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RESEARCH ARTICLE

Microbial soil legacies of crops under different water and nitrogen levels determine succeeding crop performance

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Abstract

Background and aims Soil legacies mediated by abiotic and biotic factors can greatly influence succeeding plants, a phenomenon called plant-soil feedback (PSF). To date, the patterns and mechanisms of PSF remain largely unexplored in agroecosystems, especially how soil microbial legacies of crop species and management practices interact is poorly understood.

Methods We subjected four common arable crop species (wheat, maize, soybean and rapeseed) to water (sufficient or drought) and nitrogen (high or low) treatments to condition living soil. We analyzed soil nutrient properties and microbiome composition, and then grew the four crops in conspecific and heterospecific soils to examine intra- and inter-specific PSFs.

Results We found that crop species, nitrogen and water treatments created differential effects on soil bacteria and fungi diversity and community composition. Wheat grew better in conspecific-conditioned soil than in heterospecific-conditioned soil, whereas maize and soybean performed better in heterospecific-conditioned soils regardless of water and nitrogen treatments. The PSFs of rapeseed depended on the water and nitrogen treatments. The dissimilarity of both soil bacterial and fungal communities showed a consistently positive correlation with the feedback effect for wheat, while it negatively correlated for maize, rapeseed and soybean. Path analysis showed that soil abiotic, bacterial and fungal legacies all impacted the corresponding crop growth.

Conclusions We show that via selecting crop species and by changing management practices we can create positive legacies that can enhance the growth

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of the succeeding crop. Hence, this work proposed a new way to capitalize on soil legacies for enhancing agricultural productivity.

Keywords Legacy effect · Plant-soil feedback · Soil microbiome · Soil bacteria · Soil fungi · Crop rotation

Introduction

Intensive agriculture characterized by simplified cropping systems with substantial inputs of agrochemicals have made an enormous contribution to meeting food demands of a rapidly increasing population in the world. However, this has come at the cost of severe environmental consequences and instability in global food production (Renard and Tilman 2019). In agricultural systems, growing the same crop repeatedly can lead to soil nutrient imbalances, the build-up of host specialized soil-borne pathogens and root-feeding herbivores ultimately resulting in reduced crop growth and yields (van der Putten et al. 2013). Globally, yield losses of major food crops caused by pathogens and pests can reach e.g. 17% in potato to more than 30% in rice, and soil-borne pathogens caused by continuous monoculture with large inputs of chemical fertilizer are a key contributor (Savary et al. 2019). Therefore, it is critical to innovate sustainable cropping systems to simultaneously meet food security demands and reduce negative environmental consequences (Dias et al. 2015).

Enhancing biodiversity in sustainable agricultural systems is key to promote and stabilize sustainable food and nutritional security (Ratnadass et al. 2012). Crop rotation is a traditional and practical way to manage temporal crop diversity in agroecosystems. It can suppress soil-borne pathogens, pest and disease outbreaks (Barbieri et al. 2019), and therefore increase soil biodiversity and health (Yang et al. 2020), and as a result, increase crops yield. However, there is limited theoretical guidance to design and optimize crop rotation schemes. And systematic research into the mechanisms underlying sustainable crop rotation systems is lacking.

Plants can influence soil abiotic and biotic properties via root exudation and litter input, which can, in turn, influence productivity and health of the succeeding plant, a phenomenon termed plant-soil feedback, hereafter called PSF (van der Putten et al. 2013). The effects of PSFs can be positive, negative or neutral, if the subsequent plant grows better, worse or similar in its own soil compared to soil conditioned by other plant species (Bever et al. 1997; van der Putten et al. 2013). The various effects of PSFs are species-specific. Recently, PSFs have been proposed to be an effective tool to design and optimize the appropriate rotational sequence of crop species in agricultural systems (Mariotte et al. 2018). A recent study showed that plant-soil feedbacks vary widely among crops and this knowledge can be used to select crop rotation sequences with higher crop yields (Koyama et al. 2021).

Besides from crop-specific effects, management practices can also greatly influence the directions and magnitude of PSFs through affecting root traits, soil biota as well as through their interactions (Berendsen et al. 2012; Chen et al. 2019). Fertilization and irrigation are two common management practices in arable farming systems that can greatly impact soil biota and other soil properties. For example, N fertilization has been shown to reduce soil bacterial and fungal diversity (Sun et al. 2015), and protist diversity (Zhao et al. 2019). It is well known that water shortage in soil can severely affect soil microbial communities and functions (Kaisermann et al. 2017). To our best knowledge, no studies have ever designed optimal crop rotation schemes with PSF principles under varying N and water conditions, and understood the underlying abiotic and biotic mechanisms.

The main goal of the present study is to understand the PSF patterns of different crop rotation combinations under N and water management and to examine the underlying abiotic and biotic drivers. We grew four crop species, namely winter wheat (*Triticum aestivum* L.), summer maize (*Zea mays* L.), summer soybean (*Glycine max* L.) and winter rapeseed (*Brassica napus* L.), at different water and N application levels. After the soil conditioning phase, we measured soil abiotic characteristics and soil bacterial and fungal community composition, and then four crop species were grown in conspecific and heterospecific soils. We hypothesized that soil conditioning with different crops that are exposed to different water and N regimes will result in distinct microbial soil legacies, that differ in the accumulation of particular bacterial and fungal taxa, and that this will impact the growth of the following crop species. Specifically, we hypothesized that the strength of PSFs will be related to the dissimilarity of the microbiota composition between the own and foreigner soil. We then compared the predicted yields of different combinations of summer and winter crops based on the PSFs to identify the rotation with the highest yield.

Materials and methods

Experimental set-up

Four crop species (winter wheat, summer maize, winter rapeseed and summer soybean) were chosen in this study. Seeds of the four crops were surface sterilized with 10% v/v hydrogen peroxide for 30 min, washed with deionized water and germinated at 25/20 ℃ (day/night) before sowing. 250 kg soil was collected at 0–20 cm depth in April 2019 from the Shangzhuang Experimental Station of China Agricultural University, Beijing, China. Soil pH was 7.33, organic carbon (C) 13.3 g kg^{-1}, total N 0.74 g kg^{-1}. The field soil was sieved (1 cm mesh size) to remove coarse fragments and all macro-arthropods. Pots (15 cm length × 13 cm width × 10 cm height) were filled with a sieved soil (total 2 kg soil per pot). Part of the soil was used to analyze soil properties.

