Asian Journal of Agriculture and Biology
https://doi.org/10.35495/ajab.2025.058

Original Article

Archaeal abundance as a negative indicator of soil fertility

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Received: 04 May 2025 / Accepted: 11 September 2025 / Published Online: 20 September 2025

Abstract

Fertiliser application can enhance soil fertility while influencing the structure and diversity of archaeal communities in croplands. However, the relationship between soil fertility and Archaea remains insufficiently explored. Here, we examined this interaction in a 34-year vegetable fertilisation experiment in Northeast China. Six treatments were selected: an unfertilised control (CK), organic fertiliser alone (MN_0), nitrogen fertiliser combined with organic fertiliser (MN_1 and MN_2), and nitrogen fertiliser alone (N_1 and N_2). Results indicated that Organic fertilizer treatments (MN0/MN1/MN2) significantly increased soil organic matter (36.1%–51.1%), total nitrogen (51.1%–88.9%), available phosphorus (2.2–5.1-fold), and available potassium (3.0–4.0-fold), whereas sole nitrogen fertilization (N1/N2) induced soil acidification and salinization risk. Combined fertilization (MN1) stimulated hydrolase activities (urease increased by 149%–217%, invertase increased by 60–130%), boosted enhanced nitrogen-phosphorus transformation (neutral phosphatase increased by 102%); Thaumarchaeota (87%) dominated as the core phylum, exhibiting significant negative correlations with SOM, EC, and catalase (CAT) activity ($P<0.05$); Sole nitrogen fertilization enriched Euryarchaeota (N1:10%) and Marine Group II (N1:9.5%); Organic amendments promoted unclassified archaeal proliferation (MN1:29%), with LEfSe identifying Soil Crenarchaeotic Group SCG as a biomarker for organic treatments; The tomato yield under combined fertilization (MN1) reached 2.5 times that of CK, showing significant correlation with Thaumarchaeota abundance ($P<0.05$). These results suggested that integrated organic-inorganic fertilization synergistically improves nutrient use efficiency and sustains soil health by optimizing archaeal community structure (elevating Thaumarchaeota/unclassified taxa) and enhancing enzymatic networks, providing microbial regulation targets for precision agriculture in greenhouse systems.

Keywords: Archaea, Soil fertility, Soil enzymes, High throughput sequencing

How to cite this article:
Sun SK, Li M, Zhao LL and Liu SJ. Archaeal abundance as a negative indicator of soil fertility. Asian J. Agric. Biol. 2025: e2025058. DOI: https://doi.org/10.35495/ajab.2025.058

Introduction

Soil fertility is generally evaluated based on physical, chemical, and biological properties (Yan et al., 2008). Given the complexity of these indicators, simple and reproducible parameters are often preferred for assessing key aspects of soil fertility (Zheng et al., 2004). Soil microorganisms, as the most dynamic components of the soil ecosystem, serve as highly sensitive indicators of soil fertility (Zhang et al., 2013). With advancements in molecular ecology, the relationship between soil microbial communities and fertility has become a focal area in edaphology. Soil microbial community structure significantly influences soil fertility and nutrient cycling, with microorganisms can decompose organic matter to release nutrients, enhancing the mineralization of soil organic matter (Xu et al., 2023). Their activities also drive nutrient transformation and translocation processes, regulate nutrient availability and accessibility, and respond rapidly to agricultural management practices—making them a key driver of soil environmental quality and function (Antonio and Ramdas, 2023). Therefore, maintaining an optimal microbial community structure is essential for improving soil fertility and nutrient use efficiency. Soil beneficial microorganisms primarily encompass three major groups: bacteria, fungi, and archaea, each performing critical roles in ecosystem functions. Specifically, bacteria decompose organic matter, mineralize nutrients, and fix atmospheric nitrogen; fungi contribute to organic matter humification, nutrient transport, and soil aggregate formation; and archaea participate in nitrogen cycling, methane metabolism, and extremophilic adaptation (Shi et al., 2023). While extensive research has examined the interactions between soil bacteria or fungi and fertility, studies on archaea remain relatively limited.

The discovery of Archaea in marine environments in 1992 by Delong and Fuhrman (Delong, 1992; Fuhrman et al., 1992), expanded our understanding of microbial diversity. Initially, only Euryarchaeota and Crenarchaeota were recognised, but Korarchaeota was later identified (Tahon et al., 2021). Subsequent research led to the reclassification of mesophilic Crenarchaeota into a distinct phylum, Thaumarchaeota (Tahon et al., 2021). More recently, additional archaeal lineages such as Nanoarchaeota, Aigarchaeota, Parvarchaeota, Lokiarchaeota, and Aenigmarchaeota have been proposed (Tupinambá et al., 2016; Aparici-Carratalá et al., 2023), though their classification remains under debate.

Molecular ecology studies have revealed the widespread presence of Archaea across diverse ecosystems, including marine, freshwater, and terrestrial environments, where they play key roles in biogeochemical cycles, particularly in carbon and nitrogen transformations (Aparici-Carratalá et al., 2023). Ammonia-oxidising archaea (AOA), for instance, contribute to nitrification, especially in acidic soils (Kim et al., 2021). Previous studies have reported that the initial amount of AOA in soil is higher than that of ammonia oxidizing bacteria (AOB), but the use of inorganic nitrogen fertilizer significantly inhibits AOA and promotes AOB growth and ammonia oxidation (Sterngren et al., 2015; Ouyang et al., 2017; Meinhardt et al., 2018). It is widely accepted that high nitrogen levels stimulate the growth and activity of AOB, while AOA dominate in nitrogen-poor environments due to their higher ammonia affinity (Di et al., 2009; Pan et al., 2023). However, emerging research has identified AOA strains within the genus *Nitrosocosmicus* exhibiting ammonia affinity comparable to AOB (Jung et al., 2022). This finding challenges the established paradigm that AOB primarily drive nitrification in high-nitrogen soils, whereas AOA prevail in low-nitrogen soils. Hence, with the research on AOA and AOB in agricultural soil, the metabolic mechanisms, functional activities, and relative roles of the two in different habitats are still controversial.

Previous reports have pointed out that the dominant archaeal phyla in paddy soils are Euryarchaeota (65.49%–92.69%), Thaumarchaeota (2.14%–6.41%), Candidatus Bathyarchaeota (1.72%–22.93%), and Candidatus Thermoplasmatota (0.90%–3.62%) (Wang et al., 2025). In the rhizosphere soils of soybean, Aenigmarchaeota emerges as the most abundant archaeal group (Xu and Mao, 2019). Soil total nitrogen (TN) indirectly influences crop yield by modulating both α-diversity (within-sample diversity) and β-diversity (between-sample compositional variation) of soil archaeal communities (Wang, 2023). However, current research predominantly focuses on archaeal diversity, community composition, and specific lineages (Tejerizo et al., 2017), with limited progress in understanding their ecological functions, particularly in soil ecosystems.

