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REVIEW ARTICLE

Nutrient stress in plant cells: Mechanisms, adaptations and implications for crop resilience

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Abstract

Nutrient stress, caused by a lack of necessary macronutrients such as nitrogen, phosphate and potassium and micronutrients such as iron, zinc and copper, is a major environmental issue that has an impact on plant health, growth and agricultural output. The purpose of this study is to currently understand the molecular, cellular and physiological mechanisms used by plants to perceive, respond to and adapt to nutrient limitations. We investigate the complex signalling networks involved in nutrition sensing, as well as the adaptive methods that maintain cellular homeostasis, such as root architectural remodelling, nutrient recycling via autophagy and antioxidant defence mechanisms. A significant focus is on phytohormones such auxins, cytokinins and jasmonates, which mediate nutritional stress responses. We additionally emphasize emerging technologies, such as CRISPR-based gene editing and sophisticated omics methods (transcriptomics, proteomics and metabolomics), which provide new opportunities for producing crops with higher nutrient use efficiency and stress tolerance. This review emphasizes the importance of interdisciplinary research that integrates fundamental molecular biology with applied agricultural strategies, providing solutions to improve crop yields under nutrient-limited conditions, especially in the face of climate change and soil degradation. The application of these results in agriculture has the potential to improve food security and promote sustainable farming techniques.

Keywords: cross-talk; macronutrients; micronutrients; nutrient stress; omics; phytohormones

Introduction

Plants, as sessile organisms, are profoundly influenced by their immediate environment. Among the most critical environmental factors affecting plant growth and productivity is nutrient availability in the soil. Nutrient stress-defined as the insufficient supply of essential macro- and micronutrients-has a substantial impact on plant cellular functions, physiology and overall performance. Deficiencies in macronutrients such as nitrogen (N), phosphorus (P) and potassium (K) and micronutrients including iron (Fe), manganese (Mn) and zinc (Zn) (Fig. 1), disrupt fundamental metabolic processes. These deficiencies can lead to stunted growth, poor biomass accumulation, reduced crop yields and, in severe cases, plant death (1-3). The functional roles of key nutrients in plants are summarized in Table 1.

Nutrient limitations are widespread in natural and agricultural ecosystems. To cope with such constraints, plants have evolved a variety of adaptive strategies, including morphological, physiological and molecular modifications (4, 5). However, anthropogenic influences such as soil degradation, intensive agriculture and climate change have exacerbated nutrient imbalances and deficiencies, posing a growing threat to global agricultural productivity (6-8). Nutrient stress impairs critical processes such as photosynthesis, protein synthesis and hormone regulation, ultimately reducing crop quality and yield (9, 10).

Understanding how plants sense and respond to nutrient stress at molecular, cellular and physiological levels is essential for developing cultivars that can thrive under suboptimal soil conditions. The primary goal of this review is to provide an in-depth examination of the molecular mechanisms underlying nutrient sensing, stress signalling and adaptive responses in plants. Special focus will be given to the signalling pathways activated during specific nutrient deficiencies, as well as the cellular and systemic adaptations that enable survival under stress (11, 12). Moreover, this review explores recent advances in biotechnological tools, such as genetic engineering and multi-omics approaches, to enhance crop resilience to nutrient stress-ultimately contributing to food security and agricultural sustainability in the face of climate change (13-15). Therefore, the overarching goal of this review is to synthesize current knowledge about the molecular mechanisms of nutrient sensing, signalling and adaptive responses in plants, as well as to highlight how biotechnological strategies, such as genetic engineering and omics-based tools, can be used to improve crop resilience to nutrient stress. Finally, this analysis seeks to enlighten sustainable agriculture practices and contribute to global food security in the face of growing environmental difficulties.

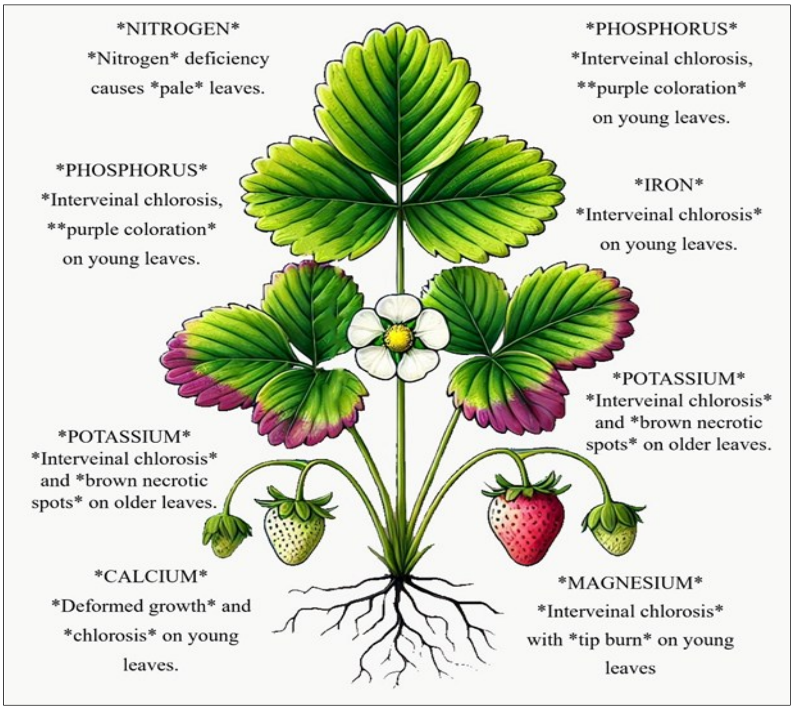

Fig. 1. Symptoms of macro and micronutrients lack on strawberry.

