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RESEARCH ARTICLE

Soil health and microbial network analysis in a wheat-maize cropping system under different wheat yields

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KEYWORDS

Soil health index, soil microbial network, subsoil, topsoil, yield categories

HIGHLIGHTS

- Improving soil health has the potential to increase wheat yields.
- Fields with maximum wheat yield had more complex soil bacterial and fungal networks.
- Soil health index at a depth of 0–15 cm was positively correlated with wheat yield.
- Microbial phyla, Actinobacteria, Thaumarchaeota, and Ascomycota, were the important drivers of soil health.

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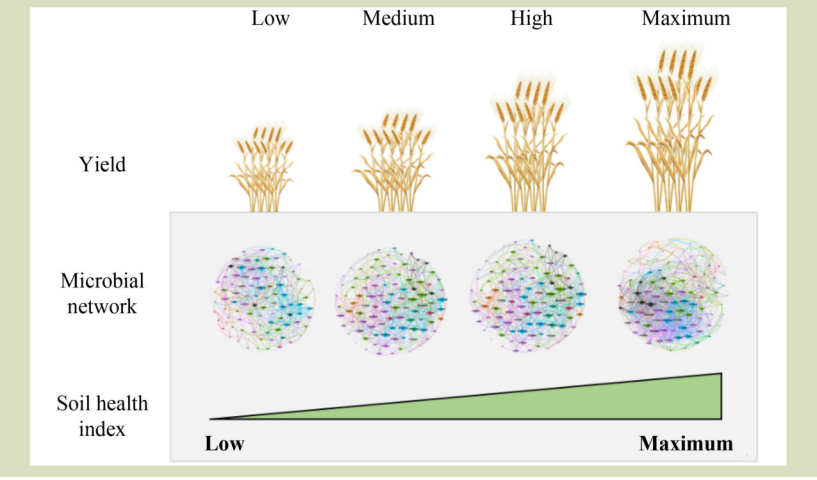
GRAPHICAL ABSTRACT



ABSTRACT

Healthy soil is crucial for sustainable agriculture with soil microbiomes being key to soil health. However, comprehensive assessments of soil health and microbial community structures under different wheat yields have not been made. Therefore, soil samples were collected from wheat fields with differing yields at depths of 0–15 and 15–30 cm. The yields were categorized as low (Y1, 3.75 t·ha^{-1}), medium (Y2, 6.00 t·ha^{-1}), high (Y3, 8.25 t·ha^{-1}), and maximum (Y4, 10.1 t·ha^{-1}), and soil health and microbial communities determined. The results showed that both yield category and soil depth significantly influenced SOC, TN, mineral nitrogen, AP and AK, enzyme activity, and soil bacterial communities. The soil health index in Y4 (0.51–0.87) was significantly higher than in Y3 (0.39–0.63), Y2 (0.27–0.45), and Y1 (0.21–0.52) at both 0–15 and 15–30 cm (expect Y1). Significant correlation was only found between soil health index at 0–15 cm and wheat yield, not at 15–30 cm. The bacterial and fungal network structure in Y4 was more complex and densely connected.

Actinobacteria, Thaumarchaeota, and Ascomycota were identified as key drivers of soil health. Based on these results, the regulation of microbes has the potential to improve soil health and crop yields.

1 Introduction

The global population is projected to reach 9.6 billion by 2050 with food demand increasing rapidly making it challenging to achieve sustainable development goals[1–3]. Healthy soil is crucial for achieving sustainably agricultural development as defined by the 17 sustainable development goals established by the FAO in 2015 with 13 of these directly or indirectly related to soil. China is a major agricultural country need more efficient use of agricultural resources due to only 9% the croplands feeding 22% the global population. However, nearly 70% of Chinese cultivated land only produces low to medium yields, and has serious issues such as soil acidification, underground water pollution and greenhouse emissions[4,5]. Therefore, improving or maintaining high soil quality is of great significance for enhancing crop productivity.

Soil health is crucial for improving sustainable land use[6]. There are many ways to evaluate soil health, for example, soil quality index[7], soil management assessment framework[8] and the Comprehensive Assessment of Soil Health (CASH) framework[9]. The CASH framework was proposed by Cornell University with this framework integrating soil physical, chemical, and biological indicators. It has been widely used to assess soil health in different soil types, cropping systems, and coffee plantations[10–12]. Although many studies had reported soil health assessment in cereal crops[11,13–16], these studies have mainly focused on surface soil (0–20 cm soil depth). However, subsoil is also key for crop growth with physicochemical characteristics and microbial community structure that differs from the topsoil[17–19]. In addition, some studies have shown that crop yields have a strong positive correlation with soil health index, meaning that higher soil health index lead to higher yields[13,16,20]. However, these studies primarily focused on surface soil and did not examine the correlation between the subsoil health and crop productivity. Therefore, it is important to examine the importance of soil health in both topsoil and subsoil.