To address this gap, we investigated the ecological role of Archaea in agricultural soils by assessing their relationship with soil fertility. Fertility was evaluated

https://doi.org/10.35495/ajab.2025.058

through key physical and chemical properties alongside soil enzyme action. Our study was conducted at a long-term (34-year) fertilisation research site established in 1988. Based on the 34-year long-term fertilization experiment in vegetable systems, this study proposes a central hypothesis: Long-term fertilization regimes drive the restructuring of archaeal communities by regulating soil physicochemical properties (organic matter, N/P/K speciation, EC, pH) and enzyme activities (urease, dehydrogenase, etc.), thereby influencing soil fertility evolution. Utilizing Illumina high-throughput sequencing to characterize archaeal community composition, we integrate microbial functional diversity, key soil enzyme activities, and multidimensional fertility indices to achieve three objectives: 1) elucidate archaeal community succession patterns across fertilization gradients; 2) quantify interaction networks between archaeal community structure and soil fertility parameters; 3) identify core archaeal taxa responsive to fertilization as diagnostic biomarkers for soil health. These findings will provide microbiological foundations for innovating fertility evaluation systems in greenhouse vegetable production and establish the theoretical basis for precision fertilization guided by archaeal community homeostasis.

Material and Methods

Experimental site and treatments

Soil samples were obtained in June 2021 from the long-term vegetable fertilisation research station at Shenyang Agricultural University (41°31′N, 123°24′E) in Liaoning Province, Northeast China. The soil type was classified as meadow soil. This region experiences a sub-humid north temperate continental climate, with an average annual temperature ranging from 6.2 °C to 9.7 °C and annual precipitation of 600–800 mm. The frost-free period lasts approximately 155–180 days. The long-term fertilisation experiment was established in 1988, with initial surface layer nutrient levels as follows: organic matter 24.30 g/kg; total nitrogen 1.164 g/kg; available nitrogen 86.41 mg/kg; available phosphorus 70.80 mg/kg; available potassium 56.14 mg/kg; exchangeable base cations 14.56 cmol/kg; pH value 6.75 (Ge et al., 2004).

Six fertilisation treatments were selected: an unfertilised control (CK), organic fertiliser only (MN_0), nitrogen fertiliser combined with organic fertiliser (MN_1, MN_2), and nitrogen fertiliser alone (N_1, N_2). The organic fertiliser consisted of decomposed horse manure applied at 75 t ha^{-1}. The nutrient content of well-decomposed horse manure is as follows: organic matter 21%; nitrogen 0.4%-0.55%; phosphorus 0.2%-0.3%; potassium 0.35%-0.45%. The N_1 and N_2 treatments involved urea application at rates of 307.5 and 615 kg N ha^{-1} (converted to pure N), respectively. A completely randomised block design was used, with each treatment replicated three times in 1 × 1.5 m^2 plots. Organic manure and half of the nitrogen fertiliser were incorporated as a basal treatment via ploughing, while the remaining nitrogen was applied during the fruit swelling stage. Each plot contained eight tomato plants (*Lycopersicon esculentum* Mill. 'Liaoyuanduoli'), with four fruit panicles per plant and 3–5 fruits per panicle.

Soil sampling and chemical analyses

Soil samples (0–20 cm depth) were collected from each replicate plot using a five-point composite sampling method with a soil auger, 40 days after the final fertilisation (15 June 2021). Fresh samples were sieved through a 2 mm mesh to remove stones, crop residues, and visible soil fauna. Samples were then divided into two portions: one was stored at −80 °C for high-throughput sequencing, while the other was air-dried at room temperature for soil physicochemical and enzyme activity analyses.

Soil physicochemical properties were assessed following Bao (2000) and Lu (2000). Soil water content (SWC) was determined by oven-drying at 105 °C for 12 h. Soil organic matter (SOM) was quantified using low-temperature external-heated $K_2Cr_2O_7$ oxidation spectrophotometry. Total nitrogen (TN) was measured via Kjeldahl digestion. Ammonium nitrogen (NH_4^+-N) was extracted with 2 M KCl and analysed by the indophenol blue colorimetric method, while nitrate nitrogen (NO_3^--N) was extracted using saturated $CaSO_4$ solution and measured by the phenol disulfonic acid colorimetric method. Available phosphorus (AP) was extracted with HCl-NH_4F and determined via molybdenum blue spectrophotometry, whereas available potassium (AK) was extracted using NH_4OAc and analysed by flame photometer. Soil pH and electrical conductivity (EC) were measured in a 1:5 (w/v) soil-to-water suspension.

Soil enzyme activity assays

Soil enzyme activities were determined using standard methods described by Yan (1988) and Li et al. (2008). Catalase (CAT) activity was measured by $KMnO_4$

https://doi.org/10.35495/ajab.2025.058

titration (0.002 M $KMnO_4$, mL g^{-1}, 37 °C, 30 minutes). Polyphenol oxidase (PPO) activity was assessed using purpurogallin colourimetry (purpurogallin, mg 100 g^{-1}, 37 °C, 3 hours). Invertase (INT) activity was determined by sodium thiosulfate titration (0.1 M $Na_2S_2O_3$, mL g^{-1}, 37 °C, 24 hours). Urease (URE) activity was analysed by sodium–hypochlorite colorimetry (NH_3-N, mg g^{-1}, 37 °C, 24 hours). Neutral phosphatase (NPP) activity was quantified using disodium phenyl phosphate colourimetry (PhOH, mg g^{-1}, 37 °C, 12 hours). Cellulase (CEL) activity was measured with 3,5-dinitrosalicylic acid colourimetry (glucose, mg g^{-1}, 37 °C, 72 hours). To ensure the accuracy and reliability of the experimental results and eliminate the influence of soil original substances on the experimental results, no matrix or soil controls were included in enzyme activity measurements.

Nucleic acid isolation and high-throughput sequencing

Total DNA was extracted from fresh soil using a FastDNA® Spin Kit for Soil (MP Biomedicals, U.S.), following the manufacturer's protocol. DNA concentration and purity were assessed using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, U.S.). Archaeal community composition and diversity were analysed via high-throughput sequencing of the 16S rRNA gene, amplified using the primer pair 344F (5'-ACGGGGYGCAGCAGGCGCGA-3') and 915R (5'-GTGCTCCCCCGCCAATTCCT-3') (Caliz et al., 2015).

A 20 μL PCR reaction contained 4 μL of 5× FastPfu buffer, 2 μL of 2.5 mM dNTP mix, 0.8 μL of each primer (5 μM), 0.4 μL of TransStart FastPfu DNA polymerase (TransGen), 0.2 μL of BSA, and 10 ng of template DNA, with double-distilled H_2O added to a final volume of 20 μL. PCR amplification was performed in an ABI GeneAmp® 9700 thermocycler using the following program: initial denaturation at 95 °C for 3 min, followed by 27 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 1 min, followed by a final elongation at 72 °C for 10 min. PCR products were purified with an AxyPrep DNA Gel Extraction Kit and quantified with a Quant-iT PicoGreen dsDNA assay (Invitrogen, Carlsbad, CA, U.S.). Concentration and purity were verified by 2% agarose gel electrophoresis with ethidium bromide staining, confirming product integrity and suitability for pyrosequencing.

