REVIEW



Research Progress on Microbial Nitrogen Conservation Technology and Mechanism of Microorganisms in Aerobic Composting

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Abstract

With economic development and improvements in living standards, the demand for livestock products has steadily increased, resulting in the generation of large amounts of livestock manure, which seriously pollutes the ecological environment and poses a threat to human health. High-temperature aerobic composting is an effective method for treating livestock manure; however, traditional composting processes often lead to considerable nitrogen loss, reduced efficiency of soil conditioners, and increased emissions of harmful gases. The incorporation of physical, chemical, and biological additives can effectively retain nitrogen within the compost. Among these, microbial agents are particularly noteworthy as they precisely regulate the microbial community structure associated with nitrogen transformation during aerobic composting, altering the abundance of functional genes and enzyme activities involved in nitrogen transformation. This approach significantly reduces nitrogen loss and harmful gas emissions. This paper reviews the application effects of microbial agents on nitrogen retention during aerobic composting and explores the underlying regulatory mechanisms, aiming to provide theoretical guidance and new research directions for the application of microbial agents in enhancing nitrogen retention during aerobic composting.

 $\textbf{Keywords} \ \ Aerobic \ composting \cdot Nitrogen \ transformation \cdot Microbial \ nitrogen \ retention \ technology \cdot Regulatory \ mechanisms$

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Introduction

With rapid economic development and improvement in living standards, the demand for livestock products in China has been steadily increasing. According to data from the Ministry of Agriculture, as of 2021, the slaughter volumes of poultry, pigs, and cattle reached 15.74 billion, 671.28 million, and 47.07 million, respectively [1]. However, the livestock industry has produced a substantial amount of manure. The Ministry of Agriculture reports that China produces approximately 3.8 billion tons of livestock manure annually [2]. This manure is rich in nitrogen and phosphorus, and during storage, it releases ammonia (NH₃) and hydrogen sulfide (H₂S), both of which are odorous gases. The emission of these pollutants not only severely contaminates the ecological environment but also poses a threat to human health. Therefore, effectively treating livestock manure has become a crucial research topic in efforts to protect the environment and safeguard human health.

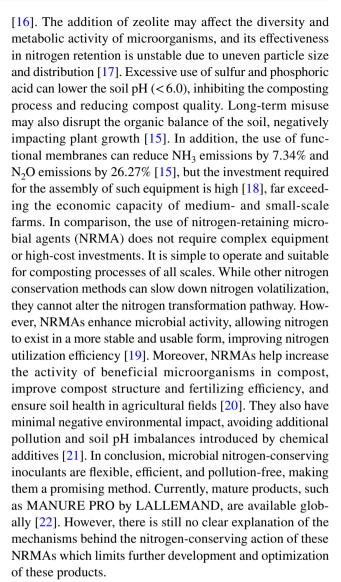
Aerobic composting is an efficient technological method for treating livestock manure. By conducting aerobic



fermentation under high-temperature conditions, livestock manure is transformed into safe, stable, and nutrient-rich soil conditioners. This process not only significantly reduces the emissions of environmental pollutants from livestock manure but also effectively enhances composting efficiency, thereby improving soil quality and promoting sustainable agricultural development [3].

However, studies have demonstrated that the aerobic composting process leads to nitrogen losses accounting for 12-25% of the initial nitrogen content, with NH₃ volatilization losses representing 60-99% of this amount, along with a smaller portion of nitrous oxide (N_2O) emissions [4, 5]. This not only reduces the efficiency of composting but also contributes to air pollution. Regulating nitrogen transformation to mitigate NH₃ emissions during composting is a primary focus of nitrogen retention technologies in aerobic composting. The nitrogen loss during the composting process is influenced by factors such as the composition of raw materials, C/N ratio, and oxygen (O₂) concentration within the compost pile. The composition of compost materials (such as organic waste, discarded food, and crop residues) directly affects the microbial community structure and their metabolic activities. For example, materials rich in protein and nitrogen sources may promote microbial nitrogen assimilation and degradation activities [6]. The C/N ratio of compost plays a crucial role in nitrogen loss. When the C/N ratio is below 10 or above 30, nitrogen loss significantly increases. A lower C/N ratio leads to excessive mineralization of nitrogen, increasing nitrogen loss, while a higher C/N ratio directly results in nitrogen volatilization losses [7]. To optimize nitrogen conversion efficiency and reduce NH₃ loss, the optimal C/N ratio is between 24 and 30 [8]. Denitrifying microorganisms in compost prefer low-oxygen concentrations (<0.2 mg/L) under low-oxygen conditions. Within the compost pile, the aggregation and compaction of materials usually limit oxygen penetration, and low O₂ concentrations are a major factor driving N₂O emissions [9]. Therefore, to reduce N₂O emissions, an appropriate aeration rate (e.g., 0.5 L·min⁻¹·kg⁻¹) should be maintained to ensure oxygen supply and suppress N₂O production [10]. An appropriate moisture content in compost also helps increase the porosity of the compost mixture, thereby increasing O₂ content, enhancing maturity, and reducing nitrogen loss [11].

