International Journal of Agriculture and Plant Science
www.agriculturejournal.in
Online ISSN: 2664-7664, Print ISSN: 2664-7656
Received: 23-06-2025, Accepted: 24-07-2025, Published: 08-08-2025
Volume 7, Issue 4, 2025, Page No. 81-87

Physiological disruptions in maize (*Zea mays L.*) from indiscriminate nitrogen fertilization: A review

Chavan Syam Raj Naik[1], Himakara Datta M[2], CVCM Reddy[3*]

[1] Principal scientist, Department of Crop Physiology, Regional Agriculture Research Station, Acharya NG Ranga Agriculture University, Lam, Guntur, Andhra Pradesh, India.

[2] *Research Associate*, Department of Genetics and Plant Breeding, ANGRAU-Regional Agricultural Research Station, Lam, Guntur, Andhra Pradesh, India.

[3] Principal Scientist, Department of Genetics and Plant Breeding, (Millets & Maize), ANGRAU-Regional Agricultural Research Station, Acharya NG Ranga Agricultural University-RARS, Lam, Guntur, Andhra Pradesh, India.

Abstract

Nitrogen (N) is an indispensable nutrient for maize (*Zea mays* L.) production. However, its indiscriminate application beyond physiological requirements represents a central paradox in modern agriculture, posing significant threats to both productivity and environmental sustainability. The review examines the effects of excess nitrogen on root and shoot morphophysiology, developmental phenology, yield components, and, most critically, Nitrogen Use Efficiency (NUE). Supra-optimal N supply disrupts the hormonal balance, particularly the auxin-cytokinin axis, leading to inhibited root system development and an unfavourably high shoot-to-root ratio, making the plant prone to lodging. The yield response to N follows a law of diminishing returns, with rates beyond the optimum causing yield stagnation or decline due to source-sink imbalances and physical limitations. Concurrently, NUE declines quickly with increasing N rates. The concept of incremental NUE (iNUE) is critically examined, revealing the profound inefficiency of marginal N applications near the economic optimum, where over 90% of the applied N may be lost or unutilized for grain production. These disruptions are underpinned by the plant's perception of N excess as a metabolic stress, triggering widespread changes in gene expression. This underscores the urgent need for a paradigm shift from N-surplus to N-synchrony management strategies. Future research should focus on elucidating the genetic basis of N tolerance, understanding the molecular drivers of iNUE, and developing dynamic, sensor-based N management systems. The implications for agricultural practice and policy are clear: enhancing the sustainability of maize production hinges on recalibrating nitrogen (N) inputs to align with actual crop demand, thereby improving profitability while safeguarding environmental health.

Keywords: Maize, Nitrogen fertilization, Nitrogen use efficiency (NUE), Source-Sink relationship, Root architecture, Yield components

Introduction

The advent of synthetic nitrogen (N) fertilizers, produced via the Haber-Bosch process, was a cornerstone of the Green Revolution, enabling unprecedented increases in global crop yields and supporting a rapidly growing human population (Vicente & Dean, 2017) [26]. Maize (*Zea mays* L.), a crop of immense global importance for food, animal feed, and biofuel production, is exceptionally responsive to N inputs, which are fundamental to its vigorous growth and high yield potential. While essential for productivity, the mismanagement of N, characterized by application rates that exceed the crop's capacity for uptake and utilization, has become a principal source of agricultural inefficiency and a major driver of environmental degradation (Asibi *et al*., 2019) [1].

