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When Plants Fight Back: How Nutrition Helps Crops Survive Stress

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Plants may appear passive, but life beneath the surface tells a very different story. Every day, plants must acquire nutrients from soil, transport them through their tissues, use them to build proteins and membranes, maintain energy production, and defend themselves against an astonishing range of threats. Drought can deprive roots of water. Salinity can flood tissues with toxic ions. Heat and cold can disrupt cellular processes. Pathogens and insects can attack leaves and roots. And all of these challenges can occur at the same time. What makes the problem even more fascinating is that nutrition and stress are not separate issues. They are deeply connected. A plant under attack may need more of certain nutrients to activate its defenses. At the same time, the stress itself may make those nutrients harder to obtain. Roots may change their architecture, nutrient transporters may be switched on or off, hormones may redirect nutrient movement, and beneficial microorganisms may help the plant acquire resources that would otherwise be inaccessible. In other words, a plant does not simply "need fertilizer." It needs to constantly decide what to acquire, where to send it, and how to use it. A review by Wang et al., (2025) brings together recent discoveries about this remarkable interaction between plant nutrition and both biotic and abiotic stress. The nutrient uptake and use efficiency are fundamental to plant growth, productivity, and resilience, and that understanding these processes under stress is increasingly important for developing stress-tolerant, nutrient-efficient crops and more sustainable agriculture (Maathuis and Diatloff, 2013; Oldroyd and Leyser, 2020; Wang et al., 2025).

The plant's nutritional toolbox

Plants require a surprisingly diverse collection of mineral elements. There are 14 essential mineral nutrients: six macronutrients namely nitrogen (N), phosphorus (P), potassium (K), sulfur (S), calcium (Ca), and magnesium (Mg) and eight micronutrients namely iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), molybdenum (Mo), boron (B), chloride (Cl), and nickel (Ni) (Maathuis and Diatloff, 2013; Vatansever et al., 2017). There are also elements that are not universally essential but can nevertheless promote plant growth. Sodium, selenium, cobalt, and silicon fall into this category (Pilon-Smits et al., 2009; Vatansever et al., 2017). The classification of some elements, particularly sodium and silicon, remains debated, and they are cautiously described as beneficial elements (Vatansever et al., 2017; Singhal et al., 2023).

Each nutrient has a job, but these jobs overlap. Nitrogen helps build proteins and nucleic acids. Phosphorus is central to ATP, nucleic acids, and membrane phospholipids.

Potassium regulates water relations and ion balance. Sulfur contributes to proteins and defensive compounds. Calcium functions both structurally and as a major signaling molecule. Magnesium is central to chlorophyll and many enzymes. The micronutrients are required in much smaller amounts, but their importance is anything but small. Iron, zinc, manganese, copper, molybdenum, boron, chlorine, and nickel participate in enzyme activity, electron transport, signaling, metabolism, and defense. Beneficial elements such as silicon and selenium can also contribute to stress resistance.

The crucial point is that plants do not acquire these nutrients in isolation. Their uptake is influenced by the surrounding environment, by other nutrients, by microorganisms, and by the plant's own physiological condition. Stress can therefore transform the nutritional needs of an otherwise healthy plant. Biotic stresses including pathogens and herbivores can reduce photosynthetic capacity, change root exudates, alter nutrient availability, and force plants to divert resources toward defense rather than growth (Saijo and Loo, 2020; Singh et al., 2022). Abiotic stresses such as drought, salinity, extreme temperatures, and heavy-metal contamination can alter soil properties and water availability while disrupting physiological processes, potentially causing nutrient deficiencies or imbalances (Gong et al., 2020; Zhang et al., 2022). Plants therefore need a flexible nutritional strategy. They modify root architecture, adjust nutrient transporter activity, activate stress-responsive signaling pathways, and alter nutrient metabolism and allocation (Li et al., 2016; Gong et al., 2020; Chen et al., 2021).

