inc., USA) and WinRhizotron root graphical analysis software (Win RHIZO TRON 2008, Regent Instruments, Canada). After scanning, SRL was determined using the measured RL-to-biomass ratio. Then, the BGB and AGB of maize were measured by the dry weight method, that is, the stems and roots of maize were dried in an oven (60 °C) for 72 h and then removed and weighed. R: S was obtained using the root dry weight divided by the branch dry weight.

# 2.4. Measurements of physical and chemical properties of soil

Soil organic carbon (SOC) was determined using the  $H_2SO_4-K_2Cr_2O_7$  method (Nelson et al., 1982). Soil total nitrogen (TN) was determined using the Kjeldahl method (Bremner and Mulvaney, 1982). Soil total

phosphorus (TP) was determined by colorimetric method (digestion with  $H_2SO_4$  and  $HClO_4$ ) (UV-1800, Shimadzu, Japan). Soil available phosphorus (AP) content was determined using the colorimetric method with sodium bicarbonate and molybdenum-antimony (Olsen and Sommers, 1982).

# 2.5. Measurements of dissolved organic matter of soil

We homogenized 40 g of soil by adding 120 mL of distilled water to obtain a soil solution, and the soil solution was placed on a high-speed centrifuge for 10 min (4000 rpm·min<sup>-1</sup>) (Liu et al., 2017). The supernatant was filtered using a 0.45  $\mu$ m cellulose acetate membrane, and the filtered solution was stored frozen for subsequent determination. Soil dissolved organic carbon (DOC) content was determined using a TOC analyzer (Liquid TOC II, Elementar, Germany). Soil total dissolved nitrogen and phosphorus (TDN and TDP) were determined using soil alkaline persulfate digestion-UV spectrophotometry and ammonium molybdate spectrophotometry, respectively (Galhardo and Masini, 2000; Doyle et al., 2004). Soil ammonium nitrogen (NH<sub>4</sub><sup>+</sup>) and soil nitrate nitrogen (NO<sub>3</sub><sup>-</sup>) contents were determined using a continuous flow autoanalyzer (AutoAnalyzer3-aa3, Bran + Luebbe, Germany).

#### 2.6. Measurement of soil microbial characteristics

The chloroform fumigation method was used to measure soil microbial biomass carbon, nitrogen, and phosphorus content (MBC, MBN, and MBP) (Brookes et al., 1982; Vance et al., 1987). According to the method of German et al. (2011), the activities of four extracellular enzymes were determined by the fluorescence microplate method: alkaline phosphatase (ALP),  $\beta$ -1,4-glucosidase (BG), leucine aminopeptidase (LAP), and N-acetyl- $\beta$ -D-aminoglucosidase (NAG). Chen et al. (2020) provided the study with the corresponding assay for enzyme activity. Specifically, microtitre plates were incubated at 25 °C for 0.5 h (ALP), 2 h (LAP and BG), and 4 h (NAG). At the end of the incubation, fluorescence readings were measured using a multifunctional enzyme spectrometer (Spectra Max M2, Molecular Device, California, US).

### 2.7. Statistical analysis

The statistical analyses used for the study were performed in SPSS software (version 21.0; IBM Corp., Armonk, NY, USA) and R environment (version 4.1.3; https://www.r-project.org) (R Core Team, 2019). Firstly, the data are tested for normality and variance homogeneity. When the homogeneity test of variance was passed and significant difference was observed (P < 0.05), the least significant difference test (LSD) was performed on multiple comparisons. Subsequently, two-way analysis of variance (ANOVA) was used to examine the effects of MPs particle size and content on soil properties, microbial characteristics, functional traits, and growth characteristics of maize before and after fertilization. Also, paired t-tests were performed to assess the effects of environmental variables (MPs particle size, content, soil properties, microbial characteristics, and maize functional traits) on maize growth characteristics under different nutrient conditions. While the soil properties included SOC, TN, TP, DOC, TDN, TDP, AP, NH<sub>4</sub><sup>+</sup>, and NO<sub>3</sub><sup>-</sup>, microbial characteristics comprised MBC, MBN, MBP, ALP, BG, LAP, and NAG. Further, maize functional traits mainly included photosynthetic parameters (Pn, Ci, Gs, and Tr) and root traits (RL, RD, and SRL), whereas, its growth parameters consisted of PH, R:S, BGB, and AGB.

Firstly, we used variance partitioning analysis (VPA) to estimate the relative contribution of (non-) biotic factors affecting maize growth under nutrient-poor conditions. Then, we examined the interactions among the environmental factors by correlation analysis. Random forest model (RFM) was used to assess the relative importance of environmental factors affecting maize growth in nutrient-poor soils. In addition, we used Pearson's rank correlation, multiple linear regression, and ANOVA to elucidate the relationship between nutrient-rich

environmental variables and maize growth and to quantify the contribution of the aforementioned environmental factors to maize growth. Also, we used principal component analysis (PCA) to map the effects of environmental variables on maize growth. Subsequently, we determined the importance of environmental variables on maize growth under nutrient-rich conditions by hierarchical partitioning. Finally, to explore the pathways and (potential) drivers of MPs disturbances on maize growth under different nutrient conditions, we applied partial least squares path models (PLS-PMs) to determine the direct and indirect contributions of environmental variables. Two-way ANOVA, LSD, and paired *t*-test were performed using SPSS software. Hierarchical partitioning, PLS-PMs, and multiple linear regression were performed in the R environment using the "plspm" and "relaimpo" software packages, respectively, while Pearson rank correlation, VPA, PCA, and RFM were performed using the "vegan" package and "randomforest" package.

### 3. Results

# 3.1. Effect of MPs disturbance in different nutrient environments on soil properties

With the increase of MPs content, the SOC content increased in both nutritional environments, while the TP and TN did not change significantly (Fig. 1A–C; P < 0.05). Compared with CK, the SOC content of P500 increased significantly from 4.65 to 21.45 g·kg<sup>-1</sup> in the nutrient-rich environment (Fig. 1A; P < 0.05). Further, the DOC content considerably decreased in the nutrient-poor environment; however, there was no significant change in the nutrient-rich environment (Fig. 1D; P < 0.05). In addition, the SOC and DOC contents in both soil environments increased markedly with increasing MPs particle size (Fig. 1A and D; P < 0.05). Compared with CK, the contents of SOC and DOC in C2 increased significantly from 4.65 to 21.45 g·kg<sup>-1</sup> and 51.37 to 88.1 mg·kg<sup>-1</sup>, respectively (Fig. 1A and D; P < 0.05). We also observed the independent and interactive effects of fertilization, MPs content and particle size on soil properties (Table 2). Among them,