Quality control followed the method described by Liu et al. (2015). To determine the counts of bacterial species, genera, and other taxa in a sequencing sample, sequences must be clustered into Operational Taxonomic Units (OTUs) based on similarity. Typically, OTUs clustered at a 97% similarity threshold undergo subsequent bioinformatic analysis using the Usearch platform (version 7.1: http://drive5.com/uparse/). Post-filtering, high-quality sequences were aligned against the SILVA v111 16S rRNA gene database (http://www.arb-silva.de), with community composition quantified at each taxonomic level: domain, kingdom, phylum, class, order, family, genus, and species. Taxonomic classifications lacking scientific names were labelled as *norank*, while those with confidence scores below the threshold (80%) were marked as *unclassified.* The non-parametric factorial Kruskal-Wallis (KW) sum-rank test was employed to detect features with significant abundance differences and identify taxa exhibiting these variations. Linear Discriminant Analysis (LDA) Effect Size (LEfSe) was applied to estimate the effect size of each component (species) abundance contributing to the observed differences. The LEfSe statistical outputs comprise three elements: (1) an LDA value distribution histogram, (2) a cladogram illustrating phylogenetic distribution, and (3) a comparison table displaying biomarker taxa with statistically significant abundance differences among experimental groups. Environmental factor correlation analyses were implemented via the Majorbio Cloud Platform (https://www.majorbio.com/).

Statistical analysis

Soil physicochemical properties and enzyme activities were analysed using one-way ANOVA, with treatment means compared via least significant difference (LSD) tests. All experiments were conducted in triplicate, and statistical significance was set at $P < 0.05$, with different lowercase letters indicating significant differences.

Results

Soil characteristics

Table-1. Soil physicochemical characteristics under different fertilisation treatments.

Treatments	SOM [a] (g kg^{-1})	TN (g kg^{-1})	NH_4^+-N (mg kg^{-1})	NO_3^--N (mg kg^{-1})	AP (mg kg^{-1})	AK (mg kg^{-1})	EC (mS cm^{-1})	SWC (%)	pH
CK	17.2 b [c]	0.79 b	5.8 d	5.0 d	55.8 b	40.2 b	0.14 e	15.0 ab	7.1 ab
N_1	18.0 b	0.90 b	17.6 cd	45.8c	40.4 b	46.5 b	0.28 d	13.7 ab	6.6 bc
N_2	19.1 b	0.72 b	58.8 a	147.6 b	77.2 b	49.8 b	0.60 bc	12.6 b	5.3 d
MN0	24.9 a	1.44 a	12.4 cd	15.0 d	223.0 a	215.8 a	0.55 c	19.1 a	7.3 a
MN_1	26.0 a	1.36 a	25.5 bc	198.6 a	244.6 a	200.6 a	0.68 ab	18.7 ab	6.7 bc
MN_2	25.4 a	1.35 a	40.2 b	245.9 a	205.7 a	222.3 a	0.77 a	16.3 ab	6.3 c
OV[b]	24.3	1.164	- [d]	-	70.8	56.14	-	-	6.75

[a] Abbreviations are expanded in ‘‘Materials and Methods.’’
[b] OV (original value) refers to the original soil agrochemical properties at the beginning of the long-term fertilisation test.
[c] Means accompanied by the same lowercase letter in the same column were not significantly different by LSD’s test ($P < 0.05$).
[d] Means not measured at the original time.

The concentrations of SOM, TN, AP and AK were significantly higher under organic fertiliser treatments (MN_0, MN_1, and MN_2) compared to both the single nitrogen fertiliser treatments (N_1 and N_2) and the unfertilised control (CK). Taking the MN1 treatment as an example, its organic matter content increased by 36.1%–51.1% compared to no fertilization or nitrogen-only treatments, total nitrogen rose by 51.1%–88.9%, available phosphorus surged 2.2- to 5.1-fold, and available potassium elevated 3.0- to 4.0-fold. In contrast, ammonium nitrogen (NH_4^+-N), nitrate nitrogen (NO_3^--N), and EC increased with urea application. SWC did not differ significantly among treatments, except between MN_0 and N_2. Over the long term, the sole application of nitrogen fertiliser led to a pronounced depletion of AP and AK, along with substantial SOM loss. Notably, soil pH remained stable under the unfertilised control and with sole organic fertiliser application, but declined progressively with increasing nitrogen input. Among them, N2 treatment decreased by 1-2 units compared to other treatments. Above all, well-decomposed horse manure (organic fertilizer) optimized soil structure and water retention by enhancing organic matter and nutrient content. In contrast, nitrogen-only fertilization, while improving nitrogen availability, caused soil acidification and salinization risks. The combined organic-inorganic fertilization (MN1/MN2) partially mitigated these adverse effects while sustaining high nutrient levels, though excessive nitrate accumulation requires attention.

Soil enzyme activities and tomato yield

Table-2. Impact of fertilisation on soil enzyme activities.

Treatments	URE [a] mg (g·d)$^{-1}$ [b]	INT mL (g·d)$^{-1}$	CEL mg (g·72 h)$^{-1}$	NPP mg (g·12 h)$^{-1}$	PPO mg (100g·3 h)$^{-1}$	CAT mL (g·30 min)$^{-1}$	Yield kg plot^{-1}
CK	0.98 b [c]	1.12 bc	0.08 b	0.45 e	60.5 bc	15.3 a	9.5 d
N_1	1.25 b	0.83 c	0.09 b	0.88 c	73.5 b	9.8 b	14.6 c
N_2	0.53 c	0.78 c	0.08 b	0.69 d	39.8 c	4.7 c	14.8 c
MN_0	3.01 a	2.24 a	0.18 a	1.23 b	75.6 b	14.6 a	20.9 b
MN_1	3.11 a	1.79 ab	0.18 a	0.91 c	75.1 b	15.6 a	24.2 a
MN_2	2.84 a	1.81 ab	0.21 a	1.57 a	98.8 a	16.4 a	22.2 ab

[a] Abbreviations are expanded in ''Materials and methods''.
[b] Unit of Soil enzymatic activities are outlined in ''Materials and methods''.
[c] Means accompanied by the same lowercase letter in the same column were not significantly different by LSD's test ($P < 0.05$).

The activities of key hydrolases—including urease (URE), invertase (INT), and cellulase (CEL)—exhibited similar trends across treatments. These enzymes were significantly more active under organic fertiliser treatments (MN_0, MN_1, and MN_2) compared to both nitrogen-only treatments (N_1, N_2) and the control (CK; Table 2). Taking the MN1 treatment as an example, its urease activity increased by 1.5- to 4.9-fold compared to no fertilization or nitrogen-only treatments, invertase rose by 60.0%–129.5%, and cellulase elevated by 1.0- to 1.25-fold. Neutral phosphatase (NPP) was especially responsive to fertilisation, showing significant variation across all six treatments. Interestingly, polyphenol oxidase (PPO) activity peaked under the two high-nitrogen treatments (N_2 and MN_2), while remaining relatively unchanged in the remaining treatments. Catalase (CAT) activity did not significantly differ between CK and organic fertiliser treatments, suggesting that organic amendments alone or in combination with nitrogen did not affect CAT levels. However, sole nitrogen application appeared to suppress CAT activity, decreased by 56.1% to 2.3-fold compared to CK. Collectively, these findings indicate that the co-application of chemical nitrogen fertiliser with organic manure enhances a broad range of soil enzyme activities, whereas the absence of fertilisation or use of nitrogen alone markedly suppresses enzymatic function.

