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Nutrient Dynamics in Thawing Permafrost

Vasudha Agnihotri*

G.B.Pant National Institute of Himalayan Environment, Himachal Pradesh Regional Centre, Mohal, Kullu 175 126, India

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Abstract: As the climate warms, permafrost thawing impacts nutrient cycling and biogeochemical processes by altering their availability and timing, which in turn affects ecosystem productivity and greenhouse gas emissions. Phosphorus has been identified as a more significant regulator of gross primary productivity (GPP) and the net ecosystem carbon balance compared to nitrogen, which has traditionally been considered the primary limiting nutrient along thaw gradients. The timing mismatch between peak nitrogen release due to permafrost thawing and plant uptake leads to increased nitrogen loss as nitrous oxide emissions. During permafrost thaw, microbial communities face co-limitation by nitrogen and phosphorus, which affects nutrient cycling rates and potential carbon loss. Additionally, changes in hydrological processes driven by the deepening of the permafrost thaw layer alter nutrient mobilization and transport to aquatic ecosystems, impacting freshwater biogeochemistry. The intricate interactions between nitrogen and phosphorus dynamics govern carbon distribution in ecosystems during permafrost thaw, underscoring the importance of incorporating nutrient co-limitations, microbial processes, and temporal nutrient availability patterns to enhance the predictions of permafrost responses to climate change.

Key words: Dissolved organic carbon, dissolved nitrogen, dissolved phosphorus, nutrient export, High-altitude ecosystem, Himalaya.

Correspondence
Vasudha Agnihotri
vasudha@gbpihed.nic.in

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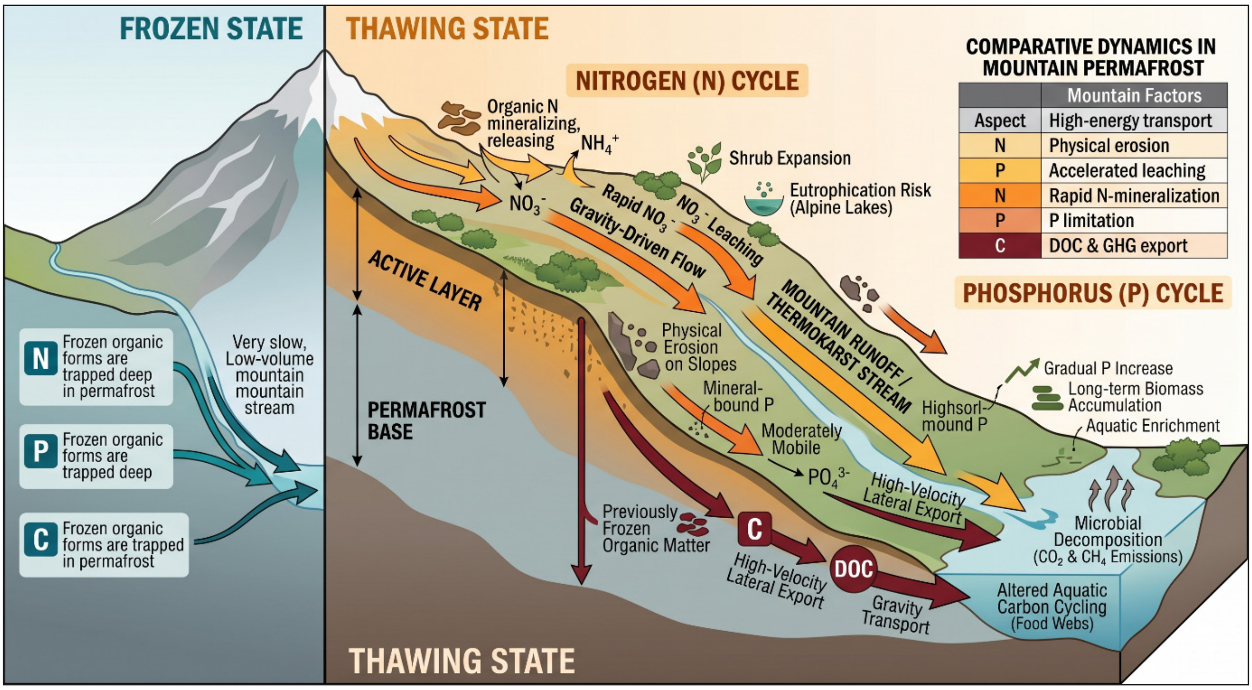
Permafrost refers to ground that remains at or below 0°C for a minimum of two consecutive years. It is not located directly on the surface but exists in layers, including the active layer, permafrost, and unfrozen ground. The permafrost table separates the active layer from the permafrost. The active layer is the uppermost soil layer that thaws in summer and refreezes in winter, thereby supporting biological activity. Permafrost is found in high-altitude areas such as the Arctic (Alaska, Canada, Russia, and Greenland) and as Alpine Permafrost in mountain ranges such as the Himalayas and the Alps. The cold-arid regions of the Himalayas are characterized by permafrost-affected soils that remain frozen for most of the year. Unlike Arctic permafrost, Himalayan permafrost is typically found in steep, high-altitude areas where freeze-thaw cycles are influenced by intense solar radiation and low precipitation. It contains a vast amount of organic carbon, including partially decomposed dead plants and animals, and preserves microbes that have been frozen for tens of thousands of years. The thawing process releases nutrients and carbon, thereby affecting soil health and the biogeochemistry of proglacial streams. Rising temperatures due to human activities are accelerating permafrost thawing, leading to the release and redistribution of previously trapped nutrients and the emission of greenhouse gases such as methane (CH_4) and carbon dioxide (CO_2) from the microbial decomposition of long-preserved biomass, which further raises local temperatures and deepens the active layer (IPCC, 2022). This process also causes gradual deepening of the active layer and sudden thermokarst collapse, worsened by the reduced albedo of the exposed ground (Riihel¨a *et al.*, 2021; Leal Filho *et al.*, 2023). During thawing, nutrient immobilization shifts the system from closed nutrient cycles to one dominated by lateral exports, affecting nearby aquatic ecosystems and the terrestrial productivity. This also affects the infrastructure in high-altitude mountain regions. Nutrient dynamics during permafrost thawing involve the reactivation and redistribution of previously frozen reserves of carbon (C), nitrogen (N), phosphorus (P), and other nutrients as ground ice and nutrient-rich permafrost soil melt. This process makes these nutrients available to microbes and plants and facilitates their movement into water bodies. Thawing shifts the equilibrium between nutrient release, immobilization, and export, transitioning from a closed-loop cycle to significant lateral export (Kendrick *et al.*, 2018; Yang *et al.*, 2021; Heffernan *et al.*, 2024). This paper reviews research conducted in various permafrost regions worldwide to understand the patterns of nutrient release during permafrost thawing and its impact on nearby water bodies and other ecosystems.