**Fig. 1.** Effect of MPs on soil properties under different nutrient conditions. (A) Represents the change of soil organic carbon (SOC), (B) represents the change of soil total nitrogen (TN), and (C) represents the change of soil total phosphorus (TP). (D) Represents changes in dissolved organic carbon (DOC), while (E) and (F) represent changes in total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP), respectively. (G) Represents the change of available phosphorus (AP), while (H) and (I) represent the change of ammonium nitrogen (NH<sup>+</sup><sub>4</sub>) and nitrate nitrogen (NO<sup>-</sup><sub>3</sub>), respectively. Capital letters indicate the difference after treatment with MPs with the same concentration and different particle sizes, lowercase letters indicate the difference after adding MPs with the same particle size and different concentrations, and \* indicates the difference before and after fertilization (P < 0.05). N means no fertilization treatment (Nutrient-poor conditions). P20 represents 20 µm MPs treatment; P200 represents 200 µm MPs treatment; P500 represents 500 µm MPs treatment. CK (white): Control; C0.5 (blue): 0.5 % MPs addition; C1 (yellow): 1 %; C2 (red): 2 %. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2

P-values and contribution of independent factors (Fertilization, Content, and Size) and their interactions to various parameters studied by three-way ANOVA.

Variables	bles Fertilization		Content Size			Fertilization *Content		Fertilization * Size		Content *		Fertilization *		Residual	
										Size		Content * Size			
	Р	%	Р	%	Р	%	Р	%	Р	%	Р	%	Р	%	%
SOC	< 0.01	14.36	< 0.01	11.42	< 0.01	63.40	< 0.05	0.30	< 0.01	2.99	< 0.01	6.88	< 0.01	0.57	0.07
TN	< 0.05	18.68	< 0.01	23.28	0.58	2.30	0.61	2.09	< 0.05	13.18	0.60	2.86	< 0.01	33.43	4.17
TP	< 0.01	83.60	0.55	0.41	< 0.01	4.63	0.66	0.28	< 0.01	6.94	< 0.01	3.32	0.92	0.15	0.67
AP	< 0.01	98.13	0.09	0.17	< 0.01	0.50	< 0.05	0.25	< 0.01	0.55	0.05	0.17	0.06	0.16	0.07
DOC	< 0.01	25.62	0.25	0.84	< 0.01	34.65	< 0.01	12.43	< 0.01	15.07	< 0.05	1.65	< 0.01	9.14	0.60
TDN	< 0.01	87.81	0.15	1.34	0.09	1.67	0.18	1.20	< 0.05	2.57	< 0.01	2.99	< 0.05	1.73	0.69
$NH_4^+$	< 0.01	56.69	0.74	0.41	$<\!0.01$	28.03	0.86	0.21	< 0.01	10.57	0.14	2.40	0.92	0.33	1.36
$NO_3^-$	< 0.01	78.24	< 0.01	2.34	$<\!0.01$	5.50	< 0.01	1.92	< 0.01	10.34	0.46	0.23	< 0.01	1.18	0.25
TDP	< 0.01	90.09	< 0.01	1.87	< 0.01	2.39	< 0.05	0.94	< 0.01	2.38	0.38	0.32	< 0.01	1.71	0.30
MBC	0.24	2.95	< 0.01	38.15	< 0.01	22.69	< 0.01	12.48	< 0.05	8.19	< 0.05	5.77	< 0.01	7.69	2.09
MBN	< 0.01	24.39	< 0.05	1.24	< 0.01	34.34	< 0.01	12.78	< 0.01	7.96	< 0.01	11.06	< 0.01	6.87	1.36
MBP	< 0.01	32.33	< 0.01	23.81	< 0.05	4.29	< 0.01	15.55	< 0.05	3.62	< 0.01	10.52	< 0.01	8.86	1.02
ALP	< 0.01	71.85	< 0.01	1.21	< 0.01	3.26	< 0.01	2.90	< 0.01	15.26	< 0.01	2.87	< 0.01	2.59	0.06
BG	< 0.01	14.83	0.07	5.10	< 0.05	7.79	0.11	43.72	< 0.01	4.36	< 0.01	12.86	< 0.01	9.43	1.90
LAP	< 0.01	26.42	< 0.01	10.82	$<\!0.01$	42.09	0.75	0.52	0.17	3.33	0.29	2.33	< 0.01	12.66	1.82
NAG	< 0.01	78.19	< 0.05	1.40	$<\!0.01$	2.28	< 0.01	5.06	< 0.01	6.23	< 0.01	3.39	< 0.01	3.14	0.31
Pn	< 0.01	33.78	< 0.05	31.14	$<\!0.01$	5.31	< 0.01	14.02	< 0.01	13.12	0.29	1.12	0.27	1.42	0.09
Ci	< 0.05	7.95	< 0.05	25.87	$<\!0.01$	40.33	< 0.01	8.62	< 0.01	12.06	0.82	0.93	0.57	1.79	2.46
Gs	< 0.01	60.02	< 0.01	10.93	$<\!0.01$	22.10	0.10	0.40	< 0.01	4.73	< 0.05	1.16	< 0.05	0.49	0.17
Tr	< 0.01	67.86	< 0.01	5.22	$<\!0.01$	19.48	0.45	0.39	< 0.05	1.87	< 0.01	2.96	< 0.01	1.73	0.48
RL	< 0.01	54.24	0.88	0.56	< 0.01	25.86	0.58	2.39	$<\!0.01$	7.33	0.67	2.57	0.65	2.70	4.36
RD	< 0.01	53.57	< 0.05	8.55	< 0.01	15.38	< 0.05	4.69	< 0.01	14.58	0.29	1.76	0.22	1.23	0.24
SRL	< 0.01	22.96	< 0.01	3.49	$<\!0.01$	33.01	< 0.01	16.47	< 0.01	14.22	< 0.01	3.56	< 0.01	5.80	0.49
BGB	< 0.01	40.40	< 0.01	14.50	$<\!0.01$	23.20	< 0.01	11.00	< 0.01	4.10	< 0.01	5.46	< 0.05	1.13	0.22
AGB	< 0.01	54.55	< 0.01	20.10	< 0.01	10.72	< 0.01	5.40	< 0.01	3.65	< 0.05	3.21	< 0.05	2.33	0.04
R:S	< 0.01	66.96	< 0.01	7.77	< 0.01	6.18	0.11	2.53	< 0.01	9.01	0.37	1.19	< 0.01	5.25	1.11
PH	< 0.01	52.23	< 0.01	11.17	$<\!0.01$	17.44	< 0.01	6.70	< 0.01	7.07	< 0.01	3.11	< 0.01	2.25	0.04

Soil properties include SOC, TN, TP, DOC, TDN, TDP, AP,  $NH_{4}^{+}$ , and  $NO_{3}^{-}$ . Microbial characteristics consist of MBC, MBN, MBP, ALP, BG, LAP, and NAG. Maize functional traits consist mainly of photosynthetic parameters (Pn, Ci, Gs, and Tr) and root traits (RL, RD, and SRL). Maize growth parameters included PH, R:S, BGB, and AGB. Size includes 20  $\mu$ m, 200  $\mu$ m, and 500  $\mu$ m. Content includes 0 %, 0.5 %, 1 %, and 2 %. Abbreviations for soil properties, microbial characteristics, functional traits, and growth parameters of maize were applied to the above methods.

