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PLANT RESPONSE TO AMMONIUM TOXICITY: MECHANISTIC INSIGHTS INTO YIELD LOSS AND ADAPTIVE MECHANISMS

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Abstract

Ammonium (NH_4^+) is a key form of nitrogen (N) source for plant growth and development. However, when present in high amounts or as the primary nitrogen supply, it causes physiological imbalance in plants. Ammonium toxicity in plants disrupts carbon-nitrogen metabolism by depleting TCA cycle intermediates necessary for amino acid synthesis. This metabolic imbalance raises energy requirement, slows root and shoot development, and decreases yield. Toxicity also causes oxidative stress by accumulating ROS and disrupting ion homeostasis, particularly iron, intensifying damage.

This article delves into the mechanistic basis of ammonium-induced stress, elucidating its impacts on plant metabolism, morphology, and development that collectively contribute to yield diminution. Furthermore, it outlines the adaptive responses at the cellular, metabolic, and genetic levels that plants deploy to counteract this toxicity.

Introduction

Nitrogen (N) is widely acknowledged as one of the most important macronutrients for plant development and production, since it serves as the foundation for critical biomolecules such as amino acids, proteins, nucleic acids, and chlorophyll (Marino & Moran, 2019). Plants get nitrogen from soil in two inorganic forms: nitrate (NO_3^-) and ammonium (NH_4^+). Their relative availability is determined by soil pH, microbial activity, and environmental circumstances (Esteban et al., 2016). Although nitrate is the predominant form of nitrogen in most aerobic soils due to rapid microbial nitrification, ammonium is more energy efficient to assimilate than nitrate (Wang, 2021), and its uptake is mediated by specific ammonium transporters (AMTs) located in root cell membranes (Rivero-Marcos et al., 2024). Once inside the plant, ammonium is rapidly metabolized *via* the glutamine synthetase/glutamate synthase (GS/GOGAT) pathway, which efficiently incorporates NH_4^+ into amino acids, minimizing the potential for toxic accumulation (Li et al., 2014; Esteban et al., 2016).

However, ammonium uptake beyond the plant's metabolic demand, can cause accumulation of unassimilated ammonium in tissues, leading to downstream physiological disturbances like rhizospheric and cytosolic acidification, disruption of ion and pH homeostasis, metabolic imbalance of carbon–nitrogen (C–N) due to the depletion of tricarboxylic acid (TCA) cycle intermediates (Figure 1), and oxidative stress from increased mitochondrial respiration (Marino and Moran, 2019).

Growth inhibition is more closely associated to the imbalance in C-skeleton supply and the buildup of H^+ during NH_4^+ absorption than to ATP depletion alone (Figure 1). Thus, rather of being just the result of increased energy

consumption, NH_4^+ toxicity manifests as a multifactorial stress including metabolic, ionic, and signaling abnormalities (Esteban et al., 2016).

Mechanistic Basis of Ammonium Toxicity

pH Homeostasis and Rhizospheric Acidification

Ammonium uptake by roots is typically accompanied by the extrusion of protons (H^+), leading to rhizosphere acidification (Di, 2023). This disrupts pH homeostasis both extracellularly and intracellularly, altering membrane potentials and enzyme activities (Figure 1). The acidification impairs nutrient availability, particularly of cations like Ca^{2+}, Mg^{2+}, and K^+, exacerbating nutrient imbalances (Marino and Moran, 2019).

Ionic and Nutritional Imbalances

Ammonium competes with other cations for uptake and transport channels. Its dominance disrupts the homeostasis of essential mineral nutrients, leading to deficiencies that hinder metabolic processes and structural development. For instance, reduced K^+ uptake affects osmoregulation and stomatal functioning, while Ca^{2+} deficiency impairs membrane integrity and cell signaling (Esteban et al., 2016).

Carbon-Nitrogen Metabolic Disequilibrium

Assimilation of NH_4^+ into amino acids *via* the glutamine synthetase/glutamate synthase (GS/GOGAT) pathway is carbon-intensive, requiring substantial 2-oxoglutarate derived from the TCA cycle (Figure 1) (Esteban et al., 2016). Under high NH_4^+ conditions, the carbon demand increases, leading to carbon depletion and reduced availability for other biosynthetic processes (Di, 2023). This uncoupling of C-N metabolism negatively impacts growth and biomass accumulation.