The regulation of nitrogen transformation through physical, chemical, and biological pathways to reduce nitrogen loss during composting is a key area of focus for nitrogen conservation in aerobic composting. Physical and chemical additives such as zeolite, biochar, sulfur, and phosphoric acid can reduce NH₃ emissions in the short term [12–15], but they also have significant drawbacks. For instance, biochar, while adsorbing nitrogen, may also adsorb other essential nutrients (e.g., phosphorus and potassium), thus affecting the availability of other nutrients during composting



Studies have shown that the addition of exogenous microorganisms not only promotes the maturity and quality of compost materials but also balances the succession of native microbial communities [23]. Adding NRMAs further improves nitrogen retention efficiency by enhancing nitrogen-related enzyme activities, thereby positively influencing nitrogen cycling and retention in the compost [24]. Consequently, the addition of NRMA represents a low-cost, highly efficient, and pollution-free nitrogen retention technology. However, the mechanisms underlying the effects of NRMA remain inadequately understood [25].

This paper will begin with an overview of the principles of nitrogen transformation during aerobic composting, review the nitrogen retention effects of NRMA as reported in existing studies, discuss the impact of NRMA on the microbial community in aerobic composting, analyze the regulatory mechanisms of nitrogen-related genes and enzyme activities, elucidate the nitrogen retention mechanisms, and propose future research directions. The aim is to



provide theoretical support and technical guidance for the application of NRMA in nitrogen retention during aerobic composting.

Nitrogen Transformation Mechanism in Aerobic Composting

The nitrogen transformation process in aerobic composting primarily involves ammonification, nitrification, denitrification, and other nitrogen-related processes in composting.

Ammonification

Ammonification is the process by which microorganisms decompose organic nitrogen compounds to produce ammonia, representing the mineralization of organic nitrogen [26]. These microorganisms, aided by various enzymes, convert complex nitrogen-containing organic substances into simpler nitrogen-containing compounds, such as amino acids and peptides. Under the action of microbial deaminase, these compounds undergo deamination, resulting in the formation of NH_4^+ -N or NH_3 [27]. Ammonium (NH_4^+) can be converted into NH3 under alkaline conditions, leading to its volatilization into the atmosphere [28, 29]. Furthermore, NH₄⁺-N is highly soluble in water and can leach into the soil through leachate [30]. Consequently, ammonification contributes to nitrogen loss by transforming organic nitrogen into ammonia during composting, which negatively impacts nitrogen retention efficiency.

Nitrification

Nitrification occurs under aerobic conditions, where $\mathrm{NH_4}^+$ serves as a substrate and is oxidized to hydroxylamine (NH₂OH) by ammonia monooxygenase (AMO). Subsequently, hydroxylamine is further oxidized to nitrite (NO₂⁻) by hydroxylamine oxidoreductase (HAO). $\mathrm{NO_2}^-$ is then converted to nitrate (NO₃⁻) under the action of $\mathrm{NO_2}^-$ oxidoreductase [31]. This process is completed through a three-step oxidation reaction. Nitrification, primarily carried out by nitrifying bacteria, mainly occurs during the heating and cooling phases of composting at temperatures below 40–55 °C [32, 33]. Throughout the composting process, nitrification transforms $\mathrm{NH_4}^+$ to $\mathrm{NO_3}^-$, preventing the conversion of $\mathrm{NH_4}^+$ to $\mathrm{NH_3}$ and thereby reducing nitrogen loss [31].

Denitrification

Denitrification is the process by which NO_3^- or NO_2^- is reduced to nitrogen (N_2). This process is facilitated by the synergistic action of complex enzyme systems, including

nitrate reductase, nitrite reductase, nitric oxide reductase, and N_2O reductase [34]. Nitrate nitrogen (NO_3^- -N) is gradually reduced to nitrite nitrogen (NO_2^- -N), nitric oxide (NO), N_2O , and ultimately nitrogen gas (N_2) [34]. This process typically occurs in compost that is deficient in oxygen, which can result from factors such as high moisture content, low porosity, or inadequate aeration [34]. Denitrification can lead to a relatively small loss of nitrogen in the compost, estimated at approximately 5% [35].

Other Nitrogen Transformation Processes Related to Composting

Ammonium assimilation involves the conversion of $\mathrm{NH_4}^+$ into organic nitrogen through the coordinated action of glutamate dehydrogenase, glutamine synthetase, and glutamate synthetase [36]. This process significantly reduces nitrogen loss during composting, enhances nitrogen retention in the compost, and improves the soil conditioner efficiency of the compost [37]. A small amount of nitrogen-fixing bacteria present in the compost can convert limited amounts of atmospheric nitrogen or nitrogen produced from denitrification into $\mathrm{NH_4}^+$, contributing to nitrogen retention [38].

In summary, nitrogen loss during aerobic composting primarily occurs through NH₃ volatilization, NH₄⁺-N leachate leaching, and incomplete denitrification, such as NO, N₂O, and N₂ emission [39]. The addition of NRMA to aerobic composting can enhance the nitrification process by introducing nitrifying bacteria, which promote the conversion of NH₄⁺-N into NO₃⁻-N. Simultaneously, the ammonifying bacteria present in these NRMA effectively facilitate ammonium assimilation, converting NH₄⁺-N into amino acids and other nitrogen-containing organic compounds. This process not only reduces the volatilization loss of NH₄⁺-N but also increases the nitrogen content in the compost, thereby improving the efficiency of nitrogen utilization [40, 41].

