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REGULAR ARTICLE

Soil biota suppress maize growth and influence root traits under continuous monoculture

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Abstract
Aims This study investigated maize-soil biota interactions as well as the soil legacy effects of continuous monoculture (CM) on maize performance.
Methods We conducted a glasshouse experiment that compared the performance of maize inoculated with living or sterilized soil inocula collected from experimental field plots with cropping histories of 1 to 5 years of continuous maize monoculture, where the soil type is Nicollet clay loam with moderate fertility. We measured the biomass, yield, root traits and leaf nutrients of maize as well as eukaryotic soil organisms.
Results Inoculation with living soil dramatically reduced maize biomass and yield compared to inoculation with sterilized soil, showing CM to have strong negative soil biotic legacy effects on maize. Nonetheless, the strength of soil biotic effects on most maize variables were relatively stable over time under CM. The response of maize total biomass to living soil inoculation correlated positively with arbuscular mycorrhizal (AM) fungal abundance but negatively with soil fauna abundance, whereas it did not relate with the abundance of plant pathogenetic fungi or herbivorous nematodes. The roots showed acquisitive syndromes (high specific root length but low root diameter) in sterilized soil but conservative syndromes (opposite traits) in living soil. The responses in root system structure were tightly related with AM fungal diversity and community composition.
Conclusions Our study shows strong and stable negative effects of soil biota on maize under CM. The complex effects of soil biota on maize performance highlight the need to explore the functions of different groups of soil organisms to better understand and control negative soil legacy effects in agroecosystems.

Keywords *Zea mays* · Soil legacy · Mycorrhiza · Plant-soil feedback · Root traits · Crop rotation

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Introduction

There is increasing awareness of the importance of plant-soil interactions in determining plant growth, plant population dynamics and ecosystem functioning (Chen et al. 2019; Kuebbing et al. 2015; van der Putten et al. 2016). As plants grow, they will change soil biotic and abiotic properties, and these soil changes can exert feedbacks (i.e. plant-soil feedbacks), or remain as 'legacy effects' influencing, the growth of subsequent conspecific or heterospecific plants (Bennett and Klironomos 2019; van der Putten et al. 2013). Over the past decades, the studies of plant-soil feedbacks or soil legacy effects mainly focused on wild plant species in natural ecosystems (e.g. Bennett et al. 2017; in 't Zandt et al. 2019, 2020; Kulmatiski et al. 2008; Mangan et al. 2010), whereas relatively few experimental studies have been conducted in agroecosystems, despite a long history of recognition of plant-soil interactions in agriculture and horticulture (van der Putten et al. 2013).

Diverse organisms including bacteria, fungi and fauna inhabit agricultural soils and play vital roles in crop yields, biogeochemical cycling and agricultural sustainability (Bender et al. 2016). A range of soil organisms interact directly with roots of crop plants, including mutualists that improve plant nutrition (e.g. mycorrhizal fungi and rhizobia) and antagonists that cause root damage or necrosis (e.g. root herbivores and pathogens), while other organisms can affect crops indirectly via participating in nutrient cycles (e.g. earthworms; Bardgett and van der Putten 2014; De Deyn and van der Putten 2005). It is well documented that agricultural practices can influence the biodiversity and communities in soils (e.g. Liu et al. 2012; Strom et al. 2020), but how and to what extent these changes affect crop performance and productivity as well as the roles of soil biota in driving the direction and magnitude of soil legacy effects are still poorly understood (Mariotte et al. 2018). Filling these knowledge gaps may help to develop better agricultural practices.

Continuous monoculture (i.e. growing the same crop species on the same soil year after year; CM) is a common practice due to the simplification and specialization of cropping systems (Shipton 1977). However, under CM crop yields often decline over time, and this can be mostly attributed to the accumulation of natural enemies and depletion of soil nutrients (Bennett et al. 2012; Cook 2006; Mariotte et al. 2018). It is well known that CM influences the communities of soil organisms. For example, CM enriches crop species/cultivar-specific soil pathogenic fungi and root herbivores (Liu et al. 2019; McDonald and Stukenbrock 2016; Strom et al. 2020) and even causes proliferation of less beneficial or perhaps detrimental mycorrhizal fungi (Johnson et al. 1992). So far, however, responses of the community structure and function of soil biota to CM, and which soil biological groups are responsible for yield declines, remain largely unknown.

Inoculation with soil biota is a widely used approach to study soil biological functions (Johnson et al. 2015; Wagg et al. 2019), plant-soil feedbacks (Cortois et al. 2016; Martín-Robles et al. 2020) and soil biotic legacies (Kostenko and Bezemer 2020; Meisner et al. 2013). However, most of these studies have only focused on soil biotic effects on plant performance in terms of total biomass and/or nutrient uptake (e.g. Dudenhöffer et al. 2018; Jiang et al. 2018; Johnson et al. 2015), and relatively little is known about how soil biota affect root traits, which can be highly plastic in response to changing environments (Bardgett et al. 2014; in 't Zandt et al. 2020) and associated organisms (Cortois et al. 2016; Wilschut et al. 2019). Since soil organisms can mobilize nutrients (e.g. N-cycling microbes) and extend root nutrient-uptake zones (e.g. mycorrhizal fungi; Smith and Smith 2011), it is predicted that without soil biota, plants might shift root traits towards maximizing acquisition of limited nutrients (i.e. acquisitive strategy), exhibiting high specific root length but low root diameter and root tissue density (Bergmann et al. 2020; Roumet et al. 2006). Thus, identifying the response patterns of root traits to soil biota may facilitate a more mechanistic understanding of plant-soil biota interactions.

To better understand the interactions between crops and soil biota as well as the soil biotic legacy effects of CM, we conducted a glasshouse study to compare the biomass, yield, root traits and leaf nutrients of maize inoculated with living or sterilized soil inocula collected from experimental field plots with different duration (1-5 yrs) of CM. We also characterized the communities of soil eukaryotic organisms and determined their relationships with the responses of maize to inoculation with living soil biota. We hypothesized that (1) soil biota under CM will suppress maize growth and the strength of suppression will increase with the duration of CM; (2) CM will exert strong effects on soil biotic communities, and the changes of some functional groups (e.g. pathogens, mycorrhizal fungi, nematodes) will be highly

related with the responses of maize to inoculation with soil biota; (3) when maize is grown in the absence of soil biota, its root traits will shift to a more acquisitive strategy (e.g. greater fine root length and higher specific root length), resulting in better performance of maize.

