REVIEW ARTICLE Agricultural Reviews, Volume 47 Issue 3: 375-384 (June 2026)

Nitrogen Mineralization in Cool Temperate Soils: Microbial and Organic Matter Perspectives: A Review

Kamrun Nahar Sheuly[1], Ishrat Alam[2], Bijoya Saha[3], Md. Shamsuzzoha[4], Nahid Hossain[5] Rebaka Sultana[6], Khalid Syfullah[7], Rashiduzzaman Emran[8], Ronzon Chandra Das[9]

10.18805/ag.RF-389

ABSTRACT

Nitrogen (N) mineralization in cool temperate soils is a complex, microbially driven process that acts as a vital bridge between organic matter decomposition and plant-available nitrogen pools. These ecosystems are uniquely characterized by prolonged low temperatures, frequent freeze-thaw cycles and seasonal moisture fluctuations, which impose significant selective pressures on microbial physiology. Despite these constraints, cold-adapted microbial communities sustain N cycling through specialized metabolic adaptations, including the production of psychrophilic enzymes and membrane modifications. Depolymerization remains the rate-limiting “gatekeeping” step, regulated by the extracellular breakdown of complex organic N compounds into soluble monomers. This review highlights the critical role of organic matter quality and organo-mineral stabilization in modulating N availability, noting that environmental pulses-such as thawing and rewetting-frequently trigger transient flushes of mineralization. As climate change alters winter temperature regimes and snow cover, understanding these microbially mediated mechanisms becomes essential for predicting N availability and developing sustainable nutrient management strategies to mitigate leaching and gaseous losses in cool agroecosystems.

Key words: Cool temperate soils, Freeze-thaw cycles, Microbial adaptation, Nitrogen mineralization, Organic matter dynamics.

Nitrogen (N) mineralization in cool temperate soils represents a complex, microbially driven transformation of organic N into inorganic forms that sustain plant productivity (Schimel and Bennett, 2004; Robertson and Groffman, 2024). This process is strongly modulated by soil temperature regimes, substrate quality and microbial community adaptation. Unlike warm regions, cool temperate systems are characterized by prolonged low-temperature periods, frequent freeze-thaw cycles and pronounced seasonal moisture fluctuations, which collectively impose strong selective pressures on microbial physiology and enzymatic function (Grogan *et al*., 2004; Henry, 2007). Despite these constraints, microbial communities in these soils exhibit specialized metabolic, structural and genetic adaptations that enable continued N cycling even at temperatures near or below freezing (Schimel *et al*., 2007; Frank, 2010).

Microbial activity governs the magnitude, timing and stability of nitrogen mineralization in cool temperate soils. Through enzymatic flexibility, physiological acclimation and ecological resilience, soil microorganisms maintain N turnover across seasons (Allison *et al*., 2010; Burns *et al*., 2013). However, strong environmental variability-particularly freeze-thaw events and spatial heterogeneity of organic substrates-frequently results in temporal decoupling between microbial N mineralization and plant N demand (Jaeger *et al*., 1999). A mechanistic understanding of these microbially mediated processes is therefore critical for predicting nitrogen availability under future climate scenarios and for developing sustainable nutrient management strategies in cool agroecosystems (Davidson *et al*., 2012).

[1]The UWA Institute of Agriculture, UWA School of Agriculture and Environment,Agricultural Central Wing (2.106), Perth WA 6009, Australia.
[2]Department of Soil Science, Sher-e-Bangla Agricultural University, Dhaka1207, Bangladesh.
[3]Soil Science Division Bangladesh Rice Research Institute. Bangladesh.
[4]Bangladesh Institute of Research and Training on Applied Nutrition, Bangladesh.
[5]Department of Soil Science, Khulna Agricultural University, Khulna -9100. Bangladesh.
[6]Department of Horticulture, Sher-e-Bangla Agricultural University, Dhaka1207 Bangladesh.
[7]Department of Genetics and Plant Breeding, Sher-e-Bangla Agricultural University,Dhaka 1207, Bangladesh.
[8]Additional Agriculture Officer Nalitabari, Sherpur, Department of Agricultura Extension, Ministry of Agriculture, Bangladesh.
[9]Department of Soil Science, Agronomy Division, Bangladesh Jute Research Institute, Bangladesh.

Corresponding Author: Khalid Syfullah, Department of Genetics and Plant Breeding, Sher-e-Bangla Agricultural University, Dhaka 1207, Bangladesh. Email: syfullahkhalid11@gmail.com

How to cite this article: Sheuly, K.N., Alam, I., Saha, B., Md. Shamsuzzoha, Hossain, N., Sultana, R., Syfullah, K., Emran, R. and Das, R.C. (2026). Nitrogen Mineralization in Cool Temperate Soils: Microbial and Organic Matter Perspectives: A Review. *Agricultural Reviews.* **47(3):** 375-384. doi: 10.18805/ag.RF-389.