Fertilization \* Content (0.30 % and 12.43 %), Fertilization \* Size (2.99 % and 15.07 %), and Fertilization \* Content \* Size (0.57 % and 9.14 %) showed significant interaction effects on SOC and DOC (Table 2).

# 3.2. Effect of MPs disturbance in different nutrient environments on microbial characteristics

The MBC content in both environments showed a decreasing trend with increasing MPs content, while MBN showed a significant decreasing trend only in the nutrient-rich environment (Fig. 2A and B; P < 0.05). Compared with CK, the contents of MBC and MBN in the nutrient-rich environment were significantly decreased. The MBC in P200 decreased from 103.19 to  $68.82\ \text{mg}\,\text{kg}^{-1}\text{,}$  while MBN in P20 decreased from 12.48 to 2.15 mg·kg<sup>-1</sup> (Fig. 2A and B; P < 0.05). In addition, the MBC and MBN contents in both environments increased markedly with increasing MPs particle size (Fig. 2A and B; P < 0.05). Compared with CK, the MBC content in the nutrient-rich C2 treatment decreased significantly, from 103.19 to 68.82 mg·kg<sup>-1</sup> (Fig. 2A; P <0.05). We also observed the independent and interactive effects of fertilization, MPs content and particle size on microbial characteristics (Table 2). Among them, Fertilization \* Content (12.48 % and 12.78 %), Fertilization \* Size (8.19 % and 7.96 %), and Fertilization \* Content \* Size (7.69 % and 6.87 %) showed significant interaction effects on MBC and MBN (Table 2).

# 3.3. Effects of MPs disturbance in different nutrient environments on functional traits of maize

With increasing MPs content, the Pn and Ci of maize decreased in the nutrient-poor soil environment, while only Pn decreased in the nutrient-rich environment (Fig. 3A and B; P < 0.05). Compared with CK, the Pn in the nutrient-rich P500 treatment significantly increased from 24.4 to

25.78 μmol·m<sup>-2</sup>·s<sup>-1</sup> (Fig. 3A; P < 0.05). In addition, both Pn and Ci of maize in the nutrient-poor environment decreased with increasing MPs particle size, while Ci in the nutrient-rich environment increased significantly (Fig. 3A and B; P < 0.05). Compared with CK, the Ci in the nutrient-rich C0.5 treatment increased significantly from 55.72 to 78.57 μmol·mol<sup>-1</sup> (Fig. 3B; P < 0.05). Further, we observed the effects of fertilization, MPs content and particle size on photosynthetic parameters of maize (Table 2). Among them, Fertilization \* Content (14.02 % and 8.62 %) and Fertilization \* Size (13.12 % and 12.06 %) showed significant interactions on Pn and Ci (Table 2).

With the increase in the MPs content, the SRL of maize increased in both environments, but RL and RD did not change significantly in the nutrient-poor environment (Fig. 3E-G; P < 0.05). Compared with CK, the SRL of P200 decreased from 7.33 to 5.88 cm·g<sup>-1</sup> (Fig. 3G; P < 0.05). The RL and RD of P500 increased significantly from 25.12 to 53.73 cm and 0.32 to 0.42 mm·plant<sup>-1</sup>, respectively (Fig. 3E and F; P < 0.05). In addition, fertilization, MPs content, and particle size affected the root traits of maize (Table 2). Among them, Fertilization \* Content (4.69 % and 16.47 %) and Fertilization \* Size (14.58 % and 14.22 %) exhibited significant interaction effects on RD and SRL, while Fertilization \* Size (7.33 %) affected RL (Table 2).

# 3.4. Effects of MPs disturbance in different nutrient environments on maize growth characteristics

The BGB and AGB of maize in the nutrient-rich environment decreased with increasing MPs content (Fig. 4A and B; P < 0.05). Compared with the CK, the BGB and AGB of P500 increased significantly from 7.11 to 20.81 g and 61.11 to 118.26 g, respectively (Fig. 4A and B; P < 0.05). With the increase in the MPs particle size, both BGB and AGB of C0.5 increased significantly from 7.11 to 20.81 g and 61.11 to 118.26 g, respectively (Fig. 4A and B; P < 0.05). With the increase in the MPs particle size, both BGB and AGB of C0.5 increased significantly from 7.11 to 20.81 g and 61.11 to 118.26 g, respectively (Fig. 4A and B; P < 0.05). Further, we observed the



**Fig. 2.** Effects of MPs on microbial characteristics under different nutrient conditions. (A), (B), and (C) represent changes in microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and microbial biomass phosphorus (MBP), respectively. (D) represents the change of alkaline phosphatase (ALP), (E) represents the change of  $\beta$ -1,4-Glucosidase (BG), (F) represents the change of leucine aminopeptidase (LAP), and (G) represents the change of N-acetyl- $\beta$ -D-glucosaminidase (NAG). Capital letters indicate the difference after treatment with MPs with the same concentration and different particle sizes, lowercase letters indicate the difference after adding MPs with the same particle size and different concentrations, and \* indicates the difference before and after fertilization (P < 0.05). N means no fertilization treatment (Nutrient-poor conditions), and F means fertilization treatment (Nutrient-rich conditions). P20 represents 20 µm MPs treatment; P200 represents 200 µm MPs treatment; P500 represents 500 µm MPs treatment. CK (white): Control; C0.5 (blue): 0.5 % MPs addition; C1 (yellow): 1 %; C2 (red): 2 %. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

independent and interactive effects of fertilization, MPs content and particle size on maize growth characteristics (Table 2). Among them, Fertilization \* Content (11.00 % and 5.40 %), Fertilization \* Size (4.10 % and 3.65 %), and Fertilization \* Content \* Size (1.13 % and 2.33 %) also showed significant interactions on BGB and AGB (Table 2).