Key Nutrient Releases

As permafrost thaws, it releases nutrients such as nitrogen, phosphorus, and carbon, potentially impacting microbial activity, plant growth, and greenhouse gas emissions in the ecosystems it affects (Fig. 1; Table 1) (Vonk *et al.*, 2015; Mao *et al.*, 2020; Yun *et al.*, 2023). This thawing transforms the system from frozen storage to an active cycle, where easily degradable organic matter and mineral nutrients become accessible to microbes and plants. This process liberates substantial amounts of organic carbon, nitrogen, and phosphorus for microbial processing and hydrological movement, thereby increasing the dissolved organic carbon and nutrient concentrations in rivers and lakes and altering food-web dynamics and carbon cycling in these aquatic environments (Reyes &



COMPARATIVE DYNAMICS IN MOUNTAIN PERMAFROST

	Mountain Factors
Aspect	High-energy transport
N	Physical erosion
P	Accelerated leaching
N	Rapid N-mineralization
P	P limitation
C	DOC & GHG export

Fig. 1. Diagrammatic representation of the nutrient dynamics during permafrost thaw, specifically highlighting the processes in mountain environments (AI-generated)

Lougheed, 2015; Kendrick *et al*., 2018; Heffernan *et al*., 2024).

Nitrogen and phosphorus release: The active layer of permafrost is rich in organic nitrogen (N) and contains small amounts of reactive inorganic nitrogen, both of which can be released as temperatures rise and microbial activity increases during thawing (Reyes & Lougheed, 2015; Kashi *et al*., 2023). Microbial processes convert organic nitrogen into ammonium (NH_4^+). In cold environments, ammonium ions accumulate in acidic permafrost soils because the subsequent steps of the nitrogen cycle are inhibited. Total dissolved nitrogen, which includes dissolved organic nitrogen (DON) and dissolved inorganic nitrogen (DIN), generally increases along the thaw gradient (Finger *et al*., 2016). In well-drained, oxygen-rich soils, ammonium ions are transformed into nitrate ions (NO_3^-), which are more mobile than ammonium ions and can easily leach into groundwater and surface water (Salmon *et al*. 2018). Francis *et al*. (2022) noted active nitrogen cycling and denitrification in thaw zones of large river systems, such as the Kolyma, using ^{15}N isotope analysis. Under waterlogged and anaerobic conditions, nitrate ions are converted into nitrous oxide (N_2O), a potent greenhouse gas with a global warming potential nearly 300 times that of CO_2 (Voigt *et al*., 2017). As thaw depth increases, water flows through deeper layers with higher concentrations of nitrates and DON. This increase in nitrogen content in high-altitude water bodies can lead to ecological changes by boosting algal growth and altering aquatic microbial communities. An increase in bioavailable nitrogen can promote the growth of woody plants, mainly shrubs, replacing moss or lichens (Koven *et al*., 2015). Cyanobacteria and legumes in cold regions can enhance their nitrogen fixation rates as temperatures rise. Salmon *et al*. (2018) found that permafrost thawing changes nitrogen (N) stratification in the Alaskan tundra, shifting ecosystems from surface-level N limitation to subsurface enrichment. The findings indicate that newly thawed deep soil layers are significantly richer in nitrogen than the organic-rich but nitrogen-poor active layers. The inorganic nitrogen released from deep pools was found to be roughly equivalent to the accelerated mineralization in warming surface soils, meeting plant demand and highlighting the importance of deep-layer mobilization of nutrients. In the Tibetan alpine permafrost region, thawing significantly affects nitrogen dynamics owing to increased plant nitrogen demand and accelerated gaseous nitrogen losses. A deficit in nitrogen availability acts as a critical bottleneck for terrestrial carbon-climate feedback by limiting the carbon-sequestration capacity of high-altitude ecosystems (Salmon *et al*., 2018).

Phosphorus (P) is present in these regions, primarily attached to iron (Fe) or aluminum (Al) oxides of other minerals, and can be liberated when redox conditions or pH levels change, such as in anoxic or acidic environments (Yang *et al*., 2021; Hefferman *et al*., 2024). Dissolved inorganic phosphorus (DIP) is easily accessible for biological use and is often regulated by mineral adsorption and iron-redox cycles, whereas dissolved organic phosphorus (DOP) is mainly found in peat-rich permafrost, is highly mobile, and is less influenced by mineral adsorption. As temperatures rise in permafrost areas, microbial communities break down dissolved organic phosphorus and convert it into an inorganic form. Under aerobic conditions, inorganic phosphorus binds to Fe (III)-oxyhydroxides, preventing the release of DIP into surface waters. However, in anaerobic or waterlogged conditions, typical of thermokarst features, these iron oxides can dissolve, releasing adsorbed phosphates into soil solutions (Reyes and Lougheed, 2015). Freeze–thaw cycles can break soil aggregates, facilitating the release of moderately active phosphorus forms; however, the concurrent formation of secondary Fe and Al minerals can act as a long-term buffer, re-sequestering phosphate, and limiting its movement to nearby headwater rivers (Reyes and Lougheed, 2015; Liao *et al*., 2019; Wang *et al*., 2022). Phosphorus mobilization is also influenced by the hydrological connectivity between surface water and deeper soil layers (Schade *et al*. 2016). High-altitude areas significantly alter phosphorus biogeochemistry by shifting regions from stable reservoirs to active nutrient sources. Hong *et al*. (2025) noted a 36.1% decrease in soil P stock since the 1980s, driven by a negative nutrient budget in which outflows greatly surpass inflows. This reduction is partly due to dissolved phosphorus runoff and plant uptake; however, over 80% of the total soil P export is attributed to water erosion.