Table 1. Examples of macronutrient and micronutrient functions in plants

Nutrient	Function in plants	Deficiency symptoms
Nitrogen (N)	Protein synthesis, chlorophyll production	Stunted growth, yellowing leaves
Phosphorus (P)	Energy transfer, DNA/ RNA synthesis	Poor root development
Potassium (K)	Osmoregulation, enzyme activation	Leaf scorch, weak stems
Iron (Fe)	Chlorophyll synthesis, electron transport	Chlorosis of young leaves
Zinc (Zn)	Hormone production, enzyme activity	Interveinal chlorosis

Nutrient sensing and signalling mechanisms

Nitrogen (N) sensing

Nitrogen is a fundamental macronutrient required for the biosynthesis of amino acids, nucleic acids, chlorophyll and secondary metabolites, thereby directly influencing photosynthesis, protein synthesis and overall plant productivity. Plants have evolved sophisticated signaling mechanisms to optimize nitrogen acquisition and assimilation under fluctuating environmental conditions. Under nitrogen-deficient conditions, the NIN-like protein 7 (NLP7) transcription factor becomes activated and translocates to the nucleus, where it regulates a suite of nitrogen-responsive genes involved in nitrate and ammonium uptake, assimilation and remobilization (1). These genes, which include nitrate transporters (NRTs), ammonium transporters (AMTs) and nitrate reductases (NIA1 and NIA2), are illustrated in Fig. 2.

The regulation of nitrogen signaling occurs through complex and multilayered mechanisms. Transcription factors such as NLP7, TCP20 and LBD family members interact with microRNAs (e.g., miR169, miR393, miR444) that fine-tune gene expression in response to nitrogen status. Moreover, nutrient transporters act not only as

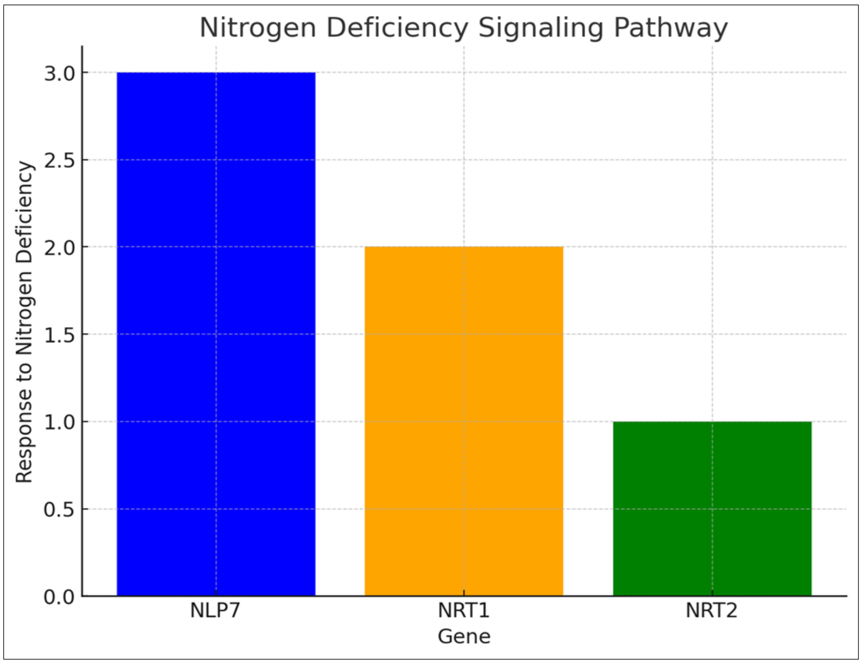

Fig. 2. Nitrogen-responsive genes under nitrogen deficiency.

carriers but also as sensors. A well-documented example is NRT1.1 (also known as CHL1), which functions as a dual-affinity nitrate transporter and a nitrate sensor, integrating external nitrate signals with internal plant nitrogen demands (2). NRT1.1 also plays a central role in root-to-shoot signaling, mediating the systemic regulation of nitrogen assimilation pathways.

Nitrogen deficiency induces significant morphological and physiological modifications in roots. Plants exhibit enhanced lateral root proliferation, increased root hair density and elongation, expanding the soil exploration zone to maximize nitrogen acquisition (3). These changes are coordinated with hormonal crosstalk, particularly auxin and cytokinin, which integrate nitrogen status with root system architecture. In addition, nitrogen starvation triggers the upregulation of high-affinity nitrate transporters (NRT2 family) and ammonium transporters (AMTs), which together increase the efficiency of nitrogen uptake in low-nitrogen soils.

At the cellular level, nitrogen availability affects carbon–nitrogen balance and primary metabolism. Under deficiency, plants upregulate glutamine synthetase (GS) and glutamate synthase (GOGAT) to assimilate available inorganic nitrogen efficiently, while simultaneously reallocating nitrogen from older tissues through the action of amino acid transporters and proteases. Furthermore, emerging studies highlight the role of Target of Rapamycin (TOR) signaling in coordinating nitrogen status with growth and development, suggesting that nitrogen signaling is tightly integrated with global metabolic regulation (16).