Submitted: 22-05-2025 **Accepted:** 16-01-2026 **Online:** 03-02-2026

In cool temperate soils, nitrogen mineralization constitutes a crucial biological bridge between organic

matter (OM) decomposition and plant-available N pools. The process is predominantly governed by microbial depolymerization and assimilation of organic substrates, which is tightly linked to the physicochemical properties of organic matter and the environmental constraints of these ecosystems (Cotrufo *et al*., 2013). Due to low mean annual temperatures, recurrent freeze-thaw cycles and often elevated soil moisture, decomposition rates are reduced, leading to substantial organic matter accumulation and a delayed release of inorganic N relative to plant uptake requirements (Van Groenigen *et al*., 2015). Understanding nitrogen mineralization through the lens of organic matter dynamics is therefore essential for improving nutrient use efficiency and anticipating climate-driven feedbacks in temperate agroecosystems.

Organic matter acts simultaneously as the substrate and regulator of nitrogen mineralization in cool temperate soils. Its chemical composition, degree of biochemical recalcitrance and extent of physical and mineral stabilization determine whether microbial activity results in net N mineralization or immobilization (Six *et al*., 2002; Schmidt *et al*., 2011). Microbial consortia adapted to cold environments sustain enzymatic activity through membrane modifications, production of cold-active enzymes and stoichiometric adjustments that optimize nutrient acquisition under energy-limited conditions (Sollins, 1996). The tight coupling between organic matter decomposition, microbial adaptation and environmental controls defines the distinctive nitrogen cycling dynamics of cool temperate ecosystems, ultimately shaping soil fertility and carbon-nitrogen balance under a changing climate (Manzoni *et al*., 2012; Wieder *et al*., 2013).

This review was conducted using a systematic synthesis of peer-reviewed literature to evaluate the mechanisms governing nitrogen (N) mineralization in cool temperate ecosystems. The methodology focused on three primary phases: literature identification, thematic categorization and conceptual synthesis.

Literature identification and selection

A comprehensive search was performed across major scientific databases, including Web of Science, Scopus and Google Scholar. The search targeted studies published between 1980 and 2024, using key terms such as “nitrogen mineralization” “cool temperate soils” “microbial psychrophily” “depolymerization” and “freeze-thaw cycles.” Priority was given to long-term field studies, meta-analyses and high-resolution laboratory incubations that specifically addressed nitrogen transformations in regions characterized by seasonal freezing and low-temperature regimes.

Thematic categorization and integration

Selected literature was categorized into three foundational pillars:

- **Microbial regulation:** Analysis of physiological aptations, cold-active enzymes and community resilience during seasonal transitions.
- **Substrate quality and chemistry:** Evaluation of the role of the carbon-to-nitrogen (C:N) ratio and the stabilization of Mineral-Associated Organic Matter (MAOM).
- **Environmental forcing:** Assessment of how temperature fluctuations, moisture content and freeze-thaw cycles drive “pulses” of nitrogen release.

Evaluation of predictive models and indicators

The review analyzed the efficacy of various diagnostic tools and mathematical frameworks used to estimate N availability. This included an assessment of first-order kinetic models for Potentially Mineralizable Nitrogen (PMN) and chemical extraction methods (*e.g*., hot water and $CaCl_2$ extractions) to determine their reliability as biological indicators in cool climates.

Synthesis and gap analysis

Finally, the findings were synthesized to develop a mechanistic framework of the “gatekeeping” steps in N mineralization. A gap analysis was performed to identify areas where current biogeochemical models fail to account for “shoulder-season” dynamics, providing a basis for the future research directions proposed in the conclusion.

Mechanisms of nitrogen mineralization

Depolymerization of organic nitrogen compounds

Depolymerization is widely recognized as the rate-limiting step of nitrogen mineralization, involving the extracellular enzymatic breakdown of complex macromolecular organic nitrogen compounds-such as proteins, nucleic acids and chitin-into soluble monomers including amino acids, amino sugars and short oligopeptides (Schimel and Bennett, 2004; Burns *et al*., 2013). This process is primarily mediated by heterotrophic bacteria (*e.g.*, *Bacillus*, *Pseudomonas*) and filamentous fungi (*e.g., Aspergillus*, *Penicillium*), which secrete a suite of extracellular hydrolytic enzymes, including proteases, peptidases, chitinases and nucleases, to access polymeric organic N pools stabilized within soil organic matter matrices (Sinsabaugh *et al*., 2008).

Recent metagenomic and metatranscriptomic studies indicate that depolymerization efficiency in temperate soils is strongly regulated by enzyme diversity, microbial community composition and microbial stoichiometric demands, particularly under fluctuating temperature and moisture regimes (Allison *et al*., 2010). The availability of labile carbon substrates further modulates enzyme synthesis, linking carbon (C) and nitrogen (N) cycles at the rhizosphere-microbe interface and reinforcing the principle of coupled C-N acquisition strategies in soil microorganisms (Schimel and Weintraub, 2003; Kuzyakov and Blagodatskaya, 2015).

In cold or acidic soils, extracellular enzymatic activity is substantially reduced, creating a bottleneck for N release despite high total organic N content (Henry, 2007). Consequently, ecological regulation of depolymerization reflects the combined influence of substrate chemical recalcitrance, mineral protection and climatic constraints.