Nitrogen: more than plant food

Nitrogen is often associated simply with vigorous green growth, but its role is much broader. It is a fundamental component of proteins and nucleic acids, and plants acquire it from both inorganic and organic sources in the soil (Wang et al., 2012). At the molecular level, nitrogen acquisition is controlled by specialized transport proteins. Nitrate uptake involves several transporter families, including NRT1/PTR, also known as NPF, NRT2, CLC, and SLAC1/SLAH proteins (Wang et al., 2012; Léran et al., 2014; Noguero and Lacombe, 2016). One of the most intriguing proteins is NRT1.1, which does double duty: it transports nitrate and also acts as a nitrate sensor. Through phosphorylation, it can switch between high- and low-affinity transport modes (Liu and Tsay, 2003; Ho et al., 2009). Nitrate is also a signal. When perceived by NRT1.1, it can initiate calcium signaling involving CNGC15, phospholipase C, and inositol triphosphate. Calcium-dependent protein kinases then phosphorylate NLP7, helping it move into the nucleus and activate genes involved in the primary nitrate response (Liu et al., 2017b; Wang et al., 2021b). NLP7 has additionally been proposed to function as an intracellular nitrate sensor (Liu et al., 2022c). This signaling network becomes especially important during drought. Nitrogen supplied as NH_4NO_3 can improve water-use efficiency by increasing plant dry mass while reducing water loss (Song et al., 2019). Ammonium can also lessen drought damage by increasing root numbers, potentially improving water acquisition (Ye et al., 2022). In Arabidopsis, NRT1.1 influences stomatal movement, while disruption of NLP7 can reduce water loss and improve drought tolerance (Araus et al., 2020). In maize, drought can stimulate genes involved in nitrogen uptake and assimilation, contributing to improved drought tolerance (Wang et al., 2017).

But more nitrogen is not always better. Abscisic acid (ABA), a central stress hormone, can negatively regulate nitrate acquisition. Under nitrogen deficiency, SnRK2 proteins phosphorylate NRT1.1, while ABA-induced signaling can interfere with the CBL1-CIPK23 module that activates nitrate transport (Su et al., 2021). In rice, the DST–OsNR1.2 regulatory system connects nitrogen assimilation with drought tolerance (Han et al., 2022). The story becomes even more complicated under salt stress. Excess sodium disrupts the balance between sodium and potassium, and salinity can suppress nitrate uptake. In tomato roots exposed to NaCl, several genes involved in nitrate uptake and assimilation-including *LeNRT1.1, LeNRT1.2, LeNRT2.1*, and *LeGS1.2*-were reduced, resulting in lower nitrate uptake (Yao et al., 2008). Yet moderate salt stress can sometimes increase activities of nitrogen-metabolizing enzymes, illustrating that the relationship between stress intensity and

nutrient metabolism is not simply linear (Yang et al., 2015). Nitrogen also interacts with other nutrients. Phosphate deficiency can reduce nitrogen uptake, helping maintain a balanced nitrogen-to-phosphorus ratio (Rufty et al., 1990). The phosphate sensor OsSPX4 can interact with OsNLP3 and OsPHR2, while NIGT1 represses nitrate influx genes under phosphate deficiency and promotes phosphate transporter expression (Wang et al., 2020b).

When nutrition becomes part of immunity

Nitrogen also has a complicated relationship with plant disease. Low nitrogen can sometimes increase resistance. Tomato plants supplied with nitrate as their sole nitrogen source showed greater resistance to *Pseudomonas syringae* and *Ralstonia solanacearum* under low-nitrogen conditions (Ding et al., 2021). Limited nitrogen also increased tomato resistance to the insect pest *Spodoptera litura*, potentially through greater production of the volatile compound α-humulene (Li et al., 2024d). But the opposite can happen. Increased nitrogen application has been associated with greater powdery mildew severity in barley (Jensen and Munk, 1997). Other studies, however, found that higher nitrogen improved tomato resistance to *Fusarium oxysporum* and *Botrytis cinerea* (Mur et al., 2017). The lesson is clear: nutrient status does not have a universally predictable effect on immunity. The outcome depends on nutrient form, concentration, plant species, and pathogen.