Reactive Oxygen Species (ROS) Accumulation

Excess ammonium induces the overproduction of ROS such as hydrogen peroxide (H_2O_2) and superoxide radicals (O_2^-), which cause oxidative stress (Esteban et al., 2016). ROS damage cellular macromolecules, including lipids, proteins, and nucleic acids, leading to membrane lipid peroxidation, protein oxidation, and DNA strand breaks. Elevated malondialdehyde (MDA) levels are commonly observed in ammonium-stressed tissues (Hasanuzzaman et al., 2020).

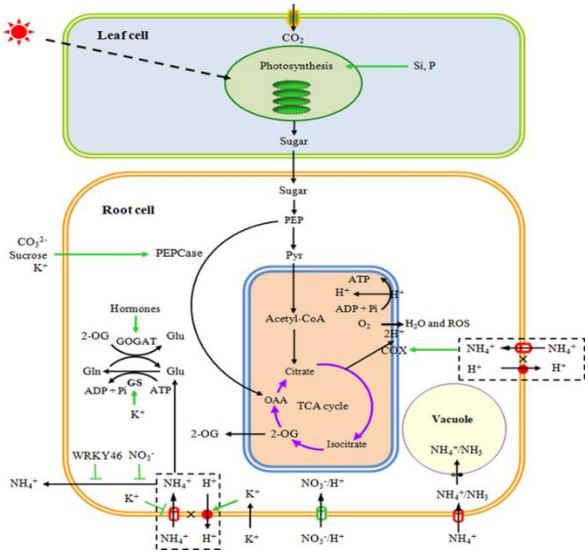

Figure 1. The schematic illustration for NH4+ toxicity and alleviation in plants

Hormonal Imbalance and Developmental Disruption

Ammonium stress alters endogenous hormone levels, particularly ethylene, abscisic acid (ABA), and auxins (Sabagh et al., 2022). Elevated ethylene and ABA levels inhibit cell expansion and division, while disrupted auxin gradients interfere with root architecture and gravitropism. These hormonal perturbations contribute to morphological abnormalities and reduced root-to-shoot ratios (Marino and Moran, 2019).

Yield Diminution under Ammonium Stress

Ammonium toxicity causes significant yield reduction in plants by initiating a series of physiological and morphological changes that impair growth and reproductive potential. When plants are exposed to high levels of external ammonium, their capacity to quickly absorb NH_4^+ *via* the GS/GOGAT pathway is overwhelmed, resulting in the buildup of free ammonium in tissues (Di, 2023). This excess ammonium induces cytosolic acidification as a result of proton extrusion, affects cellular pH homeostasis,

and interferes with critical metabolic activities such as photosynthesis. Ammonium toxicity is characterized by significant inhibition of primary root extension, changes in lateral root growth, decreased root/shoot ratios, and lower fresh weights of both roots and stems (Marino and Moran, 2019). High NH_4^+ levels also have a significant impact on leaf growth, causing chlorosis through retrograde signaling and chloroplast damage, which can occasionally result in necrosis or early senescence (Rivero-Marcos et al., 2024).

Increased malondialdehyde level and membrane lipid peroxidation are signs of oxidative stress, which frequently coexists with these symptoms and further reduces photosynthetic efficiency and biomass accumulation. The severity of yield loss is determined on species sensitivity, developmental stage, and environmental context; however, excessive ammonium exposure can result in yield decreases ranging from mild to severe, and in extreme cases, seedling mortality. Furthermore, ammonium toxicity can affect micronutrient homeostasis, notably iron metabolism, exacerbating the deleterious effects on plant growth and nitrogen utilization efficiency (Esteban et al., 2016). These complex impacts highlight the significance of properly controlling ammonium diet to prevent physiological problems and assure long-term crop output.