Depolymerization: The gatekeeping step

Depolymerization-the enzymatic cleavage of high-molecular-weight organic N compounds into soluble low-molecular-weight forms-is the primary control point

governing nitrogen mineralization rates (Schimel and Bennett, 2004). Extracellular hydrolytic enzymes act on organic substrates often adsorbed onto clay minerals and humic substances, where enzyme-mineral interactions can enhance enzyme persistence and catalytic stability, particularly in cool soils (Burns *et al*., 2013).

Cold-adapted microorganisms, including *Pseudomonas fluorescens*, *Arthrobacter* spp. and psychrotolerant fungi such as *Mortierella* spp., produce cold-active (psychrophilic) enzymes characterized by flexible tertiary structures, reduced hydrogen bonding and expanded active sites. These adaptations lower activation energy barriers and enhance substrate affinity under low-temperature conditions (Feller and Gerday, 2003). The resulting release of amino acids and amino sugars enables microbial uptake *via* high-affinity transport systems, supplying substrates for intracellular ammonification.

Ammonification: Microbial mineralization of organic N

Ammonification, often referred to as mineralization proper, involves the conversion of soluble organic N intermediates-such as amino acids, amides and urea-into ammonium (NH_4^+) through enzymatically mediated deamination reactions (Robertson and Groffman, 2024f). This process is carried out by a broad range of soil microorganisms, including heterotrophic bacteria (*Bacillus*, *Arthrobacter*), saprotrophic fungi (*Trichoderma*, *Penicillium*) and actinomycetes (*Streptomyces*), reflecting its fundamental role in microbial metabolism.

Dominant biochemical pathways include:

I. **Oxidative deamination**, catalyzed by glutamate dehydrogenase (GDH):

$$\text{Glutamate} + NAD^+ \rightarrow \alpha\text{-ketoglutarate} + NH_4^+ + NADH$$

II. **Hydrolytic deamination**, mediated by amino acid deaminases and amidases, releasing NH_4^+ directly from amino acids and amides

III. **Ureolysis**, catalyzed by urease, converting urea into CO_2 and NH_4^+.

These enzymatic reactions exhibit strong temperature sensitivity, with apparent activation energies ranging from 40 to 80 kJ mol^{-1} (Davidson and Janssens, 2006). However, cold-adapted enzymes maintain functional turnover rates through enhanced molecular flexibility and reduced substrate-binding enthalpy, allowing ammonification to proceed at temperatures as low as 2-5°C.

Microbial membrane lipid unsaturation and the synthesis of cryoprotectants such as trehalose and glycine betaine further sustain enzymatic secretion, substrate uptake and intracellular metabolism under cold stress (D'Amico *et al*., 2006; Schimel *et al*., 2007). As a result, NH_4^+ is released continuously but at subdued rates throughout cold seasons.

Following depolymerization, soluble organic N compounds are assimilated into microbial biomass, with a portion mineralized to NH_4^+ *via* deamination. Ammonification therefore represents the balance between gross mineralization and microbial immobilization. Isotopic tracer studies using ^{15}N pool dilution techniques reveal that gross mineralization and immobilization fluxes often exceed net mineralization rates by 5-10-fold, indicating rapid internal N cycling within microbial communities (Hart *et al*., 1994; Murphy *et al*., 2003). Environmental drivers-including temperature, redox conditions and substrate C:N ratios-determine the magnitude and direction of these fluxes.

Nitrification and the fate of inorganic nitrogen

Ammonium produced during ammonification is subsequently subject to nitrification, a two-step aerobic oxidation process converting NH_4^+ to nitrate (NO_3^-). The first step-oxidation of NH_4^+ to nitrite (NO_2^-)-is performed by ammonia-oxidizing bacteria (AOB; *e.g*., *Nitrosomonas*, *Nitrosospira*) and ammonia-oxidizing archaea (AOA; *e.g*., *Nitrososphaera*, *Nitrosopumilus*), while nitrite-oxidizing bacteria (NOB; *Nitrobacter*, *Nitrospira*) catalyze the oxidation of NO_2^- to NO_3^- (Prosser and Nicol, 2012; Robertson and Groffman, 2024).

In cool temperate soils, nitrification is frequently constrained by low temperature, limited oxygen diffusion and acidic pH, resulting in transient NH_4^+ accumulation (Booth *et al*., 2005; Zhang *et al*., 2012). Under warmer, well-aerated conditions, nitrification rates increase and NO_3^- becomes the dominant inorganic N form. However, because NO_3^- is highly mobile, excessive nitrification enhances leaching and denitrification losses, particularly under fluctuating soil moisture regimes typical of temperate climates (Butterbach-Bahl *et al*., 2011).

The classical nitrification pathway is catalyzed by the following reactions:

I. Ammonia oxidation (AOB and AOA):

$$NH_4^+ + 1.5\ O_2 \rightarrow NO_2^- + 2\ Hz^+ + H_2O$$

Enzymes: Ammonia monooxygenase (amoA) and hydroxylamine oxidoreductase (hao).

II. Nitrite oxidation (NOB):

$$NO_2^- + 0.5\ O_2 \rightarrow NO_3^-$$

Enzyme: Nitrite oxidoreductase (nxrA/B)

Emerging evidence highlights the role of complete ammonia oxidizers (comammox), particularly *Nitrospira* spp., which can oxidize NH_4^+ directly to NO_3^- within a single organism (Daims *et al*., 2015; van Kessel *et al*., 2015). This discovery challenges the traditional two-organism paradigm and introduces new complexity into nitrogen cycling models.