The major genes and proteins implicated in nitrogen signaling and assimilation are summarized in Table 2, providing a comprehensive overview of molecular players governing nitrogen homeostasis.

Table 2. Key genes and proteins involved in nutrient sensing

Nutrient	Key genes/proteins	Function
Nitrogen	NLP7, NRT1.1	Nitrogen sensing, root-shoot signaling
Phosphorus	PHR1, miR399	Phosphate acquisition, homeostasis
Iron	FIT, IRT1	Iron uptake and translocation

Phosphorus (P) signalling

Phosphorus is essential for energy transfer, nucleic acid synthesis and cell membrane structure. Phosphorus deficiency induces the activation of the Phosphate Starvation Response 1 (PHR1) transcription factor, which regulates the expression of genes involved in phosphate acquisition, such as phosphate transporters (PHT1) and phosphatases (4). Plants also employ a range of mechanisms to solubilize and mobilize soil-bound phosphorus, including the exudation of organic acids like citric acid, which helps in the chelation and mobilization of phosphorus from the soil matrix (5). Furthermore, the recent discovery of the miR399 regulatory network has highlighted the role of microRNAs in regulating phosphate homeostasis and signaling under nutrient-limited conditions (6). Plants also secrete organic acids like citrate and malate, along with acid phosphatases and ribonucleases, which act on phosphorus complexes by releasing the P from insoluble complexes into the soil (17). Root architecture modifications also help with P acquisition: lateral root branching, root hair elongation and for some particular species, the formation of cluster roots augment the root surface available for soil exploration (18).

Furthermore, systemic signaling integrates shoot and root responses. Long-distance signaling of P is made possible by mobile miR399 and SPX proteins that convert phosphorus status from shoots into the nucleus to the roots for coordinated regulation of uptake and redistribution (19). Consequently, such responses ensure that plants can both acquire the necessary phosphate from limited pools in the soil and maintain cellular homeostasis of phosphate, which is essential for supporting growth and reproductive capacity under nutrient stress conditions.

Iron (Fe) homeostasis

Iron is an essential micronutrient for processes like chlorophyll production, respiration and electron transport. Iron deficit activates a unique signaling network, including the FER-like Iron Deficit-Induced Transcription Factor (FIT) pathway, which upregulates genes including Iron-Regulated Transporter 1 (IRT1) to aid iron intake (7). Nicotianamine, a metal chelator, also aids in the transport of iron inside plant tissues, resulting in efficient iron distribution. Recent research has revealed the strategies plants utilize to adapt to iron deficiency, including significant alterations in root architecture, such as increased root hair density and lateral root proliferation, which enhance soil exploration and iron acquisition (8, 20, 21). Additionally, plants upregulate the expression of iron transporter genes (e.g., IRT1) and ferric chelate reductases (e.g., FRO_2), thereby improving iron solubilization and uptake from the rhizosphere (10, 22, 23). In Strategy I plants, such as *Arabidopsis thaliana*, these responses also involve increased proton extrusion via H^+-ATPases to acidify the rhizosphere, facilitating iron mobilization (12, 24). Strategy II plants, such as *Oryza sativa* and *Zea mays*, release phytosiderophores (e.g., mugineic acid) that chelate Fe^{3+} and create soluble complexes that are absorbed through specialized transporters such YS1 (13, 25, 26). These adaptive reactions collectively improve iron acquisition efficiency in conditions of low iron availability (15).

2.4. Boron stress

Boron (B) is required for plant growth (9) and its availability in soil and irrigation water is a crucial factor influencing agricultural production (10). In soil solution, B exists largely as boric acid (H_3BO_3), which is easily leached under heavy rainfall circumstances (11, 12), resulting in deficits in plants that thrive there. On the contrary, under low rainfall conditions, B cannot be properly leached and may accumulate to dangerous levels for plant growth (13). This commonly occurred in dry and semiarid regions with high-boron groundwater, where evaporation leads to boron accumulation in the topsoil at toxic levels, ultimately reducing agricultural productivity (10). B shortage is well recognized to affect a wide range of vascular plant functions, including root elongation, indole acetic acid (IAA) oxidase activity, sugar translocation, carbohydrate metabolism, nucleic acid synthesis and pollen tube formation (14). An ongoing boron depletion treatment (0.25 mg L^{-1}) hindered elongation of trifoliate orange roots, enlarged root tips and severe necrosis. It also significantly decreased soluble boron and IAA levels in seedling root tips. A short-term boron deprived treatment resulted in substantial reductions in soluble boron and IAA contents after 3 hr, hours of treatment (HOT) and 1 day, day of treatment (DOT) (15). Plants have evolved sophisticated signaling mechanisms for detecting and responding to B imbalances. Changes in cell wall integrity caused by diminished rhamnogalacturonan II cross-linking are seen in B deficient cells, activating downstream signaling cascades (27). Furthermore, specialized boron transporters such as

NIP5;1 (influx) and BOR1 (efflux) are activated to improve B absorption and redistribution (28). The deficit also stimulates calcium signaling, reactive oxygen species (ROS) buildup and the mitogen-activated protein kinase (MAPK) pathways, all of which regulate stress-responsive genes (29). Hormones such as auxin, ethylene and abscisic acid (ABA) also influence root development and water balance under stress circumstances (30). Excess boron, on the other hand, causes toxic buildup and oxidative stress, mostly via ROS formation, which damages cellular components and activates antioxidant defense mechanisms such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) (29). ABA levels frequently rise during toxicity, causing stomatal closure and stress response (30). BOR1 and other transporters, such as BOR4 and BOR2, are downregulated or internalized to prevent excessive boron translocation (28). In response to toxicity, transcription factors such as WRKY, NAC and MYB are activated to coordinate gene expression changes (27). Both deficiency and toxicity have overlapping signaling networks, such as calcium and ROS signaling and MAPK cascades, which allow plants to integrate various abiotic stress responses. Understanding these mechanisms can help produce boron-efficient crops that thrive in nutrient-depleted soils.