Globally, it is estimated that less than half of the N fertilizer applied to maize is recovered by the crop, with recovery rates in some intensive systems falling as low as 30–40% (Kitchen *et al*., 2022) [8]. The unrecovered N is lost to the environment through multiple pathways, including nitrate (NO_3^-) leaching into groundwater, gaseous emissions of ammonia (NH_3) and the potent greenhouse gas nitrous oxide (N_2O), and surface runoff leading to the eutrophication of aquatic ecosystems (Zhang *et al*., 2023) [34]. This inefficiency not only represents a significant economic loss for producers but also incurs a substantial environmental cost, estimated at hundreds of billions of dollars annually in regions like Europe (Asibi *et al*., 2019) [1]. The common practice of applying "insurance" nitrogen (N) fertilizer in excess of the scientifically recommended rate to mitigate perceived risks of deficiency is a primary contributor to this problem, driven by economic incentives that prioritize maximum yield and uncertainty about weather and soil nitrogen dynamics (Kitchen *et al*., 2022) [8]. Despite decades of research on optimizing N management, a comprehensive review that connects the observable agronomic outcomes of N over-application to the underlying cascade of physiological, morphological, hormonal, and molecular disruptions within the maize plant is crucial. There is a critical need to move beyond simple dose-response curves and develop a mechanistic understanding of why and how excess N becomes detrimental. This review aims to fill that gap by providing a holistic analysis of the physiological consequences of indiscriminate N fertilization in maize. The objectives of this article are fourfold: (1) To synthesize the morpho-physiological responses of maize to supra-optimal N, from root architecture to shoot development; (2) To critically analyze the impact of N excess on yield components and the non-linear dose-response relationship that governs final grain yield; (3) To understand why

Nitrogen Use Efficiency (NUE) drops so steeply at high nitrogen rates, focusing on how the incremental NUE (iNUE) concept can help diagnose and explain this trend; and (4) to explore the underlying hormonal and molecular control mechanisms that mediate the plant's response to N excess as a physiological stressor.

The Physiological Imperative of Nitrogen in Maize

To comprehend the disruptions caused by an excess of nitrogen, it is first essential to appreciate its fundamental and indispensable role in the life of the maize plant. Nitrogen is not merely a nutrient; it is the structural and functional backbone of the plant's most critical biological machinery (Gheith *et al*., 2022) [2]. Its availability is a primary determinant of growth, development, and ultimately, grain yield. The physiological importance of N is rooted in its presence as a core constituent of a vast array of essential biomolecules. First and foremost, N is a central component of the chlorophyll molecule, the pigment that captures light energy for photosynthesis. An adequate supply of N is therefore directly linked to the plant's photosynthetic capacity, influencing leaf area development and the rate of carbon fixation, which generates the sugars that fuel all metabolic processes (Wani *et al*., 2021) [29]. Furthermore, N is the defining element of amino acids, which are the monomers that polymerize to form proteins. These proteins are not only structural components of cells and tissues but also function as enzymes, the catalysts that drive virtually every biochemical reaction in the plant, from nutrient uptake by roots to the synthesis of complex carbohydrates in the grain. Nitrogen is also a key component of nucleic acids such as deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), which carry the genetic blueprint and orchestrate the synthesis of proteins, thereby controlling all aspects of growth and development (Leghari *et al*., 2016) [9].

Crucially, plant growth is not regulated by the absolute quantity of N alone, but by a finely tuned homeostatic balance between nitrogen and other elements, most notably carbon. The carbon-to-nitrogen (C/N) balance is a central metabolic sensor that plants use to coordinate growth with resource availability (Ying *et al*., 2024) [33]. An influx of N must be matched by an adequate supply of carbon skeletons, derived from photosynthesis, to be assimilated into amino acids and other N-containing compounds. When this balance is severely perturbed by an excessive, non-physiological supply of N, the plant's homeostatic mechanisms are overwhelmed. This disruption of the C/N balance is one of the first and most fundamental systems to be disturbed by indiscriminate fertilization, initiating a cascade of stress responses that will be detailed in subsequent sections (Ying *et al*., 2024) [33]. Therefore, understanding N's role is not just about recognizing its necessity, but also appreciating that its physiological function is contingent upon balance and integration within the plant's entire metabolic network.

Morpho-physiological Alterations under Supra-optimal Nitrogen Supply

While optimal N levels are synonymous with vigorous growth, supra-optimal concentrations trigger a series of counterintuitive and detrimental alterations to the plant's morphology and physiology. These changes are not uniform across the plant; instead, they represent a systemic imbalance where investment in one part of the plant comes at a severe cost to another, ultimately compromising the integrity and productivity of the entire organism (Table 1).

Disrupted Root System Architecture and Function

The most profound and foundational disruption caused by excess N occurs belowground. Contrary to the intuitive notion that fertilizer universally promotes growth, a supra-optimal supply of N is specifically detrimental to the development and function of the maize root system. This belowground failure is a primary disruption that precipitates a host of subsequent problems, including poor water and nutrient uptake, as well as reduced structural stability.