In cool temperate soils, nitrification often declines below 10°C; however, AOA exhibit higher affinity for NH„ z and greater tolerance to low substrate availability, allowing them to dominate nitrification under cold and oligotrophic conditions (Leininger *et al*., 2006; Prosser and Nicol, 2012). Seasonal shifts in microbial community composition therefore regulate nitrification dynamics, with AOA prevailing during colder periods and AOB becoming more competitive under warmer conditions.

Microbial regulatory mechanisms

Enzyme induction and genetic regulation

Microbial nitrogen mineralization is governed by tightly coordinated genetic and enzymatic regulatory mechanisms that enable rapid microbial responses to fluctuations in substrate availability and environmental conditions (Schimel and Weintraub, 2003; Allison *et al*., 2010). The synthesis of extracellular hydrolases-such as proteases, chitinases and nucleases-is predominantly substrate-induced, with enzyme expression upregulated in response to the presence of specific organic nitrogen compounds. This inducible strategy minimizes energetic costs while maximizing nutrient acquisition efficiency in heterogeneous soil environments (Sinsabaugh *et al*., 2008).

At the molecular level, genes encoding key enzymes involved in nitrogen transformations-including *gdhA* (glutamate dehydrogenase), *ureC* (urease) and *amoA* (ammonia monooxygenase)-are widely used as functional markers for assessing mineralization and nitrification potential across soil ecosystems (Prosser and Nicol, 2012). Their transcriptional regulation is sensitive to nitrogen availability, cellular C:N balance and redox conditions, reflecting the close integration of metabolic and regulatory pathways governing nitrogen turnover.

Cold-adapted microorganisms display distinctive transcriptional strategies that maintain enzyme synthesis at reduced energetic cost, including modifications in promoter architecture, altered sigma-factor usage and enhanced regulatory protein flexibility (D'Amico *et al*., 2006; Schimel *et al*., 2007). In addition to transcriptional control, post-translational mechanisms-such as allosteric regulation and enzyme stabilization through adsorption onto mineral and organic surfaces-optimize catalytic efficiency and prolong enzyme lifespan under low-temperature conditions (Burns *et al*., 2013). The coordinated regulation of these enzymatic systems ensures that nitrogen mineralization proceeds even under energy-limited and thermally constrained environments.

Microbial biomass turnover, immobilization and mineralization-immobilization turnover (mit) dynamics

Microbial biomass constitutes both a sink and a source of mineral nitrogen, functioning as a dynamic and highly active reservoir within soil nitrogen cycling networks (Wardle and Ghani, 1995). The mineralization-immobilization turnover (MIT) framework describes the rapid and continuous exchange of nitrogen between microbial biomass and the soil solution. During periods of elevated substrate supply or favorable temperature and moisture conditions, microorganisms immobilize inorganic nitrogen into biomass to support growth and enzyme synthesis. Conversely, under substrate limitation, environmental stress, or microbial senescence, microbial necromass is decomposed, releasing ammonium back into the mineral nitrogen pool (Booth *et al*., 2005; Schimel and Bennett, 2004).

In cool temperate soils, MIT processes operate at reduced rates but remain continuous, contributing to a buffered and temporally stabilized nitrogen supply (Van Groenigen *et al*., 2015). The balance between immobilization and mineralization is regulated by microbial growth efficiency, substrate C:N ratios and stoichiometric requirements for maintenance metabolism (Manzoni *et al*., 2012). High microbial turnover during thaw periods can generate transient pulses of inorganic nitrogen, whereas prolonged low-temperature dormancy sustains slow but persistent recycling of organic nitrogen through microbial residues, necromass accumulation and extracellular polymeric substances (Schimel *et al*., 2007; Wieder *et al*., 2023).

Isotopic studies using ^{15}N pool dilution techniques demonstrate that gross mineralization and immobilization fluxes frequently exceed net mineralization by several-fold, underscoring the dominance of internal microbial nitrogen cycling over observable changes in inorganic nitrogen pools (Hart *et al*., 1994; Murphy *et al*., 2003).

Ecophysiological adaptations to cold

Microbial communities inhabiting cool temperate soils employ a suite of ecophysiological adaptations that permit nitrogen mineralization under persistent low-temperature stress. Psychrophilic and psychrotolerant microorganisms maintain membrane fluidity by increasing the proportion of unsaturated and branched-chain fatty acids, thereby preserving membrane permeability and transport efficiency at low temperatures (Russell, 2002; D'Amico *et al*., 2006). Concurrently, the synthesis of cryoprotective solutes-such as trehalose, glycine betaine and extracellular polysaccharides-prevents ice crystal damage, stabilizes proteins and maintains osmotic balance during freeze-thaw cycles (MacIntyre *et al*., 2020).