Material and methods

Soil inocula collection and experimental design

Soil inocula were collected from a long-term maize-soybean rotation experiment at the University of Minnesota's Agricultural Experiment Station in Waseca, Minnesota (44°04′N, 93°33′W). The soil type is Nicollet clay loam (fine-loamy, mixed, mesic Aquic Hapludoll; pH: *c*. 6.5, organic matter: *c*. 5.5%) and the field experiment includes various maize-soybean cropping sequence treatments that have been maintained continuously since 1982 (Grabau and Chen 2016b). All treatments are replicated four times with a randomized complete block design, and the experimental plots were 4.57 m wide by 7.62 m long with six crop rows. For the purpose of this study, we examined a 5-years sequence of continuous maize monoculture, in which 5 years of soybean is followed by 5 years of maize. We sampled only the maize phase in the years 1, 2, 3, 4, and 5. Soil inocula were collected from each of the 20 plots (5 treatments by 4 replicates) in October 2017, immediately following harvest when the maize stubble was standing. In each plot, nine shovels to *c*. 15–20 cm depth were randomly taken along the central two rows of maize plants, and a representative soil slice from each shovel was mixed to create a composite sample for each plot. All soil samples were stored in sealed bags in coolers with ice or in a 4 °C room until use as inocula. Background soil for the pot experiment was collected from a nearby harvested maize field (*c*. 0–30 cm deep), and this soil was steam-sterilized twice (1 d interval, *c*. 90 °C for 3 h each), air-dried, sieved and mixed. Three subsamples of the sterilized background soil were stored in sealed bags at room temperature and used for measuring soil nutrients.

All soil samples were transported to Northern Arizona University at Flagstaff, Arizona to conduct a microcosm experiment, in which plastic pots filled with the sterilized background soil were inoculated with living or sterilized (steam-sterilized twice at 121 °C for 1 h each, 1d interval) soil of the plots of different CM durations. Each pot was filled with 1850 ml of sterilized background soil, and 150 ml of living or sterilized soil inoculum was added as a middle layer. Each inoculation treatment was replicated five times with a random block design, resulting in 200 pots (5 CM durations × 4 replicate plots (blocks) × 2 inoculation types × 5 replicates). Surface-sterilized organic maize seeds (Item Lot# 57590, Johnny's Selected Seeds, USA) were pregerminated and sown in each pot, and one seedling was retained in each pot. Plants were grown in a glasshouse with temperature ranging from 18 to 24 °C in the day and 13 to 21 °C in the night, and the natural daylight was supplemented by 600 W metal halide lamps. All pots were randomly located in each block, and the block position and the pot position within each block were randomly changed every 2 weeks. All pots were watered every 3 days with tap water, and no other practice was used during the period of plant growth. After 16 weeks, all plant individuals were harvested using the methods described below.

Plant harvest, sampling, root scanning and staining

For each pot, ears of maize (including husks, seeds and cobs) were collected and the shoot was clipped at the surface of soil. Three subsamples of topsoil (*c*. 0–6 cm depth; *c*. 20 cm^3 each; soil biodiversity in the upper soil layer is often higher than in deeper layers; Delgado-Baquerizo et al. 2017) were collected and mixed into one composite soil sample. Samples of the five inoculation replicates were pooled (40 pooled samples in total) and used to measure soil nutrients (air-dried and stored at room temperature) and for DNA extraction (freeze-dried and stored at −20 °C). Roots from each pot were washed, scanned using an Epson Perfection V700 scanner (Epson America, Inc), air-dried and weighed. Subsamples of roots were stained with ink and vinegar (Vierheilig et al. 1998), and the percentages of root length colonized by arbuscular mycorrhizal (AM) fungi or non-AM fungi were quantified using the magnified intersection method (McGonigle et al. 1990). AM fungal structures were distinguished from non-AM fungal structures according to morphological characteristics and color (Antoninka et al. 2009; See Fig. S1).

Analyses of plant biomass, root traits and N and P concentrations in plants and soils

All plant biomass samples were dried at 60 °C for 72 h and weighed. Shoot, root, total and ear biomass were recorded or calculated (note that shoot biomass included

the ear biomass). The dry mass of ears was used as maize yield. Scans of root systems were analyzed using WINRHIZO Pro v.2012b (Regent Instruments Inc., Canada) to calculate mean root diameter, total root length and root volume. Specific root length (SRL) was calculated as total root length divided by root biomass, and root tissue density (RTD) was calculated as root biomass divided by fresh root volume (Kramer-Walter et al. 2016).

Subsamples of all dried leaves were grinded into powder, digested with sulfuric acid, and used to measure the leaf N and P concentrations using a FIAstar 5000 system (FOSS, Hillerød, Denmark). Soil available N (NO_3-N + NH_4-N) and soil available P (PO_4-P) were extracted with 2 M KCl (1:5, *w/v*) and 0.5 M $NaHCO_3$ (1:5, w/v), respectively, and their concentrations were quantified via colorimetry on a QuikChem 8000 Series FIA+ (Lachat Instruments, Milwaukee, USA). Available soil N and P concentrations at the onset (sterilized background soil) and completion (soil collected from pots at the time of harvest) of the experiment are listed in Table 1.