Crop yield is a direct indicator of soil fertility and nutrient supply capacity. The tomato yield of MN1 was the highest, with 2.5 times that of CK, representing a 66.0% increase over N1, N2 and even exceeding MN0 by 16%, confirming the synergistic effects of the combined fertilization strategy (Table 2). Conversely, reliance on nitrogen fertiliser alone resulted in notably lower yields. Above all, the integrated organic-inorganic fertilization maximized crop yield by synergistically regulating enzyme activities, particularly enhancing nitrogen-phosphorus transformation (URE and NPP) and redox metabolism (PPO and CAT). In contrast, high-rate chemical fertilizer alone (N_2) inhibited most enzymes, underscoring the essential role of integrated fertilization in sustaining soil health and productivity.

Soil archaeal community structure

Taxonomic classification based on the SILVA v111 16S rRNA gene reference database identified seven archaeal phyla, including a notable proportion of unclassified groups (Fig. 1a). Among these, only Thaumarchaeota and Euryarchaeota had relative abundances exceeding 1%. Thaumarchaeota overwhelmingly dominated the archaeal community in greenhouse soil, accounting for an average of 87% of sequences. Euryarchaeota abundance peaked under the N_1 and N_2 treatments, reaching 10% and 8%, respectively, but it was lowest in MN_1 (0.2%) and remained around 1% in other treatments. The presence

of up to 29% unclassified archaea in MN_1 suggests a rich diversity of potentially novel archaeal taxa under organic fertilisation conditions.

At the genus level, seven taxa surpassed the 1% relative abundance threshold, including unclassified groups (Fig. 1b). Excluding N_2, the *Soil Crenarchaeotic Group* (*SCG*) *norank* was the most prevalent genus across treatments, ranging from 48% to 67% in relative abundance. *Candidatus Nitrososphaera* ranked second, with its highest abundance (40.8%) recorded in CK, progressively declining with increased nitrogen input. *Candidatus Nitrosotalea* was detected only in MN_2, N_1, and N_2, exhibiting a remarkably high relative abundance (63%) in N2, indicating its dominance under high-nitrogen conditions; however, its presence in MN_2 and N_1 remained below 0.5%. *Marine Group II norank* was predominant only in N_1 and N_2, with relative abundances of 9.5% and 8.0%, respectively, but remained below 0.8% in other treatments. The *unclassified Crenarchaeotic Group SCG* maintained consistent relative abundance (~3%) across all treatments. *Norank SIGW621* peaked at 6% in N_1 but remained below 3% elsewhere. Notably, MN1 had the highest proportion of unclassified archaea at the genus level, further underscoring the biodiversity-promoting effect of organic fertilisation. These results collectively demonstrate that fertilisation strategies, particularly nitrogen input levels and organic amendments, substantially influence the structure and diversity of archaeal communities in greenhouse soils.

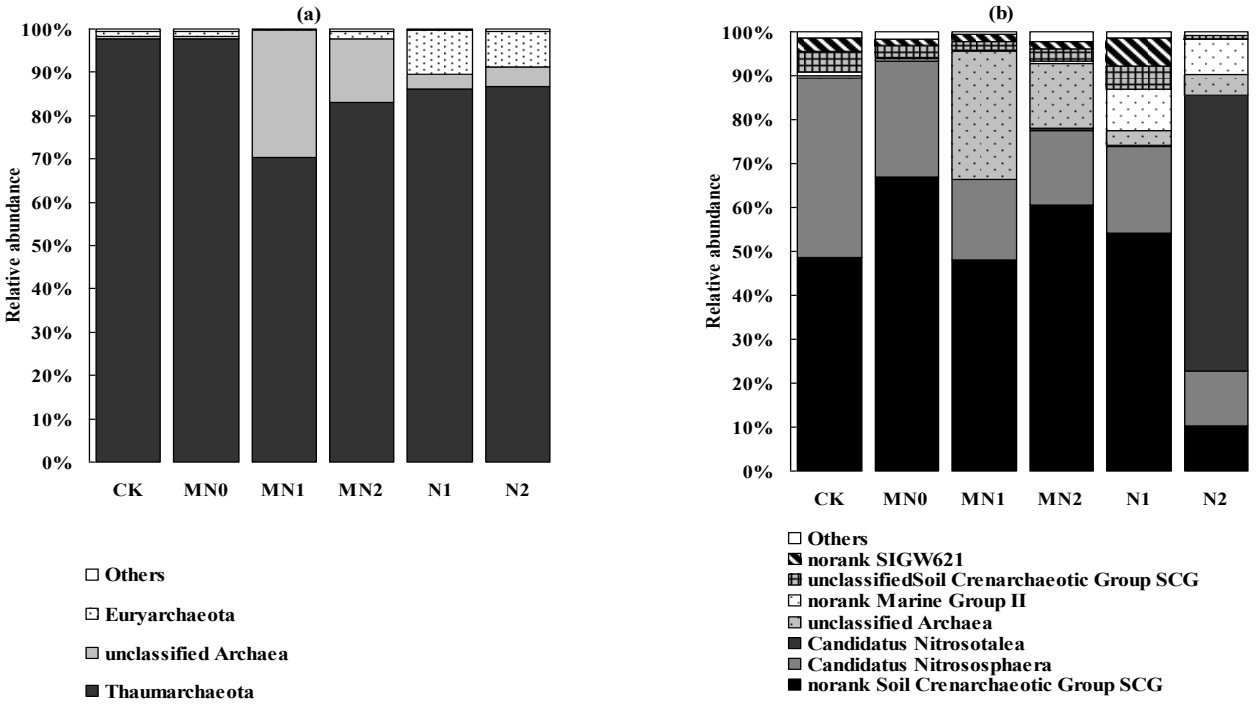

Figure-1. The abundance of archaea at the phylum (a) and genus levels (b). The relative abundance of Archaea below 1% was classified as "others." CK-unfertilised control, N1, N2-nitrogen fertiliser alone .MN0-organic fertiliser only, MN1, MN2-nitrogen fertiliser combined with organic fertiliser. The specific amount of fertilizer can be found in the Materials and Methods.

Correlation between Archaea and soil fertility factors at the phylum level

Pearson correlation analysis was conducted to examine the relationships between archaeal abundance and soil physicochemical properties, enzyme activities, and tomato yield at the phylum level (Table 3). Thaumarchaeota, the dominant archaeal group, displayed a significant negative correlation with SOM, EC, and CAT activity ($P < 0.05$), and was significantly correlated with tomato yield. Euryarchaeota, the second most abundant phylum, exhibited a significant negative correlation with URE activity and PPO

activity ($P < 0.05$). Parvarchaeota abundance showed a negative correlation with SWC and PPO activity ($P < 0.05$), while demonstrating a positive association with soil pH ($P < 0.05$). Other archaeal phyla showed only non-significant correlations with soil fertility and yield ($P > 0.05$).

Table-3. Correlation between Archaeal abundance (phylum level) and physicochemical parameters, soil enzyme activities, and yield.