Enzymes produced by cold-adapted microorganisms exhibit enhanced conformational flexibility, reduced hydrogen bonding and enlarged active sites, which collectively lower activation energy barriers and permit catalytic activity near or below freezing (Feller and Gerday, 2003). The formation of extracellular polymeric matrices and biofilms further enhances resilience by creating hydrated microscale environments that concentrate enzymes and substrates, buffer physicochemical fluctuations and promote cooperative metabolic interactions (Flemming and Wingender, 2010).

Together, these physiological, biochemical and structural adaptations ensure sustained depolymerization, ammonification and nitrification under cold and seasonally variable conditions. Consequently, microbial processes in cool temperate soils exhibit remarkable resilience and functional continuity, maintaining nitrogen cycling despite pronounced oscillations in temperature, moisture and substrate availability (Schimel *et al*., 2007).

Organic matter perspectives

Organic matter quality and mineralization potential

Organic matter (OM) quality is a primary determinant of both the rate and extent of nitrogen mineralization in cool temperate soils, as it governs microbial accessibility, enzymatic degradability and stoichiometric constraints on

microbial metabolism (Schimel and Bennett, 2004). The chemical composition, molecular complexity and degree of humification of organic substrates regulate the balance between nitrogen release and immobilization. Labile organic fractions-such as simple carbohydrates, free amino acids and proteins-are rapidly decomposed, leading to short-term increases in mineral nitrogen availability. In contrast, recalcitrant compounds rich in lignin, tannins and polyphenols resist microbial depolymerization, suppress enzymatic activity and promote nitrogen immobilization within microbial biomass and organic matter pools (Sinsabaugh *et al*., 2008).

In cool temperate climates, low temperatures, prolonged snow cover and reduced enzyme kinetics slow the decomposition of both labile and stabilized organic pools, resulting in substantial OM accumulation and a shift toward nitrogen storage rather than rapid turnover (Davidson and Janssens, 2006). The carbon-to-nitrogen (C:N) ratio remains a robust predictor of mineralization potential; substrates with narrow C:N ratios generally favor net nitrogen mineralization, whereas wide C:N ratios increase microbial nitrogen demand, enhancing immobilization and carbon preservation (Booth *et al*., 2005; Manzoni *et al*., 2012). However, in cold systems, enzymatic constraints can override stoichiometric controls, further decoupling organic matter decomposition from nitrogen release.

Organic matter stabilization and organo-mineral associations

The persistence of organic matter and its regulatory influence on nitrogen cycling are closely linked to physical and chemical stabilization mechanisms within the soil matrix. Organic compounds sorbed onto clay minerals, metal oxides (Fe and Al) and entrapped within microaggregates are physically and chemically protected from microbial attack and extracellular enzyme activity (Six *et al*., 2002). In cool temperate soils, the reduced turnover of mineral-associated organic matter (MAOM) contributes to long-term nitrogen retention while limiting short-term nitrogen availability for plants and microorganisms (Cotrufo *et al*., 2013; Schmidt *et al*., 2011).

Freeze-thaw cycles and seasonal wetting-drying events characteristic of cool temperate climates periodically disrupt organo-mineral associations and soil aggregates, exposing previously protected organic substrates to enzymatic degradation and stimulating short-lived pulses of nitrogen mineralization (Grogan *et al*., 2004; Henry, 2007). The dynamic balance between protection and exposure regulates both the timing and magnitude of nitrogen release. In fine-textured soils and those enriched in iron and aluminum oxides, strong organo-mineral complexes enhance the sorption of amino acids, peptides and microbial necromass, slowing their mineralization while promoting long-term stabilization of soil organic nitrogen (Kögel-Knabner *et al*., 2008, Fitriani *et al.,* 2025).

Interactions between organic matter and nitrification / heterotrophic nitrification

Organic matter not only supplies substrates for nitrogen mineralization but also exerts direct and indirect control over nitrification processes. Labile organic carbon influences soil redox conditions, oxygen diffusion and microbial competition, thereby regulating the activity of nitrifying communities (Prosser and Nicol, 2012; Booth *et al*., 2005). High concentrations of easily decomposable carbon can suppress autotrophic nitrification by stimulating heterotrophic microbial respiration and oxygen consumption, whereas low carbon availability favors chemolitho autotrophic ammonia oxidizers.

Under carbon-rich or low-oxygen conditions, heterotrophic nitrifiers-primarily fungi and some bacteria-can oxidize organic nitrogen compounds directly to nitrate, bypassing the conventional ammonia oxidation pathway (Zhang *et al*., 2012). In cool temperate soils, substantial organic inputs from litterfall and root residues create microsites with contrasting oxygen and substrate availability, allowing autotrophic and heterotrophic nitrification to coexist spatially and temporally (Bengtson *et al*., 2012).

Furthermore, organic acids and phenolic compounds derived from partially decomposed plant residues can inhibit ammonia-oxidizing bacteria while favoring ammonia-oxidizing archaea adapted to acidic, low-nutrient conditions (Leininger *et al*., 2006; Zhang *et al*., 2012). Consequently, the quality, quantity and spatial distribution of organic matter strongly influence nitrifier community composition and activity, thereby determining the dominant inorganic nitrogen forms and their fate within the soil profile.