Molecular analyses of the soil eukaryotes

Composite soil samples representing each of the 20 living soil inocula were used to determine the communities of eukaryotes. We also analyzed communities in four composite samples of the sterilized control inoculation treatments (i.e. the five CM treatments of each field block were pooled) to rule out the potential microbial contaminations by seeds, air and/or water. For each sample, DNA was extracted from 0.25 g of soil using a soil DNA isolation Kit (MoBio Laboratories, CA, USA), and subjected to PCR amplification of the V4 region of 18S rDNA with universal eukaryotic primers TAReuk454FWD1 and TAReukREV3 (*c*. 420 bp; Stoeck et al. 2010). Since 18S rDNA is not a good barcode region for fungi (with the exception of AM fungi; Davison et al. 2015), we also amplified the ITS1 region of rDNA with the primers ITS1f and ITS2 (*c*. 280 bp; Gardes and Bruns 1993; White et al. 1990) to analyze the soil fungal communities. For each DNA sample, the target DNA regions were amplified in three technical replicates using Phusion® High-Fidelity PCR Master Mix (New England Biolabs, MA, USA) and the corresponding primer combination tagged with a unique barcode. We employed a two-step PCR approach (Miya et al. 2015) to construct the paired-end libraries, with the following cycling conditions: 95 °C for 5 min, 25 cycles of 95 °C for 30 s, 50 °C for 30 s, 72 °C for 40 s; and 10 cycles of 98 °C for 10 s, 65 °C for 30 s, 72 °C for 30 s, and a final extension at 72 °C for 5 min. The amplicons of each soil sample were pooled and purified using the AxyPrepDNA Gel Extraction Kit (Axygen Biosciences, CA, USA). Purified PCR products were quantified by QuantiFluor™-ST (Promega, USA), pooled in equimolar amounts and used for paired-end sequencing using an Illumina HiSeq 2500 sequencer (Illumina Inc., CA, USA). For each target rDNA region, about 1.9 million raw read pairs (18S: 1,860,741; ITS: 1,915,567) were obtained from the 24 soil samples. The raw sequencing data have been deposited in the NCBI Sequence Read Archive (Accession numbers: PRJNA667971 and PRJNA667992).

Bioinformatic analyses of the sequence data were performed using the online BMKCloud Platform (www.biocloud.net). Briefly, raw reads were merged to paired-end reads using FLASH v1.2.7 (Magoč and Salzberg 2011), followed by trimming, demultiplexing and quality filtering using TRIMMOMATIC v0.33 (Bolger et al. 2014). Chimeric sequences were identified and removed using UCHIME v4.2 (Edgar et al. 2011). The filtered sequences (18S mean length = 382 bp, ITS mean length = 266 bp) were clustered into operational taxonomic units (OTUs) at 97% similarity threshold using UPARSE-OTU algorithm, and during the clustering process the singletons were removed simultaneously (Edgar 2013). Taxonomical assignments were made using the RDP Bayesian classifier (Wang et al. 2007) with SILVA v.132 (for 18S; Quast et al. 2013) or UNITE v.8 (for fungal ITS; Nilsson et al. 2019) as reference databases. To further confirm the taxonomical assignments, the representative sequences of each OTU were compared with the database of Nucleotide Collection using BLAST (https://blast.ncbi.nlm.nih.gov), and some ambiguous taxonomies were corrected manually. The OTUs that affiliated with *Zea mays* (*c*. 33.7% of the total 18S reads) were removed before analysis.

To obtain the eukaryotic OTUs that specifically originated from the living soil inocula collected from the field, we compared the read numbers of each OTU between inoculated and sterilized control samples, and the OTUs that were only recorded in inoculated samples, or those whose mean read numbers in inoculated samples were at least tenfold higher than those in the sterilized inoculum controls, were selected for further analyses (319 and 289

Table 1 Soil available nitrogen and phosphorus concentrations at the onset of the experiment (sterilized background soil) and from the pots after completion of the experiment

Soil type / treatments		PO_4-P (mg kg^{-1})	NO_3-N (mg kg^{-1})	NH_4-N (mg kg^{-1})
Sterilized background soil		17.9±1.0 a	0.33±0.01 c	20.3±0.09 a
Soil from the experimental pots				
Living soil inoculation	1 yr	14.8±1.0 ab	2.8±0.3 ab	8.1±0.3 b
	2 yr	13.7±0.6 ab	3.0±0.8 ab	8.5±0.2 b
	3 yr	15.5±1.3 ab	1.6±0.5 ac	8.2±0.2 b
	4 yr	14.6±1.3 ab	1.9±0.5 ac	8.4±0.4 b
	5 yr	12.1±0.4 b	3.1±0.8 a	7.7±0.2 b
Sterilized control	1 yr	15.3±0.9 ab	1.2±0.2 ac	8.1±0.2 b
	2 yr	12.9±0.6 ab	0.7±0.2 bc	7.7±0.2 b
	3 yr	15.5±1.4 ab	1.5±0.8 ac	7.8±0.6 b
	4 yr	14.0±0.8 ab	1.0±0.3 ac	7.6±0.5 b
	5 yr	13.4±0.8 ab	0.7±0.2 bc	8.2±0.3 b

Maize plants in pots were inoculated with living or sterilized soil inocula collected from field plots with 1 to 5 years of continuous maize monoculture. Each pot was filled with a total of 2 L soil and had been grown in the glasshouse for 16 weeks

Means and standard errors are shown ($n = 3$ for background soil and $n = 4$ for the others). Values within the same column with different letters differ significantly from each other according to Tukey HSD tests

OTUs for 18S and ITS, respectively). Although it is possible that this procedure may omit OTUs that have different growth rates in sterile versus living soil, we believe that this is a conservative approach for removing glasshouse contaminants from the community datasets. Representative sequences of all OTUs in living soil inoculum communities have been deposited in the GenBank database under the accession numbers MT530776-MT531383. We grouped the 18S OTUs into protists (including Amoebozoa, Cercozoa, Bacillariophyta, Chlorophyta, Ciliophora, Alveolata, Choanoflagellata, etc.), metazoans (including Nematoda, Arthropoda, Rotifera, etc.) and fungi (including AM fungi and other fungi). After these procedures, seven microbial community datasets, including one fungal ITS OTU table and six 18S OTU tables (all eukaryotic organisms, protists, metazoans, nematodes, fungi and AM fungi), were obtained. For the fungal ITS dataset, we identified the OTUs that probably belong to the plant pathogenic guild using the online version of FUNGuild database (Nguyen et al. 2016; accessed on Apr. 10, 2020; http://www.stbates.org/guilds/app.php). Based on the taxonomical information of nematode OTUs (genera or families), we also identified the root-feeding nematodes (herbivores) according to the descriptions by Yeates et al. (1993) and online NEMAPLEX database (accessed on Apr. 10, 2020; http://nemaplex.ucdavis.edu).