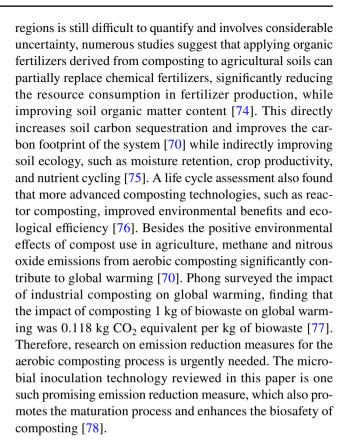
Microbial Additives, Their Effects on Nitrogen Retention, Environmental Benefits, and Trade-offs

Microbial additives can consist of a single strain or a composite agent composed of several different microorganisms [42, 43]. Previous studies have investigated various NRMAs for aerobic composting, The primary types of NRMA employed include *Bacillus*, ammonia-oxidizing bacteria, cellulose-degrading bacteria, nitrifying bacteria, and nitrogen-fixing rhizobia [35, 42–45]. The microbial communities with outstanding performance are summarized as follows: The use of *Bacillus megaspora*, *Thiobacillus* sp., *Saccharomyces exiguus*, or *Bacillus licheniformis* individually can effectively reduce NH₃ emissions from livestock



manure, reduction of odor emissions by 31.3–90% [46–49]. Strains of the Geobacillus have been shown to reduce N₂O emissions by 89.3% [50]. The synergistic application of different strains to construct a composite microbial consortium has further enhanced nitrogen retention efficiency. For instance, the addition of a chicken manure-integrated microbial consortium increased the total nitrogen content by approximately 28.3% while simultaneously reducing NH₃ and N₂O emissions [51]. In cow manure substrates, adding ammonia-oxidizing microbial consortia increased the total Kjeldahl nitrogen content by 24.43–38.87% [19]. When Bacillus subtilis, Bacillus licheniformis, Trichoderma viride, and Aspergillus niger were added to cow manure at proportions of 0.1–0.4%, the total nitrogen content increased by 5.5–20.6% [52]. In pig manure, the addition of a composite microbial consortium composed of Bacillus subtilis sp. NF1 and other strains increased the total nitrogen content by up to 55.35% [53]. The types of nitrogen-retaining microbial agents (NRMAs) utilized and their effects on nitrogen retention are summarized in Table 1. Studies have shown that the addition of microbial inoculants during aerobic composting significantly enhances compost maturity while reducing odor emissions and nitrogen losses. Consequently, various mature NRMA products are now available in the market, such as MANURE PRO by LALLEMAND, livestock manure fermentation inoculant VT1010 (Beijing VOTO Biotech Co., Ltd.), and deodorant VT400 (Beijing VOTO Biotech Co., Ltd.).

In addition, based on economic analysis and life cycle assessment (LCA), the ratio of ecological efficiency, economic benefits, and potential environmental impacts of improved technology applications has become an important indicator for measuring the integrated economic and environmental impacts [69]. Research on the microbial inoculation technology for nitrogen conservation in composting, assessed through LCA and/or techno-economic studies, has not been reported. Therefore, this study attempts to elucidate the process through the aerobic composting technology itself. The organic matter and nutrients, such as nitrogen and phosphorus, in the matured compost are essential for crop growth. However, the production of nitrogen and phosphorus fertilizers requires land use, depleting mineral resources while consuming large amounts of energy. Studies have shown that the land-use impact of producing 1 kg of nitrogen fertilizer is 0.31 m² per crop equivalent [70, 71]. In terms of mineral resource scarcity, according to the Ecoinvent database, the production of 1 kg of nitrogen fertilizer results in 0.027 kg of copper equivalent [70]. The energy demand for nitrogen fertilizer production is high, as it requires high process temperatures and pressures, accounting for 90% of the total energy needed for fertilizer production [72, 73]. Although the actual substitution rate of compost for chemical fertilizers across different



Mechanisms of Microbial Agents Affecting Nitrogen Transformation in Composting

Regulation of Nitrogen-Transforming Microbial Abundance

During aerobic composting, nitrogen exists in various forms, including NH₄⁺-N, NO₃⁻-N, and organic nitrogen. The transformation of these nitrogen forms relies heavily on the activities of diverse microorganisms, such as ammonifying bacteria, nitrate-reducing bacteria, nitrifying bacteria, nitrogen-fixing bacteria, and other functional microorganisms [79]. *Sphingobacterium*, a nitrifying bacterium, is frequently observed in composting and plays a crucial role in the conversion of ammonia to NO₃⁻ and NO₂⁻ [24]. *Sporosarcina* is an efficient nitrogen-fixing bacterium, and its metabolic processes are essential for nitrogen formation and retention during composting, which is critical for compost quality and fertility [80].