Adaptive Mechanisms to Ammonium Toxicity

Metabolic Reconfiguration

Metabolic reconfiguration is a fundamental adaptive approach in plants for mitigating ammonium stress, requiring dynamic adjustments in nitrogen absorption, carbon metabolism, and redox balance. In high NH_4^+ conditions, plants increase glutamine synthetase (GS)/glutamate synthetase (GOGAT) activity to quickly assimilate toxic ammonium into amino acids (Figure 1), while also upregulating alternative pathways like asparagine synthetase (AS) to sequester excess nitrogen into less harmful compounds like asparagine. This detoxification is combined with enhanced antioxidant enzyme synthesis (e.g., superoxide dismutase, catalase) to combat reactive oxygen species (ROS) caused by ammonium-induced oxidative stress (Marino and Moran, 2019). Plants also reorganize carbon metabolism to provide organic acids (e.g., 2-oxoglutarate) as carbon skeletons for ammonium absorption, generally through improved photorespiration or glycolysis (Miao et al., 2024). Additionally, transporter regulation (e.g., AMT2 ammonium transporters) limits excessive NH_4^+ uptake, while pH homeostasis mechanisms, such as proton pump activation, counter cytosolic acidification (Rivero-Marcos et al., 2024). Tonoplast-localized NH_4^+ transporters aid in vacuolar sequestration of ammonium, reducing cytosolic accumulation.

Antioxidant Defense Systems

Plants under ammonium stress produce more reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2) and superoxide (O_2^-), which can cause oxidative damage to proteins, lipids, and nucleic acids (Marino and Moran, 2019). Plants react by activating a variety of antioxidant enzymes, including glutathione reductase (GR) to replenish reduced glutathione (GSH), superoxide dismutase (SOD) to dismutate O_2^- into H_2O_2, catalase (CAT), and ascorbate peroxidase (APX) to breakdown H_2O_2. In addition, non-enzymatic antioxidants such as GSH and ascorbate (AsA) directly scavenge ROS and take part in the ascorbate-glutathione cycle, which helps to preserve cellular redox equilibrium and reduce oxidative stress when exposed to ammonium (Hasanuzzaman et al., 2020).

Hormonal Crosstalk Modulation

Hormonal crosstalk regulation is a critical adaptive response that allows plants to resist ammonium toxicity by integrating and fine-tuning the signaling pathways of major phytohormones such as abscisic acid (ABA), jasmonates, auxins, and gibberellins (GAs) (Thilakarathne et al., 2025). Under ammonium stress, ABA signaling is immediately triggered, prompting antioxidant defense systems, osmotic adjustment, and stomatal modulation to reduce cellular damage and preserve homeostasis. Simultaneously, jasmonate signaling pathways are altered to control root development and iron homeostasis, both of which are frequently affected by high

ammonium levels (Pandey et al., 2024; Thilakarathne et al., 2025). The interaction of these hormones, together with auxin and GA, regulates root architectural remodeling, nutrient absorption, and metabolic changes, improving plant resistance and survival under extended ammonium exposure. This dynamic hormonal crosstalk ensures that plants can adaptively balance growth and stress responses, minimizing the detrimental effects of ammonium toxicity on productivity and health (Sabagh et al., 2022; Thilakarathne et al., 2025).

Agronomic and Genetic Approaches to Amelioration

Balanced Fertilization

Ammonium toxicity can be decreased by balanced fertilizers with the ideal NO_3^-\NH_4^+ ratios. Optimizing fertilizer management can lower the risk of ammonium toxicity. This includes avoiding excessive ammonium fertilization in cool or low light conditions when plant metabolic activity is reduced, using a blend of ammonium and nitrate sources, and applying nitrification inhibitors to control the conversion of ammonium to nitrate (Wang, 2021; Xiao et al., 2023). Furthermore, preserving the ideal pH of the soil and guaranteeing sufficient availability of carbon substrate, such as by providing organic acids like α-ketoglutarate, might promote effective ammonium absorption and lessen poisoning symptoms.

Genotype Selection and Breeding

Ammonium-tolerant genotypes exhibit traits such as robust GS/GOGAT activity, strong antioxidant systems, and efficient ion homeostasis. Breeding programs targeting these traits can enhance tolerance (Esteban et al., 2016). Marker-assisted selection and QTL mapping facilitate the identification of tolerance-conferring loci.