The experiment consisted of two phases. In the conditioning phase, we used the four crop species to condition soil by growing them as monoculture receiving water and nitrogen treatments. In the test phase, we then grew each crop species on its conspecific and heterospecific soils to measure the effects of the species-specific conditioned soils combined with water and nitrogen treatments on the performance of following crop species (Fig. 1).

Phase I: conditioning phase

The experiment was conducted in a greenhouse at 25–30/18–22 °C (day/night) and 60–80% relative humidity during the growth period. In total, the conditioning phase comprised of 192 pots (4 crop species × 2 N treatments × 2 water treatments × 12 replicates) as shown in Fig. 1. The N treatment levels included low N (LN) input with 65 kg N ha^{-1} (165 mg urea per pot) to represent the optimized rate of N fertilizer and high N (HN) input with 170 kg ha^{-1} (432 mg urea per pot), which is the N fertilization rate commonly practiced by farmers. The water treatment levels included sufficient irrigation (60–65% of soil water holding capacity, S) and insufficient irrigation (30–35% of soil water holding capacity, hereafter called drought, D). All other basal nutrients were provided as follows (mg per pot): KH_2PO_4 878; K_2SO_4 340; $MgSO_4{\cdot}7H_2O$ 380; $CaCl_2$ 5300; $FeSO_4{\cdot}7H_2O$ 0.8; $MnSO_4{\cdot}H_2O$ 1.2; $ZnSO_4{\cdot}7H_2O$ 4.4; $CuSO_4{\cdot}5H_2O$ 4; H_3BO_3 1; $(NH_4)_6Mo_7O_{24}{\cdot}4H_2O$ 0.14. Six seedlings of each crop were planted in each pot and two seedlings with similar size were kept after one week. In order to accurately control soil moisture level, all pots were watered to a defined weight to obtain the designated soil moisture content three times per week.

Plants were harvested 60 days after transplanting. The whole plant including roots was carefully removed from the soil by loosening the soil and gently shaking. The soil from each pot was then homogenized and stored in a plastic bag at 4℃ (1 bag for each pot) for less than one week prior to the test phase. Soil subsamples used to analyze soil microbial community composition, were stored at -80℃ until analysis. Roots were carefully washed to remove adhering soil. Shoot and root biomass of each crop were dried and weighed (Table S1).

Phase II: test phase

In the test phase, we investigated the effect of soil conditioning by conspecific and heterospecific plants under N and water treatments on crop growth. For the selection of heterospecific soils, we took actual cropping systems in the North China Plain into consideration by combining winter and summer crops. Wheat and rapeseed are winter crops, and soybean and maize are summer crops. Each winter crop was followed by two different summer crops, and vice versa. Specifically, in the experiment, wheat was tested on wheat, maize and soybean soil, rapeseed on rapeseed, maize and soybean soil, maize on maize, wheat and rapeseed soil, and soybean on soybean, wheat and rapeseed soil. Hence, there were 12 treatments (four conspecific soils + eight heterospecific soils) for each crop species. Each treatment was replicated four times. In total, there are 48 pots for each crop species. In this way, the testing phase comprised of 192 pots (48 pots per crop species × 4 crops). All pots were randomly arranged in the greenhouse and kept under the same conditions as described for the conditioning phase and were watered regularly to ensure sufficient