Cross-talking among nutrients and signalling in plant

A lack or excess of any mineral element can cause physiological and metabolic abnormalities in plants and have a negative impact on plant growth (31). However, nutrient availability is heavily influenced by soil physicochemical qualities (32); as a result, plants have evolved a variety of mechanisms to deal with alterations ranging from deficiency to excess (33-35). Recent research on stresses associated with nutrient deprivation has shown that the intricate cross-talks between N, phosphate ions (Pi), Zn and Fe absorption and plant homeostasis have a significant impact on plant growth response. Pi has been shown to interact with zinc and iron in plants (8, 36, 37). However, various local techniques have revealed multiple cross-talks between macro- and micronutrients; thus, it is vital to investigate the dynamics of the plant ionomic globally. A detailed knowledge of ionomic homeostasis necessitates a thorough examination of plant nutrient networks. Although ionomic homeostasis is insufficiently understood, some current investigations have shown diagrams of ionomic networks and multiple cross-talks in plant species (38-41). The previous study examined the crosstalk between nutrient stress-induced and pathogen-induced signalling pathways in rice, focusing on regulatory microRNAs (42). Cross-talks between N, Pi, S, Zn and Fe homeostasis may aid in better understanding how these nutrient interactions influence mineral uptake and signalling in plants (43). Phytohormonal crosstalk in plant response to nitrogen stress helps to detect current advances in the interaction between phytohormones and N through physiological and morphological modification. As a result, crosstalk between phytohormones results in synergistic or antagonistic relationships, which are critical for maintaining the appropriate equilibrium between plant responses to abiotic stresses and plant development and defense (44).

Scaffold elasticity and nutrients stress

Tissue engineering scaffolds in plant biotechnology are increasingly investigated as artificial extracellular matrices that closely mimic the natural plant cellular environment to support cell, tissue and organ development *in vitro*. These scaffolds typically possess an interconnected porous architecture lined with plant cells, allowing the diffusion of nutrient-rich culture media which supplies essential minerals, carbohydrates, phytohormones (such as auxins, cytokinins and gibberellins) and oxygen required for sustained metabolic function (45, 46). Such continuous circulation within scaffolds not only maintains cellular proliferation and differentiation but also facilitates the removal of toxic metabolites and phenolic exudates, which can otherwise inhibit growth or induce oxidative stress (47, 48).

Several intrinsic and extrinsic factors influence tissue growth dynamics within plant scaffolds. The rate of nutrient flow and the nutrient concentration within the culture medium critically affect morphogenetic responses such as callus formation, organogenesis and somatic embryogenesis (49). Scaffold porosity and mechanical flexibility modulate mass transport properties and influence cell adhesion, orientation and differentiation. For instance, higher porosity increases nutrient diffusion but may reduce scaffold mechanical integrity, whereas more compliant scaffolds favor cellular expansion but might limit structural support (50, 51). The physiological state of cultured cells, including their metabolic rate and hormone sensitivity, also governs scaffold performance and tissue regeneration outcomes (47).

At the molecular and biochemical levels, biomimetic mineral deposition within plant scaffolds plays a pivotal role in directing tissue differentiation and enhancing functional properties such as mechanical strength and stress tolerance. Mineral nucleation and polymerization commonly occur on cellulose- or pectin-based scaffolds enriched with bioactive minerals, such as silica and calcium salts. These deposits reinforce cell walls by enhancing lignification and modulating cellular defense pathways, ultimately leading to improved vascular differentiation and overall tissue robustness (52-54). The availability of silicic acid and calcium ions, along with scaffold chemical groups like hydroxyl and carboxyl moieties, regulate the extent and pattern of mineral deposition (55). This mineralization process not only increases scaffold rigidity but also positively affects reactive oxygen species (ROS) scavenging mechanisms and osmotic balance under abiotic stresses, promoting enhanced regenerative capacity *in vitro* (56, 57).

Emerging scaffold designs incorporate bioactive compounds and nanomaterials that further simulate the plant extracellular matrix, enhancing cell signaling and differentiation. For example, incorporation of silicon nanoparticles or calcium phosphate nanocrystals into scaffolds has shown promising results in accelerating vascular tissue formation and improving tolerance to oxidative and drought stress in cultured explants (58, 59). Moreover, dynamic culture systems integrating perfusion bioreactors have been employed to optimize nutrient delivery and waste removal, further advancing the physiological relevance and scalability of plant tissue engineering (60).

Cellular adaptations to nutrient stress

Inorganic mineral nutrients are essential for the growth and development of plants. The supply of nutrients directly controls the several processes that underlie crop yield creation, such as biomass accumulation and partitioning. In essence, plants need 17 components to create the most biomass and yield, while certain other elements help them survive stress and/or increase the quality of economically valuable output (61). The concept of nutritional stress is viewed from the perspective of how cells recognize and react to a lack of nutrients to meet their bioenergetic requirements. But food overload can also cause stress in cells, causing them to produce more reactive oxygen species (ROS) than are necessary for regular physiological reactions (62).