Soil microorganisms are crucial for maintaining soil health and function, with a combination of abundant microbial species provide functions such as nutrient cycling and carbon sequestration. Analyzing microbial networks provides a deeper understanding of the interactions between microorganisms. Root-associated microbial groups are key contributors to aboveground productivity[21,22], but agricultural intensification has reduced the complexity of soil microorganisms[23,24]. Analysis of the network diagrams of diseased and healthy soils revealed that the fungal network structure in healthy soil is more ordered and closely connected[25]. Intercropping systems with diversified planting also had more nodes and were more stable than those with long-term monoculture soils[26]. Keystone microbial taxa associated with plants promote soil health and plant growth[27]. For example, the enrichment of specific microbial taxa, such as AMF[28], Actinobacteria[29], and *Pseudomonas*[30], is associated with soil quality and plant health. Therefore, there is merit in conducting further research on the structure and networks of soil microbial under different levels of crop productivity. This study was conducted in Quzhou County situated on the North China Plain (NCP) where winter wheat–summer maize is the predominant cropping system and contributes to about 50% and 33% of national wheat and maize production, respectively[31]. The study was conducted at the time of wheat harvest. The objectives were to (1) assess the soil health in topsoil and subsoil in four wheat yield categories, and (2) reveal any linkages between microbial taxa and soil health.

2 Materials and methods

2.1 Study area

This study area was located in Quzhou County (36.9° N, 115.0° E), Hebei Province, China. This region has a warm temperate semi-humid continental monsoon climate. The annual average temperature is 13.4 °C, and the annual average precipitation is 792 mm, with 60% of the precipitation occurring from July to September. The main cropping system in Quzhou County is the wheat–maize rotation, with an average yield of 7.0 t·ha^{-1} for wheat and 7.3 t·ha^{-1} for maize.

2.2 Soil sampling

Before collecting soil samples, we interviewed the local farmers and analyzed historical data on wheat yields for 12 fields in the

Wangzhuang Science and Technology Backyard, Quzhou County. Based on survey data, the wheat yields in the sampled plots was categorized as low (Y1), medium (Y2), high (Y3), and maximum (Y4) with mean (n = 3) yields of 3.75, 6.00, 8.25, and 10.1 t·ha^{-1}, respectively. Soil samples were collected in May 2018 after wheat harvest at depths of 0–15 and 15–30 cm. After removing crop residues from surface soil, five core samples were collected per field using an S-shaped sampling method and then thoroughly mixed to provide one composite sample. The topsoil (0–15 cm) and subsoil (15–30 cm) samples were separately divided into three parts then stored separately in sealed bags. One subsample was air-dried in room for the determination of soil physicochemical properties. The second undried subsample was stored at −20 °C for measurements of soil inorganic nitrogen and enzyme activity. The third undried subsample was stored at −80 °C for the analysis of microbial communities.

2.3 Indicators and methods of determination

For chemical indicators, soil pH was measured using a 1:2.5 ratio of soil to water. Dissolved organic carbon (DOC) extracted by 0.5 mol·L^{-1} K_2SO_4, soil organic carbon (SOC), and total nitrogen (TN), then were analyzed using a carbon–nitrogen autoanalyzer (Elementar Corp., Langenselbold, Germany). Soil inorganic nitrogen (N_{min}) was extracted using 0.01 mol·L^{-1} $CaCl_2$ (extraction solution-to-soil ratio of 20:1) and then measured using a continuous flow analyzer (TRACS 2000 system, Bran and Luebbe, Norderstedt, Germany). Available phosphorus (AP) was determined by the phosphomolybdate method after extraction with 0.5 mol·L^{-1} $NaHCO_3$ and available potassium (AK) were measured using flame photometry after extraction with 1 mol·L^{-1} NH_4OAc. For biological indicators, soil enzyme activities, including α-glucosidase, β-glucosidase, β-xylosidase, leucine aminopeptidase, and N-acetyl-β-D-glucosaminidase, were assayed using a multimode reader (Thermo Multiskan GO, Thermo Fisher Scientific Inc., Waltham, MA, USA) by the method of Koch et al.[32].

To assess soil microbial community structure, total DNA was extracted from 0.5 g fresh soil using a soil microbial DNA extraction kit (MP Biomedicals, Cleveland, OH, USA) following the manufacturer's instructions. DNA quality was then determined using a NanoDrop 2000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). Amplification of soil bacterial 16S rRNA used the primers 515F (5′-GTGCCAGCMGCCGCGG-3′) and 907R (5′-CCGTCAAT TCMTTTRAGTTT-3′). For fungal ITS amplification, the primers ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′) were used. The PCR reaction mixture for both bacterial 16S rRNA and fungal ITS amplification consisted of 20 μL, including 10 ng of template DNA, 0.8 μL of each 5 μmol·L^{-1} forward and reverse primer, 4 μL of 5 × FastPfu buffer, 2 μL of 2.5 mmol·L^{-1} dNTPs, and 0.4 μL of FastPfu polymerase with sterile ddH_2O added to make up the final volume. The PCR amplification conditions for bacteria were as follows: initial denaturation at 94 °C for 5 min, followed by 37 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 45 s with a final extension at 72 °C for 10 min. For fungi, the PCR conditions were: initial denaturation at 94 °C for 4 min, followed by 38 cycles of denaturation at 94 °C for 45 s, annealing at 55 °C for 30 s, and extension at 72 °C for 45 s with a final extension at 72 °C for 10 min. Purified PCR products were mixed in equimolar ratios for subsequent sequencing. All samples were sequenced using the Illumina MiSeq platform. Bacterial and fungal sequences were quality-filtered using the QIIME software package. Non-redundant sequences were clustered into operational taxonomic units (OTUs) based on 97% similarity. Representative sequences were annotated using the SILVA 16S rRNA database for bacteria and the UNITE database for fungi. Then the relative abundances of bacteria and fungi were calculated for assessing structure and composition soil microbial community.