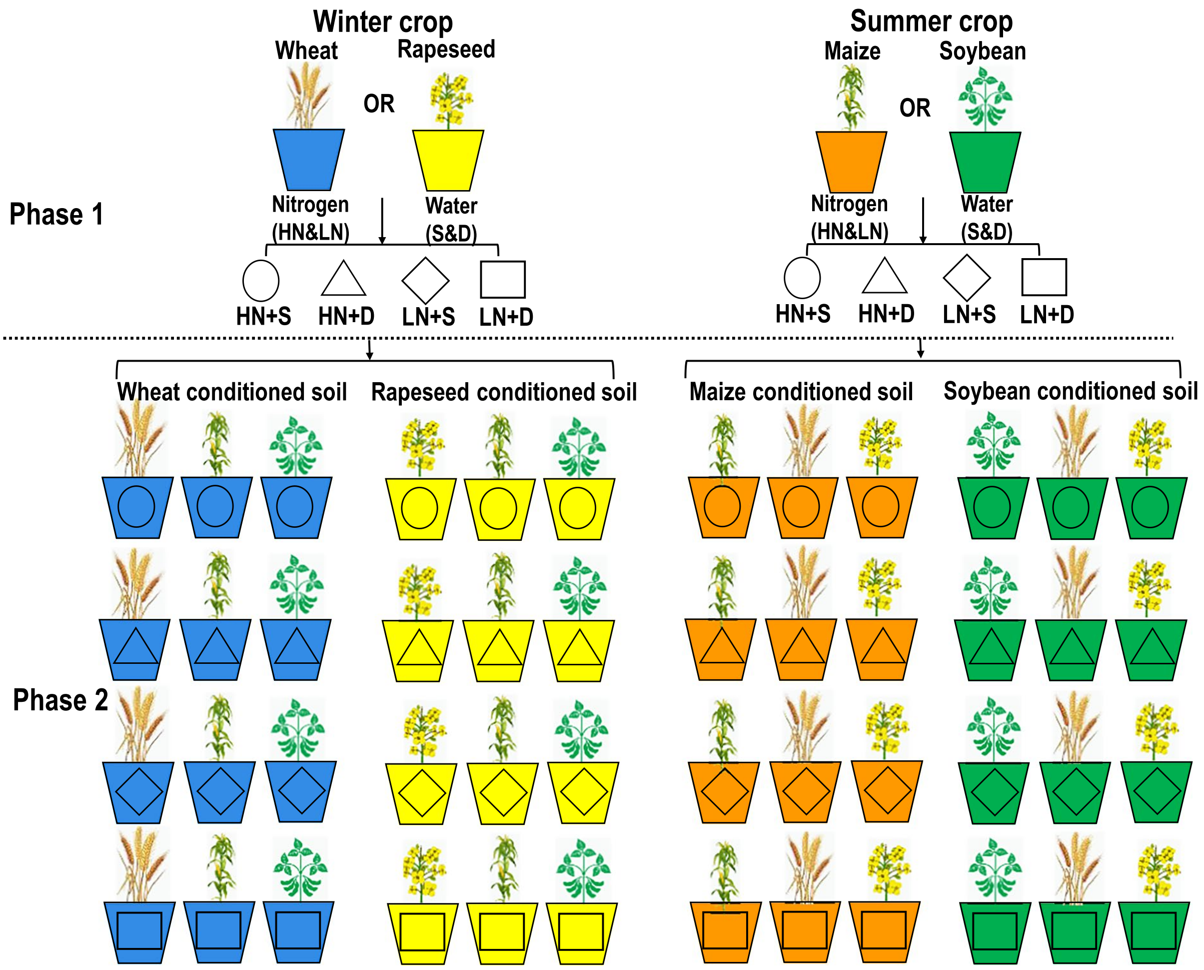


Fig. 1 Graphical illustration of the experimental design consisting of both conditioning phase and testing phase. A factorial design with two nitrogen (N) treatments: high nitrogen (HN) and low nitrogen (LN) and two water treatments: drought (D) and sufficient (S) were included in the conditioning phase. In the testing stage, plants were grown in conspecific soil or two interspecific soil for each combination of nitrogen and water treatments, which was replicated four times

water supply. Plants were harvested after growing for 42 days. Plant shoots were harvested and oven-dried (72 h, 80 °C) for biomass determination.

Soil analysis

Soil samples collected at the end of the conditioning phase were analyzed for soil chemical properties. Soils were sieved (2 mm mesh size), thoroughly homogenized, and divided into two portions. One part was stored at 4 °C to the measure the soil inorganic N (N_{min}), and the other was air-dried prior to determination of other abiotic properties. Soil total N and total carbon (C) were determined in duplicate using C/N analyzers (vario MACRO Elemental Analyzer, Elementar Company, Hanau, Germany). Soil N_{min} (NO_3^--N and NH_4^+-N) of a filtered 0.01 mol L^{-1} $CaCl_2$ extract was analyzed by continuous flow analysis (TRAACS 2000, Branand Luebbe, Norderstedt, Germany).

DNA extraction and processing of sequencing data

Soil subsamples stored at -80 °C were used for DNA extraction. Microbial community genomic DNA was extracted from 0.5 g of freeze-dried soil of each of the 64 samples (four crop species×four treatments×four replicates) using the FastDNA® Spin Kit (MP

Biomedicals, U.S.) following manufacturer's instructions. The DNA quantity and purity were determined using NanoDrop 2000 UV-vis spectrophotometer (Thermo Scientific, Wilmington, USA). Bacterial 16 S rRNA gene V3-V4 region was amplified using primers 338 F and 806R, and fungal ITS2 region was amplified using primers ITS1F and ITS2R. Sequencing was performed on an Illumina MiSeq platform with a paired-end protocol. The raw bacterial and fungal sequencing reads were demultiplexed, quality-filtered by fastp version 0.20.0 (Chen et al. 2018) and merged by FLASH version 1.2.7 (Magoč and Salzberg 2011). After filtering and merging, an average number of 71,016 and 65,978 sequences per sample for bacterial and fungal communities were obtained, respectively. Operational taxonomic units (OTUs) with 97% similarity cutoff were clustered using UPARSE version 7 (Edgar 2013), and chimeric sequences were identified and removed. The taxonomy of each OTU representative sequence was analyzed by RDP Classifier version 2.2 (Wang et al. 2007) against the Silva v138 database for the bacteria and UNITE database for fungi using confidence threshold of 0.7. The data were rarefied to the minimum sequence number per soil sample (20,489 and 34,774 for bacteria and fungi, respectively).

Data analysis

Differences in soil abiotic properties at the end of conditioning phase and shoot biomass in the feedback phase were analyzed using three-way ANOVA with crop species, N treatment, and water treatment as fixed factors. Before conducting analysis, data were checked for normality and homogeneity of variance. A Tukey's post-hoc test was used for pair-wise comparisons among different treatments. Plant-soil feedbacks were calculated as:

$$\text{Feedback} = \ln(Biomass_{conspecificsoil} / Biomass_{\text{heterospecificsoil}})$$

This was done for each replicate separately. Three-way ANOVA was used to study the overall effects of crop species, N treatment and water treatment on PSFs. For each treatment, we used a one-sample t-test to analyze whether the effect of PSFs differed from zero.

To examine whether bacterial and fungal alpha diversity was affected by different crop species, N and water treatments, we performed three-way ANOVA analysis. Data were first checked for normality and homogeneity of variance prior to ANOVA analysis. Furthermore, Non-metric multidimensional scaling (NMDS) based on the Bray-Curtis distance metric was performed using the R 'vegan' package to investigate the differences in bacterial and fungal communities. Then, we assessed the effects of crop identity, N and water treatment on the soil bacterial and fungal community using Permutational multivariate analyses of variance (PERMANOVA, adonis, permutation = 999). We used linear regression to investigate relationships between biotic and abiotic properties at the end of the conditioning phase and crop performance during the feedback phase. All correlation matrices were constructed using the package 'corrplot' in R (R Core Team 2017).

Path analysis was performed to test the biotic and abiotic legacies on the performance of the responding crop species. We established an a-priori model (Fig. S1). In this model, we assumed that soil abiotic properties and the composition of soil bacterial and fungal communities can influence the growth of the responding crop. Bray-Curtis dissimilarities were calculated between all samples for fungi, bacteria and plants. Euclidean distances were calculated for the soil abiotic properties. Mantel tests were conducted to explore the correlations between the distance matrices using Pearson's correlation coefficients with 999 permutations. The analyses were done using 'vegan' package.

To design the optimal crop rotation, we used the results from the plant-soil feedback experiment. We calculated relative biomass of crops in different rotation schemes (4 four-species rotations, 8 three-species rotations and 4 two-species rotations) in the different water and nitrogen regimes. In order to correct for crop specific differences in absolute biomass, relative values were calculated by dividing the actual biomass of the focal species in a specific rotation scheme by the average biomass of this species across all heterospecific-conditioned soils.