# 3.5. Drivers of MPs disturbance in different nutrient environments affecting maize growth

The study simulated the effects of biotic (microbial characteristics and functional traits of maize) and abiotic (soil properties and MPs diversity) factors on maize growth in different nutrient environments to explore the main role of MPs interference in regulating the functional traits of maize and mediating its growth in different nutrient environments. The results showed that MPs and photosynthetic parameters contributed more and microorganisms second in explaining the variation in maize growth parameters in nutrient-poor environments (Fig. 5A). Further, correlation analysis also revealed a high correlation between MPs and maize photosynthetic parameters in nutrient-poor environments (Fig. 5B). In addition, Pn and Ci were important variables affecting maize growth characteristics in each of the maize photosynthetic performance parameters assessed (Fig. 5C). This result was confirmed by a simple linear regression between photosynthetic indicators and growth parameters (Fig. 5D). Moreover, this negative effect increased significantly with increasing MPs particle size (Fig. S2).

In multi-nutrient soil environments, we observed that joint changes between soil properties and maize root traits play an important role in regulating maize growth. Further, the soil properties and maize root traits explained the variation in maize growth characteristics (Fig. 6A). When the relationship between soil properties and root traits was considered, there was a significant interaction between the two and that SOC was positively correlated with root traits for each soil property parameter assessed (Fig. 6B). The analysis between soil properties and root traits at different MPs levels showed that maize trait parameters exhibited varying degrees of increase even in the presence of different levels of MPs addition; however, significant changes were observed only in the moderate and high levels of MPs addition (C1 and C2 treatments) (Fig. 3). The pattern of reciprocal response between soil properties and root traits was significant only in >0.5 % MPs disturbance, regardless of the variation in particle size (Fig. S3). In addition, the study examined



**Fig. 3.** Effect of MPs on functional traits of maize under different nutrient conditions. Maize photosynthetic parameters: (A) represents the variation of net photosynthetic rate (Pn), (B) represents the variation of intercellular carbon concentration (Ci), (C) represents the variation of stomatal conductance (Gs), and (D) represents the variation of transpiration rate (Tr). Maize root traits: (E), (F), and (G) represent the changes in root length (RL), root diameter (RD) and specific root length (SRL), respectively. Capital letters indicate the difference after treatment with MPs with the same concentration and different particle sizes, lowercase letters indicate the difference after adding MPs with the same particle size and different concentrations, and \* indicates the difference before and after fertilization (P < 0.05). N means no fertilization treatment (Nutrient-poor conditions), and F means fertilization treatment (Nutrient-rich conditions). P20 represents 20  $\mu$ m MPs treatment; P200 represents 200  $\mu$ m MPs treatment; P500 represents 500  $\mu$ m MPs treatment. CK (white): Control; C0.5 (blue): 0.5 % MPs addition; C1 (yellow): 1 %; C2 (red): 2 %. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the role played by this pattern in maize growth, and the results showed that the variance could be explained more when the root traits of maize were also considered, instead of just soil properties (Fig. 6C and S4). The study was partitioned hierarchically to quantify the contribution of changes in root functional structure to maize growth (Fig. 6D) to explore the relative importance of the pattern in maize growth. Overall, in nutrient-rich soil environments, MPs (>0.5 %) indirectly promoted maize growth by initiating a cascade effect between abiotic soil properties and root traits. The results were further validated by PLS-PMs (Fig. 7).

#### 4. Discussion

### 4.1. MPs disturbance and limited nutrients affect maize growth

Changes in crop growth are the most visual manifestation of environmental disturbances, including MPs (Zhang et al., 2022b). This study found that MPs may be the stress source affecting the photosynthetic capacity and growth of maize when the environmental nutrients are limited, and the interaction between Pn and Ci of maize and the particle

size of MPs is strong (Fig. 3A and B). The main reason for this result may be related to MPs limiting root (water) nutrient uptake and diminishing photosynthetic performance (Zhao et al., 2022). It is reported that MPs directly (physical attachment and chemical derivatives) and indirectly (plant functional traits and microbial competition) affect plant growth (Zhang et al., 2022c). MPs are small, have low density, and are highly hydrophobic, and easily cover the surface of the root system to form a "MPs barrier", which disrupts the normal absorption of water and nutrients by the root system and damages plant growth (Fig. S5) (Boots et al., 2019). Photosynthesis is an important process that characterizes the physiological state of plants; water is the raw material for photosynthesis, having a direct impact, and a lack of water will weaken the photosynthetic intensity and directly affect plant growth (Reich et al., 2018). A previous study reported that MPs disturbance affects soil water movement, with large size MPs accelerating water loss by increasing the number of macropores associated with soil water conductivity (Guo et al., 2022). This study reports similar evidence, that is, when MPs with larger particle sizes are present, the soil water content is low (Fig. S6). When MPs disturbances result in dehydrated soils, this may exacerbate the limited uptake of (water) nutrients by the root system, further



**Fig. 4.** Effect of MPs on growth characteristics of maize under different nutrient conditions. (A) and (B) represent changes in belowground (BGB) and aboveground biomass (AGB) of maize, (C) represents changes in maize plant height (PH), and (D) represents changes in the root shoot ratio (R:S) of maize. Capital letters indicate the difference after treatment with MPs with the same concentration and different particle sizes, lowercase letters indicate the difference after adding MPs with the same particle size and different concentrations, and \* indicates the difference before and after fertilization (P < 0.05). N means no fertilization treatment (Nutrient-poor conditions), and F means fertilization treatment (Nutrient-rich conditions). P20 represents 20 µm MPs treatment; P200 represents 200 µm MPs treatment; P500 represents 500 µm MPs treatment. CK (white): Control; C0.5 (blue): 0.5 % MPs addition; C1 (yellow): 1 %; C2 (red): 2 %. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

affecting the photosynthetic intensity and growth status of the plant.

We also found that the interaction between MPs and microorganisms in nutrient-poor environments was also one of the crucial factors affecting maize growth. Specifically, low concentrations of MPs (0.5 %) attenuated maize growth by enhancing microbial competition for limited nutrients. In addition to nutrient acquisition through the root system, crops often rely on nutrient turnover by microorganisms to ensure their growth (de Jager and Giani, 2021). Competition among organisms for nutrients may be activated when nutrients become limiting (Tiemann et al., 2015). We speculated that 0.5 % MPs indirectly attenuated maize growth by enhancing nutrient competition among microorganisms. Previous studies have reported similar evidence, indicating that MPs can change soil properties and thus affect the activity and function of microorganisms (Lozano et al., 2021). MPs can increase the pore number and aeration of soil, especially in loose sandy soil, and the improvement in the environmental conditions is beneficial to the growth of microorganisms (Sanchez-Monedero et al., 2018). A recent study also found that MPs act as a microbial "thriving circle" in the soil environment, providing more space for microbial growth by widening the ecological niche (Zhu et al., 2022). Thus, low-intensity MPs addition provides, to some extent, favorable growth conditions (air) and sufficient space (ecological niche), which can help microorganisms dominate the limited competition for nutrients. Interestingly, however, the competitive advantage of microorganisms disappeared with increasing MPs concentration (>0.5 %). This phenomenon was evident when soil

disturbance by MPs was further enhanced. Even when a favorable growth environment existed, the absence of an adequate food source weakened microbial growth. At this point, the negative effects of MPs may dominate and weaken maize growth. Although MPs may affect the carbon cycle by becoming soil carbon (Rillig et al., 2021), there is no evidence that MPs can become a source of carbon available to microorganisms in the short term.