Numerous studies have demonstrated that high N application rates significantly inhibit root growth. Field and pot experiments consistently show that as N supply increases beyond an optimal point, key root parameters decline (Zheng-rui *et al*., 2008) [35]. This is not merely a resource allocation shift but is a direct inhibitory or toxic effect of high N concentrations on root meristematic activity and cell elongation. This inhibition of root growth is coupled with a dramatic alteration in biomass partitioning between the shoot and the root. Under high N conditions, the plant preferentially allocates resources to developing lush, green foliage, leading to a significant increase in the shoot-to-root ratio. This creates a dangerously imbalanced plant: a large, heavy shoot with a high transpirational demand, supported by a stunted and inefficient root system, making it highly vulnerable to secondary stresses like drought and structurally predisposed to lodging (Liu *et al*., 2013) [13].

The response of maize roots to nitrogen (N) availability is distinctly biphasic. Under low N conditions, maize adopts an adaptive ‘foraging strategy,’ increasing the elongation of axial roots to explore a greater soil volume in search of scarce nitrogen patches. This root plasticity is vital for survival and productivity in N-limited environments. In sharp contrast, when nitrogen levels are too high, the opposite occurs: root exploration and growth are suppressed (Sun *et al*., 2020) [24]. This highlights that the plant’s physiological response to nitrogen availability is not linear; instead, excess nitrogen is perceived as a stress signal, prompting a defensive strategy that restricts root development.

Aberrant Vegetative Growth and Phenological Shifts

The morphological disruptions caused by excess nitrogen are clearly visible aboveground, often appearing as abnormal vegetative growth that can be mistaken for better plant health. Although high nitrogen rates do produce taller plants with a larger leaf area index (LAI) (Yang *et al*., 2024) [31]. The combination of high N supply and imbalanced levels of other nutrients, particularly potassium (K), creates an ideal environment for the development of stalk rot diseases. High N promotes lush, succulent tissue growth, while insufficient K compromises cell wall strength and stalk integrity. This synergy renders the plant highly susceptible to pathogens, resulting in premature stalk death and a significantly increased risk of stalk lodging. The timing of N application is also critical; excessive N applied late in the season can exacerbate this problem by promoting weak, late-season stem growth that is particularly liable to lodging. This physical collapse can lead to devastating yield losses, as ears may be unharvestable or subject to rot on the ground (Liu *et al*., 2021) [12].

Supra-optimal N also alters the plant's phenology, or developmental timeline. Moderate increases in N can accelerate development, shortening the time required to reach key reproductive stages, such as tasseling and silking, a consequence of quicker overall growth (Shrestha *et al*., 2022) [22]. However, very high N levels can have the opposite effect, prolonging the vegetative growth period as the plant continues to invest in leaf and stem production at the expense of transitioning to the reproductive phase. This can delay overall maturity, potentially exposing the critical grain-filling period to less favourable late-season conditions, such as frost or drought. Nitrogen supplementation has been shown to shorten the anthesis-silking interval (ASI), which is the period between pollen shed and silk emergence and is a key factor for successful pollination and kernel set. Although a shorter ASI is generally beneficial, this advantage must be balanced against the significant drawbacks of weakened stalks and potentially delayed maturity that often accompany the high nitrogen rates needed to achieve it (Molla *et al*., 2014) [16].

Impact on Yield Components and Final Grain Yield

The relationship between nitrogen application and maize grain yield is a classic example of the law of diminishing returns. While yield increases with N supply up to a point, there is an optimal rate beyond which further additions provide progressively smaller benefits, eventually leading to a yield plateau and, under conditions of significant excess, a yield decline (Zhang *et al*., 2023) [34]. This non-linear response is a direct agronomic manifestation of the integrated physiological disruptions detailed in the previous sections.

Numerous studies and large-scale meta-analyses have sought to define this optimal range, which varies depending on genotype, soil type, climate, and management practices. For instance, a meta-analysis in Northwest China identified an optimal N application rate of 175–225 kg/ha for maximizing the yield-increasing effect (Jiang *et al*., 2025) [6]. Another meta-analysis for Northeast China pinpointed the optimum at approximately 205 kg/ha (Zhang *et al*., 2023) [34]. These studies consistently demonstrate that applying N beyond such thresholds is not only economically wasteful but can become agronomically counterproductive. The yield response curve flattens, and in many cases, begins to slope downward as excessive N rates significantly reduce yield.