Results

Legacy effects of crop species, N and water regimes on subsequent crop growth

Soil conditioning had significant effects on crop growth, but this effect differed greatly among the four crop species and depended on conditioning crop identity, N and water treatments (Fig. 2; Table S2). Specifically, wheat grew best on its own soil with high N addition, and worst in soils conditioned by maize and soybean with low N addition (Fig. 2a). Maize plants produced most biomass in soil conditioned by wheat with high N addition, followed by soil conditioned by wheat under LN + D treatment, and soil conditioned by rapeseed under HN + D treatment (Fig. 2b). Rapeseed had the highest biomass in its own soil under HN + D and produced least biomass at low N addition across the three crop-specific soils (Fig. 2c). Interestingly, for each crop conditioned soil, rapeseed always had the highest biomass in the HN + D treatment. Soybean grew best in soil conditioned by rapeseed with HN + D, while it had the lowest biomass on its own soil (Fig. 2d).

The patterns of the PSFs of the four-crop species differed greatly (Fig. S2; Table S3). The N and water treatments had significant main effects on the PSFs of all four crops (Fig. S2a, b, c, d). Specifically, wheat exhibited a positive PSF (Fig. 2a). For maize (Fig. 2b) and rapeseed (Fig. 2c), the PSF effects depended on the identity of the heterospecific crop species that conditioned the soil. Soybean exhibited an overall negative PSF indicating that soybean grew better in wheat and rapeseed conditioned soil than in own soil, except that there was no significant difference in PSF in the LN + S treatment (Fig. 2d).

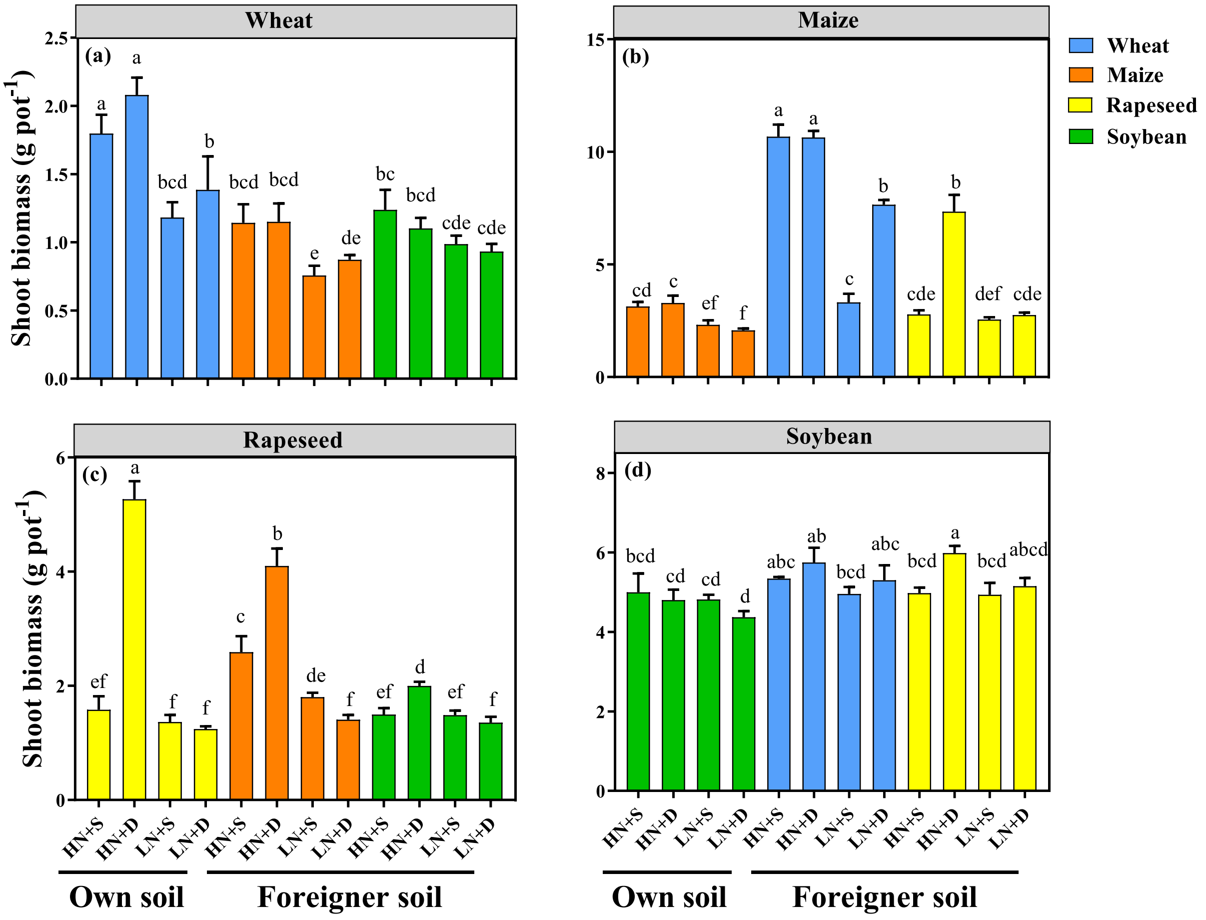


Fig. 2 Shoot biomass (**a**-**d**) of wheat (**a**), maize (**b**), rapeseed (**c**), and soybean (**d**). "HN", "LN", "S" and "D" represent high nitrogen, low nitrogen, sufficient water and drought, respectively. Different letters represent that the effects were significantly different ($P < 0.05$) between treatments. "*" denotes that the effect was significantly different from zero ($P < 0.05$). The detailed statistics were shown in Table S2

Impacts of soil conditioning on soil microbial communities and abiotic parameters

Crop species identity significantly influenced bacterial and fungal communities (Fig. 3; Table 1). For bacterial α-diversity, the effect of crop species depended on the nitrogen level (Table 1). Soils conditioned by soybean at low N tended to have lower bacterial α-diversity than at high N, while the opposite pattern was observed in soil conditioned by wheat (Fig. 3a). Sufficient water promoted bacterial α-diversity compared to drought. Relative abundance of the bacterial community at phylum level varied with species identity, N and water treatments (Table 1). For example, soils conditioned by soybean at low N level had higher abundance of proteobacteria, while soils conditioned by maize at high