Environmental modulators in cool temperate soils

Temperature and freeze-thaw dynamics

Temperature is a dominant regulator of nitrogen mineralization, exerting direct control over enzyme kinetics, microbial metabolic rates and the diffusion of substrates within the soil matrix (Davidson and Janssens, 2006; Schimel *et al*., 2007). In cool temperate regions, prolonged periods of low temperature suppress microbial growth and enzymatic turnover; however, nitrogen mineralization does not completely cease under freezing conditions. Thin, unfrozen water films persist around soil particles and within micropores, permitting limited extracellular enzymatic hydrolysis, microbial respiration and ammonification to continue even at subzero temperatures (Schimel *et al*., 2004).

Freeze-thaw cycles exert both stimulatory and inhibitory effects on nitrogen mineralization. Physical disruption of soil aggregates and microbial cell membranes during freezing can release intracellular nitrogen and carbon substrates upon thawing, enhancing substrate availability and stimulating microbial activity (Grogan *et al*., 2004; Henry, 2007). At the same time, repeated or intense freeze-thaw events may denature extracellular enzymes, reduce microbial viability and destabilize microbial communities, thereby constraining mineralization rates (Grogan *et al*., 2004, Nandy *et al*., 2025).

The net effect of freeze-thaw dynamics depends strongly on event frequency and intensity. Gradual thawing typically promotes microbial recovery and net nitrogen mineralization, whereas rapid or repeated freeze-thaw cycles can lead to nitrogen immobilization or losses through leaching and gaseous emissions, particularly when thaw coincides with high soil moisture (Brooks *et al*., 1998).

Soil moisture, aeration and redox pulses

Soil moisture availability regulates oxygen diffusion, solute transport and microbial respiration, thereby exerting strong control over nitrogen mineralization and subsequent transformation pathways (Davidson *et al*., 2012). In cool temperate soils, elevated moisture during snowmelt and spring thaw frequently creates transient anaerobic or hypoxic conditions, suppressing nitrification and favoring ammonium accumulation due to reduced activity of aerobic ammonia oxidizers (Booth *et al*., 2005; Butterbach-Bahl *et al*., 2013).

As soils dry and aeration improves during warmer periods, oxidative processes intensify, promoting ammonium oxidation and increasing nitrate production. However, periodic drying-rewetting events characteristic of temperate climates generate redox oscillations that can stimulate short-lived bursts of nitrogen mineralization. Upon rewetting, microbial cells release osmolytes and intracellular nitrogen compounds, which are rapidly mineralized, resulting in transient increases in inorganic nitrogen availability (Birch, 1958; Fierer and Schimel, 2002).

Moisture pulses also enhance the diffusion of enzymes and substrates, temporarily accelerating nitrogen turnover. In contrast, prolonged waterlogging restricts oxygen diffusion and favors anaerobic pathways, including denitrification, leading to nitrogen losses as nitrous oxide (N_2O) or dinitrogen (N_2) gases (Butterbach-Bahl *et al*., 2013). Thus, soil moisture dynamics regulate not only the rate of mineralization but also the retention versus loss of mineral nitrogen.

Texture, pH and physical protection

Soil texture and mineralogical composition strongly influence nitrogen mineralization by determining the surface area available for organic matter sorption, microbial colonization and enzyme stabilization (Six *et al*., 2002). Fine-textured soils with high clay and silt contents promote the physical protection of organic matter within microaggregates and organo-mineral complexes, thereby slowing decomposition and nitrogen release. In contrast, coarse-textured soils typically exhibit greater aeration and lower physical protection, facilitating faster organic matter turnover and nitrogen mineralization (Cotrufo *et al*., 2013).

Soil pH exerts a critical control over the activity and stability of key nitrogen-transforming enzymes, including urease, proteases and ammonia monooxygenase (Burns *et al*., 2013). Acidic conditions often inhibit bacterial nitrifiers and reduce overall nitrification rates, while favoring ammonia-oxidizing archaea adapted to low pH and low substrate availability (Leininger *et al*., 2006; Prosser and Nicol, 2012). pH also influences microbial community composition, enzyme persistence and nutrient availability, thereby shaping the balance between ammonification and nitrification.

Physical protection of organic substrates within aggregates further constrains microbial access and enzymatic attack, creating microsites with distinct physicochemical conditions. Within these microsites, nitrogen mineralization proceeds at variable rates depending on local oxygen status, moisture and substrate availability, contributing to pronounced spatial heterogeneity in nitrogen cycling processes across cool temperate soils (Kuzyakov and Blagodatskaya, 2015).

Organic amendments, nitrogen supply assessment and loss mitigation

Organic amendments and C:N strategies

In cool temperate agroecosystems, maintaining optimal nitrogen mineralization while minimizing environmental losses requires careful management of organic inputs. The application of compost, farmyard manure, crop residues and green manures supplies both carbon and nitrogen substrates, stimulating microbial activity during periods when temperature and moisture conditions are favorable (Diacono and Montemurro, 2010). The carbon-to-nitrogen (C:N) ratio of organic amendments is a critical determinant of nitrogen transformation pathways: materials with narrow C:N ratios promote rapid microbial decomposition and net nitrogen mineralization, whereas amendments with wider C:N ratios favor microbial immobilization and longer-term nutrient retention within soil organic matter pools (Booth *et al*., 2005).