This yield stagnation and decline can be deconstructed by examining the impact of N on the primary yield components: the number of kernels per ear and the weight of individual kernels (Li *et al*., 2020) [10]. Moderate N rates have a positive influence on these components, leading to more and heavier kernels. However, the physiological state of a plant under supra-optimal N can severely compromise its ability to realize this potential during the critical grain-filling period (Lixia *et al*., 2006) [14].

The breakdown occurs due to a fundamental disruption of the plant's source-sink dynamics. The "source" refers to the photosynthetic machinery (primarily the leaves) that produces carbohydrates, while the "sink" refers to the grains that store these carbohydrates. Excess N creates an oversized, dense canopy (Lihua *et al*., 2010) [11]. This can lead to intense self-shading, causing lower leaves to become photosynthetically inefficient or to senesce prematurely, which reduces the plant's overall net carbon gain. At the same time, the transport system that moves photosynthates from source to sink is compromised by weakened stalks and an inefficient root system. As a result, the plant is unable to meet the metabolic demands of its large vegetative structure while also filling a high number of kernels. This can lead to kernel abortion, which reduces the number of kernels, or incomplete grain fill, which lowers kernel weight, ultimately negating the initial benefits of a large leaf canopy. The resulting yield plateau and eventual decline mark the point at which the adverse effects of structural instability, transport inefficiency, and source limitation from self-shading outweigh the advantages of increased photosynthetic capacity.

Declining Nitrogen Use Efficiency with Over-fertilization

The primary consequence of excessive nitrogen fertilization, both economically and environmentally, is a significant decline in Nitrogen Use Efficiency (NUE). Increasing nitrogen beyond crop needs creates a paradox: more fertilizer leads to greater waste, with much of the added nitrogen doing little for grain yield and instead being lost to the environment.

Deconstructing NUE by Examining Uptake and Utilization Decoupling

Nitrogen Use Efficiency is a composite measure, broadly defined as the amount of grain yield produced per unit of N available to the crop (from soil and fertilizer) (Wang *et al*., 2019) [28]. To understand how it fails under N excess, it must be deconstructed into its two primary physiological components (Souza *et al*., 2008) [23]:

1. **Nitrogen Uptake Efficiency (NUpE):** The ability of the plant's root system to acquire N from the soil and transport it into the plant.

2. **Nitrogen Utilization Efficiency (NUtE):** The ability of the plant to assimilate the N it has taken up and convert it into grain biomass.

The overall NUE is the product of these two efficiencies ($NUE=NUpE\times NUtE$). In a well-managed system, these two components work in concert. However, indiscriminate fertilization fundamentally decouples them. High concentrations of mineral N in the soil may initially maintain or even increase the total amount of N taken up by the plant (NUpE), but as detailed previously, the plant's physiological capacity to utilize this N for productive purposes (NUtE) diminishes rapidly. The internal systems become saturated, the C/N balance is disrupted, and structural limitations prevent the efficient conversion of N into grain. This sharp drop in NUtE becomes the driving factor behind the collapse of the overall NUE, even if N uptake remains high (Souza *et al*., 2008) [23].

The Inverse Relationship between N Rate and NUE

The scientific literature presents overwhelming and unequivocal evidence of a strong, inverse relationship between the rate of N application and the resulting NUE. As farmers apply more N fertilizer, the percentage of that fertilizer recovered in the grain plummets. This trend is observed globally across diverse maize production systems (Varga *et al*., 2008; Rawal *et al*., 2024) [19, 25]. Crop recovery of applied N fertilizer rarely exceeds 50% and is often much lower, with figures of 30–35% commonly cited for intensive systems in regions like China (Asibi *et al*., 2019) [1]

A Critical Perspective with Incremental NUE (iNUE)

While the concept of overall NUE is valid, it can mask the true extent of inefficiency, as it represents an average over the entire amount of fertilizer applied. A more powerful and diagnostically precise concept is incremental NUE (iNUE), which is defined as the change in NUE for each additional, marginal unit of N applied (Zhang *et al*., 2023) [34]. This approach moves beyond farm-scale averages to reveal the real-time efficiency of fertilization decisions, particularly for the final kilograms of N applied to reach a target yield.