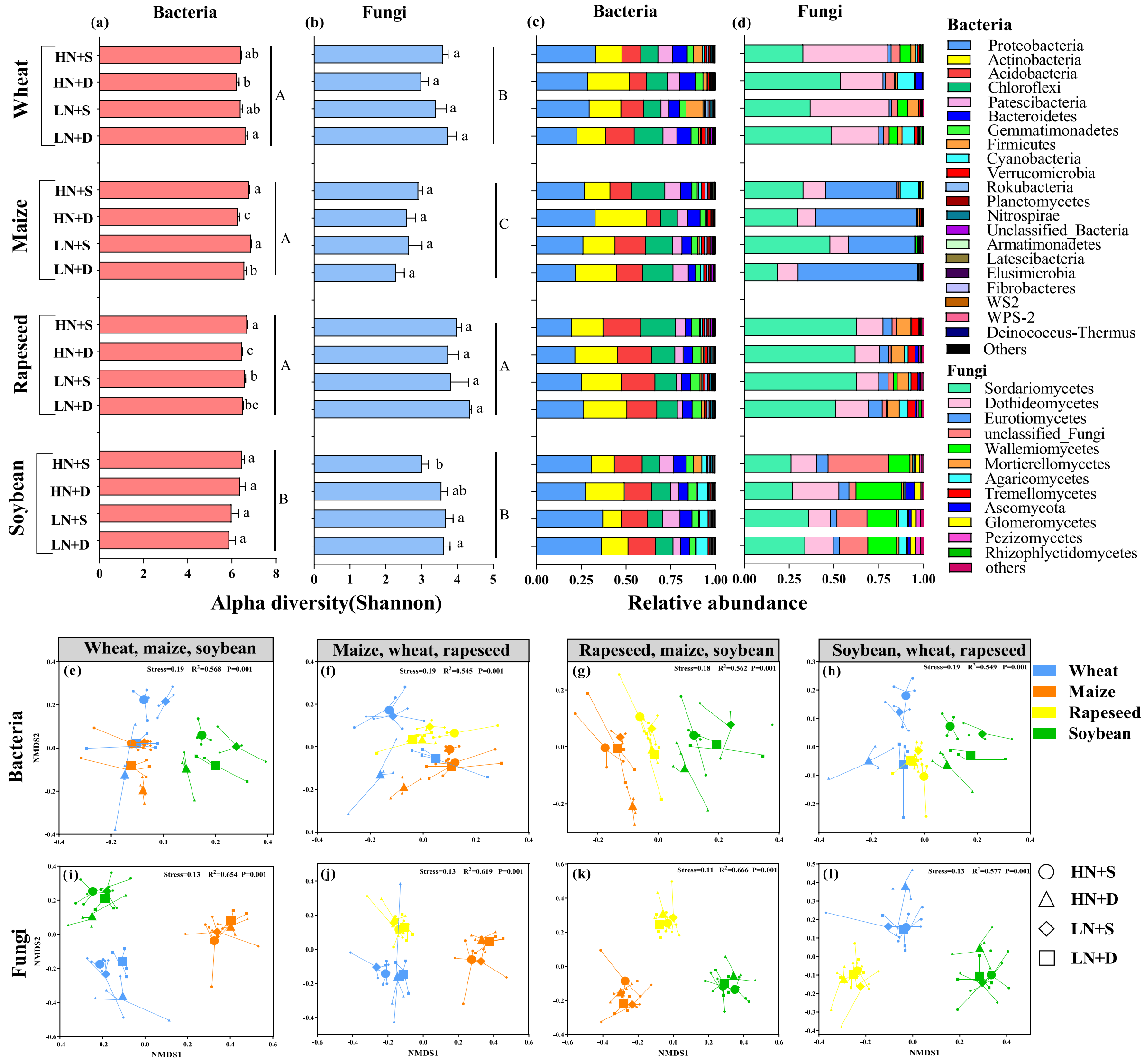


Fig. 3 The Shannon diversity of the bacterial (**a**) and fungal (**b**) community, relative composition of the bacterial community at phylum level (**c**) and fungal community at class level (**d**), and the dissimilarity of bacterial and fungal community composition (**e-l**) in the conditioning soil at the end of conditioning phase. Nonmetric multidimensional scaling (NMDS) patterns of bacterial and fungal community composition in wheat, maize and soybean (**e**, **i**), in maize, wheat and rapeseed (**f**, **j**), in rapeseed, maize and soybean (**g**, **k**), in soybean, wheat and rapeseed (**h**, **l**). Diamond, circle, triangle and rectangle in figure (**e**, **l**) represent four treatments with the combination of different water and nitrogen levels, respectively

Table 1 The effects of soil conditioning by four crop species, two nitrogen (N) treatments and two water (W) treatments on Shannon index (alpha diversity) and community composition (beta diversity) of bacteria and fungi. Bold numbers indicate significant differences

		Bacteria				Fungi			
		Shannon index		Community composition		Shannon index		Community composition	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Crop identity (C)	3	**8.27**	**0.000**	**0.24**	**0.001**	**22.02**	**0.000**	**0.73**	**0.001**
Nitrogen (N)	1	0.12	0.730	**0.06**	**0.004**	1.41	0.241	0.31	0.96
Water (W)	1	**5.71**	**0.021**	**0.07**	**0.005**	0.04	0.837	0.12	0.412
C*N	3	**4.96**	**0.004**	**0.25**	**0.001**	1.42	0.249	**0.74**	**0.001**
C*W	3	1.70	0.179	**0.3**	**0.001**	1.23	0.309	**0.78**	**0.001**
N*W	1	1.55	0.222	**0.06**	**0.011**	1.23	0.272	0.19	0.758
C*N*W	3	0.46	0.712	**0.35**	**0.001**	2.23	0.097	**0.83**	**0.001**

N and drought condition hosted higher abundance of actinobacteria (Fig. 3b). In contrast, fungal α-diversity was only significantly affected by crop species identity (Table 1), with the highest diversity in soil conditioned by rapeseed, the lowest in maize soil, and intermediate in wheat and soybean soil (Fig. 3c). Regarding the relative abundance of fungal communities at class level, maize hosted a higher abundance of eurotiomycetes than the other species, while wheat harbored the highest abundance of dothideomycetes and soybean hosted the highest abundance of wallemiomycetes (Fig. 3d). The NMDS and PERMANOVA results revealed significant main effects and interactive effects of crop identity, N and water treatment on the bacterial community (Fig. 3e-h, Table S5). In contrast, only crop identity and its interaction with N and water significantly influenced fungal community composition (Fig. 3i-l, Table S5).