Changes in the oxygen and glucose supplies produce cellular and subcellular alterations in tumor models *in vitro*. Many of these alterations could have significant effects on therapeutic responsiveness and are anticipated to take place in tumor microregions *in vivo* (63).

Both boric acid and borate can form complexes with a wide range of biological molecules that have two hydroxyl groups in cis-configuration. To date, one of B's principal activities in higher plants has been attributed to its ability to create borate esters with rhamnogalacturonan II (RG-II) apiose residues (64). The creation of this complex is critical for cell wall structure and function (65), since it plays an important role in controlling cell wall porosity (66) and tensile strength (67). For example, excessively inflated cell walls and reduced RG-II dimer production have been linked to B deficiency (68, 69). Furthermore, the RGII-borate complex is required for normal plant growth, as demonstrated by *Arabidopsis thaliana* mutant mur1-1 and mur1-2 plants with lower amounts of this complex (70). An earlier study found that *Arabidopsis* bor1-1 mutants had less cross-linking in their cell walls than wild-type plants under reduced B availability, which appeared to be due to decreased shoot B concentrations (71). The existence of borate complexes in the phloem explains what has been noticed boron transportation in canola, wheat and other species by creating the bis-sucrose borate molecule (72).

Autophagy and nutrient recycling

Autophagy is an evolutionarily conserved catabolic process that enables plants to recycle intracellular components, thereby maintaining cellular homeostasis and supporting survival under diverse environmental stresses, including nutrient deficiency. In response to nitrogen (N) or carbon (C) deprivation, autophagy-related (ATG) genes regulate the selective degradation of damaged or superfluous organelles such as chloroplasts, mitochondria and peroxisomes, facilitating the release of amino acids, sugars and other metabolites for reuse (73, 74). Chloroplasts, which constitute a significant proportion of leaf nitrogen, are preferentially targeted by ATG8-mediated autophagy during prolonged nutrient stress, a process termed chlorophagy, supplying essential amino acids and nitrogenous compounds critical for sustaining metabolic activities (75, 76).

Autophagic flux increases substantially during nutrient starvation and leaf senescence, underscoring its fundamental role in nutrient remobilization. This process ensures the efficient redistribution of nutrients from senescing leaves to developing tissues such as seeds, thus directly influencing plant fitness and yield (77, 78). Importantly, autophagy not only mediates nitrogen recycling but also facilitates remobilization of other macronutrients and micronutrients, including phosphorus and metals such as iron and zinc, highlighting its broad impact on nutrient homeostasis (79, 80).

Despite its recognized importance, the precise mechanisms by which autophagy modulates foliage longevity and coordinates with other nutrient recycling pathways remain to be fully elucidated. Recent genetic studies using *Arabidopsis* atg mutants reveal that deficiency in autophagy results in impaired nitrogen remobilization, premature leaf senescence and reduced seed yield, indicating a critical function in plant nutrient economy (81, 82). Moreover, autophagy intersects with hormonal signaling pathways, such as those involving salicylic acid and abscisic acid, to fine-tune senescence and stress responses (83, 84).

Emerging biotechnological approaches are now exploiting the modulation of autophagy-related genes to enhance crop tolerance to nutrient limitation and abiotic stresses. For example, overexpression of key ATG genes in crops like rice and maize has demonstrated improved nitrogen use efficiency and biomass accumulation under low-nitrogen conditions (85, 86). A comprehensive overview of plant engineering strategies that harness autophagy pathways to improve yield and stress resilience, emphasizing the potential to manipulate autophagic flux for sustainable agriculture (85).

Furthermore, autophagy is indispensable for plant survival during dark-induced carbon starvation, a condition mimicking extended shading or darkness, by maintaining energy balance and nutrient recycling (87, 88). In *Arabidopsis*, mutant's defective in core ATG genes show compromised growth and accelerated senescence under carbon and nitrogen starvation, reinforcing the notion that autophagy integrates environmental signals to regulate developmental and metabolic adaptations (89, 90).

In summary, autophagy serves as a central hub for nutrient recycling and remobilization under nutrient-limited conditions, supporting plant growth, development and reproductive success. Its modulation represents a promising avenue for crop improvement in nutrient-poor soils and fluctuating environmental conditions.

Oxidative stress management

An imbalance in nutritional availability frequently results in the overproduction of reactive oxygen species (ROS), which can cause oxidative damage to plant cells. Plants use antioxidant defense mechanisms, including enzymes like superoxide dismutase (SOD), catalase (CAT) and glutathione (GSH), to neutralize ROS and protect cellular structures (91). Iron deficiency, for example, increases ROS levels; nonetheless, plants have evolved systems to maintain oxidative equilibrium and protect plant cells from oxidative damage (92).

Plant's oxidative stress and antioxidant responses to macronutrient deprivation (Fig. 3). Reactive oxygen species can target biological components including cell membranes and diverse macromolecules like proteins and nucleic acids, resulting in lipid peroxidation and protein degradation (93). Eliminating oxidative stress may increase N, P and K use efficiency and promote plant development in the face of N, P and K deficit (94). N, P and K supplementation reduced cold stress-induced adversity by increasing soluble protein, superoxide dismutase, peroxide dismutase, catalase and proline levels when compared to control conditions (95). A micronutrient deficiency generates ROS in cellular compartments. Micronutrient insufficiency frequently modulates enzymatic and non-enzymatic antioxidant defense systems, regulating redox balance and scavenging harmful ROS for cellular components integrity (96).