# 4.2. Cascading effects of MPs disturbance and soil properties on the functional traits of maize roots

In the MPs–soil system, the complex interaction between (non-) biological factors leads to an apparent negative net effect, which may be due to the inability of environmental collaborators to compensate for the adverse effects of MPs in most cases (Zhao et al., 2019). Roots absorb water and nutrients, which is the basis of plant growth and production (de la Riva et al., 2021). The environmental nutrient availability leads to morphological changes in the roots, and roots often become highly plastic in response to environmental clues (Giehl and von Wiren, 2014). The widespread interference of MPs is currently one of the main knowledge gaps in plant underground ecology. In this study, we selected different MPs interference modes to test the growth status of maize in multi-nutrient environments. We found that the change in the root traits mediated the interaction between MPs and maize growth in the multi-nutrient environment (Fig. 6). The root economic spectrum (RES) is a



**Fig. 5.** Drivers affecting maize growth characteristics under nutrient-poor conditions. (A) Variation partition analysis (VPA) was used to determine the relative contribution of abiotic factors (MPs and soil properties) and biological factors (microbial characteristics and maize photosynthetic performance) to maize growth characteristics. (B) Pearson rank correlation analysis between maize growth characteristics and environmental factors. Red represents negative correlation and blue represents positive correlation. (C) Based on random forest model (RFM) to estimate the contribution of environmental variables to maize growth (MSE increased by %). (D) The relationship between growth parameters and photosynthetic performance (Pn and Ci) of maize was estimated by simple linear regression analysis. Shaded areas represent 95 % confidence intervals. Soil properties (SP), microbial characteristics, photosynthetic performance, root traits (Root), and maize growth characteristics were expressed by the first component of principal component analysis (PCA) (63.75 %, 77.00 %, 58.50 %, 53.29 %, and 66.29 %). SP includes SOC, TN, TP, AP, DOC, TDN, TDP, NH<sup>†</sup><sub>4</sub>, and NO<sup>-</sup><sub>3</sub>. Microbial characteristics include MBC, MBN, MBP, ALP, BG, LAP, and NAG. Photosynthetic performance includes Pn, Ci, Gs, and Tr. Root traits include RL, RD, and SRL. Maize growth characteristics include BGB, AGB, PH, and R: S. Size includes 20  $\mu$ m, 200  $\mu$ m, and 500  $\mu$ m. Content includes 0 %, 0.5 %, 1 %, and 2 %. Abbreviations for SP, microbial characteristics, maize functional traits and growth parameters were applied to the above methods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

common hypothesis in underground ecology, which assumes a balance between conservative (slow foraging) and acquisition (fast foraging) strategies for root resources (Freschet et al., 2010; Reich, 2014). In nutrient-rich environments, combinations of traits disturbed by MPs tend to evolve in the root system, e.g., expensive (low SRL) and cheap (high SRL) roots (Fig. 3G). The two different phenotypic combinations are beneficial for plants to adapt to changing environments, and an increase in MPs interference will promote the evolution of maize roots from resource protection to acquisition. adaptive phenotypic plasticity to occur in response to possible effects of environmental signals on plant growth processes (Ma et al., 2018). This study reports corresponding evidence that the maize root system in a multi-nutrient environment is more inclined to choose resourceconserving economic strategies (low SRL), especially under lowconcentration (0.5 %) MPs perturbation (Fig. 3G). The inconsistency between the external nutrient status and plant growth correlations suggests that root plasticity responses may be largely masked by environmental perturbations, which is consistent with root traits selecting conservative strategies. Water availability is a potentially important

Plant root systems with a high degree of tectonic freedom allow







**Fig. 6.** Drivers affecting maize growth characteristics under nutrient-rich conditions. (A) Variation partition analysis (VPA) was used to determine the relative contribution of abiotic factors (MPs and soil properties) and biological factors (microbial characteristics and root traits) to maize growth characteristics. (B) Based on correlation and optimal multiple regression models the contribution of abiotic factors (particle size, concentration and soil properties) and biological factors (microbial characteristics and root traits) to growth parameters of maize was determined (\*\*\* indicates that the explanation variation is over 40 %). In this study, the correlation between environmental variables and maize growth characteristics was investigated, and the important indicators indicating maize growth parameters were determined. Color represents Pearson correlation, blue represents negative correlation, and red represents positive correlation. Circles of different sizes represent the importance of variables (the proportion of explanatory variables calculated by multiple regression models and variance decomposition). (C) Principal component analysis (PCA) showed the abiotic and biological factors affecting the growth of maize. According to the content of MPs and particle size, the sampling points were colored. (D) Indicate the relative importance of each variable and independently interpret the total changes quantified by applying a hierarchical algorithm. Abiotic and biotic factors were used as explanatory variables, and maize growth characteristics (MGC) were used as response variables. Soil properties (SP), not traits and MGC were expressed by the first component of PCA (66.39 %, 64.14 %, 57.55.77 %, and 79.24 %). SP includes SOC, TN, TP, AP, DOC, TDN, TDP, NH\_4^+, and NO\_3^-. MC includes MBC, MBN, MBP, ALP, BG, LAP, and NAG. PSN includes Pn, Ci, Gs, and Tr. Root traits include RL, RD, and SRL. MGC includes BGB, AGB, PH, and R: S. Size includes 20 µm, 200 µm, and 500 µm. Content includes 0 %, 0.5 %, 1 %, and 2