Incorporation of organic matter prior to winter allows slow decomposition under cold conditions, facilitating the gradual release of plant-available nitrogen during spring thaw when crop demand begins to increase (Brooks *et al*., 1998; Schimel and Bennett, 2004, Raju *et al.,* 2025). Conversely, excessive inputs of readily decomposable organic materials with low C:N ratios can accelerate nitrification during wet and cool periods, increasing the risk of nitrate leaching beyond the root zone (He *et al*., 2011). Integrating organic amendments with mineral fertilizers and synchronizing application timing with crop nitrogen uptake improves nitrogen-use efficiency, stabilizes yields and enhances the long-term sustainability of soil fertility in temperate agroecosystems (Cassman *et al*., 2002).

Soil testing, potentially mineralizable nitrogen (PMN) and predictive modelling

Quantifying the capacity of soils to supply nitrogen through mineralization is essential for adaptive nutrient management in cool climates. Potentially mineralizable nitrogen (PMN) is commonly estimated using laboratory-based aerobic incubations, short-term anaerobic assays, or chemical extraction techniques designed to approximate biologically available organic nitrogen pools (Curtin *et al*., 2006). While these methods provide useful indices of soil nitrogen-supplying power, they often overestimate field-scale mineralization

because they are conducted under optimal temperature and moisture conditions that rarely persist in cool temperate environments (Dessureault-Rompré *et al*., 2015).

Incorporating temperature response functions, moisture correction factors and seasonal constraints into predictive models substantially improves the reliability of nitrogen release estimates (Davidson *et al*., 2012). Mechanistic and process-based models that integrate microbial growth kinetics, enzyme-mediated depolymerization and substrate availability can simulate temporal patterns of mineralization and immobilization across seasons (Wieder *et al*., 2015). These modeling approaches are increasingly used to refine fertilizer recommendations, reduce nitrogen surpluses and improve nitrogen-use efficiency under the variable climatic conditions characteristic of cool temperate agroecosystems.

Mitigation of nitrogen losses (Leaching and N_2O Emissions)

Effective mitigation of nitrogen losses in cool temperate regions depends on synchronizing nitrogen mineralization with crop demand while limiting pathways for nitrate leaching and nitrous oxide (N_2O) emissions. Cover cropping, residue retention and winter ground cover enhance nitrogen capture during non-growing seasons by taking up residual nitrate and reducing leaching losses during snowmelt and early spring rainfall events (Tonitto *et al*., 2006).

Reducing soil disturbance through conservation tillage preserves aggregate structure and enhances the physical protection of organic nitrogen, slowing rapid mineralization and reducing nitrogen losses (Six *et al*., 2002; Blanco-Canqui and Lal, 2008). The use of nitrification inhibitors can suppress the conversion of ammonium to nitrate, thereby reducing both nitrate leaching and N_2O emissions under moist and cool conditions (Akiyama *et al*., 2010; Butterbach-Bahl *et al*., 2013). Biochar amendments further contribute to nitrogen retention by adsorbing ammonium and nitrate, improving soil aeration and modifying microbial activity, collectively reducing gaseous nitrogen losses (Davys *et al*., 2023).

When combined with accurate soil nitrogen diagnostics and climate-responsive predictive models, these integrated management strategies support sustainable nitrogen cycling, enhance nitrogen-use efficiency and contribute to the mitigation of greenhouse gas emissions in cool temperate agroecosystems.

Implications of climate change for nitrogen mineralization in cool temperate soils

Climate change is expected to fundamentally alter nitrogen mineralization dynamics in cool temperate soils through shifts in temperature regimes, snow cover duration and soil moisture patterns. Rising mean annual temperatures and warmer winters are likely to increase microbial metabolic activity during traditionally dormant periods, thereby enhancing off-season nitrogen mineralization (Schimel *et al*., 2004). Winter soil processes, once considered negligible, are now recognized as critical contributors to annual nitrogen fluxes, particularly under reduced snow insulation and increased soil freezing intensity.

Changes in freeze-thaw dynamics represent a key mechanism by which climate warming may affect nitrogen availability and loss. Reduced snowpack can increase soil frost depth, intensifying freeze-thaw disturbance and stimulating episodic pulses of ammonium and nitrate during thaw periods (Henry, 2007). These transient mineralization flushes may become increasingly decoupled from plant nitrogen demand, elevating the risk of nitrate leaching and nitrous oxide (N_2O) emissions during early spring (Risk *et al*., 2013).

Warming trends may also shift the composition and functional dominance of microbial communities involved in nitrogen cycling. Enhanced winter and shoulder-season activity is expected to favor ammonia-oxidizing archaea (AOA), which are better adapted to low substrate availability and cold, acidic conditions, while ammonia-oxidizing bacteria (AOB) may dominate under warmer and more nutrient-rich conditions (Prosser and Nicol, 2012). Such shifts could alter the balance between ammonium retention and nitrate production, with cascading effects on nitrogen use efficiency and loss pathways.