The iNUE concept provides a paradigm-shifting perspective on nitrogen management. Analysis of extensive datasets has revealed a striking truth: for the final units of nitrogen fertilizer applied to reach the Economic Optimal Nitrogen Rate (EONR), which is the rate that maximizes profit, the iNUE is critically low at about 6 percent. In other words, that final increment of 'insurance' fertilizer added to maximize profit leads to over 90 percent of the nitrogen being either lost to the environment during the growing season, retained in the soil as a pollution risk, or sequestered in non-grain biomass such as stover and roots. (Kitchen *et al*., 2022) [8].

This finding reshapes the entire economic and environmental assessment of nitrogen fertilization. It shows that applying extra nitrogen to gain the last few kilograms of grain yield comes at a disproportionately high environmental cost and delivers minimal physiological efficiency. The iNUE concept clearly illustrates the law of diminishing returns in practical terms, providing strong evidence to challenge the practice of maximizing yield at any cost. It suggests that meaningful improvements in overall NUE and significant reductions in environmental losses could be achieved by slightly lowering nitrogen rates below the EONR, with only a slight loss in yield and minimal impact on profit (Wang *et al*., 2020; Kitchen *et al*., 2022) [8, 27].

Table 1: Synthesis of Maize Responses to Optimal vs. Supra-Optimal Nitrogen Fertilization

Parameter	Optimal N Fertilization	Supra-Optimal N Fertilization	Key Literature
Root System	Balanced shoot: root ratio, robust root elongation, and biomass	High shoot: root ratio, inhibited root elongation, reduced root biomass	(Liu *et al*., 2013; Sun *et al*., 2020) [13, 24]
Phenology	Normal progression through growth stages	Accelerated early growth, potential delay in maturity	(Lixia *et al*., 2006; Moose & Below, 2009) [14, 17]
Grain Yield	Reaches maximum potential (yield plateau)	Stagnation or significant decline from the maximum	(Kitchen *et al*., 2022) [8]
Yield Components	High kernel number and kernel weight	Reduced kernel fill, potential kernel abortion	(Hisse *et al*., 2022) [4]
Overall NUE	Maximized for the system (e.g., 30-50%)	Sharply reduced (e.g., <20%)	(Ordóñez *et al*., 2021) [18]
Incremental NUE (iNUE)	High for initial N units, drops to ~6% at optimum	Becomes zero or negative, indicating net loss	(Kitchen *et al*., 2022) [8]
Hormonal State	Balanced auxin/cytokinin signalling	High cytokinin levels, disrupted auxin gradients	(Wilkinson & Ohlrogge, 1964) [30]
Environmental Impact	Minimized N loss per unit of yield	High N losses (leaching, volatilization, N2O emissions)	(Moose & Below, 2009; Kitchen *et al*., 2022) [8, 17]

Hormonal and Molecular Responses to Nitrogen Excess

The macroscopic morphological and physiological disruptions observed in maize under supra-optimal N are orchestrated by a complex network of internal signalling pathways at the hormonal and molecular levels. The plant does not passively accumulate excess N; it actively perceives the imbalance and initiates a cascade of responses. Understanding these control mechanisms is key to explaining why the plant behaves as it does and opens avenues for genetic improvement.

The Auxin-Cytokinin Axis

The stunted root system architecture previously discussed is not a random occurrence but a direct consequence of a fundamental disruption in the plant's hormonal signalling. The development of the root system, particularly the formation of lateral roots, which are crucial for nutrient and water uptake, is tightly controlled by an antagonistic balance between two key classes of phytohormones: auxins and cytokinins (CKs). In simple terms, auxin generally promotes the initiation of lateral roots, while cytokinin acts as an inhibitor (Rivas *et al*., 2022) [20].

It is well-established in plant science that the availability of nitrogen in the soil directly modulates the biosynthesis of cytokinins, primarily in the roots (Jan *et al*., 2024) [5]. When N is abundant, roots synthesize higher levels of cytokinins, which are then transported via the xylem to the shoot, acting as a long-distance signal that communicates the plant's N status (Kiba *et al*., 2011) [7]. Under conditions of supra-optimal N fertilization, this system is pushed into overdrive, leading to an overproduction of cytokinins in the roots.