Statistical analysis

The responses of each plant variable to inoculation with living soil biota were calculated using the following formula: response value = $\log_e$(Inoculated/$\text{Sterilized}_{\text{mean}}$), where 'Inoculated' was the measured variable of maize in a pot inoculated with living soil, and 'Sterilized' was the mean of the corresponding sterilized controls (i.e. the mean of the five pot replicates). Significant differences between the response values under each CM treatment and the null expectation of zero were determined by *t*-tests. A positive response means that maize benefited from soil biota in terms of the corresponding variable, whereas a negative response indicates that maize was suppressed by soil biota. For the soil biotic communities, OTU tables were rarefied to the median read number of all samples ('rrarefy' function) and the Shannon's diversity indices ('diversity' function) were calculated using the R package 'VEGAN' (Oksanen et al. 2015). The relative abundances of taxonomic (protists, metazoans, fungi, nematodes, AM fungi) or functional (plant pathogenic fungi

and herbivorous nematodes) groups and the major phyla or OTUs were calculated on the basis of the read numbers.

Effects of soil inoculation and/or CM duration on the measured or calculated variables were analyzed by linear mixed-effects (LME) models, in which soil inoculation and/or CM duration were treated as fixed effects, and the greenhouse block nested within field block or only field block as random effects ('lme' function from R package 'NLME'). Relationships between any two variables or between measured or calculated variables with the CM years (i.e. the number of years of CM) of soil inocula were determined by Pearson's correlation analysis or by linear or nonlinear regression models ('cor.test' and 'lm' functions from 'STATS' package). Effects of CM duration on the OTU composition of each community were analyzed, using Bray-Curtis dissimilarity by permutational multivariate analysis of variance (PERMANOVA) with constraining permutations within field block ('adonis' function from 'VEGAN' package). The community dissimilarities among CM treatments were depicted by principle coordinates analysis (PCoA) ordination ('cmdscale' function from 'STATS' package). To explore the relationships between the community structure of soil biota and maize performance, we used Mantel tests ('mantel' function from 'VEGAN' package) to measure the correlations between OTU composition of each community and the matrices of maize response variables to soil biota inoculation in terms of biomass (including shoot, root, total biomass, yield and root:shoot biomass ratio), root traits (total root length, mean root diameter, SRL and RTD) or plant nutrients (leaf N and P concentrations and N:P ratio). Soil biotic communities and maize response variables were represented by Bray-Curtis and Euclidean distance, respectively ('vegdist' function from 'VEGAN' package). All statistical analyses were conducted in R version 3.6.3 (https://www.r-project.org).

Results

Maize responses to soil biota inoculation and continuous monoculture

Inoculation with living soil dramatically reduced maize biomass and yield compared to the sterilized control (Fig. 1a-d), and the negative effects of living soil on both root biomass and root:shoot biomass ratio gradually increased as the duration of CM increased (Fig. 1b,e). Interestingly, both shoot biomass and total biomass showed negative correlations with CM years regardless of soil inoculation (all Pearson $r \leq -0.25$, $P < 0.02$, $df = 98$), whereas the negative relationship between root biomass and CM years was only detected under living soil treatment ($r = -0.46$, $P < 0.0001$, $df = 98$; Fig. S2a-c). The concentrations of leaf P responded positively but leaf N responded mostly neutrally to living soil inoculation under each CM treatment, resulting in a significantly negative effect of soil biota on leaf N:P ratio (Fig. 1f-h). Across all samples, leaf N:P ratio showed positive correlations with all biomass variables (all $r > 0.30$, $P < 0.0001$, $df = 198$) and yield ($r = 0.33$, $P < 0.0001$, $df = 198$).

Root traits were also very responsive to soil inoculation, with much higher mean root diameter and lower total root length and SRL under the living soil treatment compared to the sterilized control (Fig. 1i-k; Fig. S2e-g). The response of RTD to soil biota inoculation was generally positive and showed considerable variation among CM treatments (Fig. 1l). With increasing years of CM, the responses of root diameter and root length showed quadratic and negatively linear patterns, respectively (Fig. 1i, j). Analysis of the data from all samples revealed that, SRL was positively related with total biomass, yield and leaf N:P ratio (Fig. 2a-c), whereas the RTD correlated negatively with both yield and leaf N:P ratio (Fig. 2e, f). Under the living soil treatment, RTD responded negatively to the increasing years of CM (Pearson $r = -0.28$, $P = 0.004$, $df = 98$; Fig. S2h) and correlated positively with total biomass but negatively with leaf N:P ratio (Fig. 2d, f).

Root colonization by fungi under different experimental treatments

Root colonization by AM fungal structures was exclusively observed in samples inoculated with living soil (Fig. 3a). Non-AM fungal structures were observed in almost all samples, but levels of colonization by non-AM fungi was about three-fold higher in roots inoculated with living soil (23.4 ± 1.4%; mean ± SE; $N = 100$) compared to sterilized soil (8.0 ± 0.9%; Fig. 3b). We did not detect significant effects of CM duration on any of the fungal colonization variables (Fig. 3a, b). AM fungal colonization showed a marginally positive relationship with total biomass under the living soil treatment (Fig. 3c), while non-AM fungal colonization was negatively