Genetic Engineering

Transgenic approaches overexpressing ammonium transporters (AMTs), GS, or antioxidant genes have shown promise in conferring NH_4^+ tolerance (Di, 2023). CRISPR/Cas9-mediated editing of regulatory genes involved in stress response pathways is a future avenue for precision breeding (Kumar et al., 2023).

Conclusion

Ammonium toxicity poses a multifaceted challenge to plant health and crop productivity. Deciphering the mechanistic intricacies of NH_4^+-induced stress and adaptive pathways offers valuable insights for designing resilient cropping systems. Integrating physiological, molecular, and agronomic strategies will be pivotal for achieving sustainable nitrogen management and mitigating yield losses in ammonium-sensitive crops. Future research is highly needed to confirm the positive effects of ammonium in increasing plant quality, productivity, and resilience to biotic and abiotic stressors and their mechanisms behind. Moreover, the combined use of physiological and multi-omics studies will allow the exploration of the molecular intricacies of ammonium toxicity and tolerance in the future.

References

1. Di, D. W. (2023). New molecular mechanisms of plant response to ammonium nutrition. *Applied Sciences*, *13*(20), 11570.
2. Esteban, R., Ariz, I., Cruz, C., & Moran, J. F. (2016). Mechanisms of ammonium toxicity and the quest for tolerance. *Plant Science*, *248*, 92-101.
3. Hasanuzzaman, M., Bhuyan, M. B., Zulfiqar, F., Raza, A., Mohsin, S. M., Mahmud, J. A., Fujita, M., & Fotopoulos, V. (2020). Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants*, *9*(8), 681.
4. Kumar, M., Prusty, M. R., Pandey, M. K., Singh, P. K., Bohra, A., Guo, B., & Varshney, R. K. (2023). Application of CRISPR/Cas9-mediated gene editing for abiotic stress management in crop plants. *Frontiers in Plant Science*, *14*, 1157678.
5. Marino, D., & Moran, J. F. (2019). Can ammonium stress be positive for plant

performance? *Frontiers in Plant Science*, *10*, 1103.

6. Miao, F., Wang, Y., Haq, N. U., Lyu, M. J. A., & Zhu, X. G. (2024). Rewiring of primary metabolism for ammonium recycling under short-term low CO_2 treatment–its implication for C4 evolution. *Frontiers in Plant Science*, *15*, 1322261.
7. Pandey, A., Devi, L. L., Gupta, S., Prasad, P., Agrwal, K., Asif, M. H., Pandey, A. K., Bandyopadhyay, K., & Singh, A. P. (2024). Jasmonate signaling modulates root growth by suppressing iron accumulation during ammonium stress. *Plant Physiology*, *196*(4), 2213-2231.
8. Rivero-Marcos, M., Lasa, B., Neves, T., Zamarreño, Á. M., García-Mina, J. M., García-Olaverri, C., Aparicio-Tejo, P. M., Cruz, C., & Ariz, I. (2024). Plant ammonium sensitivity is associated with external pH adaptation, repertoire of nitrogen transporters, and nitrogen requirement. *Journal of Experimental Botany*, *75*(11), 3557-3578.
9. Sabagh, A., Islam, M. S., Hossain, A., Iqbal, M. A., Mubeen, M., Waleed, M., & Abdelhamid, M. T. (2022). Phytohormones as growth regulators during abiotic stress tolerance in plants. *Frontiers in Agronomy*, *4*, 765068.
10. Thilakarathne, A. S., Liu, F., & Zou, Z. (2025). Plant Signaling Hormones and Transcription Factors: Key Regulators of Plant Responses to Growth, Development, and Stress. *Plants*, *14*(7), 1070.
11. Wang, P. (2021). Friend or foe: how nitrate antagonizes ammonium toxicity. *Plant Physiology*, *186*(1), 210–211.
12. Xiao, C., Fang, Y., Wang, S., & He, K. (2023). The alleviation of ammonium toxicity in plants. *Journal of Integrative Plant Biology*, *65*(6), 1362-1368.