Systemic responses and symbiotic solutions

Root architecture remodelling: Nutrient stress causes considerable changes in root architecture, which are required for optimal nutrient uptake efficiency. In response to phosphorus (P) deprivation, plants normally increase lateral root multiplication and root hair elongation, allowing them to explore a larger soil volume and acquire more phosphate (97). This reaction is influenced by variations in auxin distribution and phosphate transporter activation

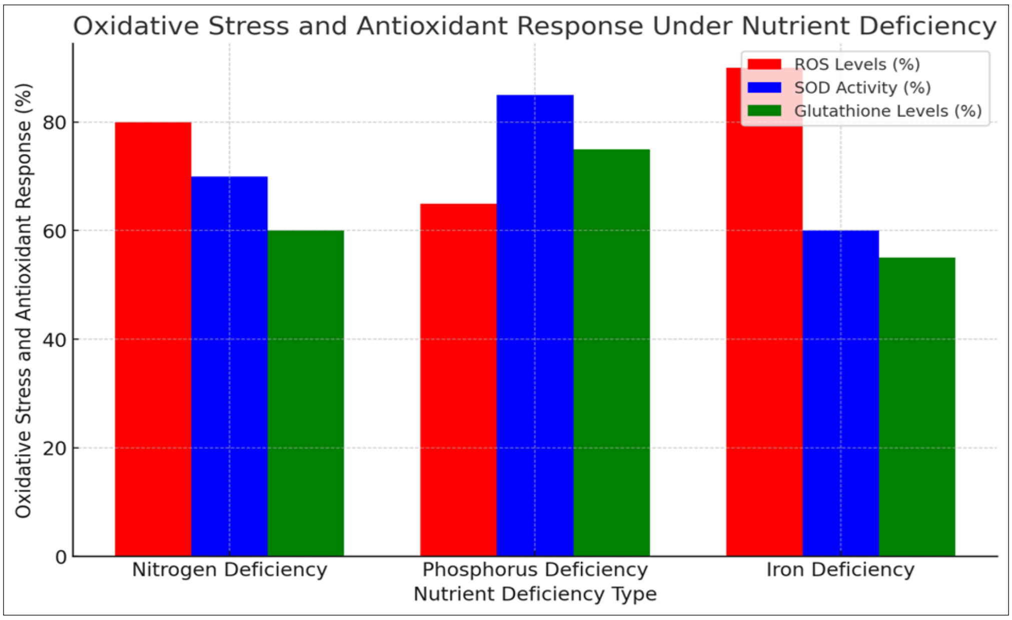

Fig. 3. Oxidative stress and antioxidant response under nitrogen deficiency.

(98). Similarly, nitrogen (N) deprivation promotes the production of fine roots and dense root hairs, which increase the root surface area and maximize nitrogen absorption from the soil (99). Boron (B) deficiency, which primarily affects cell wall stability and membrane integrity, prevents root extension and results in bloated or stubby roots. In some species, B shortage results in enhanced lateral root development. The nutrients deficiency is illustrated in Fig. 4. In some species, B shortage causes enhanced lateral root development as a compensatory mechanism (31, 100). Iron (Fe) deficiency causes the establishment of transfer cells and cluster roots (particularly in Strategy I plants), as well as rhizosphere acidification and the production of phenolics and reductants to improve Fe solubility and absorption (101, 102). These morphological and physiological root responses to nutritional restriction are tightly regulated by hormonal crosstalk, particularly auxin, ethylene and cytokinins, resulting in optimal foraging strategies under resource-limited situations (34, 103).

Mycorrhizal and rhizobial symbiosis: Symbiotic interactions with soil bacteria are vital for nitrogen uptake. Arbuscular mycorrhizal fungi (AMF) improve phosphorus uptake in most land plants by creating symbiotic relationships with their roots (104). In nitrogen-fixing legumes, rhizobial bacteria produce nodules in the roots, converting atmospheric nitrogen into a form that the plant can use. These symbiotic partnerships are critical for dealing with nutrient-limited situations because they increase nutrient efficiency and promote plant development (105). Symbiotic interactions under nutrient deficiency are mentioned in Table 3.

In symbiotic plants, carbon and nitrogen acquisitions, as well as metabolism, must be precisely coordinated. Mutual control of the components of these pathways by C and N signals or C/N balance is the norm rather than the exception. Systemic signaling of plant N need was linked to rapid changes in sucrose distribution to nodules, resulting in differential nodule expansion (106 .(107 ,Future research into the effects of systemic and local N signals on MtSnRK1a4 activity