This flood of cytokinins disrupts the delicate auxin-cytokinin balance required for normal root development. The high concentration of inhibitory cytokinins effectively overrides the pro-growth signals from auxin, leading to the observed inhibition of lateral root formation and overall stunting of the root system (Rivas *et al*., 2022) [20]. Studies using exogenous hormone applications have confirmed this mechanism; applying high levels of cytokinin to maize roots mimics the effect of high N, reducing lateral root density, while applying auxin can partially reverse this inhibition, demonstrating that the relative balance between the two hormones is the critical determinant (Rivas *et al*., 2022) [20]. Therefore, this hormonal disruption provides a direct, causal mechanistic link between the external chemical environment (high soil N) and the resulting physical outcome (a poor root structure), explaining why the plant's foundation is the first system to fail under N excess.

Cellular and Metabolic Stress Signals

At the cellular and molecular level, maize does not perceive excess nitrogen as a harmless surplus of a vital resource but rather as a significant physiological stressor that triggers broad changes in metabolism and gene expression. This stress response helps explain the growth changes and inefficiencies observed under high nitrogen conditions (Ying *et al*., 2023) [32].

A primary metabolic disruption is the perturbation of the C/N balance. A massive influx of N without a proportional increase in carbon fixation forces the plant into a state of "metabolic stress," as it struggles to find the carbon skeletons necessary to assimilate the N into amino acids. This imbalance is a key signal that initiates downstream stress responses (Schlüter *et al*., 2013) [21].

Advanced transcriptomic analyses have provided a window into this stress response, revealing that maize plants exposed to high N levels alter the expression of thousands of genes compared to those grown under optimal conditions. Critically, some of these changes mirror responses to other known abiotic stresses. For example, a consistent finding across multiple maize hybrids and developmental stages is the significant repression of genes involved in the biosynthesis of thiamine (Vitamin B1), specifically the *Thi1* and *Thi2* genes. Since thiamine is a vital cofactor involved in stress mitigation, its downregulation under high N strongly indicates that the plant has entered a stressed state (Ying *et al*., 2023) [32]. The consistency of this response suggests that these genes could serve as robust molecular biomarkers for identifying N-induced stress in maize.

Gene expression patterns also provide the molecular basis for the phenological changes observed. High N supplementation leads to the prolonged expression of genes associated with photosynthesis and chlorophyll biosynthesis, while simultaneously repressing genes involved in the initiation of senescence, such as specific proteases (He *et al*., 2005) [3]. This explains the "stay-green" effect and the extended vegetative period that can delay maturity.

Importantly, these molecular and metabolic responses are not uniform across all maize varieties. Studies have shown that different maize hybrids exhibit markedly different sensitivities and gene expression patterns in response to high N, and these differences correlate with their ultimate yield response (Mastrodomenico *et al*., 2019) [15]. This highlights a significant genetic component to N tolerance and NUE. Hybrids that are better able to maintain metabolic homeostasis and mitigate the stress of high nitrogen (N) levels are more likely to sustain yield under such conditions. This genetic variability represents a critical target for modern breeding programs aiming to develop maize varieties that are not only efficient under low N but also resilient to the physiological disruptions of inadvertent over-fertilization.

Future Research Directions

This comprehensive review underscores key knowledge gaps and outlines clear opportunities for future research. Closing these gaps will be essential for developing more sustainable and resilient maize production systems.

- **Genetic Basis of N-Stress Tolerance:** While it is clear that maize hybrids respond differently to supra-optimal N, the specific genes and regulatory networks conferring tolerance are not well understood. Future research should employ genome-wide association studies (GWAS) and transcriptomic profiling across diverse maize germplasm to identify quantitative trait loci (QTLs) and candidate genes associated with the ability to maintain root growth, structural integrity, and NUE under high N conditions. This could lead to the development of molecular markers for breeding N-resilient cultivars.