**Fig. 7.** Partial least squares path models (PLS-PMs) of MPs disturbance affecting maize growth under different nutrient conditions. (see the Discussion section for a detailed description of the conceptual diagram). The model was evaluated using the goodness of fit (GOF). Numbers are the correlation coefficients (correlation coefficients > 0.4 are indicated in bold). Purple and red numbers represent the positive and negative effects of MPs, respectively. The green box on the left shows the effect of MPs disturbance on maize growth under nutrient-poor conditions. The orange box on the right shows the effect of MPs disturbance on maize growth under nutrient-rich conditions. The first component of PCA represents soil properties (63.75 % and 66.39 %), microbial activity (77.00 % and 64.14 %), photosynthetic performance (58.50 % and 67.41 %), root traits (53.29 % and 55.57 %) and maize characteristics (66.29 % and 79.24 %) under poor and rich nutrient conditions. Soil properties include SOC, TN, TP, DOC, TDN, TDP, AP, NH<sup>+</sup><sub>4</sub>, and NO<sup>-</sup><sub>3</sub>. Microbial activity consists of MBC, MBN, MBP, ALP, BG, LAP, and NAG. Maize functional traits consists mainly of photosynthetic performance (Pn, Ci, Gs, and Tr) and root traits (RL, RD, and SRL). Maize characteristics include PH, R:S, BGB, and AGB. Size includes 20 µm, 200 µm, and 500 µm. Content includes 0 %, 0.5 %, 1 %, and 2 %. Abbreviations for soil properties, microbial characteristics and functional traits of maize were applied to the above methods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

factor affecting the underground strategy of plants (Li et al., 2019), while MPs decrease the water-holding capacity of soil (Lozano and Rillig, 2022), which exerts great pressure on soil quality and the plant growth environment. On the other hand, root systems attached with MPs exhibit more restricted water and nutrients uptake, even when weakly disturbed (Boots et al., 2019; Shorobi et al., 2023). When faced with the dual pressures of external nutrient availability and internal nutritional status, maize root systems are more inclined to choose conservative strategies at the expense of reduced growth.

In addition, we found that, compared with a low MPs concentration, moderate and high intensity (>0.5 %) MPs interference initiated the detectable nutrient acquisition behavior of the root system. Consistent with the research hypothesis, we detected a correlation between the changes in root function structure and the positive changes in maize growth parameters (Fig. 6), which provided experimental evidence for nutrient-driven dynamic foraging behavior to promote plant growth. With the enhancement of interference signals, the cost of plant investment in root construction decreased; that is, when MPs interference increased from 0.5 % to 2 %, SRL increased by 212.77 % (Fig. 3G). The

cost of root construction was strongly regulated by the availability of soil resources, including nutrients and water (de la Riva et al., 2021). A rich nutrient environment seems to provide rich nutrient returns, but with increasing MPs attachment to roots, it may be difficult for maize to leave the "nutrient dilemma" (Boots et al., 2019). Spatial heterogeneity in soil nutrients drives plants to evolve an effective mechanism for monitoring and searching for external nutrient patches (Giehl and von Wiren, 2014), and the exploration of "nutrient-rich areas" by roots determines the plant nutrient foraging efficiency (McCormack et al., 2012). Compared with constructing expensive roots, plants with cheap roots can more accurately explore soil nutrient hotspots (Weemstra et al., 2016). After weighing the availability of external nutrients and the status of internal nutrients, plants may prefer a lower-cost root construction mode, that is, fast-renewing and cheap roots (high SRL), to cope with stronger interference frequency (Chen et al., 2021).

Interestingly, our study also identified additional root resource investments, i.e., increases in RD and RL (Fig. 3E and F). Nutrient limitation activates foraging behavior driven by morphological changes in the plant root system by stimulating the elongation of the plant root

system, i.e., by increasing the area of root-soil interaction to sustain plant growth (Giehl and von Wiren, 2014). A previous study also observed that the foraging activity of roots increases with the increase in RD, showing the strongest response signal in resource-rich patches (Kong et al., 2019). The selection of plants to adapt to environmental stress and growth homeostasis may lead to the evolution of root trait combinations (Pellegrini et al., 2023). The co-selection of root traits by MPs disturbances in multi-nutrient environments may have promoted trait correlations in the RES. In addition, coevolution, that is, plants choosing one (or two) trait to cause the evolution of another trait, among underground traits with genetic connection is not surprising (Chen et al., 2021). Root traits, i.e., SRL, RL, and RD, which are strongly correlated with changes in MPs content patterns with general MPs interference, may be one of the trait combinations that aids in the future understanding of the interaction between MPs and plant adaptability, especially in multi-nutrient environments.

### 5. Conclusions

Reliable information on the fate and potential impacts of crops is essential for policy development in managing MPs pollution and its threat to agroecosystems. This study provides experimental evidence revealing the primary role of MPs interference in regulating the functional traits of maize and mediating its growth under different nutrient environments. MPs disrupt the equilibrium of maize physiological status by weakening its photosynthetic performance. However, the increase in soil nutrients masked the negative effects of MPs on maize growth. Specifically, > 0.5 % MPs disturbance promoted the nutrient foraging activity of maize and its growth by optimizing the functional structure of root system, that is, by reducing the construction cost of input roots (high SRL). This study emphasizes that the adaptive phenotypic plasticity of roots enables them to respond to nutritional cues to mask the negative effects of MPs. The study describes the short-term effects of MPs on crop growth; however, in the long term, the role of MPs as persistent stressors in agricultural soils may change over time and accumulate and translocate in the crop. It is important to consider that crops have been or will likely be exposed to levels of MPs contamination capable of altering their physiological state, and subsequent studies may include additional comparisons using other soils and MPs types. Our results aid in the formulation of food security and risk management policies and the protection of soil health in future agricultural environments.

### Uncited references.

### CRediT authorship contribution statement

**Ziqi Guo:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft. **Peng Li:** Data curation, Investigation, Project administration. **Lihui Ma:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – review & editing. **Xiaomei Yang:** Supervision, Visualization, Writing – review & editing. **Jinqiu Yang:** Data curation, Investigation. **Yang Wu:** Investigation, Data curation. **Guobin Liu:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources. **Coen J. Ritsema:** Supervision, Visualization, Writing – review & editing. **Violette Geissen:** Supervision, Visualization, Writing – review & editing.

## 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.

### Data availability

Data will be made available on request.

### Acknowledgements

My co-authors and I thank the editorial personnel and the anonymous reviewers for the time and effort in the manuscript. We are grateful to Dr. Zhunqiao Liu for his constructive suggestions on the revision of this manuscript. This work was funded by the National Natural Science Foundation of China (41977076), Shaanxi Science Fund for Distinguished Young Scholars (2021JC-50), and Shaanxi Innovation Ability Support Plan-Science and Technology Innovation Team Plan (2023-CX-TD-37).

### Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2023.116759.