In addition to thermal effects, climate-driven changes in precipitation regimes will influence soil aeration and redox dynamics. Increased frequency of extreme rainfall events may enhance anaerobic microsite formation, stimulating denitrification and DNRA, while prolonged summer drying may suppress mineralization and nitrification (Davidson *et al*., 2012). Collectively, these interacting climatic drivers underscore the need to incorporate seasonal and winter processes explicitly into nitrogen cycling models and management strategies for cool temperate agroecosystems.

Conceptual synthesis: Integrating microbial regulation, organic matter dynamics and environmental controls

Nitrogen mineralization in cool temperate soils emerges from the tight coupling among organic matter quality, microbial regulatory mechanisms and environmental constraints. Organic matter provides both the substrate and the physicochemical context within which microbial processes operate, while temperature, moisture and soil structure regulate enzymatic accessibility and metabolic efficiency. This interaction creates a temporally heterogeneous nitrogen supply characterized by slow background mineralization punctuated by episodic pulses during thaw and rewetting events.

At the microbial level, extracellular enzyme production governs depolymerization, the principal bottleneck in nitrogen mineralization. Cold-adapted microbial communities maintain this process through psychrophilic enzymes, membrane adaptations and biofilm-mediated microscale protection, enabling continued nitrogen turnover under low-energy conditions (Schimel *et al*., 2007). Intracellular

ammonification and subsequent nitrification are regulated by microbial stoichiometry, growth efficiency and competition between immobilization and mineralization, giving rise to rapid internal nitrogen cycling that is often poorly reflected in net mineralization measurements (Kuzyakov and Blagodatskaya, 2015).

Organic matter stabilization through organo-mineral associations further modulates nitrogen availability by physically protecting substrates from enzymatic attack. Freeze-thaw and wet-dry cycles intermittently disrupt these protective mechanisms, releasing previously stabilized organic nitrogen and triggering short-lived mineralization pulses. These dynamics highlight the importance of soil structure and mineralogy in regulating not only carbon persistence but also nitrogen release timing (Six *et al*., 2002; Schmidt *et al*., 2011).

From a management perspective, this integrated framework emphasizes that nitrogen availability in cool temperate soils is governed less by total nitrogen stocks than by the synchronization of microbial activity, organic matter turnover and plant demand. Adaptive management strategies-such as optimized organic amendment timing, residue quality manipulation and climate-responsive fertilization-must therefore account for seasonal microbial dynamics and environmental variability. Conceptually, nitrogen mineralization in cool soils should be viewed as a pulsed, microbially buffered process, rather than a continuous flux, with implications for nutrient use efficiency, environmental losses and ecosystem resilience under climate change.

Future directions and research gaps

Despite extensive research on nitrogen mineralization in temperate regions, significant knowledge gaps remain in understanding microbial and environmental controls under low-temperature conditions. Most studies have focused on gross mineralization and nitrification processes, while less attention has been given to the coupling between mineralization and nitrogen retention pathways such as denitrification and dissimilatory nitrate reduction to ammonium (DNRA). The relative importance of these processes during freeze-thaw transitions and seasonal saturation cycles is poorly quantified. Future research should integrate molecular, isotopic and modeling approaches to unravel the temporal and spatial heterogeneity of nitrogen mineralization in cool soils. High-resolution metagenomics and transcriptomics can reveal gene-level adaptations that enable psychrophilic microorganisms to sustain activity under subzero temperatures. Stable isotope tracing and microsensor technologies can link these microbial functions to actual nitrogen fluxes across microscale soil environments. Long-term field experiments are required to assess how climate variability-particularly changes in snow cover, freeze duration and moisture regimes-affects nitrogen turnover and losses. Mechanistic models need to incorporate microbial physiological parameters, enzyme kinetics and organic matter quality indices to improve predictions of nitrogen availability under future climate scenarios. Greater emphasis should also be placed on management-oriented studies that evaluate how different organic amendments, residue management practices and crop rotations influence mineralization-immobilization dynamics throughout the year. Understanding these linkages will be crucial for designing adaptive nutrient management strategies that sustain productivity while mitigating nitrogen losses and green-house gas emissions in cool temperate agroecosystems.

CONCLUSION

Nitrogen mineralization in cool temperate soils is not a continuous flux but a pulsed, microbially buffered process shaped by the intricate coupling of organic matter dynamics, microbial regulation and extreme environmental variability. Microbial communities exhibit remarkable resilience, maintaining functional turnover even at subzero temperatures through evolutionary adaptations to cold stress. However, the temporal decoupling between microbial mineralization and plant N demand-driven by freeze-thaw cycles and seasonal moisture shifts-poses significant challenges for nutrient use efficiency.

Predicting the future of these systems requires moving beyond measurements of total nitrogen stocks to a mechanistic understanding of microbial growth kinetics and enzyme-mediated pathways. Adaptive management strategies, such as the synchronized application of organic amendments, the use of nitrification inhibitors and the integration of climate-responsive predictive models, are vital to optimizing nitrogen supply while mitigating environmental risks like nitrate leaching and N_2O emissions. Ultimately, explicitly incorporating winter and shoulder-season processes into biogeochemical models is essential for maintaining soil fertility and ecosystem resilience under a changing global climate.

Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. No funding or sponsorship influenced the design of the study, decision to publish or preparation of the manuscript.

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