Previous studies have demonstrated that inoculating aerobic composting with ammonia-oxidizing bacteria (AOB) as NRMA significantly impacts the microbial community and its functions within the compost [19]. AOB inoculation enhances the growth of *Bacillus*, which is particularly active during the high-temperature phase of composting. The abundance increased to 29.18%, resulting in a reduction



Table 1 Nitrogen retention effect of different NRMA on aerobic compost

Bacillus strain sp. TAT105 Ammonia oxidizing bacteria sp. AOB						the Seminas amos (%) compared to an economic stocks		INCICION
		addition (fresh weight%)	NH_3	N_2O	NO ₂ N	NO ₃ N	TN and TKN	
	Pig manure	2.38					TN ₇₂₂	[42]
	Chicken manure; rice straw	5	881		↑44.5		TN↑1.08	[43]
Microbial agents screened in pig farm waste- water and leaf litter soil	Pig manure; straw and mushroom waste; saw- dust and rice husk	0.8	†25.52					[54]
Bacillus subtilis, Bacillus licheniformis	Food waste	6.0		↓17–54				[55]
Cellulose-degrading bacteria sp. WSD.5	Chicken manure	5	↓25.9	↓34.98				[35]
Bacillus megaspora sp. 1.1870	Pig manure	5	↓31.34	↓53.16				[47]
Cellulose-degrading bacteria sp.	Cattle manure	0.3		↓ 45				[99]
Thiobacillus sp. 1904	Chicken manure	5	↓61.5			↑33.5	TN↑28.20	[48]
Denitrifying and ammonia bacteria sp.	Sludge	0.35			↑28.85	↑33.13	TKN †4.94%	<u>4</u>
Medium-temperature fungus-F1, medium- temperature bacteria-Z1, high-temperature bacteria-Z2 and their combination	Cattle manure	S	↓8.45–23.29	↓22.85–61.13			TKN ↑13.48–19.60	[57]
Ammonia oxidizing bacteria high temperature resistant strain sp. T-AOB-2, medium temperature strain sp. M-AOB-4 and compound microbial agent sp. MT-AOB-2–4 formed by compound bacteria	Cattle manure	'n	129.98–46.94		↑21.85–38.9	0 †33.90-41.79	†21.85–38.90 †33.90–41.79 TKN †24.43–38.87	[19]
Bacillus subtilis sp. NF1, thermophilic bacteria sp. NF2, and combined addition sp. NF3	Cow manure	5	U12.77–25.11	112.77–25.11		↑8.96–19.40	TKN †38.43–55.35 [46]	[46]
Carbon-based microbial agents CBMA	Chicken manure	10	↓25.06			136.59	TN ↑35.02	[31]
Azotobacter chroococcum (GCA_016406165.1), Bacillus subtilis (GCA_023612315.1), Saccharomonospora sp. (GCA_015910535.1), Streptomyces albi- doflavus (GCA_019286195.1)	Food waste	'n					TN ↑20.6	[58]
Acinetobacter radioresistens strain sp. GH16093 (HA-1) and Bacillus nitratireducens strain Bnit1 sp. HA-2	Cattle manure	S	↓ 36.1	↓32.1			TN ↑15.1	[32]
Thermophilic nitrifying bacteria sp.	Sewage sludge	5	129.7				TN ↑10.58	[33]
Chicken manure integrated microbial consortium (CMMC)	Chicken manure	10	↓21.8	↓ 44.5				[51]
Thiobacillus thioparus sp. 1904	Chicken manure	5	↓21.86	↓31.84			TN ↑28.3	[65]
Pichia membranifaciens	Pig manure	1					TN ↑4.79–29.61	[09]
Bacillus subtilis, Bacillus licheniformis, green wood mold, Aspergillus niger	Cow manure	0.1–0.4					TN ↑5.5–20.6	[52]
Bacillus sphaericus DF-2	Pig manure	0.3	† 65				TN ↑30	[61]
Bacillus subtilis CGMCC No 0.19516	Chicken manure	1	↑76.64			†220		[62]