Inorganic nitrogen and phosphorus are rapidly released as temperatures rise and water saturation increases in thaw-sensitive regions. Ammonium nitrogen was liberated at a higher rate from the upper permafrost layer than from the overlying active layer during thawing. Phosphorus, along with other micronutrients such as calcium, iron, magnesium, sulfur, and silicon, has been reported to be released from thawed permafrost under incubated warming conditions (Reyes and Lougheed, 2015). Along thermokarst or thaw-gradient sequences, soil nitrogen availability often shows an initial spike, followed by a decline as plant uptake and microbial immobilization increase, whereas phosphorus availability tends to rise as mineral weathering and phosphorus desorption accumulate. This pattern can lead to a shift from nitrogen-limited to phosphorus-limited conditions, which impacts the role of nutrients in plant productivity and carbon uptake after thawing (Yang *et al*., 2021). Thaw-released nutrients and dissolved organic carbon (DOC) can alter methane (CH_4) production and oxidation. Nitrogen-rich permafrost leachates can suppress methane production and oxidation, whereas phosphorus addition can enhance methane oxidation in some areas, demonstrating stoichiometric control over greenhouse gas emissions (Kashi *et al*., 2022; Heffernan *et al*., 2024).

Carbon release: Hundreds of megagrams of carbon per hectare (Mg C ha^{-1}) are stored in permafrost soils in high-altitude peatlands and tundra areas, which have accumulated over millennia under cold, oxygen-limited conditions. As the permafrost layer recedes and the active layer becomes deeper, ancient carbon that was once locked in frozen soil becomes susceptible to microbial breakdown (Koven *et al*., 2015; Dieleman *et al*., 2022; Vas *et al*., 2025). The major portion of total organic carbon produced by the microbial decomposition of frozen soil organic carbon consists of dissolved organic carbon (DOC) (Vonk *et al*., 2015; He *et al*., 2025). Ollivier *et al*. (2026) reported higher concentration of DOC (341 mg L^{-1}) in permafrost meltwater from in retrogressive thaw slumps of one of the Siberian lakes in comparison to DOC (29-51 mg L-1) in connected alas-lakes. Gandois *et al*. (2019) reported highest DOC level (44.1±10.1 mg L^{-1}) during thawing of early-stage thermokarst bogs in north Siberia peatland permafrost, which was characterized by high aromaticity with the significant contribution of ages permafrost carbon. DOC concentration was lower (11.0±2.4 mg L^{-1}) in fens and lakes, where dissolved organic matter shifts from plant-derived, aromatic compounds to microbially processed and photodegraded organic matter. This shows a shift in nutrient dynamics, where the initial collapse of permafrost mobilizes ancient carbon stocks before subsequent landscape stabilization dilutes these inputs (Vonk *et al*., 2015; Gandois *et al*., 2019).

High-altitude peatlands have shown a rapid loss of pre-thaw carbon stocks along the thaw gradient, which reflects direct mineralization along with lateral transport (Keskitalo *et al*., 2025). The lateral export of DOC can rival or even exceed vertical gas reflux in some permafrost systems. Leaching experiments conducted in headwater catchments on the Tibetan Plateau showed that mineral permafrost can retain a sizeable fraction of DOC migrating from the active layer, altering both the quantity and chemistry of DOC exported to streams (Kelley *et al*., 2025; He *et al*., 2025). In another study, 10% of the total soil carbon loss in the form of DOC was reported in abrupt thermokarst in upland tundra, with the remainder being released as CO_2 and CH_4 (Kelley *et al*., 2025). These findings show that DOC export, an integral component of permafrost carbon loss, is modulated by soil mineralogy, iron cycling, and hydrological connectivity (Liu *et al*., 2022; Liu *et al*., 2025a; Du *et al*., 2026). In an incubation study, Fe (III) reduction caused the release of DOC along with its partial mineralization under anoxic conditions, while Fe-bearing minerals served as sorption sites that retained DOC and limited its export (Carneiro Barreto *et al*., 2024). In Tibetan permafrost thaw sequences, permafrost collapse leads to increased Fe-oxide formation and the accumulation of iron-bound organic carbon, which tends to stabilize the fraction of organic matter despite overall soil organic carbon loss. This Fe-mediated retention and mineral-associated organic carbon formation may partially buffer the long-term impact of permafrost thawing on the atmosphere (Liu *et al*., 2022; Carneiro Barreto *et al*., 2024).