Plants can also recruit partners to solve their nitrogen problem. Nitrogen-fixing bacteria and arbuscular mycorrhizal fungi can expand the plant's access to nitrogen. In rice supplied with nitrate, approximately 42% of total nitrogen uptake in roots was reported to occur through the mycorrhizal pathway when plants were associated with *Rhizophagus irregularis*. Mycorrhizal symbiosis also increased expression of the nitrate transporter OsNPF4.5 in rice, with homologous responses reported in maize and sorghum (Wang et al., 2020a). In legumes, the conversation between nutrition and symbiosis becomes even more sophisticated. The microRNA, miR2111 helps regulate rhizobial infection and nodulation through the TML pathway. Under nitrogen deficiency, CEP signaling can stimulate nodulation through the CRA2 receptor and induce miR2111 production, effectively encouraging the plant to seek biological sources of nitrogen (Gautrat et al., 2020).

Phosphorus: energy, roots and defense

If nitrogen is central to building plant biomass, phosphorus is central to the plant's energy economy. It is a component of nucleic acids, membrane phospholipids, and ATP (Yang et al., 2024a). Plants rely on several phosphate transporter families, with PHT1 proteins playing a major role in uptake from soil. PHO1 then helps move phosphate from roots toward the shoot through the xylem (Wege et al., 2016). When phosphorus becomes scarce, plants activate a phosphate starvation response (PSR). PHR1 is a major transcriptional regulator of this response, while SPX proteins act as important negative regulators when phosphorus is plentiful (Wang et al., 2014b).

Drought can disrupt phosphorus nutrition, but phosphorus can also help plants tolerate drought. Phosphorus application and solubilization can improve root biomass and hydraulic conductance (Tariq et al., 2017). Nitrogen and phosphorus fertilization has been reported to improve photosynthesis, water-use efficiency, and membrane integrity in Moso bamboo (Wu et al., 2018). Phosphorus can also reduce hormone and reactive oxygen species accumulation while increasing drought-associated proteins and metabolites, including those associated with aquaporins (Li et al., 2020b). Intriguingly, phosphorus limitation itself can sometimes promote drought tolerance. In Arabidopsis, the PHR1PHL1 pathway contributes to drought resistance, while the long non-coding RNA, DRIR can be strongly induced by phosphorus limitation and enhance drought tolerance and ABA sensitivity (Scheible et al., 2023). MYB2 also activates miR399f under phosphorus starvation, contributing to ABA and drought responses (Baek et al., 2016).

Phosphorus is equally entangled with disease. Applying K_2HPO_4 increased rice yield by 32% while reducing neck blast caused by *Magnaporthe oryzae* by 42% in one study. Phosphorus supplementation can stimulate salicylic-acid-mediated immunity more strongly than several other nutrients (Morcillo et al., 2020). But again, excess can reverse the benefit.

High phosphorus fertilization and miR399 overexpression can increase phosphorus accumulation while suppressing defense-related genes such as OsPR1 and OsPBZ1, making rice more susceptible to blast fungus (Campos-Soriano et al., 2020). The plant is therefore not trying to maximize phosphorus. It is trying to maintain the right phosphorus status at the right time.

Potassium: the guardian of water and ion balance

Potassium is the most abundant cation inside plant cells and is essential for growth, development, and stress adaptation (Ashley et al., 2006). Its importance becomes especially obvious under salinity. Sodium and potassium are chemically similar enough that excess sodium can interfere with potassium uptake. Maintaining a sufficiently high cytoplasmic K^+/Na^+ ratio is therefore crucial for surviving salt stress (Johnson et al., 2022). Plants respond through a sophisticated network of transporters and channels. The CBL1/9-CIPK23 complex activates AKT1 and HAK5 to enhance potassium uptake, while a separate CBL-CIPK-TPK system can mobilize potassium from vacuoles when external supplies are low (Li et al., 2023b). In rice, OsHAK1, OsHAK5, OsHAK16, and OsHAK21 contribute to potassium uptake and help maintain a favorable K^+/Na^+ ratio during salinity (Nieves-Cordones et al., 2016). Potassium transport from roots to shoots is also regulated by KUP7/2, particularly during potassium deficiency and salt stress (Rajappa et al., 2020). Potassium is also part of the plant's response to drought. ABA can influence potassium channels involved in stomatal behavior, while jasmonic acid and calcium-dependent signaling can promote potassium efflux associated with stomatal closure. These processes allow plants to reduce water loss while responding to environmental stress. The broader message is that potassium is not simply an element absorbed by roots. It is part of a dynamic electrical and signaling system that helps plants control water, ions, membranes, and stomata.