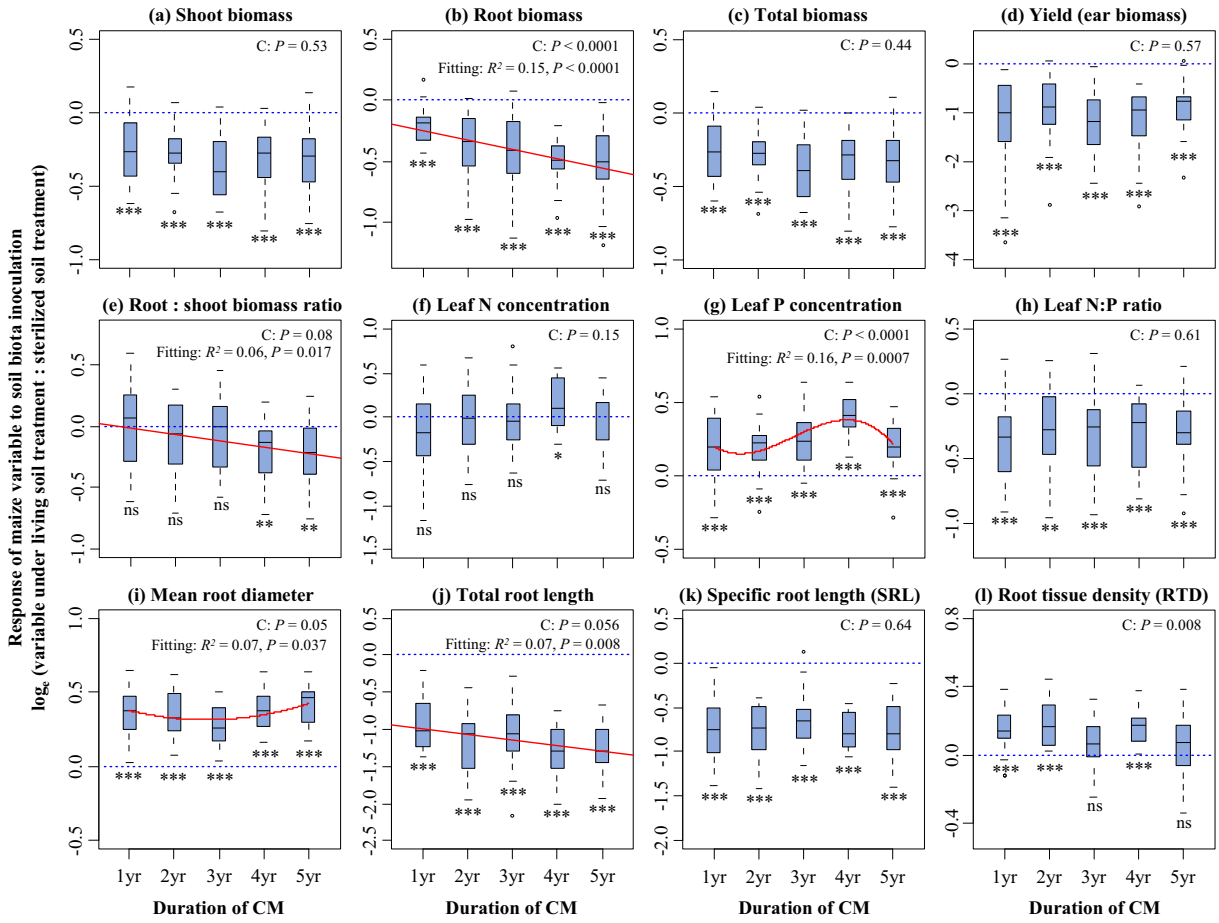

Fig. 1 Responses of maize biomass, leaf nutrients and root traits to inoculation with living soil (soil biota) collected from fields cultivated with 1-5 yrs. of continuous monoculture (CM). $N = 20$ for each boxplot. Effects of the duration of CM (C) were determined by linear mixed-effects models (*P*-values are shown). Relationships between each variable and CM duration were determined by linear or polynomial line fitting ($P \leq 0.05$). Significant differences from the null expectation of zero were determined by *t*-tests (*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$; ns, non-significant), and response values >0 and < 0 indicate positive and negative effects of inoculation with soil biota, respectively

correlated with total biomass across all samples (Fig. 3d).

Eukaryotic soil communities and their relationships with maize responses to living soil inoculation

Analysis of 18S rDNA amplicon sequences revealed that fungi (49.3 ± 4.4% of total 18S reads; mean ± SE; $N = 20$) and protists (27.8 ± 3.7%) were dominant groups in living soil, whilst the relative abundance of nematodes and AM fungi were 8.3 ± 1.6% and 3.5 ± 0.8%, respectively. The relative abundance of most soil eukaryotic groups (e.g. protists, metazoans, AM fungi and nematodes) were not influenced by the duration of CM (Fig. S3). Nonetheless, the relative abundance of fungi and nematodes showed quadratic relationships with the number of years of CM (Fig. S3a, e), and also the relative abundance of main phyla varied among CM treatments (Fig. S4). Based on the fungal ITS dataset, we found that the relative abundance of plant pathogenic fungi was 17.6 ± 3.4% (mean ± SE; N = 20), which was mostly determined by one OTU (10.2 ± 1.8%) affiliated with a culturable *Drechslera* sp. (Table S1). Based on the top ten abundant OTUs in each community dataset, we detected several OTUs whose abundance showed significant correlations with the CM years (for example, an OTU affiliated with *Claroideoglomus etunicatum* decreased and a *Glomus* sp. increased with increasing years of CM; Table S1). Among the seven community datasets, the OTU compositions of all eukaryotic