Table 1. Comparative dynamics of nutrients in thawing permafrost

Nutrient component	Predominant forms and dynamics	Impact of permafrost thaw	Notable source(s)
Organic carbon (DOC/POC)	DOC (Dissolved), POC (Particulate); includes ancient Yedoma carbon.	Thaw triggers "rhizosphere priming" and rapid decomposition. Massive concentrations of old DOC are exported to lakes and rivers.	Heffernan *et al*. (2024); Ollivier *et al*. (2026); Friggens *et al*. (2025)
Inorganic carbon (DIC)	CO_2 and CH_4	Increased microbial "Carbon Use Efficiency" (CUE) and mineral-associated carbon shifts lead to higher greenhouse gas efflux.	Qin *et al*. (2025); Liu *et al*. (2022); Vas *et al*. (2025)
Nitrogen (N)	NH_4^+, NO_3^-, N_2O	Thaw increases N availability, but "progressive nitrogen limitation" is observed on the Tibetan Plateau as plants consume available N.	Kou *et al*. (2020); Voigt *et al*. (2017); Salmon *et al*. (2018)
Phosphorus (P)	Bioavailable P, Sediment-bound P	P is often the limiting factor for C dynamics rather than N. Thaw cycles increase P loss in runoff and create a "soil phosphorus crisis."	Yang *et al*. (2021); Hong *et al*. (2025); Liao *et al*. (2019)
Iron (Fe)	Fe-bound Organic Carbon	Redox conditions modulate iron dissolution; microbial C degradation is heavily dominated by iron redox metabolism in thawing soils.	Carneiro Barreto *et al*. (2024); Romanowicz *et al*. (2023); Du *et al*. (2026)
Mineral elements	K, Ca, Mg, Trace elements	Changing tundra vegetation and increased thaw depth alter the foliar cycling of these minerals, impacting plant-soil feedbacks.	Mauclet *et al*. (2022); Wang *et al*. (2022)

Simulation studies have projected the vulnerability of permafrost carbon under 2-3°C warming, which causes the release of CO_2 and CH_4 (Reif, 2023). Warming-induced permafrost thaw reshapes both the microbial community composition and metabolic strategies. Studies have shown that an increase in Fe (III) reduction genes and related organic degradation stimulates CO_2 production while suppressing acetoclastic methanogenesis during increased thawing (Romanowicz *et al*., 2023; Qin *et al*., 2025). In other studies, microbial communities have shown acclimatization to higher temperatures, thereby gaining the functional capacity to decompose recalcitrant organic matter with increased soil respiration and CH_4 fluxes (Feng *et al*., 2020; Qin *et al*., 2025). Plant-soil interactions can further complicate these impacts. A positive rhizosphere priming effect (RPE) in thawing permafrost indicates that root extrudates and litter enhance the decomposition rate of organic matter, which can amplify net carbon loss from active layer soils (Friggens *et al*., 2025).

Ecosystem Impacts and Research Gaps

The ecological consequences of nutrient dynamics during permafrost thaw are intricate, influencing carbon cycling, aquatic ecosystems, vegetation composition, microbial communities, and the overall functioning of ecosystems (Fig. 1). As permafrost thaws, it reveals frozen organic matter and associated nutrients such as nitrogen and phosphorus, leading to notable changes in soil nutrient availability and prompting shifts in vegetation communities. In wetter lowland areas, there is often an increase in graminoids with higher silicon content. In contrast, drier upland regions tend to support shrub growth with elevated calcium and magnesium levels in their foliage. These shifts in vegetation impact mineral cycling by altering litter production and decomposition patterns, which subsequently affect nutrient availability and soil chemistry (Mauclet *et al*. 2022). The expansion of vegetation and litter inputs boosts carbon inputs, potentially altering the microbial genetic potential for biogeochemical cycling and contributing to increased greenhouse gas emissions (Chauhan and Pandey, 2024; Cuartero *et al*., 2025). Higher nutrient levels in aquatic systems also modify the carbon cycle, including changes in the production and consumption of carbon-based trace gases, which can influence the structure and biodiversity of aquatic food webs (Wrona *et al*.