- **Molecular Drivers of Incremental NUE (iNUE):** The concept of iNUE offers a powerful diagnostic tool; however, the underlying molecular mechanisms that cause its sharp decline near the EONR remain essentially a black box. Research is needed to investigate the saturation kinetics of specific nitrate and ammonium transporters (e.g., NRTs, AMTs), the feedback regulation of N assimilation pathways (e.g., nitrate reductase, glutamine synthetase), and the hormonal signalling events that occur at marginal increases in N supply. Identifying the molecular bottlenecks that cause this inefficiency could reveal novel targets for genetic engineering or management interventions aimed at "flattening" the iNUE decline.

- **Interactive Effects with Other Abiotic Stresses:** Climate change is increasing the frequency and intensity of concurrent stresses, such as drought, heat, and soil salinity. The current body of research broadly examines N effects in isolation. It is critical to investigate the synergistic or antagonistic interactions. Multi-stress experiments are needed to build more resilient agronomic recommendations for future climates.

- **Impact on the Root-Microbiome Axis:** Indiscriminate N fertilization is known to alter the soil chemical environment, which in turn profoundly impacts the composition and function of the root-associated microbiome. Future research should explore how these shifts in microbial communities affect maize health. Exploring unique maize landraces that have evolved associations with nitrogen-fixing microbes could also provide novel solutions.

- **Developing and Validating Dynamic N Management Systems:** The findings of this review make a strong case for moving beyond static, pre-season nitrogen rate recommendations. The future of sustainable nitrogen management depends on dynamic, data-driven systems that align nitrogen applications with real-time crop needs. Future research should focus on integrating proximal and remote sensing tools, such as drones and satellites, with crop models and machine learning algorithms to deliver in-season, site-specific nitrogen prescriptions. Validating these technologies across diverse environments is essential for building farmer confidence and accelerating the adoption of precision agriculture practices that prioritize nitrogen synchrony over surplus application.

Nitrogen Management for a Sustainable Future

In summary, applying nitrogen beyond the plant’s physiological needs is not only wasteful but also damaging, setting off a cascade of negative impacts on plant structure, function, and yield. Chasing maximum yield through surplus nitrogen is an unsustainable practice that threatens both economic returns and environmental sustainability.

Excess nitrogen fundamentally disrupts the plant's foundation, starting at the root. By disturbing the auxin–cytokinin hormonal balance, surplus nitrogen hampers root development, resulting in a shallow and inefficient root system. This belowground weakness is mirrored aboveground by excessive vegetative growth, producing a structurally weak plant with lush but fragile foliage prone to lodging. This imbalance creates a critical source–sink mismatch, as the plant's ability to move photosynthates to the grain is compromised. The relationship between nitrogen rate and grain yield clearly follows the law of diminishing, and eventually negative, returns — yield plateaus and then declines once nitrogen exceeds the optimum level. Nitrogen Use Efficiency also drops sharply with over-fertilization. The incremental NUE (iNUE) concept highlights this inefficiency, demonstrating that the final 'insurance' applications of nitrogen contribute almost nothing to yield and are largely lost.

The broader implications of these findings call for a fundamental recalibration of how nitrogen is managed in maize production. The common practice of applying excess nitrogen to avoid any risk of limitation must shift toward a strategy of nitrogen synchrony, where supply is closely matched to the crop's changing needs throughout its lifecycle. Achieving this shift requires a coordinated, multi-faceted effort. Advances in genetics and breeding are necessary to develop maize hybrids that utilize nitrogen more efficiently and tolerate the physiological stresses associated with excessive nitrogen. Equally important is the widespread adoption of precision agronomy, guided by the 4R Nutrient Stewardship principles (Right Source, Right Rate, Right Time, Right Place) and supported by advanced sensing and modelling tools. Finally, supportive policies should incentivize efficiency and sustainability, rewarding farmers for optimizing nitrogen use rather than simply maximizing yield. By aligning agronomic practices with the crop's physiological realities, maize production can become both highly productive and environmentally responsible.