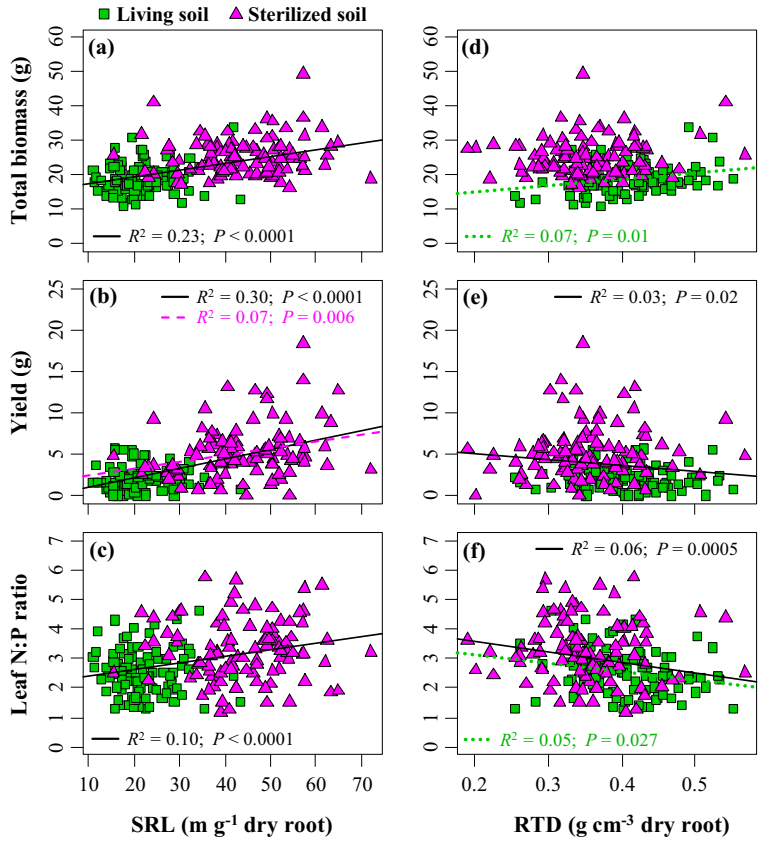

Fig. 2 Relationships between specific root length (SRL) and root tissue density (RTD) versus total biomass, yield (ear biomass) and leaf N:P ratio of maize. These data compile all five treatments of continuous monoculture and two treatments of soil inoculation (living soil and sterilized soil). Linear relationships were tested separately using the data collected from plants inoculated with living soil (green dotted line), sterilized soil (pink dashed line) or all samples combined (black solid line), and only significant relationships ($P \leq 0.05$) are indicated with regression lines

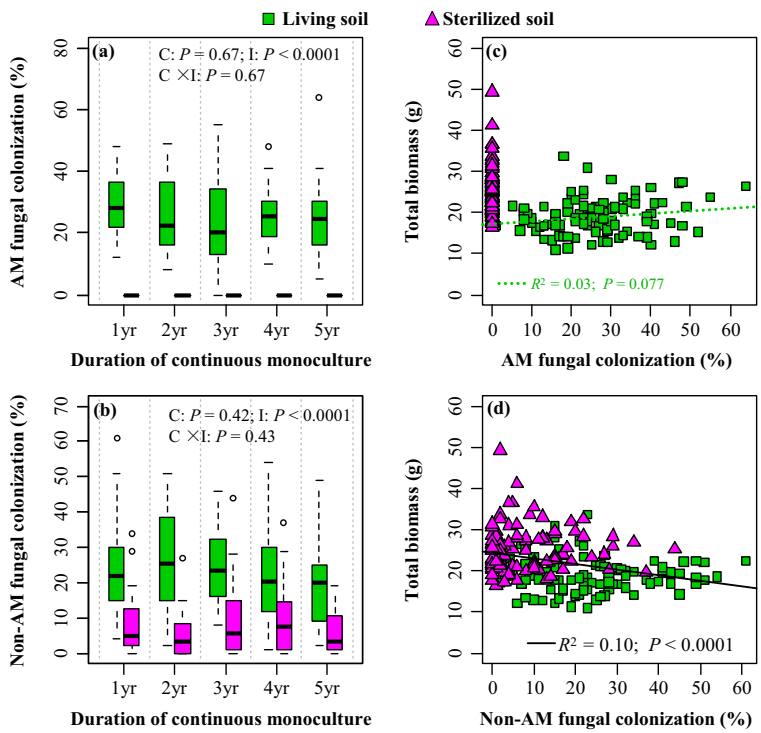

Fig. 3 Root length colonization by arbuscular mycorrhizal (AM) fungi and non-AM fungi as affected by the soil inoculation treatments ($N = 20$ for each boxplot), and their relationships with maize total biomass. For a and b, the effects of experimental treatments (C, continuous monoculture duration of soil inocula; I, inoculation with living or sterilized soil inocula; C × I, their interaction) were determined by linear mixed-effects models (P values are shown). For c and d, the regression relationships were tested using the data collected from plants inoculated with living soil (green dotted line), sterilized soil or all samples combined (black solid line), and only significant ($P \leq 0.05$) or marginally significant ($P < 0.1$) relationships are indicated with regression lines

organisms and all fungi (ITS dataset) varied significantly among CM years (Table 2, Fig. S5), whereas the CM duration only affected the Shannon's diversity indices of metazoans and nematodes (Table 2).

The response of maize total biomass to inoculation with soil biota was negatively related with metazoan abundance but positively related with AM fungal abundance (Fig. 4a, b), meanwhile the response of root biomass correlated negatively with nematode abundance (Fig. 4c). The relative abundance of plant pathogenic fungi or herbivorous nematodes did not correlate with the responses of any biomass or root variables (all $P > 0.08$). Interestingly, however, the relative abundance of the most abundant AM fungal OTU (related with *Claroideoglomus etunicatum*; Table S1) was correlated significantly with the responses of most root variables, especially the root length ($r = 0.70$, $P = 0.0007$, $df = 18$) and root diameter ($r = -0.63$, $P = 0.003$, $df = 18$). We also detected significant correlations between AM fungal diversity and the responses of root biomass, root:shoot biomass ratio, root length and root diameter (Fig. 4d-g), and positive relationships between RTD and metazoan and nematode diversity (Fig. 4h-i). Moreover, the response of SRL showed strongly negative relationships with the diversity of AM fungi ($r = -0.60$, $P = 0.005$, $df = 18$) and nematodes ($r = -0.49$, $P = 0.03$, $df = 18$), and marginally related with metazoan diversity ($r = -0.43$, $P = 0.062$, $df = 18$). Mantel tests revealed that, among the seven community datasets, only the AM fungal community composition correlated significantly with the responses of root traits (matrix of total root length, root diameter, SRL and RTD) to living soil inoculation (Mantel $r = 0.25$, $P = 0.017$; Table S2).