Soil abiotic properties were significantly influenced by conditioning treatments including crop species identity, water and N treatment, and the effects of the treatments differed among conditioned soils (Table S4). The drought treatment decreased soil pH. Soil NO_3-N concentration was affected by the three main effects as well as by the interactions between conditioning crop species and N treatment, and between the N treatment and the water treatment (Table S4). Soil NH_4-N concentration was affected by conditioning crop identity, and its interaction with the water treatment.

Linking soil abiotic, and biotic legacies with crop performance

PSF effects of wheat tented to increase with increases in both the bacterial and fungal Bray-Curtis dissimilarity, whereas the other three crops, maize, rapeseed and soybean had negative relationships with both the bacterial and fungal Bray-Curtis dissimilarity (Fig. S3). Specifically, for wheat, the positive correlations was observed under drought with either high N or low N for bacteria, and under HN+S for fungi (Fig. S3a, e). We further found a significant positive correlation between wheat shoot biomass and *Bacteroidetes* (Fig. S4). For maize, negative correlations were observed in soil conditioned with LN+S for both the bacterial and fungal community (Fig. S3d, f). Also, PSF effects in soil in the HN+D treatment were negatively correlated with fungal dissimilarity (Fig. S3f). For rapeseed, PSF was negatively correlated with bacterial dissimilarity in soil exposed to drought treatment with either high or low N (Fig. S3c) and were negatively related with fungal dissimilarity in soil with LN+S (Fig. S3g). For soybean, PSFs negatively correlated with bacterial dissimilarity in soil conditioned at low N (Fig. S3d), while they were negatively related with fungal dissimilarity both in soil conditioned at HN+D, and LN+S treatments (Fig. S3h). Taken together, the above-mentioned results indicate that management practices such as N and Water treatment can indirectly impact plant growth via influencing the dissimilarity of the soil microbial community.

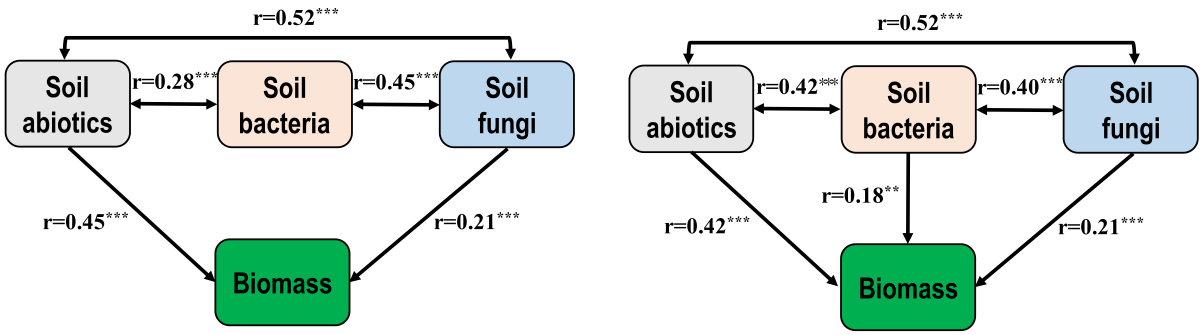
Path analysis was conducted based on Mantel tests on dissimilarity matrices to explore the components of the soil legacies from previous crop growth, N and water management on the biomass of the succeeding four crops (Fig. 4). Biomass of wheat significantly correlated with soil abiotic properties and soil fungi community (Fig. 4a). Maize biomass significantly correlated with soil abiotic, bacterial and fungal legacies (Fig. 4b). For rapeseed, only soil abiotic properties significantly explained the biomass production (Fig. 4c), while biomass of soybean significantly correlated with the soil fungal community (Fig. 4d).

Designing optimal crop rotation under different water and nitrogen regimes

Based on the PSF results, the relative performance of crops in different rotation schemes was compared (Fig. 5). This was done for rotations with four, three and two crops, respectively. In rotations with four crops the combination 'winter wheat-summer maize-winter rapeseed-summer soybean' had the overall best relative performance and this was true in all four soil treatments (Fig. 5). For the rotations with three crops, the soybean-wheat-maize combination performed the best, except for the HN + D treatment where a rotation with rapeseed-wheat-maize was the best (Fig. 5). For rotations with two crops the combination wheat-maize was the best in most treatments, expect for LN + S treatment, where a rotation with wheat-soybean performed the best (Fig. 5).

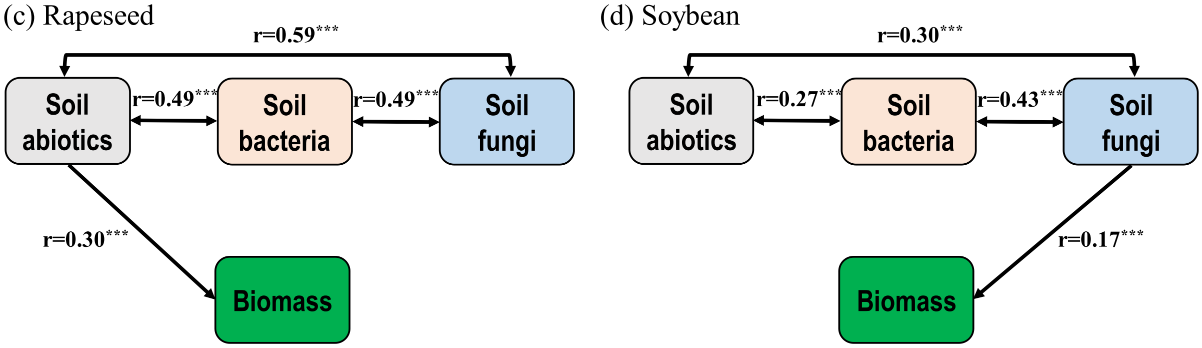
Discussion

This study assessed how different crop species shape soil abiotic and biotic factors, and how this, in turn, influences the growth of the following crop. We also examined how the legacy impacts of management practices such as fertilization and irrigation influence the directions and magnitude of PSFs. We observed that species-specific conditioning of soils leads to marked differences in diversity and composition of the soil microbiome and that it significantly impacts the growth of the following crop. Importantly, management practices such as fertilization and irrigation can enlarge or eliminate these PSF effects implying that these soil legacy effects can be managed to create sustainable agricultural systems.