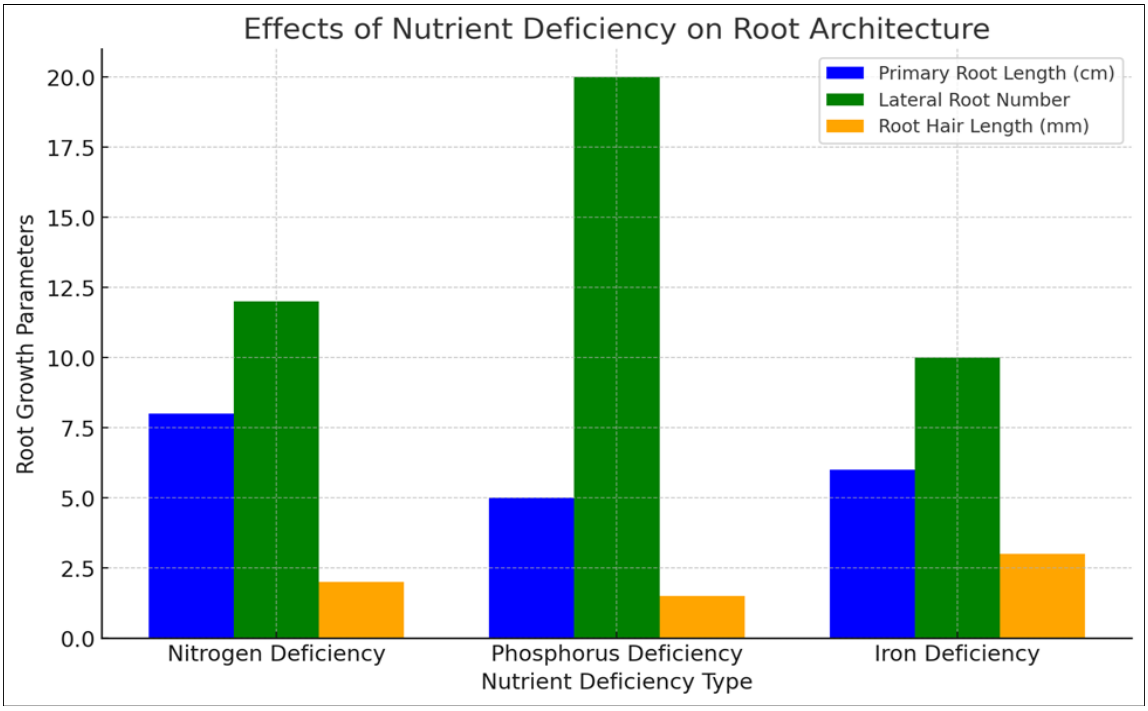

Fig. 4. Root architecture under nitrogen deficiency.

Table 3. Symbiotic interactions under nutrient deficiency

Nutrient deficiency type	AMF colonization (%)	Rhizobial nodulation (%)
Nitrogen deficiency	40	90
Phosphorus deficiency	85	20
Iron deficiency	50	10

and function is probably warranted. The plant keeps the bacteroids in microoxic conditions, allowing nitrogenase to convert atmospheric nitrogen (N_2) to ammonia (NH_3). Ammonia is not broken down by the bacteroids, but rather transported to the surrounding plant cells, where it is mixed with carbon (C) skeletons via the glutamine synthetase/glutamate synthase process. Derived amino acids and/or ureides are eventually transported throughout the entire plant (108). The significance of important nutrients, such as nitrogen, phosphorus, potassium and trace elements like iron, molybdenum and boron, in maximizing symbiosis is critically examined (109) under various environmental conditions. the regulatory circuitry had identified thereby controls the decreased expression of bacterial genes involved in NH_4^+ assimilation throughout early nodule colonization. This is a critical step in the differentiation of N_2-fixing bacteroids (the endocellular symbiotic form of rhizobia) and the formation of effective nodules (110).

Biotechnological advances and future perspectives

CRISPR-Cas9 editing: The advent of gene-editing tools like CRISPR-Cas9 has transformed the area of plant biotechnology. This method enables precise alterations to plant genomes, resulting in the production of crops with improved nutrient usage efficiency. For example, CRISPR-Cas9-mediated editing of the OsPTF1 gene in rice has been demonstrated to increase phosphorus intake in phosphorus-limited circumstances (111) as mentioned in Table 4.

Table 4. Examples of biotechnological applications in nutrient stress mitigation

Technology	Application	Example
CRISPR-Cas9	Gene editing	Enhanced phosphorus uptake in rice
Transcriptomics	Biomarker identification	Stress-responsive genes
Biofortification	Nutritional enhancement	Iron-biofortified rice

Similarly, altering nutrient transporters and transcription factors involved in nitrogen and iron uptake can boost plant growth in nutrient-deficient soils. The establishment of nutrient-efficient plants using the CRISPR-Cas approach will accelerate genetic improvement for nutrient stress tolerance in crops and promote agricultural sustainability (112). Effects of CRISPR-based genetic modifications on nutrient uptake are illustrated in Table 5.

CRISPR-Cas-based crop genome editing has been used to impart/produce qualitative enhancements in aroma, shelf life and sweetness, as well as quantitative improvements in starch, protein, gamma-aminobutyric acid (GABA), oleic acid, anthocyanin, phytic acid, gluten and steroidal glycoalkaloid content (113). CRISPR-based engineering of plant nutrient transport not only allows for the study of the process in native plants with preserved regulatory systems, but also aids in the development of non-transgenic crops with higher nutrient usage efficiency (114). CRISPR-Cas9 is the most precise, productive and rapid technology and it is widely used to withstand both biotic and abiotic stressors. This approach influences quantitative genes' ability to survive abiotic shocks, either directly or indirectly. Over twenty different crops have been engineered with CRISPR-Cas tools to tolerate stress and increase production (115).