Calcium and sulfur: nutrients that also speak the language of defense

Calcium occupies a special position because it is both a nutrient and a messenger. Changes in cytosolic calcium concentration can act as signals during salt, osmotic, temperature, and other stresses. Under prolonged salt stress, for example, signaling involving SOS2, ANN proteins, SCaBP8, and calcium transport systems helps regulate calcium levels and maintain cellular homeostasis (Ali et al., 2023). Calcium channels and sensors also participate in cold-induced signaling and freezing tolerance (Peng et al., 2024). Sulfur, meanwhile, is closely tied to plant defense chemistry. It is part of cysteine and contributes to disulfide bonds in proteins, including antimicrobial peptides such as defensins. Sulfur is also important for the formation of iron-sulfur clusters in rhizobial nitrogenase, linking sulfur nutrition to biological nitrogen fixation (Kalloniati et al., 2015). Sulfur metabolism can even influence tolerance to salinity. The plant-growth-promoting bacterium *Enterobacter* sp. SA187 was reported to reprogram sulfur-starvation responses and reduce the harmful effects of salt stress in salt-sensitive mutants (Andrés-Barrao et al., 2021). During pathogen infection, sulfur transport can itself become part of the battle. The tomato sulfate transporter ST2 is induced by bacterial flagella but repressed by pathogen effectors (Lovelace et al., 2018). In rice, the bacterial effector Tal2g activates OsSULTR3;6, and mutation of this transporter reduces bacterial growth and disease symptoms (Xu et al., 2021).

The small nutrients with enormous consequences

Micronutrients are needed in tiny quantities, but they participate in some of the plant's most important biochemical processes. They act as enzyme cofactors, components of signaling systems, and regulators of stress responses. During biotic stress, they can support antimicrobial compounds and immune signaling; during abiotic stress, they contribute to osmotic regulation, cellular homeostasis, and the scavenging of reactive oxygen species (de Bang et al., 2021).

Iron illustrates the delicate balance involved. Plants carefully regulate iron acquisition, transport, localization, and storage because both deficiency and excess can be

damaging. Iron status also affects plant-pathogen interactions. Reactive oxygen species generated during defense can be useful as signals but dangerous when uncontrolled. Proteins such as ferritin and defensins can bind iron and influence ROS production (Herlihy et al., 2020).

Zinc has similarly broad roles. It contributes to enzymes involved in gene expression, photosynthesis, and stress responses (Stanton et al., 2022). Under zinc deficiency, Arabidopsis uses bZIP19 and bZIP23 as zinc-responsive regulators to activate genes that improve zinc acquisition and tolerance (Lilay et al., 2021). Zinc deficiency can also increase susceptibility to disease and insect attack, whereas high tissue zinc can sometimes inhibit pathogen infection (Fones and Preston, 2013).

Copper, molybdenum, and nickel demonstrate another principle: too little and too much can both be harmful. Copper deficiency can impair growth and reproduction, while excess copper can damage membranes, photosynthesis, and enzyme activity. Its movement is regulated by transporter systems including COPT, ZIP, HMA, and FRO proteins, with SPL7 acting as an important copper-responsive transcription factor (Chen et al., 2022a).

Molybdenum is required for the formation of the molybdenum cofactor used by enzymes such as nitrate reductase, while nickel is essential for enzymes including urease and glyoxalase-I. Yet excess nickel is toxic and can disrupt photosynthesis and respiration (Weber et al., 2023). Chloride is another interesting example. Although often associated with salinity damage, chloride is itself an essential micronutrient involved in photosynthesis, stomatal movement, osmotic pressure, charge balance, and even disease inhibition (Geilfus, 2019). Under salt stress, plants must therefore distinguish between chloride as a necessary nutrient and chloride at toxic concentrations.