2.4 Soil health assessment

The CASH framework was used to calculate unitless scores[9] with the mean and standard deviation were used to calculate the scoring equation as a cumulative normal distribution[33]:

$$p = f(x,\mu,\sigma) = \frac{1}{\sigma\sqrt{2\pi}}\int_{-\infty}^{+\infty} e\frac{-(x-\mu)^2}{2\sigma^2}dx, \quad (1)$$

where, p is the probability (0–1), x is the measured value (−∞ to +∞,), and μ and σ are the mean and standard deviation of each indicator in the data set, respectively. Two types of scoring functions were used: more-is-better (for SOC, DOC, TN, N_{min}, AP, AK, α-glucosidase, β-glucosidase, β-xylosidase, leucine aminopeptidase, and N-acetyl-β-D-glucosaminidase) and optimum-range (for pH). The soil health index was calculated based on the scores of the evaluation indicators, and following transformation, the indicator scores were integrated into a composite index using equal weighted addition:

$$\mathrm{SHI} = \sum_{i=1}^{n} S_i/n, \quad (2)$$

where, SHI is the soil health index, S_i is the indicator scores of CASH, and n is the number of soil indicators integrated in the index.

Depending on the soil health index, the soil health was categorized as: very low (0–0.2), low (0.2–0.4), moderate (0.4–0.6), high (0.6–0.8), and very high (0.8–1.0).

2.5 Statistic analysis

The analysis of microbial network structure was conducted by selecting OTUs with relative abundances greater than 1%. Spearman correlation matrix was constructed, and correlations with a value between −0.6 and 0.6 ($P < 0.05$) were selected. The effects of yield category and soil depth on the bacterial and fungal communities structure was analyzed using permutational multivariate analysis of variance. The Gephi platform was used to calculate the microbial network and present the co-occurrence network diagram[34]. A random forest model was used to predict the keystone microbial taxa driving soil health at the phylum level. The two-way ANOVA was conducted to determine significant effects of the yield categories and soil depths ($P < 0.05$). Additionally, the multiple comparisons were using LSD ($P < 0.05$). All statistical analysis were performed using IBM SPSS 20.0 (IBM Corp., Armonk, NY, USA) and R software (version 4.2.2).

3 Results

3.1 Soil chemical properties and enzyme activity

There were significant differences in SOC, TN, N_{min}, AP and AK concentrations, and enzyme activity between the yield categories (Table 1). Soil depth significantly affected soil pH, and concentrations of SOC, DOC, TN, AP, AK, α-glucosidase, β-glucosidase, and β-xylosidase. The interaction of yield category and soil depth was significant for SOC, TN, N_{min}, AP, α-glucosidase, β-glucosidase, β-xylosidase, and N-acetyl-β-D-glucosaminidase.

At 0–15 cm, the SOC, TN, N_{min}, AK, and α-glucosidase concentrations in Y4 were higher than those in Y1, Y2, and Y3, whereas Y1, Y2, and Y3 did not differ, except for N_{min} and α-glucosidase in Y1. AP, β-glucosidase, and β-xylosidase concentrations in Y3 and Y4 were higher than those in Y1, whereas no difference in Y3 and Y4 was found. Soil pH, and concentrations of DOC, N-acetyl-β-glucosaminidase (except Y1), and leucine aminopeptidase did not differ between the yield categories (Table 1).

Table 1 Soil chemical properties and enzyme activity in four wheat yield categories at soil depths of 0–15 and 15–30 cm