Omics approaches: Advances in transcriptomics, proteomics and metabolomics have yielded important insights into the molecular networks that control plant responses to nutritional stress. Omics technologies enable the identification of stress tolerance biomarkers as well as the finding of critical regulatory genes for use in marker-assisted breeding programs. These technologies can be combined to create crops with improved nutrient absorption and stress tolerance. RNA-metabolite associations were discovered, indicating that tricarboxylic acids, azoles, carbohydrates, sterols and auxins may play positive regulatory roles in plant adaptation to macronutrient deficiency, while aromatic and aspartate amino acids, glucosamine-containing compounds, cinnamic acid and nicotianamine may play negative regulatory roles (116). To mention a few, phosphoproteomics, sophisticated proteomics methods such as PUNCH-P and high throughput protein-ligand interaction studies (117) may aid in revealing regulatory activity changes that differential proteomics cannot detect (118).

Ionomics is becoming increasingly important in identifying putative genes involved for ion uptake, transport and storage in plants. Ionomics is a key pillar in the study of structural and functional genomics. It includes estimating an organism's elemental composition and changes in composition in response to physiological, formative, environmental and genetic variables (119). The treatments had an effect on N-containing metabolites in both leaves and roots and the N form considerably influenced the phytohormone profile. Furthermore, the simultaneous application of Fe and N to Fe-deficient plants resulted in the formation of secondary metabolites such as phenylpropanoids, depending on the N form used, which was primarily urea, followed by nitrate and ammonium (120). Plant ionomic characterization is carried out utilizing a variety of analytical methods such as ICP-MS, ICP-OES, X-Ray crystallography, Neutron Activation Analysis (NAA) and so on. All these analytical methods provided a comprehensive profile of the ions that exist in plants (121).

Biofortification: Biofortification, which involves boosting the nutritional content of crops through genetic or agronomic manipulations, has significant promise for treating micronutrient shortages in human diets. For example, overexpression of the NAS gene in rice has been found to improve iron bioavailability, addressing iron deficiency anemia in underdeveloped nations (122). Biofortification solutions include other micronutrients including zinc, selenium and iodine, providing a long-term solution to malnutrition. Nitrogen deficit specifically boosted molybdenum absorption, potentially enhancing nitrogen assimilation and/or endophytic nitrogen fixation in plants. Potassium deficit significantly increased

Table 5. Effects of CRISPR-based genetic modifications on nutrient uptake

Nutrient type	Wild-type uptake (%)	CRISPR-modified uptake (%)	Key modified genes	Functional outcome
Nitrogen (N)	100	140	OsNRT2.3, NLP7	Enhanced nitrate uptake and assimilation
Phosphorus (P)	100	180	OsPTF1, PHR1	Increased phosphate transporter activity
Iron (Fe)	100	160	IRT1, FIT	Improved iron uptake and mobilization

the absorption ability of different cationic elements. These elements may function as replacements to K in osmoregulation and the antagonistic effect of organic/inorganic anions. There are several agricultural strategies for biofortification, involving selective breeding of crops to contain higher amounts of specific nutrients, an agronomic strategy that uses fertilizers and other inputs to promote crop nutrient uptake and a transgenic approach. The agronomic strategy provides a temporary but quick solution, whereas the genetic approach (breeding and transgenic) is the long-term solution but takes time to generate a nutritious cultivar (123). Biofortified kinds of staple crops, involving rice, wheat, maize and beans, with elevated amounts of vital micronutrients, such as iron, zinc, vitamin A and vitamin C, have been effectively created using ordinary and modern methods. Furthermore, recent developments in genetic engineering, such as CRISPR-Cas9 technology, have made it possible to particularly adapt crop genomes to improve their nutritional profiles (124). The crucial role of nutrients in the network of foods and their impact on health is discussed, as well as the various features of biofortification, factors influencing biofortification of key minerals in soil-plant systems, obstacles and prospective opportunities for agricultural biofortification (125).

Plant-derived extracellular vesicles: Plant-derived extracellular vesicles (P-EVs) are tiny vesicles with a lipid-rich membrane that carry nucleic acids, vitamins, antioxidant compounds, proteins and metabolites (126, 127). Extracellular vesicles (EVs) are solitary membrane-bound spheres that transport complex cargoes such as lipids, proteins and nucleic acids. They mediate cell-to-cell communication by transferring molecules between cells. Proteomic analysis of these EVs indicated that they are rich in proteins implicated in both biotic and abiotic stress responses. Thus, EVs may play a significant role in plant immune responses (128). Furthermore, Evs play an important function in nutrient sensing and information transfer across cells, particularly in nutritional stress circumstances (129). Purified from numerous edible species, these EVs are more biocompatible, biodegradable and abundant in many plants, making them suitable for cell-free therapy (126). Recent research has revealed that plant EVs are becoming participants in cross-kingdom regulation and contribute to plant immunity by regulating the trafficking of regulatory short RNA into diseases, resulting in the silencing of pathogen virulence-related genes (130).

Conclusion

Plants responses to nutritional stress are complicated and varied, involving molecular signalling, cellular adaptations and physiological changes. A thorough understanding of these mechanisms is required for creating crops that flourish in nutrient-limited environments. While substantial work has been achieved in understanding the mechanisms involved, further study is required to investigate the relationships between various nutrient stress pathways and translate these results into practical agricultural solutions. We can ensure global food security by integrating cutting-edge biotechnology with conventional agronomy to create crops that are nutrient-efficient and stress-resistant.

Authors' contributions

OHMA, YSS, AFA and SAAS contributed equally to its writing, data verification and interpretation. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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