Discussion

The phenomenon of "soil sickness" (i.e. negative plant-soil feedbacks or negative soil legacy effects) has long been associated with the practice of CM (Cesarano et al. 2017). In the present study, we found that inoculation with soil biota from a long-term experimental gradient of CM duration strongly reduced maize biomass and yield, showing negative soil biotic legacy effects of CM on maize performance. It is possible that our approach of comparing responses to living versus sterilized soil inocula may amplify soil legacy effects (Brinkman et al. 2010), however, similar patterns of negative soil legacy effects on biomass variables (but not yield) were also observed when calculated as comparisons of maize

Table 2 Effects of continuous monoculture (CM) duration of soil inocula on the structure and Shannon's diversity index of communities of soil eukaryotes. Soil eukaryotic communities were characterized by sequencing 18S or ITS rDNA markers

Community datasets	Community attributes	Effects of CM duration of soil inocula	
		F-value	*P*-value
All eukaryotes (18S)	community composition	**1.23**	**0.035**
	Shannon diversity	1.48	0.27
Protists (18S)	community composition	1.30	0.067
	Shannon diversity	2.79	0.075
Fungi (18S)	community composition	1.26	0.095
	Shannon diversity	1.48	0.27
Fungi (ITS)	community composition	**1.48**	**0.001**
	Shannon diversity	2.75	0.078
Metazoans (18S)	community composition	1.12	0.12
	Shannon diversity	**8.23**	**0.002**
Nematodes (18S)	community composition	0.96	0.38
	Shannon diversity	**11.12**	**<0.001**
AM fungi (18S)	community composition	1.58	0.095
	Shannon diversity	2.68	0.083

The effects were determined by permutational multivariate analysis of variance (PERMANOVA) and linear mixed-effects models, respectively (*F*- and *P* values are shown). Significant effects ($P \leq 0.05$) are highlighted in bold

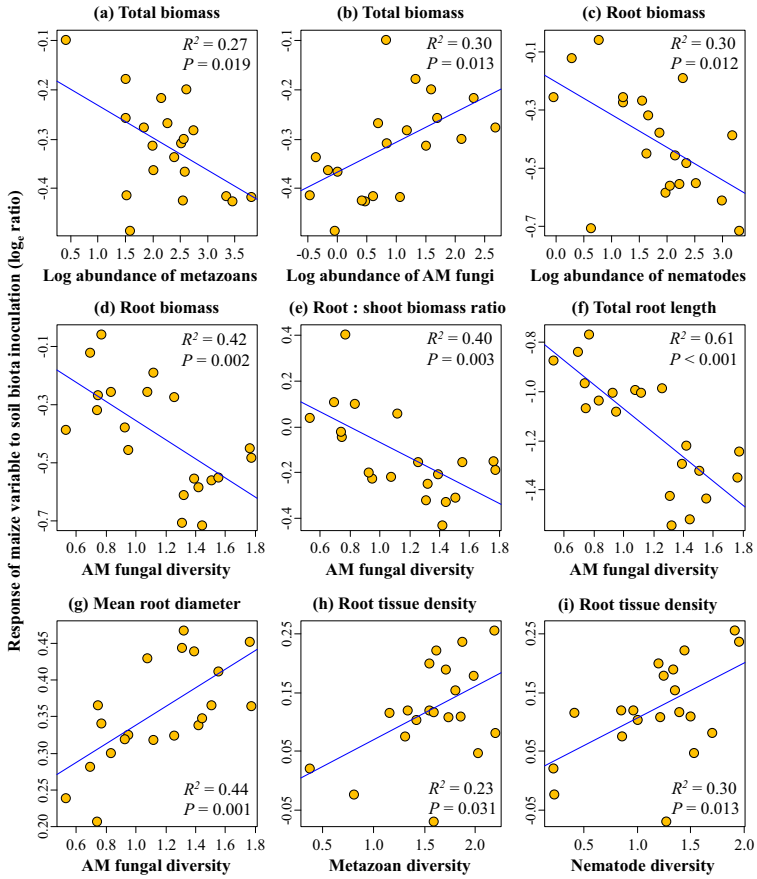

Fig. 4 Linear regressions of the relative abundance (percentage of total 18S rDNA reads; log-transformed) and diversity (Shannon's diversity index) of soil metazoans, nematodes or arbuscular mycorrhizal (AM) fungi versus biomass and root trait responses of maize to inoculation with soil biota. Response values of each maize variable are the same as in Fig. 1, but herein we used the averages of the five pot replicates to match the biota data

inoculated with living soil collected from 2 to 5 years of CM versus maize inoculated with living soil from first year of CM (Fig. S6). The observed patterns of maize responses to soil biota and CM, and shifts in root traits towards a more acquisitive strategy under sterilized soil conditions, suggest that plant-soil interactions are influenced by many interactive processes (Bennett and Klironomos 2019).

In contrast to our expectation, the degree to which soil biota suppressed total biomass production and yield did not change with increasing years of CM, indicating that maize might suffer from strongly negative soil legacy effects after only 1 year of monoculture and remain stable thereafter. This idea is supported by the fact that the yield of maize grown in the experimental field plots that were the source of our inocula showed the same pattern, with a strong yield decline in the second year of maize cultivation and a stable level thereafter (Strom et al. 2020). It has been reported that the build-up of crop species-specific pathogens and root herbivores contribute greatly to the negative legacy effects of CM (Cesarano et al. 2017; Mariotte et al. 2018; Strom et al. 2019). In our study, however, the relative abundance of known plant pathogenic fungi and root-feeding nematodes were not correlated significantly with the responses of biomass or yield to living soil inoculation. It is possible that our experimental design may have diluted the impact of the build-up of populations of potentially deleterious organisms because each pot was inoculated with only a relatively small proportion of living soil (150 ml in 1850 ml). Nonetheless, this does not imply that the negative soil legacy effects observed here were not related with those deleterious microbes. In fact, we detected a relatively high abundance of potentially plant pathogenic fungi (*c*. 18% of total fungal ITS sequences; Fig. S3) in the living soil inoculation treatments. In our experimental field, previous studies showed that the relative abundance of maize pathogenic fungi and plant-parasitic nematodes (*Helicotylenchus*) differed considerably only between the first year and the other years of CM, and that the relative abundance of both antagonists showed strong

negative relationships with maize yield (Grabau and Chen 2016a; Strom et al. 2020). Thus, a possible explanation for our results may be the similar loadings of soil-borne antagonists among CM treatments in the glasshouse, where soil biotic communities had been influenced by maize for at least two seasons (1–5 seasons in the field and one in the glasshouse).