(a) Wheat

(b) Maize



(c) Rapeseed

(d) Soybean

Fig. 4 Crop growth are differentially affected by soil abiotic and biotic legacies. Path analyses show the relationships between soil abiotic properties, soil bacterial and fungal communities at the end of conditioning phase and responding crop biomass in feedback phase. Arrows represent significant correlations between Bray-Curtis dissimilarity matrices of soil microbial communities and plant biomass and Euclidean distance for soil abiotic properties

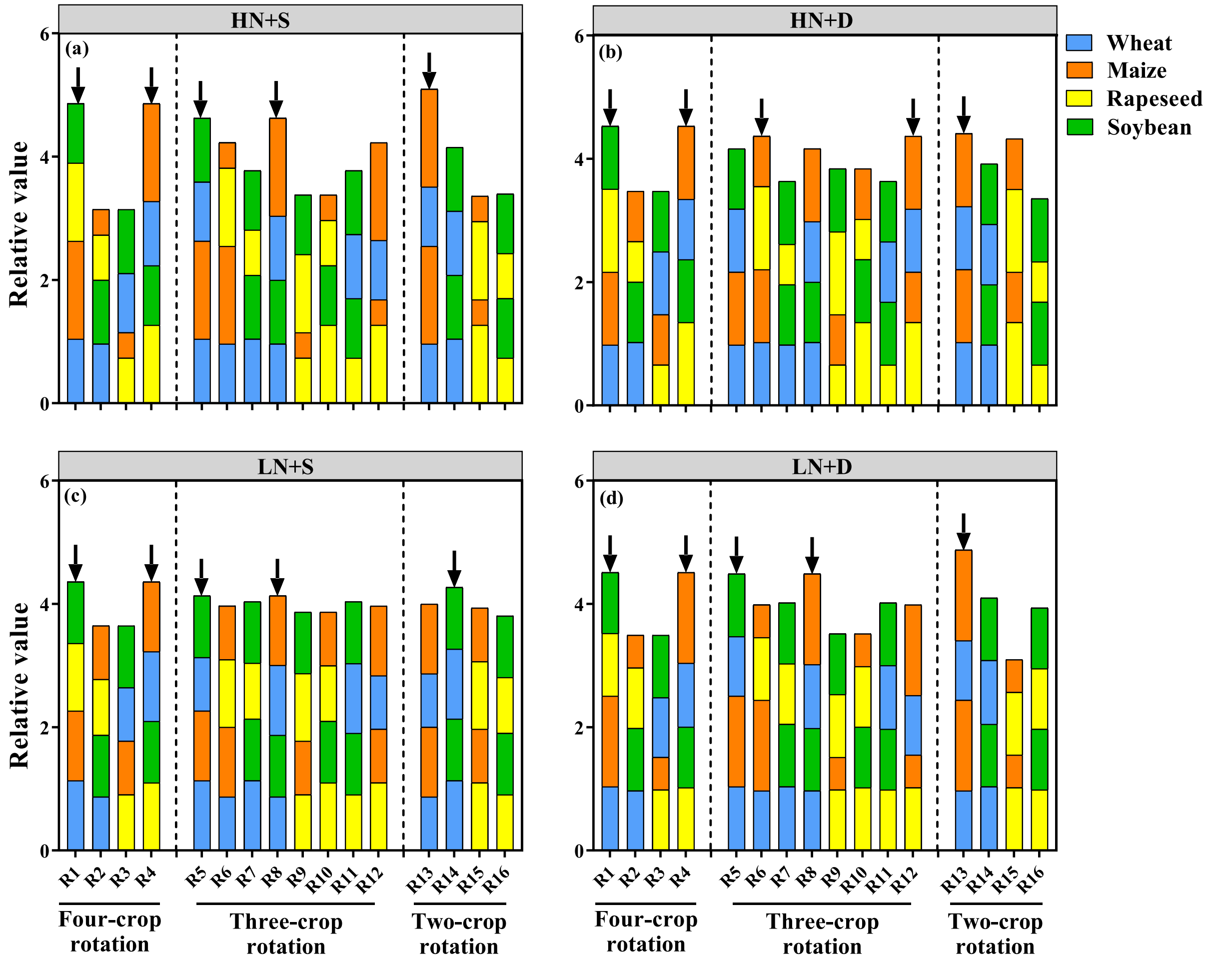


Fig. 5 Relative biomass of crops in different rotation schemes (4 four-species rotation, 8 three-species rotation and 4 two-species rotation) in different water and nitrogen treatments. The rotation direction is from bottom to top. HN and LN represents high nitrogen treatment and low nitrogen treatment, respectively. S and D represents sufficient water and drought, respectively. The rotations with the highest total value within of the 2, 3 or 4 species rotations are marked with a downward arrow