Soil depth (cm)	Yield category	pH	SOC ($g \cdot kg^{-1}$)	DOC ($mg \cdot kg^{-1}$)	TN ($g \cdot kg^{-1}$)	N_{min} ($mg \cdot kg^{-1}$)	AP ($mg \cdot kg^{-1}$)	AK ($mg \cdot kg^{-1}$)	AG ($nmol \cdot h^{-1} \cdot g^{-1}$)	BG ($nmol \cdot h^{-1} \cdot g^{-1}$)	XYL ($nmol \cdot h^{-1} \cdot g^{-1}$)	NAG ($nmol \cdot h^{-1} \cdot g^{-1}$)	LEU ($nmol \cdot h^{-1} \cdot g^{-1}$)
0–15	Y1	8.4 ± 0.0a	11.1 ± 0.4b	50.0 ± 3.7a	1.1 ± 0.1b	17.6 ± 1.0c	9.2 ± 1.4c	160 ± 21.7b	2.5 ± 0.4c	53.0 ± 13.0c	6.9 ± 1.4c	4.7 ± 1.5b	188 ± 35.4a
	Y2	8.3 ± 0.0a	10.5 ± 0.4b	55.7 ± 5.3a	1.1 ± 0.1b	23.4 ± 2.1b	10.1 ± 0.6c	214 ± 39.8b	8.9 ± 2.3bc	98.2 ± 28.1bc	12.3 ± 2.3bc	13.4 ± 4.5ab	214 ± 41.3a
	Y3	8.3 ± 0.0a	11.5 ± 0.2b	57.5 ± 6.8a	1.2 ± 0.0b	21.6 ± 1.0bc	16.1 ± 1.1b	203 ± 34.1b	11.4 ± 1.6b	185 ± 50.1ab	34.3 ± 13.1ab	20.7 ± 6.5ab	272 ± 29.8a
	Y4	8.3 ± 0.0a	17.5 ± 0.7a	60.0 ± 4.7a	1.7 ± 0.0a	41.8 ± 1.8a	42.5 ± 1.3a	562 ± 23.1a	30.6 ± 2.8a	215 ± 18.9a	43.1 ± 2.3a	27.0 ± 5.7a	264 ± 15.9a
15–30	Y1	8.2 ± 0.0a	8.3 ± 0.1a	87.7 ± 15.2a	0.9 ± 0.0ab	33.8 ± 3.9a	7.0 ± 0.6a	75.7 ± 2.2b	14.2 ± 1.2a	123 ± 16.9a	28.2 ± 4.3a	18.0 ± 1.6a	394 ± 39.6b
	Y2	8.2 ± 0.0a	7.1 ± 0.4a	83.8 ± 14.6a	0.8 ± 0.0b	16.8 ± 1.3c	12.8 ± 4.7a	116 ± 23.7b	4.5 ± 0.4c	50.8 ± 9.00b	8.5 ± 1.7b	8.4 ± 1.0b	494 ± 42.5ab
	Y3	8.2 ± 0.0a	8.7 ± 0.3a	86.6 ± 13.7a	1.0 ± 0.1ab	24.8 ± 1.3b	12.6 ± 4.9a	144 ± 20.8b	7.8 ± 1.2bc	89.0 ± 11.6ab	15.4 ± 0.8b	15.0 ± 1.3ab	454 ± 27.4b
	Y4	8.2 ± 0.0a	8.9 ± 0.8a	90.5 ± 10.4a	1.1 ± 0.1a	29.7 ± 2.0ab	18.5 ± 2.0a	342 ± 32.0a	11.3 ± 2.6ab	118 ± 16.3a	16.4 ± 1.9b	19.2 ± 5.1a	609 ± 34.5a
Yield categories (Y)		0.715	**< 0.001**	0.929	**< 0.001**	**< 0.001**	**< 0.001**	**0.006**	**< 0.001**	**< 0.001**	**0.005**	**0.009**	**0.023**
Soil depths (D)		**< 0.001**	**< 0.001**	**0.001**	**< 0.001**	0.895	**0.002**	**< 0.001**	**< 0.001**	**0.007**	**0.023**	0.071	0.651
Y × D		0.074	**< 0.001**	0.964	**0.005**	**< 0.001**	**0.001**	0.115	**0.038**	**< 0.001**	**0.010**	**0.001**	0.062

Note: The values are mean ± SE for 0–15 and 15–30 cm. Y1, Y2, Y3, and Y4 indicate the yields of 3.75, 6.00, 8.25, and 10.1 $t \cdot ha^{-1}$, respectively. SOC, soil organic carbon; DOC, dissolved organic carbon; TN, total nitrogen; N_{min}, mineral nitrogen; AP, available phosphorus; AK, available potassium; AG, α-glucosidase; BG, β-glucosidase; XYL, β-xylosidase; LEU, leucine aminopeptidase; NAG, N-acetyl-β-D-glucosaminidase. Values in bold indicate statistically significant ($P < 0.05$) differences. The different lowercase letters indicate statistically significant ($P < 0.05$) differences between different yield categories.

At 15–30 cm, soil N_{min} (except Y4) concentration, and activities of α-glucosidase (except Y4), and β-xylosidase in Y1 were higher than those in other yield categories. AK concentrations and leucine aminopeptidase activity (except Y2) in Y4 were higher than other yield categories, but no significant differences were observed between Y1, Y2, and Y3. For pH, and concentrations of SOC, TN (except Y2), AP, β-glucosidase (except Y2), and N-acetyl-β-D-glucosaminidase (except Y2), no significant differences were observed between the yield categories (Table 1).

3.2 Soil microbial community composition

After removing low-quality, non-redundant singleton, and chimeric sequences from the high-throughput sequencing data, we obtained 842,121 and 1,080,521 of 16S rRNA and ITS gene sequences, respectively. These sequences were clustered into 4090 OTUs and 1049 OTUs based on a 97% similarity threshold, which were then used for subsequent bacterial and fungal community analysis. The results of the permutational multivariate variance analysis showed that both yield category and soil depth significantly affected the bacterial community composition, but only yield category significantly affected the soil fungal community composition (Table 2). However, no interaction between yield category and soil depth was observed.