Phylum level	Thaumarchaeota	Parvarchaeota	Euryarchaeota
SOM [a]	-0.892*[b]	-0.604	-0.686
SWC	-0.444	-0.858*	-0.619
EC	-0.834*	-0.676	-0.805
pH	0.326	0.851*	0.454
PHO	-0.714	-0.888*	-0.868*
URE	-0.756	-0.538	-0.841*
CAT	-0.875*	-0.488	-0.667
Yield	-0.962**	-0.687	-0.785

[a] Abbreviations are outlined in ‘‘Materials and Methods’’.
[b] $^{*}P < 0.05$
[c] $^{**}P < 0.01$

Correlation between Archaea and soil fertility features at the species level

Table-4. Correlation between Archaeal abundance (species level) and physicochemical parameters, soil enzyme activities, and yield.

Species [a]	*Unclassified norank Soil Crenarchaeotic Group SCG*	*Unclassified Candidatus Nitrososphaera*	*Uncultured archaeon Candidatus Nitrosotalea*	*Uncultured bacterium norank Soil Crenarchaeotic Group SCG*	*Nitrososphaera viennensis EN76*	*Uncultured archaeon norank Marine Group II*
TN [b]	-0.395	-0.870*	0.532	-0.708	0.572	0.016
NH_4^+-N	-0.016	-0.689	0.261	-0.814*	0.366	-0.053
EC	0.343	0.109	-0.669	0.538	-0.725	-0.818*
pH	-0.578	-0.768	0.862*	-0.836*	0.912*	0.432
SWC	0.532	0.714	-0.866*	0.892*	-0.935** [d]	-0.606
PHO	0.546	0.510	-0.892*	0.637	-0.942**	-0.864*
NEP	0.845* [c]	-0.041	-0.696	0.041	-0.581	-0.427
URE	0.233	0.054	-0.531	0.458	-0.591	-0.861*

[a] Total relative abundance of the top 10 species
[b] Abbreviations are outlined in ‘‘Materials and Methods’’
[c] $^{*}P < 0.05$
[d] $^{**}P < 0.01$

https://doi.org/10.35495/ajab.2025.058

To further investigate the relationship between archaeal communities and soil fertility, we analysed the correlation species-level correlations, focusing on the ten most abundant species (Table 4). The most prevalent taxon, *Unclassified norank Soil Crenarchaeotic Group*, was positively correlated with soil neutral phosphatase activity ($P < 0.05$). *Unclassified Candidatus Nitrososphaera*, the second most abundant species, exhibited a significant negative correlation with TN content ($P < 0.05$). The third most abundant, *Uncultured archaeon Candidatus Nitrosotalea*, was significantly correlated with PPO activity, EC, and pH ($P < 0.05$). *Uncultured bacterium norank Soil Crenarchaeotic Group SCG*, ranking sixth in abundance, showed significant correlations with SWC, pH, and NH_4^+-N content ($P < 0.05$). *Nitrososphaera viennensis EN76*, the eighth most abundant species, demonstrated highly significant correlations with soil pH, SWC, and PPO activity ($P < 0.01$). The ninth-ranked *Uncultured archaeon norank Marine Group II* was significantly correlated with URE, PPO, and EC ($P < 0.05$). Other highly abundant taxa, including *Uncultured archaeon norank Soil Crenarchaeotic Group SCG*, *Unclassified norank Archaea*, *Uncultured crenarchaeote Candidatus Nitrososphaera*, and *Uncultured bacterium norank SIGW621*, showed non-significant associations with soil fertility parameters ($P > 0.05$). Notably, no archaeal species exhibited a significant correlation with tomato yield ($P > 0.05$, data not shown).

Responses of Archaea to organic manure and nitrogen fertiliser

A Venn diagram (Figure 2a) illustrated differences in archaeal species composition between the nitrogen fertiliser (N) and organic manure (M) groups. The N group harboured a greater number of archaeal species, with 33 species shared between the two treatments. The M group contained only two unique species—*Uncultured Methanoculleus sp.* and *Uncultured archaeon Haladaptatus*. In contrast, seven species were exclusive to the N group: *Uncultured haloarchaeon norank Marine Group II*, *Halobacteriaceae archaeon NK23*, *Uncultured archaeon norank South African Gold Mine Gp-1*, *Unclassified norank South African Gold Mine Gp-1*, *Unclassified Candidatus Micrarchaeum*, *Uncultured archaeon norank Parvarchaeota*, and *Uncultured crenarchaeote norank terrestrial group.*

Linear discriminant analysis effect size (LEfSe) identified *Uncultured archaeon Soil Crenarchaeotic Group SCG* (*Thaumarchaeota*) and *Thermophilus thermophila TM1* (*Euryarchaeota*) as key species in the M group, whereas *Uncultured archaeon norank Marine Group II* and *Unclassified norank Marine Group II* were dominant in the N group. Both archaeal taxa in the N group were classified under *Norank Marine Group II* at the genus level, which exhibited the highest relative abundance in N_1 and N_2 treatments (Figure 1).

The LDA discriminant column chart (Figure 2c) further highlighted microbial taxa with significant variability between the M and N groups. Higher LDA scores indicated a stronger influence on group differentiation. Among these, *Uncultured archaeon Soil Crenarchaeotic Group SCG* exhibited the greatest impact on distinguishing M from N treatments, whereas *Euryarchaeota* showed comparable effects in both groups. Within the N group, the LDA scores for *Uncultured archaeon norank Marine Group II* were slightly higher than those for *Unclassified norank Marine Group II* at the species level, suggesting its more prominent role in shaping archaeal community structure under nitrogen fertilisation.