Previous studies at our experimental field site detected a negative relationship between AM fungal abundance and maize yield (Strom et al. 2020), and showed that the spore abundance of some AM fungal taxa were negatively correlated with maize performance and others were positively correlated (Johnson et al. 1992), suggesting that shifts in the AM fungal abundance or community structure may contribute to the yield decline with CM. On the contrary, our study suggests that high abundance of AM fungi could alleviate the negative soil legacy effects of CM on maize total biomass (Fig. 4b) and marginally promote maize growth (Fig. 3c). Such contrasting findings may be related to the differences in soil fertility in the field (high inputs of urea and P-K fertilizer; Strom et al. 2020) and in our glasshouse experiment (relative low soil fertility), because AM benefits to plant productivity would be neutral or even negative under high fertility conditions (Jiang et al. 2018; Polcyn et al. 2019). Furthermore, different maize varieties used in our study and in the field might be another explanation, since different crop varieties have a certain degree of difference in interactions with AM fungi (Mao et al. 2014; Wang et al. 2019). We also detected significant relationships between root traits and AM fungal diversity, community composition, and abundance of the most abundant AM fungal taxon (*Claroideoglomus etunicatum*) (Fig. 4, Table S2), highlighting the influence of AM fungi on root morphology (Wang et al. 2020; Yao et al. 2009). Although the benefits of AM fungi on plant growth and ecosystem functions are well accepted (Powell and Rillig 2018; van der Heijden et al. 2015), whether these typically mutualistic microbes should be considered in agroecosystems remains debated (Rillig et al. 2019; Ryan and Graham 2018). Future studies that manipulate AM colonization are encouraged to determine whether and how AM fungal communities enhance or suppress crop growth under CM.

Interestingly, we found that a rich array of soil fauna (metazoans; mainly nematodes and rotifers in our samples) contributed to the negative soil biotic effects on total biomass (Fig. 4a). The negative effect of soil fauna on maize growth observed in our study may be related to unidentified root herbivores, such as herbivorous nematodes (Grabau and Chen 2016a) and arthropods (Levine and Oloumi-Sadeghi 1991). Previous studies of plant-soil interactions have often ignored the effects of soil fauna, but our findings highlight the importance of considering these organisms in future studies (Kutáková et al. 2018). We also found that the diversity of metazoans, nematodes and AM fungi were strongly correlated with the responses of RTD, SRL or root diameter to inoculation (Fig. 4). Since these root traits are highly related with root functions and root lifespan (Ma et al. 2018; Wen et al. 2019), our results indicate a remarkable degree of plasticity in root traits and functions in response to soil biodiversity. Collectively, our results show linkages between maize performance and communities of soil organisms, and future studies should not only focus on detrimental organisms, but also consider those organisms with potentially beneficial ecosystem functions.

As expected, we found that root traits varied significantly between the living and sterilized soil inoculation treatments (Fig. 1; Fig. S2), with acquisitive syndromes (high SRL but low root diameter and RTD) in sterilized soil but conservative syndromes (opposite traits) in living soil, suggesting that the acquisition-conservation tradeoff of root traits is highly related to soil biota (e.g. mycorrhizal fungi; Bergmann et al. 2020; Kong et al. 2019). In our case, the release of N from soil organic matter may have been reduced in the control treatments with sterilized soil due to a lack of microbes involved in mineralization and nitrification. Under such N-limited conditions, a more resource acquisitive strategy by root traits can enhance N uptake (Reich et al. 1998) and thus stimulate plant growth (Caplan et al. 2017; in ‘t Zandt et al. 2020). These explanatory hypotheses are well supported by the positive relationships among SRL, total biomass and leaf N:P ratio detected in our study (Fig. 2). Indeed, plants can optimize uptake of limiting soil resources through adjusting their root architecture and engaging with soil microorganisms (Oldroyd and Leyser 2020; Wen et al. 2019), as we detected in the tight relationships between root traits and AM fungi (see the discussion above). Thus, the remarkable proliferation of fine roots observed in sterilized soil could be the natural response of maize to nutrient limitation in the absence of mutualistic partners. Given the importance of root morphology in understanding plant-soil interactions (Cantarel et al. 2015; Wilschut et al. 2019), future

studies should consider root traits and address how nutrient availability or soil organisms induce the variations in these traits.

This study shows that many soil eukaryotes are influenced by the duration of continuous maize monoculture. These findings corroborate previous field studies in the same long-term crop rotation experiment showing that the community compositions and diversity of total fungi, AM fungi and nematodes are significantly affected by CM (Grabau and Chen 2016b; Johnson et al. 1992; Strom et al. 2020). Strong effects of CM on soil prokaryotes have also been reported for a range of crops (e.g. Chen et al. 2018; Xiong et al. 2015; Zhao et al. 2018). Since soil bacteria and archaea play pivotal roles in biogeochemical cycles and crop performance (Glick 2018), it is likely that these unmeasured groups of soil organisms interacted with the eukaryotic communities to generate the soil legacy effects that we observed in our glasshouse study. Our comparison of maize responses to living and sterile soil inocula allowed us to begin to link the structure of soil communities with their function, and this has clearly shown that soil biota respond to crop rotation and these responses may impact the biomass, yield and root traits of maize.

In summary, we have demonstrated that maize biomass and yield are reduced by negative feedback from soil biota, and the strength of these legacy effect is relatively stable over successive years of maize cultivation. This finding suggests that growing maize for more than 1 year in the same field may reduce maize biomass and yield due to negative biotic soil legacies. Overall, soil fauna were negatively correlated and AM fungi were positively correlated with maize total biomass, but we did not detect obvious relationships between maize performance with putative antagonistic soil organisms. This highlights the fact that disentangling the functional roles of the many different soil organisms that interact with plants is necessary to understand and mitigate negative soil legacy effects in agroecosystems. Our study also provides evidence that root traits are tightly linked with plant performance, and will shift from a conservative to an acquisitive nutrient acquisition strategy when certain soil biota become rare. Consequently, future studies of plant-soil interactions should consider the variation in root traits and relate it to the presence and abundance of soil biota. Only one maize cultivar and one soil type were tested in this study, which does not allow generalization. Future investigations with more crop species/cultivars and soil types are encouraged to clarify how CM affects crop performance through soil legacies.

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Author contributions NCJ, YL and LM designed the study and collected field soils with the help of SC; LM and YL conducted the glasshouse and laboratory work with help of JZ, JO and NCJ; SC conducted and maintained the field experimental plots; LM and YL analyzed the data and drafted the manuscript, and all authors contributed to revisions.

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