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(continued)
Table 1

Types of microbial agents	Pile matrix	Amount of	Nitrogen-re	taining effect (Nitrogen-retaining effect (%) Compared to the control group	the control grou	dı	References
		addition (fresh weight%)	NH ₃	N_2O	NO ₂ N	NO ₃ N	TN and TKN	
Streptomyces etiolaris, Bacillus subtilis, Lacto- Cow manure bacillus acidophilus, Clostridium perfringens, Aeromonas pyogenes, Vibrio fibrosus	Cow manure	10–20						[63]
Nitrate nitrogen assimilating bacteria	Clay powder	10-200				↑40–70		<u>[49]</u>
Multi-crustal layer thermophilic complex			091					[65]
Nitrobacillus harbinensis BM62	Cow manure	10	↑6.2–36.7		18.1		TN ↑9.2	[99]
Streptomyces fines, Bacillus subtilis, Pseudomonas aeruginosa, Nitrobacter, Denitrifying bacteria	Mixture of Cow manure, pig manure, chicken manure	0.1–0.2	↓ 64				TN ↑35	[67]
Geobacillus thermodenitrificans, Geobacillus stearothermophilus, Geobacillus kaustophilus, Geobacillus Geobacillus thermoleovorans, Geobacillus caldoxylosilyticas		20	During the centration treatment ganisms v control gr suppressi	composting tre is were signific the concentra was reduced to oup, suggestin ing the emission	uring the composting treatment with $Geobacillus$ mi centrations were significantly lower than in the contractment, the concentration of N_2O in the compost vganisms was reduced to approximately 0.3 ppm, concontrol group, suggesting that the use of the microor suppressing the emission of the greenhouse gas N_2O	bacillus microc n the control. A compost with 3 ppm, compar he microorgani se gas N ₂ O	During the composting treatment with $Geobacillus$ microorganisms, N_2O concentrations were significantly lower than in the control. At the sixth week of treatment, the concentration of N_2O in the compost with $Geobacillus$ microorganisms was reduced to approximately 0.3 ppm, compared to 2.8 ppm in the control group, suggesting that the use of the microorganisms was effective in suppressing the emission of the greenhouse gas N_2O	[52]
Saccharomyces exiguus SJP6728AF1 (KCCM-10675P), Saccharomyces exiguus SJP6729AF2 (KCCM-10677P) et al		0.1–1	50-90					[49]
Bacillus licheniformis MM76 and MM172			Bacillus licanonia the computosen functions	acillus licheniformis strains in the ammonia efficiently, which helps in the composting process and at the nitrogen for plants or mushrooms	ins in the bacteris ich helps to reduc and at the same ti ishrooms	al compositions e ammonia vol me provides an	Bacillus licheniformis strains in the bacterial compositions are able to assimilate ammonia efficiently, which helps to reduce ammonia volatilization losses during the composting process and at the same time provides an available source of nitrogen for plants or mushrooms	[50]
Sphingopyxis terrae subsp. terrae YC-JH3, Methylomonas methanica R-45371, Pseudox-anthomonas mexicana GTZY Methylosinus trichosporium OB3b, Hyphomicrobium zavarzinii ATCC 27496ZV-62			Bacteria in 2.0 µmol/ day	the compositic gDW/day, with	ns are capable of 1 a maximum nitr	fixing nitrogen ogen fixation ra	Bacteria in the compositions are capable of fixing nitrogen at rates in excess of 2.0 μmol/gDW/day, with a maximum nitrogen fixation rate of 2.5 μmol/gDW/day	[68]

This table includes the following nitrogen compounds, ammonia (NH₃), nitrous oxide (N₂O), nitrite nitrogen (NO₂⁻-N), nitrate nitrogen (NO₃⁻-N), total nitrogen (TN), and total Kjeldahl nitrogen (TKN); \downarrow indicates a reduction in gas emissions, and \uparrow indicates an increase in nitrogen-related forms



of nitrogen loss rate to 24.16%; at the high-temperature stage of composting, the number of operational taxonomic units (otus) analyzed by sequencing of 16S rRNA gene amplicons was 57 in the control group, whereas the number of otus in the treatment group with the microbial additive MT-AOB-2-4 increased significantly to 313, an increase of 256 otus compared to the control group [19]. Moreover, inoculation with heat-tolerant ammonia-oxidizing bacteria AOB increased the abundance of Bacillaceae in the bacillus group to 29.18% during the high-temperature phase and reduced the nitrogen loss rate to 24.16% [19]. This suggests that inoculation greatly increased bacterial abundance and microbial diversity during the high-temperature stage. This increase may be attributed to the presence of Bacillus in the AOB inoculant, which is relatively heat-tolerant and thus highly active during composting. Bacillus has been recognized as a key genus in regulating nitrogen transformation, playing a crucial role in nitrogen retention and transformation. Pan influence microbial abundance and metabolic activity, thereby helping to reduce nitrogen loss and improve nitrogen retention efficiency [19, 43, 81, 82].

In addition to regulating nitrogen transformation, NRMAs enhance the growth environment for nitrogen-transforming microorganisms. Zhong et al. found that the addition of NRMA during aerobic composting can significantly enhance nitrogen utilization efficiency. The primary mechanism underlying this improvement is the increased abundance of microorganisms involved in nitrogen transformation, which promotes effective nitrogen conversion. Research indicates that NRMA contains ammonifying bacteria, nitrifying bacteria, nitrite-oxidizing bacteria, and nitrogen-fixing bacteria [83]. These microorganisms effectively mitigate ammonia generation and nitrogen loss by facilitating the nitrification of ammonia and the subsequent conversion of nitrite [83]. For example, the addition of the microbial agent NRMA significantly increased the abundance of nitrogen-transforming bacteria such as Paucisalibacillus, Sporosarcina, Sphingobacterium, and Oceanobacillus, especially during the hightemperature phase. Their relative abundances increased by 7.2%, 8.33%, 0.18%, and 0.01%, respectively, resulting in a 58.8% reduction in nitrogen loss and a 22.6% increase in total nitrogen content [83]. This finding suggests that the addition of the microbial agent enhanced the activity of these microbial communities, thereby reducing ammonia emissions and improving nitrogen utilization efficiency [84].