https://doi.org/10.35495/ajab.2025.058

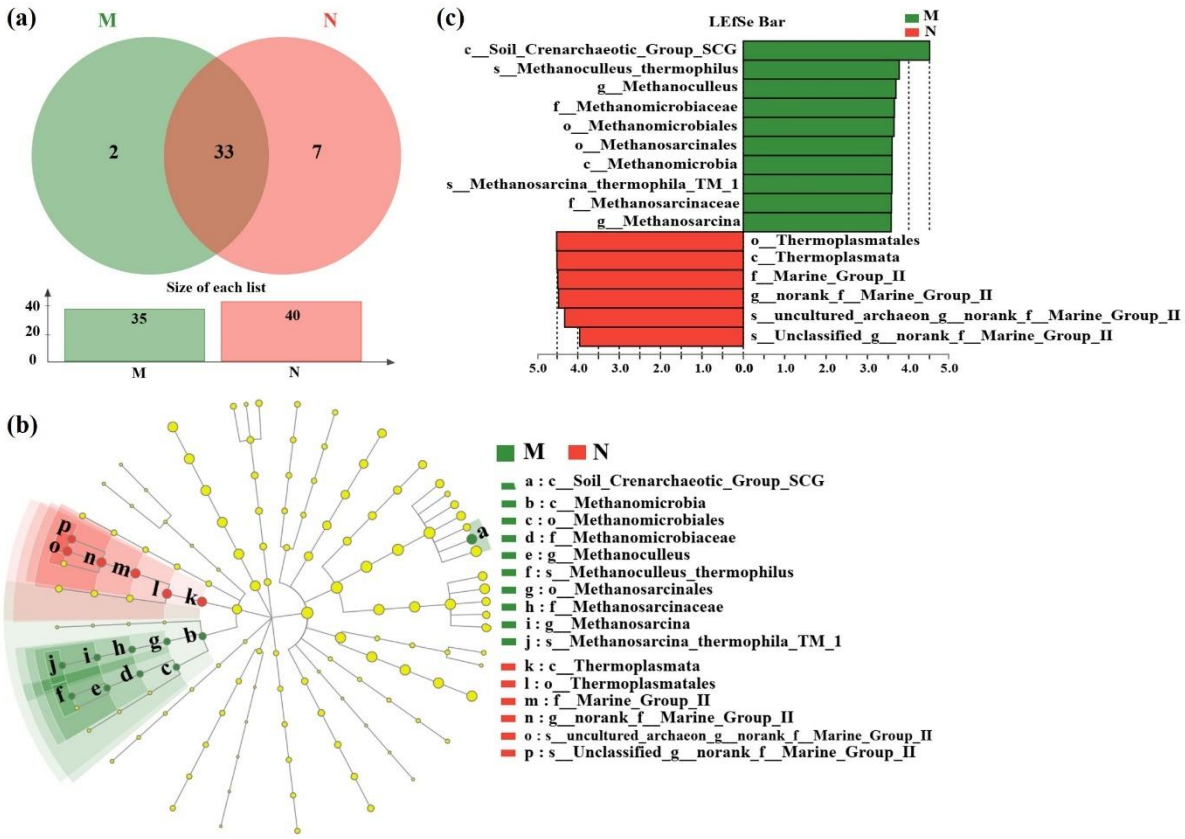

Figure-2. LEfSe identified significant differences in the marker taxa between organic manure (M) and no organic manure groups (N). M denotes organic manure treatments (MN_0, MN_1, MN_2), and N indicates no organic manure treatments (CK, N_1, N_2). (a) Venn diagram showing common and individual operational species in the M and N groups. Taxonomic cladogram from LEfSe analysis of 16S sequences. (Black) taxa enriched in the M group; (Grey) taxa enriched in the N group. Dot brightness relates to effect robustness (b). Estimating effect magnitude across component (species) abundance on differences of M and N groups by LDA score (log 10) (c).

Discussion

The Farmland ecosystems represent a critical component of terrestrial ecosystems, serving as the most actively managed environments influenced by human activities (Ren et al., 2014; Wu et al., 2015). Fertilisation plays a key role in agricultural production, significantly affecting soil fertility and microbial activity (Zhao et al., 2014). It is widely accepted that organic manure can partially substitute chemical fertilisers and contribute to the long-term sustainability of agriculture. This approach aligns with China's major agricultural policies aimed at reducing fertiliser and pesticide inputs while maintaining productivity.

Prior research demonstrates that long-term sole nitrogen fertilization induces soil acidification and reduced enzymatic activity, whereas sole organic fertilization or its combination with nitrogen significantly enhances soil nutrient content and enzyme activity—findings largely consistent with our results, which show elevated levels of soil organic matter, total nitrogen, available phosphorus, and available potassium under organic treatments compared to nitrogen-only and unfertilized controls (Zhang et al., 2022). Both TN and mineral nitrogen (alkali-hydrolyzable N, nitrate-N, ammonium-N) increased progressively with nitrogen input, with combined organic-nitrogen treatments exhibiting significantly higher nitrogen levels than sole nitrogen applications, indicating nitrogen input as the primary driver of soil nitrogen dynamics and highlighting the efficacy of long-term integrated fertilization in boosting nitrogen supply capacity in greenhouse soils

https://doi.org/10.35495/ajab.2025.058

(Hui et al., 2022). Moreover, soil electrical conductivity escalated with nitrogen input, even surpassing the critical threshold for tomato growth (Wang et al., 2023), revealing secondary salinization risks from excessive nitrogen. Comprehensive analysis by Xu et al. (2015) of global studies over 30 years confirms that chemical fertilizers, particularly ammonium-based nitrogen, accelerate soil acidification—a trend mirrored in our study as soil pH decreased with increasing nitrogen application. As critical catalysts for biochemical reactions and key indicators of soil fertility, soil enzymes' collective activity (rather than individual enzymes) more accurately reflects fertility status (Li et al., 2012), our data prove that sole or combined organic fertilization significantly enhances multiple native enzyme activities, thereby elevating comprehensive enzymatic activity to accelerate organic matter mineralization and nutrient cycling.

Numerous reports indicate that soil microbial community composition, functionality, and species diversity are closely linked to soil physicochemical features (Tamez–Hidalgo et al., 2016; Estrada et al., 2024).Archaea are ubiquitously distributed and highly abundant in diverse non-extreme environments—including lakes, oceans, and soils—while demonstrating remarkable adaptability to extreme habitats such as hyperthermophilic (>80°C), hypersaline (>30% salinity), anaerobic, hyperacidic (pH <3), and hyperalkaline (pH >10) conditions (Tahon et al., 2021; Aparici-Carratalá et al., 2023). Thaumarchaeota has been reported as the dominant archaeal group in Amazonian native forests, while Euryarchaeota predominates in oil palm-cultivated soils (Tupinambá et al., 2016). Thaumarchaeota mediate dual nitrogen transformations across redox gradients: under aerobic conditions, they oxidize ammonia (NH_3) to nitrite (NO_2^-), whereas in anaerobic environments, they derive energy by reducing nitrate (NO_3^-) to nitrite (NO_2^-) (Beam et al., 2013; Lin et al., 2015). In our study, six archaeal groups were identified (excluding unclassified Archaea), with Thaumarchaeota being the most abundant. This suggests that archaeal dominance varies across environments, likely due to their intrinsic adaptive mechanisms. Ammonia-oxidizing archaea (AOA), affiliated with the phylum Thaumarchaeota, co-participate in soil nitrification with ammonia-oxidizing bacteria (AOB) (Aparici-Carratalá et al., 2023). This study demonstrates significant negative correlations between Thaumarchaeota abundance and soil organic matter (SOM), electrical conductivity (EC), and enzyme activities—aligning with the established paradigm that high nitrogen availability stimulates AOB growth and activity, whereas AOA dominate nitrogen-depleted environments due to their superior ammonia affinity (Kim et al., 2021). Furthermore, we identified key nitrogen-cycling taxa: *Candidatus Nitrososphaera* and *Candidatus Nitrosotalea* represent distinct AOA ecotypes. *Nitrososphaera* thrives in upland soils under long-term inorganic fertilization, driving nitrification, whereas organic fertilization shifts dominance to AOB. In contrast, *Nitrosotalea* activity in paddy soils remains less responsive to fertilization but critically depends on soil pH, remaining viable only below pH 5.5 (Xu and Mao, 2019). Notably, pH was positively associated with archaeal abundance, suggesting that many archaeal taxa are well-adapted to acidic conditions (Tahon et al., 2021). Qin et al. (2015) identified pH as a primary determinant of archaeal community structure, which may explain the significant shifts observed in N_2-treated soils subjected to severe acidification. Under these conditions, *Candidatus Nitrosotalea* became the dominant archaeal species, indicating its functional role in nitrogen cycling. At the species level, *Unclassified Candidatus Nitrososphaera* abundance negatively correlated with total nitrogen (TN), while *Uncultured bacterium norank Soil Crenarchaeotic Group SCG* inversely associated with ammonium-N. Concurrently, acidification increased *Uncultured archaeon Candidatus Nitrosotalea* abundance, and *Uncultured bacterium norank Soil Crenarchaeotic Group SCG* exhibited negative correlation with pH, consistent with reports of AOA dominating nitrification in acidic, low-nitrogen soils (Aparici-Carratalá et al., 2023). While these findings highlight potential roles for archaea in nitrogen cycling, further experimental validation is necessary to confirm their functional contributions.