#### References

- Alimi, O.S., Budarz, J.F., Hernandez, L.M., Tufenkji, N., 2018. Microplastics and nanoplastics in aquatic environments: aggregation, deposition, and enhanced contaminant transport. Environ. Sci. Tech. 52 (4), 1704–1724.
- Boots, B., Russell, C.W., Green, D.S., 2019. Effects of microplastics in soil ecosystems: above and below ground. Environ. Sci. Tech. 53 (19), 11496–11506.
- Bremner, J., Mulvaney, C. (1982) Nitrogen—total. In Methods of Soil Analysis Part 2 Chemical and Microbiological Properties, pp. 595–624.
- Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurement OF microbial biomass phosphorus in soil. Soil Biol. Biochem. 14, 319–329.
- Chen, W.L., Wu, Y.Q., Fritschi, F.B., Juenger, T.E., 2021. The genetic basis of the root economics spectrum in a perennial grass. Proc. Natl. Acad. Sci. USA 118 (47).
- Chen, W., Zhou, H., Wu, Y., Wang, J., Xue, S., 2020. Direct and indirect influences of long-term fertilization on microbial carbon and nitrogen cycles in an alpine grassland. Soil Biol. Biochem., 107922
- de Jager, M., Giani, L., 2021. An investigation of the effects of hydrochar application rate on soil amelioration and plant growth in three diverse soils. Biochar 3 (3), 349–365.
- de la Riva, E.G.P., IvanMaranon, T.-R., Olmo, I.M., ManuelVillar, R., 2021. Root economics spectrum and construction costs in Mediterranean woody plants: The role of symbiotic associations and the environment. J. Ecol. 109 (4).
- Deng, L., Kim, D.-G., Peng, C., Shangguan, Z., 2018. Controls of soil and aggregateassociated organic carbon variations following natural vegetation restoration on the Loess Plateau in China. Land Degrad. Dev. 29 (11), 3974–3984.
- Doyle, A., Weintraub, M.N., Schimel, J.P., 2004. Persulfate digestion and simultaneous colorimetric analysis of carbon and nitrogen in soil extracts. Soil Sci. Soc. Am. J. 68 (2).
- Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P., Aerts, R., 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. J. Ecol. 98 (2), 362–373.
- Fuller, S., Gautam, A., 2016. A procedure for measuring microplastics using pressurized fluid extraction. Environ. Sci. Tech. 50 (11), 5774–5780.
- Galhardo, C.X., Masini, J.C., 2000. Spectrophotometric determination of phosphate and silicate by sequential injection using molybdenum blue chemistry. Anal. Chim. Acta 417 (2), 191–200.
- Gao, H., Liu, Q., Yan, C., Mancl, K., Gong, D., He, J., Mei, X., 2022. Macro-and/or microplastics as an emerging threat effect crop growth and soil health. Resour. Conserv. Recycl. 186.
- Gao, M., Qi, Y., Song, W., Xu, H., 2016. Effects of di-n-butyl phthalate and di (2ethylhexyl) phthalate on the growth, photosynthesis, and chlorophyll fluorescence of wheat seedlings. Chemosphere 151, 76–83.
- German, D.P., Weintraub, M.N., Grandy, A.S., Lauber, C.L., Rinkes, Z.L., Allison, S.D., 2011. Optimization of hydrolytic and oxidative enzyme methods for ecosystem studies. Soil Biol. Biochem. 43 (7), 1387–1397.
- Giehl, R.F.H., von Wiren, N., 2014. Root nutrient foraging. Plant Physiol. 166 (2), 509–517.
- Guo, Z., Li, P., Yang, X., Wang, Z., Lu, B., Chen, W., Wu, Y., Li, G., Zhao, Z., Liu, G., Ritsema, C., Geissen, V., Xue, S., 2022. Soil texture is an important factor determining how microplastics affect soil hydraulic characteristics. Environ. Int. 165.
- Ingraffia, R., Amato, G., Bagarello, V., Carollo, F.G., Giambalvo, D., Iovino, M., Lehmann, A., Rillig, M.C., Frenda, A.S., 2022. Polyester microplastic fibers affect soil physical properties and erosion as a function of soil type. Soil 8 (1), 421–435.
- Khalid, N., Aqeel, M., Noman, A., 2020. Microplastics could be a threat to plants in terrestrial systems directly or indirectly. Environ. Pollut. 267.
- Kong, D.L., Wang, J.J., Wu, H.F., Valverde-Barrantes, O.J., Wang, R.L., Zeng, H., Kardol, P., Zhang, H.Y., Feng, Y.L., 2019. Nonlinearity of root trait relationships and the root economics spectrum. Nat. Commun. 10.

#### Z. Guo et al.

- Kramer-Walter, K.R., Bellingham, P.J., Millar, T.R., Smissen, R.D., Richardson, S.J., Laughlin, D.C., 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. J. Ecol. 104 (5), 1299–1310.
- Li, F.L., Hu, H., McCormlack, M.L., Feng, D.F., Liu, X., Bao, W.K., 2019. Community-level economics spectrum of fine-roots driven by nutrient limitations in subalpine forests. J. Ecol. 107 (3), 1238–1249.
- Liu, Z., Cai, L., Dong, Q., Zhao, X., Han, J., 2022a. Effects of microplastics on water infiltration in agricultural soil on the Loess Plateau, China. Agric. Water Manage 271.
- Liu, Y., Xiao, M., Shahbaz, M., Zhu, Z., Lu, S., Yu, Y., Yao, H., Chen, J., Ge, T., 2022b. Microplastics in soil can increase nutrient uptake by wheat. J. Hazard. Mater. 438.
- Liu, H., Yang, X., Liu, G., Liang, C., Xue, S., Chen, H., Ritsema, C.J., Geissen, V., 2017. Response of soil dissolved organic matter to microplastic addition in Chinese loess soil. Chemosphere 185, 907–917.
- Lozano, Y.M., Aguilar-Trigueros, C.A., Onandia, G., Maass, S., Zhao, T., Rillig, M.C., 2021. Effects of microplastics and drought on soil ecosystem functions and multifunctionality. J. Appl. Ecol. 58 (5), 988–996.
- Lozano, Y.M.M., Rillig, M.C.C., 2022. Legacy effect of microplastics on plant-soil feedbacks. Front. Plant Sci. 13.
- Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R.D., Eissenstat, D.M., McCormack, M.L., Hedin, L.O., 2018. Evolutionary history resolves global organization of root functional traits (vol 555, pg 94, 2018). Nature 556 (7699).
- Machado, A.A.D., Kloas, W., Zarfl, C., Hempel, S., Rillig, M.C., 2018a. Microplastics as an emerging threat to terrestrial ecosystems. Glob. Chang. Biol. 24 (4), 1405–1416.
- Machado, A.A.D.S., Lau, C.W., Till, J., Kloas, W., Lehmann, A., Becker, R., Rillig, M.C., 2018. Impacts of microplastics on the soil biophysical environment. Environ. Sci. Tech. 52 (17), 9656–9665.
- Machado, A.A.D.S., Lau, C.W., Kloas, W., Bergmann, J., Bacheher, J.B., Faltin, E., Becker, R., Goerlich, A.S., Rillig, M.C., 2019. Microplastics can change soil properties and affect plant performance. Environ. Sci. Tech. 53 (10), 6044–6052.
- McCormack, M.L., Adams, T.S., Smithwick, E.A.H., Eissenstat, D.M., 2012. Predicting fine root lifespan from plant functional traits in temperate trees. New Phytol. 195 (4), 823–831.
- Nelson, D.W., Sommers, L.E., Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E., 1982. Total carbon, organic carbon, and organic matter. Methods Soil Anal. 9, 961–1010.
- Olsen, S.R., Sommers, L.E., 1982. Phosphorus. Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties, 2nd ed. American Society of Agronomy, Madison (WI).
- Pehlivan, N., Gedik, K., 2021. Particle size-dependent biomolecular footprints of interactive microplastics in maize. Environ. Pollut. 277.
- Pellegrini, A.F.A., Anderegg, L., Pinto-Ledezma, J.N., Cavender-Bares, J., Hobbie, S.E.E., Reich, P.B.B., 2023. Consistent physiological, ecological and evolutionary effects of fire regime on conservative leaf economics strategies in plant communities. Ecol. Lett. 26 (4), 597–608.
- Qiao, L., Wang, X., Smith, P., Fan, J., Lu, Y., Emmett, B., Li, R., Dorling, S., Chen, H., Liu, S., Benton, T.G., Wang, Y., Ma, Y., Jiang, R., Zhang, F., Piao, S., Mueller, C., Yang, H., Hao, Y., Li, W., Fan, M., 2022. Soil quality both increases crop production and improves resilience to climate change. Nature Clim. Change 12 (6), 574.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org
- Reich, P.B., 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. J. Ecol. 102 (2), 275–301.
- Reich, P.B., Sendall, K.M., Stefanski, A., Rich, R.L., Hobbie, S.E., Montgomery, R.A., 2018. Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. Nature 562 (7726), 263-+.
- Rillig, M.C., 2012. Microplastic in terrestrial ecosystems and the soil? Environ. Sci. Tech. 46 (12), 6453–6454.