The study conducted by Liu et al. demonstrates that the incorporation of NRMA HA-1 and HA-2 significantly elevates the NO₃⁻-N content in compost [45]. After inoculating with microbial agents HA-1 and HA-2, the relative abundance of *Proteobacteria* in the bacterial agent group increased by 32.3%, and the abundance of *Firmicutes* was higher, promoting nitrification and reducing nitrogen loss; the cumulative NH₃ and N₂O emissions in the bacterial agent

group were 36.1% and 32.1% lower, respectively, compared to the control group [45].

Consequently, the addition of different microbial inoculants during aerobic composting significantly increased the abundance of nitrogen-transforming microbial communities (such as *Bacillaceae*, *Proteobacteria*, *Firmicutes*, *Paucisalibacillus*, *Sporosarcina*, *Sphingobacterium*, and *Oceanobacillus*) and altered the composition of these communities, thereby reducing nitrogen losses (such as NH₃ and N₂O emissions) and enhancing nitrogen retention. The total nitrogen content and compost quality were also improved.

Changes in Nitrogen-Transforming Enzyme Activity

The nitrogen cycle during aerobic composting involves several key enzymes, each playing a crucial role in the transformation of nitrogen compounds. For instance, urease catalyzes the hydrolysis of urea, converting it into ammonia, which is subsequently transformed into ammonium ions [58]. AMO is a vital enzyme found in AOB and ammonia-oxidizing archaea (AOA) and responsible for oxidizing ammonia into NO₂, a critical step in the conversion of nitrogen from organic to inorganic forms. Nitrite oxidase then oxidizes NO₂⁻ into NO₃⁻, stabilizing nitrogen in an oxidized form for effective utilization. Nitrate reductase plays an essential role in nitrogen reduction by converting NO₃-N to NO₂-N under anaerobic conditions. Nitrite reductase further reduces NO₂⁻ to NH₃, completing the nitrogen reduction process. Nitrous oxide reductase is involved in the reduction of N₂O during the denitrification process. Additionally, nitrogenase is crucial for nitrogen fixation, converting nitrogen gas into usable nitrogen compounds during aerobic composting [85].

NRMAs significantly influence enzyme activities. The addition of these agents can regulate enzyme functions through various mechanisms, including the adjustment of compost temperature and pH, acting as enzyme activators or inhibitors, and optimizing the nitrogen cycle, thereby enhancing nitrogen utilization efficiency [58]. It was shown that the inoculation of cold-adapted microbial agent (CAMA) significantly increased the urease activity during aerobic composting of chicken manure and sawdust, with a peak urease activity of 7.82 mg NH₄⁺-N g⁻¹24 h⁻¹ in the treatment group inoculated with CAMA, while that of the control group was only 6.24 mg NH₄⁺-N g⁻¹ 24 h⁻¹ [86]. Throughout the composting process, the urease activity of the control group was consistently lower than that of the agent-added group, indicating that the addition of CAMA accelerated the decomposition of urea and its conversion into NH₄⁺-N. During the whole composting process, the urease activity of the control group was always lower than that of the group with the addition of bacteriophage, which indicated that the addition of CAMA accelerated the



decomposition of urea and converted it into NH₄⁺-N, which effectively improved the efficiency of nitrogen retention [86].

Moreover, in the process of aerobic composting, the addition of NRMA significantly influences the activity of enzymes involved in nitrogen transformation. The nitrogen-fixing microorganisms present in these agents, such as Rhizobium and Actinobacteria, effectively convert atmospheric nitrogen into ammonia, which is accessible to plants. In the composting environment, when these nitrogen-fixing microorganisms are provided with optimal growth conditions, they regulate the synthesis and activation of nitrogen-transforming enzymes by secreting specific signaling molecules [43]. The upregulation of the expression of these key enzymes not only enhances the efficiency of nitrogen fixation but also promotes the transformation of ammonia, thereby facilitating the accumulation of organic nitrogen in the compost [87]. Previous studies have reported that the addition of Thiobacillus 1904 during the aerobic composting of chicken manure and mushroom residue significantly elevated compost temperatures (P < 0.01) [48]. The expression of AMO was suppressed as temperatures increased, particularly during the late high-temperature and maturation phases (P < 0.01). This phenomenon reduces NH₃ volatilization losses, thereby benefiting nitrogen transformation and retention. Concurrently, nitrite oxidoreductase (NXR) activity exhibited a negative correlation with temperature fluctuations. In this study, the expression of NXR gene in the high-temperature and maturation stages of compost was significantly higher in the group treated with *Thiobacillus* 1904 microbial agent than in the control group (P < 0.01) [48]. The oxidation of nitrite to nitrate was catalyzed by NRX [88, 89]. So, the addition of *Thiobacillus* 1904 microbial agent promoted the conversion of NO₂⁻ to NO₃⁻, which resulted in a significantly higher NO₃-N content in the treatment group than in the control group at the end of the composting process. Thus, NRMA optimized nitrogen conversion and increased nitrogen retention capacity by modulating the activities of AMO and NXR.