While extensive research has explored the relationship between Archaea and soil physicochemical properties, their role in soil enzyme activity remains less understood. Our findings reveal significant correlations between archaeal abundance and soil enzyme activity at both phylum and species levels. Notably, oxidoreductases exhibited stronger associations with Archaea than hydrolases, with PPO displaying the closest linkage (Tables 3 and 4). PPO plays a crucial role in soil by converting aromatic compounds into quinones, which subsequently

interact with proteins, amino acids, carbohydrates, and minerals to form diverse organic matter and pigments, thereby facilitating aromatic compound turnover (Toscano et al., 2003; Li et al., 2008). This suggests that soil Archaea may potentially participate in aromatic compound transformation. Complementing Li et al.'s (2008) report of an inverse relationship between PPO activity and soil humification, our study correspondingly found that reduced humification levels favored archaeal proliferation.

Thaumarchaeota, the dominant archaeal phylum in our study, exhibited a significant negative relationship to CAT activity. Since CAT facilitates the breakdown of hydrogen peroxide, a harmful by-product in soil (Dai and Bai, 1995), this suggests that Thaumarchaeota may play a role in modulating hydrogen peroxide decomposition. Phosphatases are key enzymes in soil phosphorus cycling, accelerating the mineralisation of organic phosphorus (Li et al., 2016). Our results indicate that *unclassified norank Soil Crenarchaeotic Group SCG*, the dominant archaeal species, was specifically associated with neutral phosphatase activity, implying a functional role in phosphorus transformation, particularly the decomposition of organic phosphorus. Additionally, a significant correlation was observed between the *uncultured archaeon norank Marine Group II* and urease activity (Table 4). As urease catalyses the hydrolysis of urea (Li et al., 2008), this suggests that the archaeon may contribute to soil urea transformation. While invertase and cellulase are central to soil carbon turnover, no significant correlation was found between these enzymes and Archaea. This finding suggests that, within the tested enzymes, archaeal communities may be more involved in nitrogen cycling processes than in the specific carbon cycling processes represented by invertase and cellulase activity.

Notably, this study detected certain unclassified archaeal groups, particularly in the MN1 treatment (Figure 1), whose functions remain unknown; future research could infer potential functional pathways through phylogenetic reconstruction of archaeal communities leveraging their evolutionary relationships with known functional strains combined with metagenomic prediction tools (e.g., PICRUSt2/FUNGuild), or directly characterize their functions via metagenomic techniques, representing a promising research avenue for comprehensive functional characterization of soil archaea.

Conclusions

This study reveals that archaeal community dynamics in greenhouse vegetable soils are closely linked to soil fertility. Long-term fertilization significantly alters composition, with Thaumarchaeota dominance (87% avg.) negatively correlating with soil organic matter, electrical conductivity, catalase activity, and tomato yield ($P<0.05$), indicating its increased abundance signals declining fertility. Euryarchaeota abundance rises under high nitrogen-only fertilization, with *Marine Group II* enrichment reflecting acidification pressure. Combined organic-nitrogen fertilization enhances archaeal diversity, optimizes community structure, boosts enzyme activity, and reverses nitrogen-only inhibition. Archaeal structure sensitively responds to fertilization: Thaumarchaeota dominance implies reduced fertility, while Euryarchaeota and salt/acid-tolerant group enrichment signifies degradation. Organic manure with nitrogen fertilizer regulates diversity balance, synergistically enhancing biological activity and nutrient cycling efficiency, providing a microbial basis for soil health.

Acknowledgements

The authors are thankful for the critical input provided by anonymous reviewers.

Disclaimer: None.

Conflicts of Interest: The authors declare no conflicts of interest.

Source of Funding: This study was funded by the Liaoning Academy of Agricultural Sciences Project: Discipline construction project: Vegetable Physiology and Cultivation (2024XKJS5206). A Study of Tomato Growth Weight Distribution Model Based on Plant Real-time Weight in a Greenhouse (2023BS0802).

Contribution of Authors

Sun SK, Li M & Liu SJ: Conceived idea and designed the experiments, wrote and revised the manuscript.
Sun SK & Li M: Analysed and interpreted data.
Sun SK, Zhao LL & Li M: Conducted field trials, collected data and assisted in write up.

All the authors read and approved the final manuscript.

References

Antonio CH and Ramdas KLSS, 2023. Cover crops in citrus orchards impact soil nutrient cycling and the soil microbiome after three years but effects are site-specific. Biol. Fert. Soils, 59(6): 659–678.

Aparici-Carratalá D, Esclapez J, Bautista V, Bonete MJ and Camacho M, 2023. Archaea: current and potential biotechnological applications. Res. Microbiol., 174, 104080.

Bao SD, 2000. Soil and agricultural chemistry analysis. China Agricultural Press, Beijing, China.

Beam JP, Jay ZJ, Kozubal MA and Inskeep WP, 2013. Niche specialization of novel Thaumarchaeota to oxic and hypoxic acidic geothermal springs of Yellowstone National Park. ISME J, 8: 938–951.

Caliz J, Montes–Borrego M, Triadó–Margarit X, Metsis M, Landa BB and Casamayor EO, 2015. Influence of edaphic, climatic, and agronomic factors on the composition and abundance of nitrifying microorganisms in the Rhizosphere of commercial olive crops. PLoS One 10: e0125787.

Dai W and Bai HY, 1995. Correlations of soil catalase activity an it's kinetic characteristic with some properties, J. Beijing Fores. Univ. 1: 37–41.

DeLong EF, 1992. Archaeal in coastal marine environments. PANS. 89:5685–5689.

Di HJ, Cameron KC, Shen JP, Winefield CS, O'Callaghan M, Bowatte S and He JZ, 2009. Nitrification driven by bacteria and not archaea in nitrogen-rich grassland soils. Nat. Geosci., 2: 621−624.

Estrada R, Porras T, Romero Y, Pérez WE, Vilcara EA, Cruz J and Arbizu CI, 2024. Soil depth and physicochemical properties influence microbial dynamics in the rhizosphere of two Peruvian superfood trees, cherimoya and lucuma, as shown by PacBio-HiFi sequencing. Sci. Rep., 14: 19508.

Fuhrman JA, McCallum K and Davis AA, 1992. Novel major archaebacterial group from marine plankton. Nature. 356:148–149.

Ge XG, Zhang EP, Zhang X, Wang XX and Gao H, 2004. Studies on changes of field – vegetable ecosystem under long termfixed fertilizer experiment（I） Changes of soil organic matter. Acta. Hortic. Sin. 31: 34–38.

Hui K, Xi B, Tan W and Song Q, 2022. Long-term application of nitrogen fertilizer alters the properties of dissolved soil organic matter and increases the accumulation of polycyclic aromatic hydrocarbons. Environ. Res. 215: 114267.