- Rillig, M.C., Leifheit, E., Lehmann, J., 2021. Microplastic effects on carbon cycling processes in soils. PLoS Biol. 19 (3).
- Sanchez-Monedero, M.A., Cayuela, M.L., Roig, A., Jindo, K., Mondini, C., Bolan, N., 2018. Role of biochar as an additive in organic waste composting. Bioresour. Technol. 247, 1155–1164.
- Shorobi, F.M., Vyavahare, G.D., Seok, Y.J., Park, J.H., 2023. Effect of polypropylene microplastics on seed germination and nutrient uptake of tomato and cherry tomato plants. Chemosphere 329.
- Strand, J.A., Weisner, S.E.B., 2004. Phenotypic plasticity contrasting species-specific traits induced by identical environmental constraints. New Phytol. 163 (3), 449–451.
- Sun, C., Liu, G., Xue, S., 2017. Response of soil multifractal characteristics and erodibility to 15-year fertilization on cropland in the Loess Plateau, China. Arch. Agron. Soil Sci. 63 (7), 956–968.
- Tiemann, L.K., Grandy, A.S., Atkinson, E.E., Marin-Spiotta, E., McDaniel, M.D., 2015. Crop rotational diversity enhances belowground communities and functions in an agroecosystem. Ecol. Lett. 18 (8), 761–771.
- Valencia, E., Gross, N., Quero, J.L., Carmona, C.P., Ochoa, V., Gozalo, B., Delgado-Baquerizo, M., Dumack, K., Hamonts, K., Singh, B.K., Bonkowski, M., Maestre, F.T., 2018. Cascading effects from plants to soil microorganisms explain how plant species richness and simulated climate change affect soil multifunctionality. Glob. Chang. Biol. 24 (12), 5642–5654.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707.
- Weemstra, M., Mommer, L., Visser, E.J.W., van Ruijven, J., Kuyper, T.W., Mohren, G.M. J., Sterck, F.J., 2016. Towards a multidimensional root trait framework: a tree root review. New Phytol. 211 (4), 1159–1169.
- Xia, M.X., Valverde-Barrantes, O.J., Suseela, V., Blackwood, C.B., Tharayil, N., 2021. Coordination between compound-specific chemistry and morphology in plant roots aligns with ancestral mycorrhizal association in woody angiosperms. New Phytol. 232 (3), 1259–1271.
- Yang, W., Cheng, P., Adams, C.A., Zhang, S., Sun, Y., Yu, H., Wang, F., 2021. Effects of microplastics on plant growth and arbuscular mycorrhizal fungal communities in a soil spiked with ZnO nanoparticles. Soil Biol. Biochem. 155.
- Yang, C., Gao, X., 2022. Impact of microplastics from polyethylene and biodegradable mulch films on rice (Oryza sativa L.). Sci. Total Environ. 828.
- Zhang, Z.Q., Cui, Q.L., Li, C., Zhu, X.Z., Zhao, S.L., Duan, C.J., Zhang, X.C., Song, D.X., Fang, L.C., 2022b. A critical review of microplastics in the soil-plant system: distribution, uptake, phytotoxicity and prevention. J. Hazard. Mater. 424.
- Zhang, H., Huang, Y., An, S., Zhao, J., Xiao, L., Li, H., Huang, Q., 2022a. Microplastics trapped in soil aggregates of different land-use types: A case study of Loess Plateau terraces, China. Environ. Pollut. 310.
- Zhang, Z.Q., Li, Y., Qiu, T.Y., Duan, C.J., Chen, L., Zhao, S.L., Zhang, X.C., Fang, L.C., 2022c. Microplastics addition reduced the toxicity and uptake of cadmium to Brassica chinensis L. Sci. Total Environ. 852.
- Zhang, J., Li, Z., Zhou, X., Ding, W., Wang, X., Zhao, M., Li, H., Zou, G., Chen, Y., 2023. Long-term application of organic compost is the primary contributor to microplastic pollution of soils in a wheat-maize rotation. Sci. Total Environ. 866.
- Zhao, Z.B., He, J.Z., Geisen, S., Han, L.L., Wang, J.T., Shen, J.P., Wei, W.X., Fang, Y.T., Li, P.P., Zhang, L.M., 2019. Protist communities are more sensitive to nitrogen fertilization than other microorganisms in diverse agricultural soils. Microbiome 7.
- fertilization than other microorganisms in diverse agricultural soils. Microbiome 7. Zhao, S.L., Zhang, Z.Q., Chen, L., Cui, Q.L., Cui, Y.X., Song, D.X., Fang, L.C., 2022. Review on migration, transformation and ecological impacts of microplastics in soil. Appl. Soil Ecol. 176.
- Zhou, Y.F., Liu, X.N., Wang, J., 2019. Characterization of microplastics and the association of heavy metals with microplastics in suburban soil of central China. Sci. Total Environ. 694.
- Zhu, D., Ma, J., Li, G., Rillig, M.C., Zhu, Y.-G., 2022. Soil plastispheres as hotpots of antibiotic resistance genes and potential pathogens. ISME J. 16 (2), 521–532.