Plants do not face one stress at a time

Researchers may study drought, heat, salinity, or a pathogen separately. In a field, however, a crop may experience drought, high temperature, salinity, and insect attack simultaneously. Climate change and environmental degradation are increasing the likelihood of such combinations (Zandalinas et al., 2021). Under these circumstances, plants deploy several strategies at once. They may remodel their root systems to enlarge the area available for water and nutrient acquisition. Under drought, for example, root elongation can help expand the absorption zone (Ranjan et al., 2022). In saline or alkaline soils, plants regulate ion channels and osmotic adjustment to maintain ion homeostasis. Multiple stresses also activate hormonal and molecular signaling networks that coordinate nutrient absorption, transport, and distribution (Waadt et al., 2022).

Oxidative stress adds another layer. Environmental stress can increase reactive oxygen species, forcing plants to strengthen antioxidant systems that protect cellular structures and preserve nutrient utilization (Wu et al., 2023). Disease and pest attack can also change metabolic pathways and increase production of secondary metabolites, altering how nutrients are distributed within the plant. And once again, microorganisms can help. Plants may use rhizosphere relationships with nitrogen-fixing bacteria and mycorrhizal fungi to improve nutrient acquisition under difficult conditions (Munteanu and Schwartz, 2022).

Toward crops that are both well fed and resilient

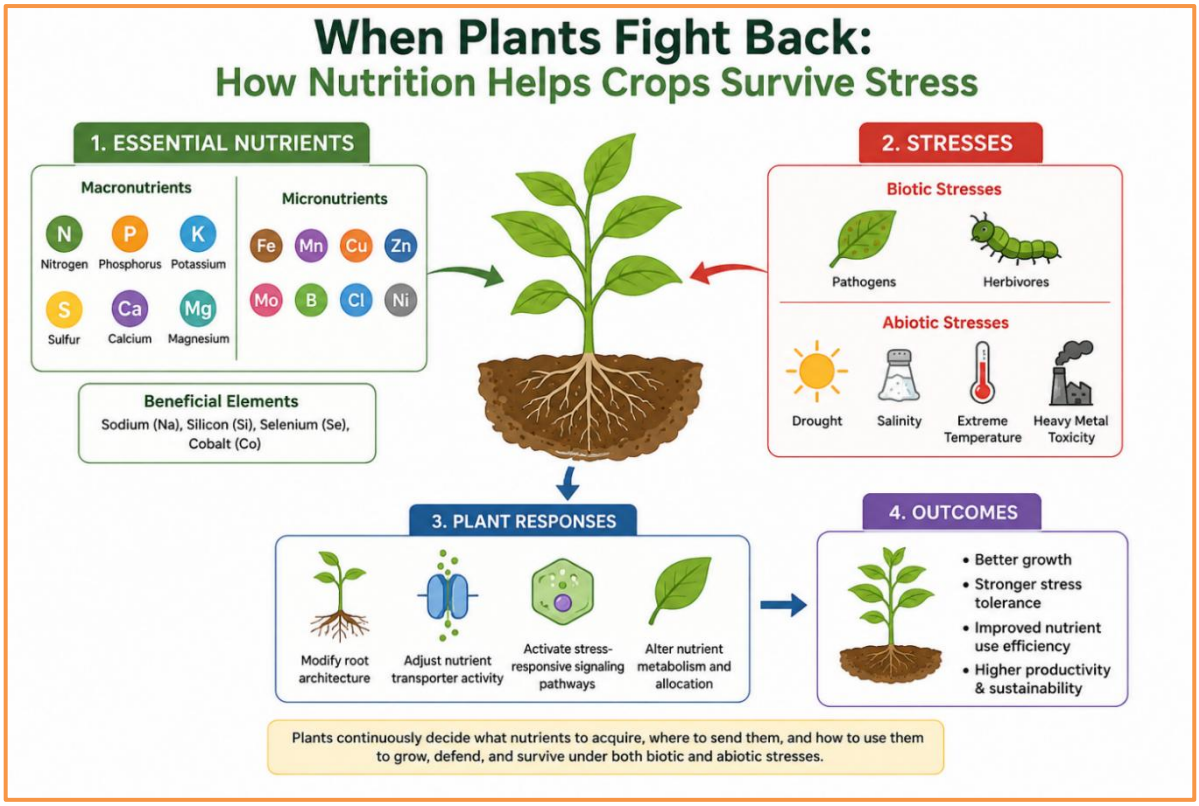
The practical implications are considerable. For decades, improving crop nutrition has often meant supplying nutrients externally. But the research summarized by Wang et al. suggests that the future may depend increasingly on understanding how plants regulate their own nutrient economy. The goal is not necessarily to give crops more fertilizer. It is to help them acquire and use nutrients more efficiently, particularly when conditions are unfavorable. This could involve breeding or engineering plants with root systems better adapted to drought, transporters that maintain nutrient uptake under salinity, or signaling networks that coordinate nutrition with immune responses.