For bacteria, the dominant phyla at the phylum level were Proteobacteria, Acidobacteria, Actinobacteria, Chloroflexi, Firmicutes, Planctomycetes, and Bacteroidetes, accounting for 91% and 88% of the bacterial sequences at soil depths of 0–15 and 15–30 cm, respectively (Fig. 1 and Table S1). For fungi, the main phyla were Ascomycota, Basidiomycota, and Zygomycota, representing over 90% of the fungal sequences at the both soil depths. At 0–15 cm, the relative abundances of soil bacterial and fungal phyla did not differ between yield categories. At 15–30 cm, the relative abundance of Firmicutes in Y4 was higher than that in Y1 and Y2, whereas no difference was observed between the Y3 and Y4. The relative abundance of Zygomycota in Y1 was 23.5%, which was higher than that in the other yield categories whereas there were no differences between Y2, Y3, and Y4. For the relative abundance of Proteobacteria (except Y3), Acidobacteria, Actinobacteria (except Y1), Chloroflexi (except Y2), Planctomycetes, Ascomycota, and Basidiomycota, there were no differences between the yield categories.

3.3 Soil health and relationship with wheat yield

The yield categories had significantly different soil health indices (Fig. 2). At 0–15 cm, soil health indices in Y1, Y2, Y3, and Y4 were 0.25, 0.37, 0.50, and 0.83, respectively. The index in Y4 was significantly higher than that in other yield categories, and the soil health index in Y3 was higher than in Y1, but no difference was observed between Y2 and Y3 (Fig. 2). At 15–30 cm, the soil health index in Y4 was higher than that in Y2 and Y3, and the soil health index in Y1 was higher than that in Y2 (Fig. 2). However, there was no significant difference between Y2 and Y3. For the soil depths, only soil health index of 0–15 cm in Y1 was lower than that of 15–30 cm. Linear regression analysis revealed a positive correlation between soil health index and wheat yield at 0–15 cm ($R^2 = 0.911$, $P < 0.05$) but there was no significant correlation between soil health index and wheat yield at 15–30 cm (Fig. 3).

3.4 Soil microbial network and keystone taxa predicting soil health

The co-occurrence network analysis indicated soil bacterial and fungal community in Y3 and Y4 had more edges and shorter average path length compared to Y1 or Y2 (Fig. 4). For the bacterial networks, the number of edges in Y1, Y2, Y3, and Y4 were 692, 981, 1408, and 1222, and average path lengths were 2.47, 2.15, 2.35, and 2.11, respectively. The most abundant bacterial taxa at the genus level within the network were *Nocardioides*, *Bacillus*, *Pseudarthrobacter*, *Pedomicrobium*, *Altererythrobacter*, and *Variibacter* in Y4 (Table S2). For fungal networks, the number of edges in Y1, Y2, Y3, and Y4 were 354, 292, 300, and 351, and average path lengths were 1.96, 2.21,

Table 2 Permutational multivariate analysis of the effects of yield categories and soil depths on bacterial and fungal communities

Source of variation	Bacterial community			Fungal community		
	F	R^2	P	F	R^2	P
Yield categories (Y)	6.46	0.43	**0.001**	4.77	0.43	**0.001**
Soil depths (D)	9.67	0.16	**0.001**	1.47	0.03	0.094
Y × D	1.24	0.08	0.167	0.88	0.08	0.742

Note: Values in bold indicate a statistically significant ($P < 0.05$) difference between factor levels with strata.