2008). Variations in temperature, precipitation patterns, and hydrological processes also impact the thickness of the active layer and soil thermal regimes across regions, affecting vegetation, microbial responses, and nutrient export dynamics, thereby influencing the ecosystem services provided by the permafrost (Fu *et al*., 2025; Gao *et al*., 2021; Lan *et al*., 2025). Collectively, these interconnected processes highlight the complexity of ecosystem responses to permafrost thawing, involving feedback mechanisms that affect nutrient cycling, carbon balance, biodiversity, and ecosystem services across various spatial and temporal scales. In arid regions of the Indian Himalaya, such as Ladakh, permafrost thawing is linked to water security issues. Dissolved carbon and other nutrients alter the nutritional profile of glacial meltwater, supporting downstream agriculture. This also leads to the loss of soil structure, resulting in desertification and land degradation in fragile, arid ecosystems (Kumar *et al*., 2024).

While numerous advanced studies have explored nutrient dynamics during permafrost thaw, most research remains site-specific and short-term in nature. There is a scarcity of long-term, high-frequency monitoring of dissolved carbon, nitrogen, phosphorus, and other nutrients, making it challenging to assess the release rates and thresholds (Gao *et al*., 2021). Metagenomic studies have shown the reorganization of microbial communities' post-thaw (Ernakovich *et al*., 2022); however, research on the assembly of nutrient-cycling microbes is still limited. Understanding how thaw-released nitrogen and phosphorus influence priming, methane production, and net carbon-climate feedback under various thaw conditions is also limited (Laurent *et al*., 2026). It is increasingly recognized that phosphorus becomes the primary limiting nutrient, rather than nitrogen, after permafrost thawing. However, predictions regarding when thaw alleviates or reinforces nitrogen limitation, particularly in low-nitrogen, high-altitude areas, are still lacking (Kou *et al*., 2020). The impact on vegetation also requires further investigation (Liu *et al*., 2025b). Research has predominantly focused on porewater or laboratory incubations, with a lack of catchment-level studies, especially in high-altitude arid regions such as Ladakh in the Indian Himalayan region. Thawing permafrost changes nutrient availability and hydrology, affecting land-use options such as pasture and agriculture, which need to be addressed to fill knowledge gaps, particularly in high-altitude regions such as the Himalayas, where nutrients are crucial for water quality and downstream ecosystems (Schuur and Mark, 2018; Ward *et al*., 2024).

Conclusions

Permafrost thaw is a major ecological transformation driven by climate warming, triggering the release of long-stored carbon and nutrients and altering biogeochemical processes across terrestrial and aquatic ecosystems. The mobilization of nitrogen, phosphorus, and dissolved organic carbon reshapes microbial activity, vegetation dynamics, hydrology, and greenhouse gas emissions, influencing both ecosystem productivity and climate feedbacks. Evidence increasingly shows that nutrient regulation during thaw involves complex interactions and co-limitations, with phosphorus often emerging as a key controlling element after initial nitrogen release. Temporal mismatches between nutrient availability and biological uptake, along with lateral nutrient export and microbial responses, introduce significant uncertainty in predicting ecosystem trajectories. Although research has advanced considerably, major gaps remain in long-term monitoring, catchment-scale studies, and investigations from high-altitude regions such as the Indian Himalaya. Integrating nutrient dynamics, microbial processes, and hydrological changes into future research will be essential for improving predictions of permafrost–climate interactions and for sustaining ecosystem services in vulnerable mountain environments.

Competing Interests

The authors declare no competing interests.

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About the Author

Vasudha Agnihotri serves as a Scientist E at the Himachal Regional Centre of the G.B. Pant National Institute of Himalayan Environment (GBPNIHE). She earned her Ph.D in Chemical Sciences from CSIR-IIP, Dehradun, and completed her M.Sc at IIT Roorkee. With more than two decades of experience, her expertise includes environmental monitoring, bioremediation, wastewater treatment, and plant product nutrition, with a particular emphasis on conserving soil, plant, and water quality in the Himalayan region. Dr. Agnihotri has published over 40 articles in SCI-indexed journals, edited or authored 12 books, and contributed to 15 book chapters, in addition to holding an Indian patent. She has successfully managed numerous high-impact projects funded by DST, DBT, and NMHS, and has guided many doctoral and postgraduate students. Dr. Agnihotri is a life member of several esteemed organizations, such as the Chemical Research Society of India and the Indian National Science Congress, making significant contributions to the field of environmental chemical sciences.

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