Our results provide clear evidence that the identity of the first crop species affects the assembly of the soil microbiome and that this influences the growth of the following crop. Plant species with different functional traits differ in the way they interact with soil microorganisms (Heinen et al. 2020). Interestingly, in our study wheat grew better in its own soil, while maize, rapeseed and soybean grew better in heterospecific soils. The PSFs for maize, rapeseed and soybean were negatively correlated with the dissimilarity of the bacterial and fungal community, indicating that these crops grow better in soils with a soil community that is distinctly different from their own. Thus, the PSF of different crop species depends on compositional differences in soil microbiota. A possible explanation is that an increase in the difference of bacterial and fungal communities could reduce co-infection by the same pathogens (Gilbert and Webb 2007; Vogel et al. 2016; Hacquard et al. 2017). Host-adapted pathogens can have cascading effects on other microbes (Hacquard et al. 2017). For example, laboratory infection of *A. thaliana* leaves by *Albugo* spp. enables the non-host pathogen *Phytophthora infestans* to grow (Belhaj et al. 2017). Different from maize, rapeseed and soybean, PSF of wheat was positively correlated with the dissimilarity of bacteria and fungi, but wheat grew best in its own soil. These contrast pattern was mainly due to that maize, soybean and wheat grew better on wheat-conditioned soil. The positive effect under high N treatment was largely attributed to higher nitrate remained in wheat-conditioned soils (Table 4S), therefore promoting the growth of those species. The over-all positive effect from wheat-conditioned soil could also due to certain beneficial microbes. For example, we found a significant positive correlation between wheat and maize shoot biomass and Bacteroidetes (Fig. S4) and previous studies have reported that the phylum Bacteroidetes contains many species that promote plant growth (Pérez-Jaramillo et al. 2018, 2019). Thus, the rhizosphere microbiome composition could be important for the choice of crop combinations in rotations. However, the results could also be related to soil nitrogen availability that varied among conditioning soils.

Both soil biotic properties (e.g., beneficial microorganisms or harmful microorganisms) and soil abiotic properties (e.g., higher nutrient availability or nutrient limitation) can cause feedback effects (Kulmatiski et al. 2017; Smith-Ramesh and Reynolds 2017; Bennett and Klironomos 2019). Abiotic factors such as nutrient availability, water and pH have been shown to strongly affect the composition of soil microbial communities (Fierer et al. 2012; de Vries et al. 2018). In our study, the legacy effect arising from N fertilization and irrigation significantly impacted the growth and PSFs of the four crops. Previous studies showed that fertilization causes significant changes in bacterial community composition without altering bacterial diversity in the short term (Zhao et al. 2014) but with significant changes in bacterial diversity in the longer term (Ramirez et al. 2010). In the current study with a short-term crop rotation, N fertilization indeed significantly changed the composition of the bacterial community. Soil fungi were affected by crop identity, but this effect depended on water and N fertilization (Table 1; Fig. 4). This is consistent with previous findings that soil bacterial communities are shaped by varying environmental conditions over time while soil fungal communities are largely shaped by plant traits (Heinen et al. 2020), and that the latter are far less affected by environmental conditions.

Drought can change the composition and activity of soil microbial communities (Barnard et al. 2013; Naylor and Coleman 2018; Lozano et al. 2021) that have a legacy effect on the following plant growth. Legacy effects from management practices such as N fertilization and irrigation can cause distinct differences in soil abiotic and biotic properties that interactively impact the growth of the following crop. For example, wheat grew better under sufficient water treatments in the conditioning stage (Table S1), taking up more N from the soil and thus leaving less residual mineral N in the soil under the HN + S treatment compared with the HN + D treatment (Table S4). But in the test phase wheat grew better in soils that had received high N fertilization independent of the water treatment than under low N fertilization in its own soils. Similarly, maize also had higher shoot biomass in wheat conditioned soil in the high N treatment which was independent of the water treatment indicating that other biotic soil legacies of the sufficient water treatment under high N play an important role in promoting plant growth. The path analysis showed that soil abiotic and biotic legacies (bacterial and fungal community composition) integrally impacted the crop growth in the feedback phase. Efforts have been made with microbial inoculation to promote plant growth, nutrient uptake and plant health (Berendsen et al. 2012; Trivedi et al. 2020). The selection of crops and combinations of crops as well as soil management decisions can be tailored to improve crop health and yield.

In this study, we compared crop rotations under different water and nitrogen regimes by applying plant-soil feedback theory. We show that the performance of crops in different rotations depended on the rotational sequence of crop species, and to a lesser extent on the water and nitrogen treatments. For example, the three-species rotation of winter wheat-summer soybean-winter wheat-summer maize performed the best under high N and low N when there was sufficient water, and low N and under drought conditions. In contrast, the three-species rotation consisting of winter wheat-summer maize-winter rapeseed-summer maize showed the highest performance under high N and drought conditions. Interestingly, the four-species rotation ‘winter wheat-summer maize-winter rapeseed-summer soybean’ consistently provided the best overall relative yields, regardless of water and nitrogen treatments, indicating that the most diverse rotation produces the best results under varying water and nitrogen regimes. A recent field-based study showed that more diverse rotations could improve crop yield by 15–25%, and that yield difference across rotational diversity was better predicted when microbial communities were considered

(Benitez et al. 2021). The rotational sequence of crop species could affect productivity of different crops (Mariotte et al. 2018; Peralta et al. 2018), hence affecting soil nutrient availability (McDaniel et al. 2014), soil water usage (Kirkegaard et al. 2008) as well as the differential effect of the previous crop species on soil communities (Mariotte et al. 2018). We acknowledge that plant-soil feedback may change when measured in the field, but the framework established in this study could still be used to design crop rotations for field-based systems.

Conclusions

We show that via selecting crop species and by changing general management practices we can create positive biotic and abiotic legacies that enhanced growth of the succeeding crop. Although the application of plant-soil feedbacks for optimizing rotation systems through steering soil microbiomes has been suggested previously, empirical evidence from agricultural systems has been lacking so far. A major challenge is now to combine the selection of appropriate crop species and management practices to steer soil microbiomes and abiotic characteristics of the soil so that throughout the crop rotation cycle it consistently enhances plant growth, plant health and nutrient acquisition, within the context of highly variable microbiomes in soil and climatic conditions. The concept of PSFs could also be used as a source of discovery of plant-specific keystone microbial taxa that increase crop growth. Our results are a first contribution to the necessary changes in the paradigm of agricultural practices. In addition to focusing on minimizing pathogenic microbes and negative feedbacks, more attention should be paid to make full use of beneficial microbes in soil and positive feedbacks among cropping systems.

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Author contribution J.J., W.C. and T.M.B. designed this study; M.K., and J.J. performed the experiment and analyzed the data; J.J. and M.K. wrote the paper; J.J., T.M.B. and W.C. revised the paper.

Data availability The sequences data are available in The National Center for Biotechnology Information (NCBI) Sequence Read Archive under accession number PRJNA764502 (available at https://dataview.ncbi.nlm.nih.gov/object/PRJNA764502).

Declarations

Conflict of interest The authors declare no competing interests.

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