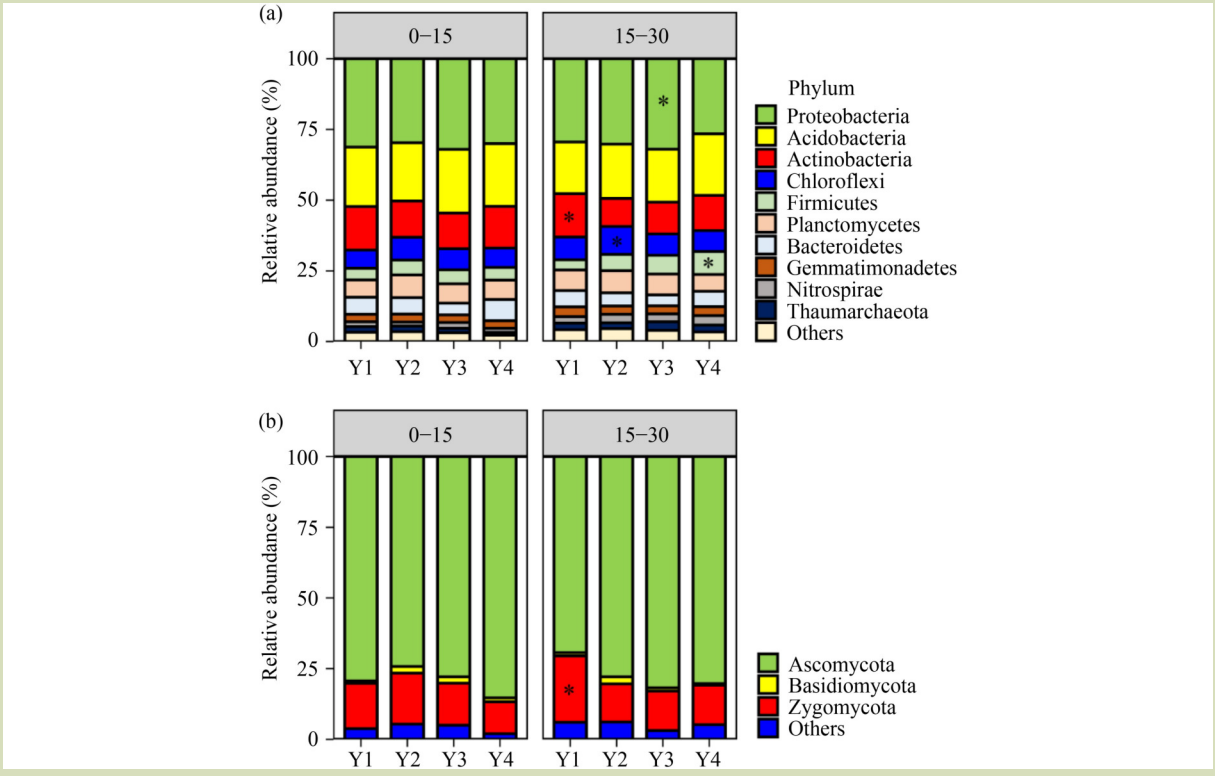


Fig. 1 Relative abundances of soil bacteria (a) and fungi (b) at phylum level in the wheat yield categories at soil depths of 0–15 and 15–30 cm. Y1, Y2, Y3, and Y4 indicate the yields of 3.75, 6.00, 8.25, and 10.1 t·ha^{-1}, respectively. * indicates the relative abundances of microbial phyla between yield categories.

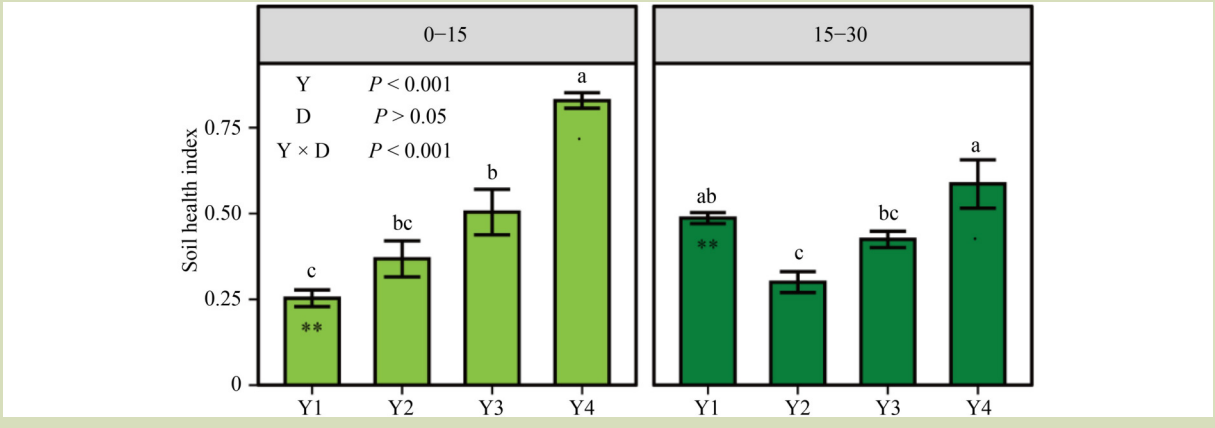


Fig. 2 Soil health index in four wheat yield categories at soil depths of 0–15 and 15–30 cm. Y1, Y2, Y3, and Y4 indicate the yields of 3.75, 6.00, 8.25, and 10.1 t·ha^{-1}, respectively. ** indicates significant differences ($P < 0.05$) in Y1 between 0–15 and 15–30 cm.

2.20, and 2.007, respectively. In the fungal networks, Y1, Y2, and Y4 included the potential pathogen *Fusarium* but Y3 included the potential pathogen *Acremonium* (Table S3). Overall, the bacterial and fungal network structure of the Y3 or Y4 was more complex and closely connected.

Random forest regression was conducted to identify the most important bacterial and fungal phyla as predictors of soil

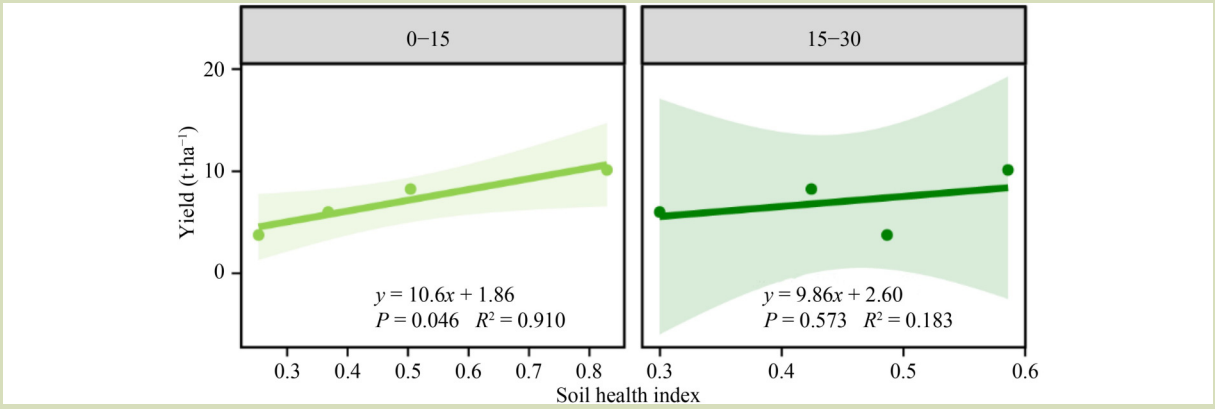


Fig. 3 Regression analysis between soil health index and wheat yield. The shaded areas are the 95% confidence bands.