Gene editing could potentially be used to modify root morphology and physiological traits, improving nutrient absorption under unfavorable conditions. Biotechnology may also

provide ways to fine-tune plant immune systems so that nutrients can be allocated more efficiently during pathogen attack. Precision nutrient management is another important direction. Because nutrient requirements depend on environmental conditions, crop species, and stress combinations, fertilizer strategies tailored to particular environments could improve resource-use efficiency. There is a need to integrate field practices with precision nutrient management while developing crops capable of efficient nutrient utilization under stress. There is also a major opportunity in plant-microbe interactions. A deeper understanding of rhizobia, mycorrhizal fungi, and other beneficial soil microorganisms could support the development of biofertilizers and microbial inoculants that improve nutrient availability and plant growth under stress (Wang et al., 2025). Modern technologies are opening additional doors. Hydroponic systems allow researchers to control trace-element concentrations precisely, while isotope tracing can reveal where nutrients travel inside plants. Genomic and transcriptomic analyses can identify genes controlling nutrient absorption, transport, and utilization (Wiggenhauser et al., 2022).

The plant's real survival strategy: balance

The central message emerging is surprisingly simple: plant nutrition is about balance. Nitrogen promotes growth, but its effects on immunity can vary with its form and concentration. Phosphorus fuels energy metabolism and can strengthen defense, but excessive phosphorus may increase susceptibility to some diseases. Potassium protects cellular ion balance, especially under salinity, but its uptake must be coordinated with sodium. Calcium is both a nutrient and a messenger. Sulfur feeds both metabolism and defense. Magnesium supports photosynthesis and can influence immunity. Micronutrients are required in tiny quantities, yet their absence or excess can profoundly affect plant health.



Plants therefore do not merely absorb nutrients. They sense them, transport them, store them, redistribute them, and use them as signals. That is why the future of sustainable agriculture may depend as much on understanding nutrient regulation as on increasing nutrient supply. The important research challenge are: understanding how roots, immune systems, nutrient metabolism, and the surrounding microbial community interact when several stresses occur simultaneously. There is need of deeper physiological, molecular, and genetic knowledge of these interactions which could guide the breeding of crops resilient to

multiple stresses and improve yields under real field conditions. This matters because the stresses faced by crops rarely arrive one by one. A farmer does not experience "drought stress" in isolation from "nutrient stress" or "pest stress." Plants certainly do not.

The crop of the future will therefore need to do more than grow quickly when conditions are ideal. It will need to recognize changing environments, maintain nutrient balance, protect itself from pathogens and pests, conserve water, manage toxic ions, cooperate with beneficial microorganisms, and continue producing biomass and seeds despite adversity. In that sense, the future of crop resilience may begin not with adding more nutrients to the soil, but with learning how plants decide what to do with the nutrients they already have. That is the hidden sophistication of plant nutrition: beneath every green leaf is a dynamic system constantly balancing growth, defense, energy, water, minerals, microbes, and stress. And the better we understand that system, the closer we may come to crops that are not simply productive-but genuinely resilient and sustainable.

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