Changes in the Abundance of Functional Genes

Nitrogen transformation during aerobic composting is a complex biochemical process that involves multiple microbial functional genes, including *amoA*, *napA*, *napB*, *nif*, *hao* [45, 54, 90, 91]. During aerobic composting, the *amoA* gene encodes the alpha subunit of AMO, a crucial enzyme involved in ammonia oxidation. Ammonia-oxidizing bacteria convert (NH₄⁺-N) into NH₂OH through the action of AMO. The expression of the *amoA* gene can mitigate ammonia volatilization, thereby reducing nitrogen loss during the composting process [54]. Liu et al. discovered that the addition of NRMAs associated with nitrogen transformation significantly enhanced the expression of the *amoA* gene in the

aerobic composting of pig manure mixed with sawdust and rice husks. This enhancement facilitated the conversion of ammonia into nitrogen compounds, decreased NH₃ volatilization, and improved nitrogen retention in the compost [54].

The *napA* and *napB* genes encode the alpha and beta subunits of nitrate reductase, which catalyzes the reduction of nitrate. Liu et al. inoculated NRMA consisting of *Acinetobacter* strain GH16093 (HA-1) and *Bacillus* sp. strain Bnit1 (HA-2) in different combinations during aerobic composting. Three groups of bacteriological treatments were formed [45]. In this study, using metagenomics analysis, the expression of napA and napB genes was reduced by up to 56.6% in the fungicide-treated group as compared to the control group, suggesting that inoculation with NRMA inhibited the expression of *napA* and *napB*. The inhibition of nitrate reduction contributed to the retention of more NO₃⁻-N in the compost, thereby improving nitrogen retention and the overall quality of the compost [45].

The *nif* gene encodes nitrogenase, an enzyme responsible for reducing nitrogen gas (N₂) into NH₃, thereby facilitating nitrogen fixation [26]. Previous studies on the aerobic composting of cattle manure and straw demonstrated that the addition of NRMA HA-1 and HA-2 suppressed the expression of the *nif* gene compared to the control group, leading to a reduction in ammonia production during biological nitrogen fixation. This suppression resulted in decreased NH₃ volatilization and nitrogen loss [45]. By more effectively regulating ammonia generation and transformation, nitrogen retention efficiency was enhanced [90].

The *hao* gene encodes HAO, an enzyme that catalyzes the oxidation of NH₃ into NO₂⁻, which is subsequently converted into NO₃⁻ [70]. This process is a crucial component of the nitrogen cycle, facilitating nitrogen transformation and mineralization and enhancing the quality and maturity of compost [92]. Although the expression level of the *hao* gene is relatively low compared to other functional genes, studies have demonstrated that inoculating with NRMA can increase *hao* gene expression, thereby promoting nitrification during the aerobic composting process [45]. This enhancement facilitates the accumulation of NO₃⁻-N, reduces NH₃ emissions, and ultimately achieves nitrogen retention during aerobic composting, leading to improved compost quality.

The nxrA gene encodes nitrate reductase, and variations in the expression of this gene can influence the conversion rate of NO_2^- to NO_3^- , thereby affecting nitrogen transformation and release [48]. Lu et al. discovered that during the high-temperature and maturation stages of composting, the expression of the nxrA gene in the microbial agent treatment groups (T3: 0.25% sulfur + 5% *Thiobacillus* 1904, and T4: 5% *Thiobacillus* 1904) was significantly higher than that in the control group (P < 0.01) [48]. At the end of composting, the NO_3^- -N content of the treatment group with added fungicide was significantly increased by 156.58% compared to the

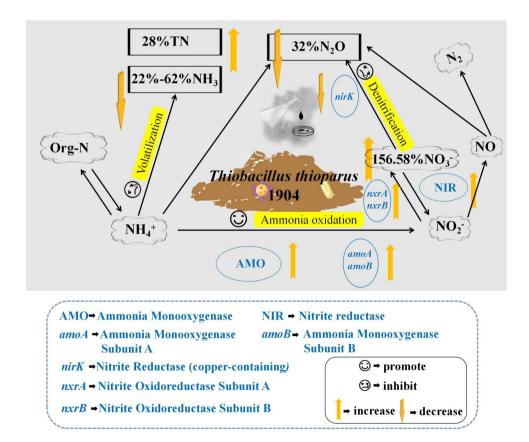


control group [48]. This finding suggests that the addition of NRMA likely enhanced the expression of the *nxrA* gene, thereby increasing nitrate production efficiency and NO₃⁻-N content, effectively fixing nitrogen and reducing nitrogen volatilization and loss. The mechanism of *Thiobacillus* 1904 in regulating the nitrogen transformation process during aerobic composting is shown as follows (Fig. 1).

The nirK, nirS, nirB, and norC genes encode nitrite reductases, which facilitate the conversion of NO₂⁻-N into N₂O during aerobic composting. Zhou et al. discovered that the addition of a microbial nitrogen-retaining agent composed of Anoxybacillus, Paenibacillus, and Geobacillus significantly influenced nitrogen transformation during the composting process [93]. The results showed that the abundance of nirK gene in the NRMA group formed by inoculation of Anoxybacillus, Paenibacillus, and Geobacillus complex was consistently lower than that of the control group throughout the composting cycle, which effectively suppressed denitrification and reduced the volatilization of nitrogen in the form of N₂O and N₂. This improved the retention of nitrogen [93]. Guo et al. also confirmed that the use of NRMA decreased *nirK* gene abundance, thereby inhibiting the conversion of NO to N₂O, significantly reducing greenhouse gas (NO_X) emissions from composting and enhancing nitrogen retention efficiency [94]. In the aerobic composting of cattle manure, the addition of a microbial nitrogen-retaining agent composed of *Acineto-bacter* strain GH16093 (HA-1) and *Bacillus* strain Bnit1 (HA-2) significantly reduced the expression levels of the nirS, nirB, and norC genes, thereby inhibiting N_2O emissions compared to the control group [32].