Jung MY, Sedlacek CJ, Kits KD and Mueller AJ, 2022. Wagner M. Ammonia-oxidizing archaea possess a wide range of cellular ammonia affinities. ISME J, 16(1): 272–283.

Kim JG, Gazi KS, Awala SI, Jung MY and Rhee SK, 2021. Ammonia-oxidizing archaea in biological interactions. J. Microbiol., 59: 298–310.

Li CH, Jia ZJ, Tang LS, Wu YC and Li Y, 2012. Effect of model of fertilization on microbial abundance and enzyme activity on oasis farmland soil. Acta. Geol. Sin. 49:567–574.

Li YF, Geng YQ, Zhou HJ and Yang Y, 2016. Comparison of soil acid phosphatase activity determined by different methods. Chin. J. Eco-Agric. 24:98–104.

Li ZG, Luo YM and Teng Y, 2008. Research methods of soil environmental microorganism. Science Press, Beijing, China.

Lin X, Handley KM, Gilbert JA and Kostka JE, 2015. Metabolic potential of fatty acid oxidation and anaerobic respiration by abundant members of Thaumarchaeota and Thermoplasmata in deep anoxic peat. ISME J., 9: 2740–2744.

Liu JW, Yu SL, Zhao MX, He BY and Zhang XH, 2015. Shifts in archaeaplankton community structure along ecological gradients of Pearl Estuary. FEMS Microbiol. Ecol. 90:424–435.

Lu RK, 2000. Methods of soil agricultural chemical analysis. China Agricultural Science and Technology Press, Beijing, China.

Meinhardt KA, Stopnisek N and Pannu MW, 2018. Ammonia-oxidizing bacteria are the primary N_2O producers in an ammonia-oxidizing archaea dominated alkaline agricultural soil. Environ. Microbiol., 20(6): 2195–2206.

Ouyang Y, Norton JM and Stark JM, 2017. Ammonium availability and temperature control contributions of ammonia oxidizing bacteria and archaea to nitrification in an agricultural soil. Soil Biol. Biochem., 2017, 113: 161–172.

Pan H, Feng HJ, Lou YH, Wang H, Yang QG, Yang ZC and Zhung YP, 2023. Advances in microbial ecology of nitrifying communities in agricultural soils. Chin. J. Soil Sci., 54(3): 750–756.

Qin J, Jiang X, Zhou J, Ma MC, Guan DW, Zhou BK, Zhao BS, Du BH and Li J, 2015. Characteristics and driving factors of soil bacterial and archaeal

communities under long–term fertilization regimes in black soil. Plant Nutr. Fert. Sci. 21: 1590–1598.

Ren P, Hong BT and Zhou JM, 2014. Assessing the farmland ecosystem sensitivity in the upper Yangtze River and the space treatment based on GIS. J. Saf. Environ. 14:290 – 294.

Shi J, Wang X and Wang E, 2023. Mycorrhizal Symbiosis in plant growth and stress adaptation: from genes to ecosystems. Annu. Rev. Plant Biol. 74: 569–607.

Sterngren AE, Hallin S and Bengtson P, 2015. Archaeal ammonia oxidizers dominate in numbers, but bacteria drive gross nitrification in N-amended grassland soil. Front. Microbiol., 6: 1350

Tahon G, Geesink P and Ettema TJG, 2021. Expanding archaeal diversity and phylogeny: past, present, and future. Annu. Rev. Plant Biol., 75: 359–381.

Tamez–Hidalgo P, Christensen BT, Lever MA, Elsgaard L and Lomstein BA, 2016. Endospores, prokaryotes, and microbial indicators in arable soils from three long–term experiments. Biol. Fertil. Soils. 52:101–112.

Tejerizo GT, Kim YS, Maus I, Wibberg D, Winkler A, Off S, Pühler A, Scherer P and Schlüter A, 2017. Genome sequence of Methanobacterium congolense strain Buetzberg, a hydrogenotrophic, methanogenic archaeon, isolated from a mesophilic industrial-scale biogas plant utilizing bio-waste. J. Biotechnol. 247:1–5.

Toscano G, Colarieti ML and Jr GG, 2003. Oxidative polymerisation of phenols by a phenol oxidase from green olives. Enzyme Microb. Technol. 33: 47–54.

Tupinambá DD, Cantão ME, Costa OY, Bergmann JC, Kruger RH, Kyaw CM, Barreto CC and Quirino BF, 2016. Archaeal community changes associated with cultivation of amazon forest soil with Oil Palm. Archaea 2:1–14.

Wang L, 2023. Responses of soil microbial community to topsoil depths in Mollisols farmland. Northeast Agricultural University.

Wang Y, Li H, Yao ZZ, Liao Q and Du TS, 2023. Effects of water and salt stresses on plant growth and xylem hydraulic properties of tomato. J App. Ecol., 34: 114–122.

Wang YX, Gao QH, Fan J, Sun G, Yin LC and Nie SA, 2025. Effects of organic-inorganic fertilization regime alterations on microbial community structures in paddy soils. Acta Microbiologica Sinica https://doi.org/10.13343/j.cnki.wsxb.20250250

Wu DN, Jiang H and Zhang JM, 2015. Research progress on the soil respiration of farmland ecosystems. Northern Hortic. 6:178 – 182.

Xu C, Han XZ, Wang XH, Guo ZX, Yan J, Lu XC and Zou WX, 2023. Inversion tillage with straw incorporation affects the patterns of soil microbial co-occurrence and multi-nutrient cycling in a Hapli-Udic Cambisol. J. Integr. Agric. 22(5): 1546-1559.

Xu JY and Mao YP, 2019. From canonical nitrite oxidizing bacteria to complete ammonia oxidizer: discovery and advances. Microbiol. Chin., 46(4): 879−890.

Xu WL, Tang GM, Ge CH, Wang XH and Liu H, 2015. Effects of long–term fertilization on diversities of soil microbial community structure and function in grey desert soil of Xinjiang. Acta. Geol. Sin. 35:468– 477.

Yan CS, 1988. Research methods of soil fertility. Agricultural Press, Beijing, China.

Yan X, Zhang YZ and Liu J, 2008. Research Progress on soil fertility quality evaluation. Hunan Agric. Sci. 5:82–85.

Zhang Q, Zhao W, Zhou Z, Huang G, Wang X, Han Q and Liu G, 2022. The application of mixed organic and inorganic fertilizers drives soil nutrient and bacterial community changes in teak plantations. Microorganisms, 10(5): 958.

Zhang R, Zhang G, Chen DQ, Ji YY, Zhang HF and Yang DL, 2013. The effects of different fertilization on the functional diversity of soil microbial community. Chin. Agric. Sci. Bull. 29:133–139.

Zhao Y, Zhou H, Ma Q, Xu YG, Jiang CM and Yu WT, 2014. Soil microbial biomass C and N as affected by fertilization and cultivation systems. Chin. J. Soil. Sci. 45:1099–1103.

Zheng LC, Yu WT, Ma Q and Wang YB, 2004. Advances in the integrated evaluation of farmland fertility. Chin. J. Ecol. 23:156–161.