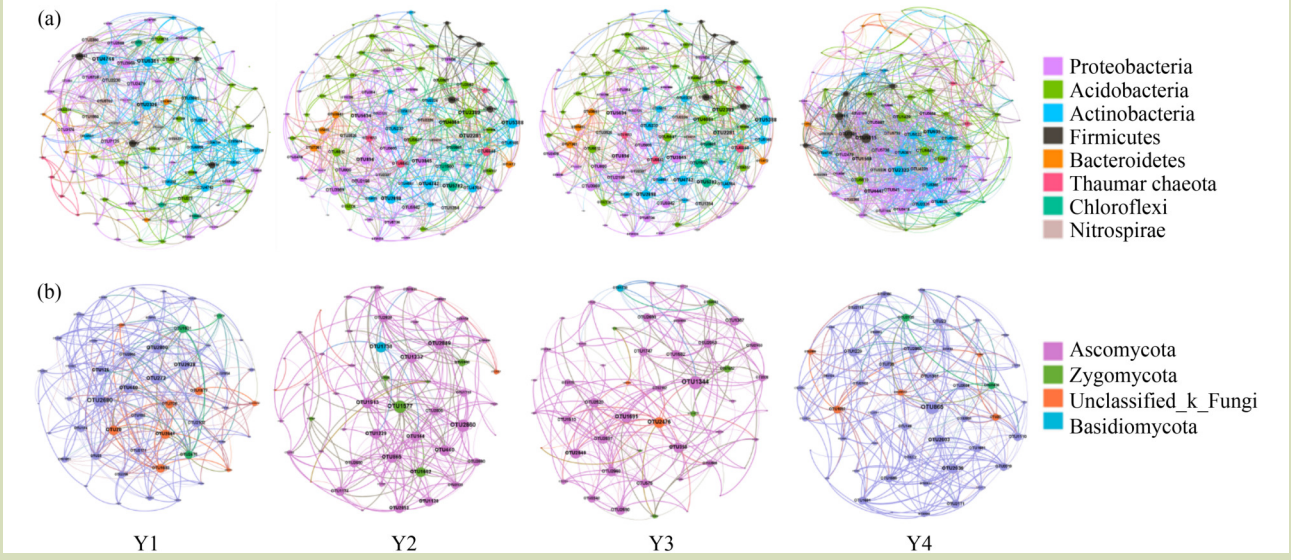


Fig. 4 Co-occurrence network structure of the bacterial (a) and fungal (b) communities at the OTU level differed between the four wheat yield categories. Y1, Y2, Y3, and Y4 indicate the yields of 3.75, 6.00, 8.25, and 10.1 t·ha^{-1}, respectively.

health. Actinobacteria, Thaumarchaeota, and Ascomycota were important microbial taxa driving soil health (Fig. 5).

4 Discussion

As expected, the soil health index in Y4 was higher than that in the other yield categories at depths of 0–15 and 15–30 cm (expect Y1 in the latter case) (Fig. 2). There was a positive correlation between the soil health index and wheat yield at 0–15 cm (Fig. 3). Consistent with previous studies in rice and wheat fields[11,13,16,35], the current results highlight the importance of healthy soils for higher productivity. The higher soil health index in Y4 with the maximum yield was most strongly related to higher SOC, soil nutrients, and enzyme activity (Table 1). SOC, soil nutrients, and enzyme activity were the important soil health indicators. SOC in Y4 was higher than that in the other yield categories. Previous studies have shown that increased SOC in most intensive agricultural contexts is positively correlated with crop yield[36]. An increase of 1 t·ha^{-1} of SOC increased wheat grain yield by 27 kg·ha^{-1} in the USA[37] and by 40 kg·ha^{-1} in Argentina[38]. Soil enzyme activity, in part, reflects the conversion capacity of soil nutrients[39]. Therefore, high yielding crops with consequent SOC input can improve the soil available nutrients in soils of the North China Plain, ensure soil metabolic activity, and

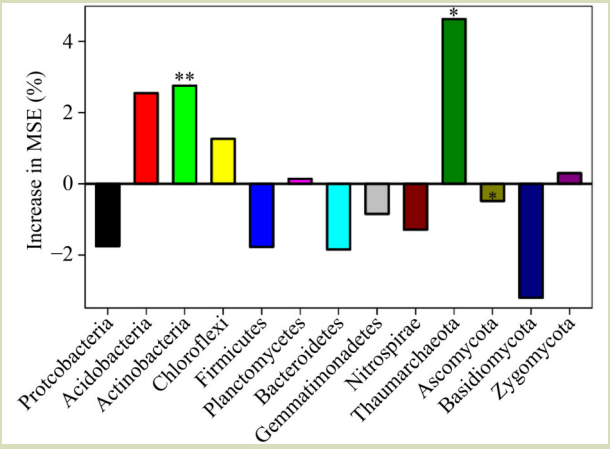


Fig. 5 Random forest regression modeling indicates the mean predictor importance (as MSE, mean square error) of microbial phyla driving the soil health in four wheat yield categories. *, $P < 0.05$, **, $P < 0.01$.