In conclusion, nitrogen transformation during aerobic composting is a complex biochemical process regulated by various microbial functional genes, primarily amoA, napA, napB, nif, hao, nirK, nirS, nirB, norC, and nxrA. Studying the regulation and abundance of these genes provides valuable insights into the mechanisms of microbial involvement in nitrogen transformation. The addition of NRMA enhances the expression of hao, amoA, and nxrA, which increases ammonia oxidation and reduces NH₃ volatilization. Furthermore, these agents inhibit the expressions of napA, napB, nirK, nirS, nirB, and norC, thereby decreasing nitrate reduction and N₂O emissions, while simultaneously promoting the expression of the nif gene, which aids in nitrogen fixation [45, 54, 93-95]. As a commonly used microbial additive Bacillus sphaericus in the nitrogen conservation process of aerobic composting, its regulation mechanism of nitrogen transformation process in aerobic composting is as follows (Fig. 2). Consequently, the incorporation of NRMA increases NO₃-N content and improves nitrogen retention efficiency in aerobic composting.

Fig. 1 Mechanism of nitrogen loss reduction in composting by *Thiobacillus thioparus* 1904





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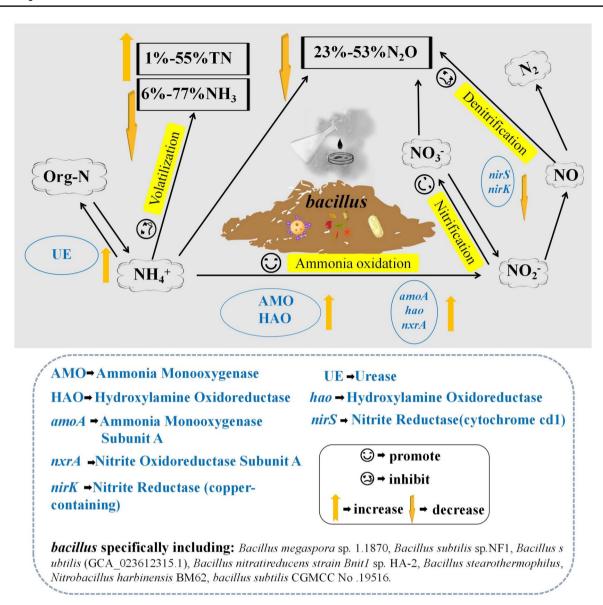


Fig. 2 Mechanism of nitrogen loss reduction in composting by Bacillus

Conclusion and Recommendations for Future Study

Aerobic composting is an effective method for the safe and efficient management of livestock manure. Microbial nitrogen-retaining technology involves the addition of microbial agents to aerobic composting, which helps regulate microbial abundance, enzyme activity, and gene expression related to nitrogen transformation, thereby achieving nitrogen retention. The regulation of nitrogen-transforming microorganisms primarily focuses on genera such as *Bacillus* and *Acinetobacter*. The incorporation of NRMA can enhance their abundance, influence nitrogen transformation processes, and increase the accumulation of NO₃⁻-N in compost, with a positive correlation

observed between microbial abundance and NO₃⁻-N content. Furthermore, the addition of these agents modifies the expression of functional genes associated with nitrogen transformation, promoting the expression of *amoA*, *nxrA*, and *hao* genes while inhibiting the expression of *napA*, *napB*, *nirK*, *nirS*, *nirB*, and *norC* genes. This modulation affects enzyme activity, regulates nitrogen transformation pathways and rates, optimizes nitrogen retention and utilization efficiency in compost, and achieves low-cost, high-efficiency nitrogen retention in the aerobic composting of livestock manure.

Future research on microbial nitrogen-retaining technologies in aerobic composting of livestock manure could provide new insights for researchers in the following directions:



- Although the addition of NRMA helps reduce NH₃ emissions, its effect on the reduction of N₂O emissions, which have a strong greenhouse effect, is often not significant and may even increase. To address this issue, enhancing specific microbial communities or adding specific enzyme preparations to achieve synergistic reduction of both ammonia and nitrous oxide can further improve the environmental benefits of composting
- Assessing the environmental impacts of microbial nitrogen-retaining technologies in long-term compost management, including potential benefits in terms of long-term nitrogen loss, soil improvement, and carbon sequestration. Long-term assessments should ensure the sustainability and long-term benefits of microbial nitrogen-retaining technologies
- Considering factors such as climate change, soil characteristics, and agricultural production needs, developing more comprehensive composting management systems that not only enhance nitrogen retention efficiency but also promote soil health and improve ecological benefits for farmland

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

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