improve soil nutrient supply capacity (Table 1). Also, the SOC, soil nutrient availability, and enzyme activity in the topsoil was higher than in the subsoil (Table 1). Fertilizer addition and straw incorporation are mainly concentrated in the topsoil, which can create a favorable soil environment for crop growth and contributing to high yields. However, there was no significant correlation between soil health index and wheat yield at soil depth of 15–30 cm given that the soil health index in Y1 did not differ from that in the other yield categories. This could be due to poor soil physical structure in Y1 leading to the leaching of nutrients from the topsoil to the subsoil. Another reason may be that crops in low-yielding fields developed less roots to absorb fewer mineral nutrients in the subsurface soil, which leads to the soil nutrient concentrations in Y1 were not lower than those in other yield categories (Table 1). The soil nutrient concentrations are used to calculate soil health index, resulting in no significant difference between Y1 and Y4. This means the high soil health index of Y1 did not lead to high yield, with no significant correlation between soil health index and wheat yield at a soil depth of 15–30 cm. However, the index in Y4 at 15–30 cm was higher than Y2 and Y3 (Fig. 2). Therefore, the subsoil management is also important for attaining high yield in intensive agricultural systems.

Our results also reveals that the microbial networks in Y3 and Y4 were more complex and closely connected. This is consistent with a previous study in potato production[25]. A complex microbial network contributes to carbon sequestration, nutrient cycling, plant growth promotion and abiotic stress tolerance[40,41], which can be beneficial for achieving higher yield. Additionally, the soil bacterial network in Y4 included *Bacillus* (Table S2), a potential beneficial bacteria that can produce auxins to promote plant growth[42]. However, the networks in Y1, Y2, and Y4 included the potential pathogen *Fusarium*, and in Y3, it included the potential pathogen *Acremonium* (Table S3). *Fusarium* is a common soilborne pathogen that can infect crop roots, affect nutrient uptake and lead to substantive yield loss[43,44]. *Acremonium* can cause root rot, impact root vitality, and be detrimental to crop growth[45–47]. These potential soil pathogens could potentially inhibit the improvement of wheat yields in Y1, Y2, and Y3 contexts. Unlike Y1, Y2, and Y3, soil in Y4 was also enriched with the beneficial bacteria *Bacillus*. Further analysis revealed a negative correlation between the relative abundances of *Bacillus* and *Fusarium* in Y4 (results not shown), indicating a trade-off between the beneficial bacteria and the pathogen.

In this study, we found that Thaumarchaeota, Actinobacteria, and Ascomycota were the most abundant taxa associated with soil health (Fig. 5). Thaumarchaeota is abundant archaea widely distributed in soils[48], and is considered to be an ammonia oxidizer archaea (AOA). The abundance of AOA was found to increase with inputs of straw[49] oxidizing ammonium derived from the mineralization of composted manure or soil organic matter[50,51]. At the sites sampled in the present study, wheat straw was returned to the field after harvest, so this could have contributed to Thaumarchaeota being one of the abundant microbial taxa associated with soil health. Actinobacteria is also one of the abundant taxa associated with soil and plant health. An earlier study revealed that the presence of Actinobacteria in sugar beet fields was associated with the suppression of diseases caused by *Rhizoctonia solani*[52]. Also, *Actinomyces* spp. have a range of activity, including decomposition of organic matter and promotion of plant growth[53]. In the present study, Ascomycota was a key species associated with a higher soil health index and the most abundant fungi. Ascomycota is a dominant phylum in the soil fungal communities worldwide[54]. Ascomycota being r-strategy fungi are typically characterized by fast-growing and are abundant in soils with high C availability[55,56]. SOC in Y4 was higher than that in the other yield categories, therefore the relative abundance of Ascomycota was also higher compared to the other yield categories. In summary, abundant microbial taxa are pivotal for soil health and crop yield. Hence, some agricultural practices such as bioorganic fertilizer application, cover crop, no-till, residue retention, and rotation are recommended to improve soil microbial networks, soil health and productivity[11,57,58].

5 Conclusions

Improving topsoil health index can potentially increase wheat yields in agricultural production. Fields with maximum yield wheat (10.1 t·ha^{-1}) had more complex soil bacterial and fungal networks, compared to other yield levels. The microbial taxa, Actinobacteria, Thaumarchaeota, and Ascomycota were found to be potentially important drivers of soil health.

Supplementary materials

The online version of this article at https://doi.org/10.15302/J-FASE-2024570 contains supplementary materials (Tables S1–S3).

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Compliance with ethics guidelines

Xinzhan Sun, Tengteng Li, and Jiangzhou Zhang declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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