References

1. Asibi AE, Chai Q, A Coulter J. Mechanisms of Nitrogen Use in Maize. Agronomy,2019:9(12):775. https://www.mdpi.com/2073-4395/9/12/775
2. Gheith E, El-Badry OZ, Lamlom SF, Ali HM, Siddiqui MH, Ghareeb RY. *et al*. Maize (*Zea mays* L.) productivity and nitrogen use efficiency in response to nitrogen application levels and time. Frontiers in Plant Science,2022:13:941343.
3. He P, Osaki M, Takebe M, Shinano T, Wasaki J. Endogenous hormones and expression of senescence-related genes in different senescent types of maize. Journal of Experimental Botany,2005:56(414):1117-1128.
4. Hisse IR, D'Andrea KE, Otegui ME. Genetic analysis of maize grain yield components and physiological determinants under contrasting nitrogen availability. Crop and Pasture Science,2022:74:182 -193.
5. Jan M, Muhammad S, Jin W, Zhong W, Zhang S, Lin Y. *et al*. Modulating root system architecture: cross-talk between auxin and phytohormones. Frontiers in Plant Science,2024:15:1343928.
6. Jiang Y, Li H, Ma W, Yu W, Chen J, Gao Y. *et al*. A meta-analysis of the effects of nitrogen fertilizer application on maize (Zea mays L.) yield in Northwest China—frontiers in Plant Science,2025:15:1485237.
7. Kiba T, Kudo T, Kojima M, Sakakibara H. Hormonal control of nitrogen acquisition: roles of auxin, abscisic acid, and cytokinin. Journal of Experimental Botany,2011:62(4):1399-1409.
8. Kitchen NR, Ransom CJ, Schepers JS, Hatfield JL, Massey R, Drummond ST. *et al*. A new perspective when examining maize fertilizer nitrogen use efficiency, incrementally. PLoS One,2022:17(5):0267215.
9. Leghari SJ, Wahocho NA, Laghari GM, HafeezLaghari A, MustafaBhabhan G, HussainTalpur K. *et al*. Role of nitrogen for plant growth and development: A review. Advances in Environmental Biology,2016:10(9):209-219.
10. Li Q, Du L, Feng D, Yun R, Li Z, Kong F-l. *et al*. Grain-filling characteristics and yield differences of maize cultivars with contrasting nitrogen efficiencies. The Crop Journal,2020:8(6):990-1001.
11. Lihua L, Pu W, Lu L. The Relationship of Source and Sink for Yield Form in Summer Maize under Different Nitrogen Fertilizer Application Rate. Journal of Maize Sciences,2010:16(4):66-71.
12. Liu X-m, Gu W, Li C-f, Jing L, Wei S. Effects of nitrogen fertilizer and chemical regulation on spring maize lodging characteristics, grain filling and yield formation under high planting density in Heilongjiang Province, China. Journal of Integrative Agriculture,2021:20:511-526.
13. Liu Y, Lai N, Gao K, Chen F, Yuan L. *et al*. Ammonium Inhibits Primary Root Growth by Reducing the Length of Meristem and Elongation Zone and Decreasing Elemental Expansion Rate in the Root Apex in Arabidopsis thaliana. PLoS One, 2013, *8*.
14. Lixia S, Yaping W, Wang P, Zhenxie Y, Zhang H, Lan L. *et al*. Effect of Nitrogen Supply on Early Kernel Development and Yield in Summer Maize (Zea mays L.). Zuo wu xue bao,2006:32(11):1746-1751.
15. Mastrodomenico AT, Bohn MO, Lipka AE, Below FE. Genomic Selection Using Maize Ex-Plant Variety Protection Germplasm for the Prediction of Nitrogen-Use Traits. Crop Science, 2019.
16. Molla S, Nakasathien S, Sarobol E, Vichukit V. Anthesis and Silking Dynamics of Maize under Contrasting Nitrogen and Water Levels. Agriculture and Natural Resources,2014:48(6):837-850.
17. Moose S, Below FE. Biotechnology approaches to improving maize nitrogen use efficiency. In Molecular genetic approaches to maize improvement Springer, 2009, 65-77.
18. Ordóñez RA, Castellano MJ, Danalatos GJN, Wright E E, Hatfield JL, Burras L. *et al*. Insufficient and excessive N fertilizer input reduces maize root mass across soil types: field Crops Research,2021:267:108142.
19. Rawal N, Vista S, Khadka D, Paneru P. Grain Yield, Nitrogen Accumulation, and Its Use Efficiency of Maize (Zea mays L.) as Influenced by Varying

Nitrogen Rates. International Journal of Agronomy, 2024. https://doi.org/10.1155/2024/4104123
20. Rivas MÁ, Friero I, Alarcón MV, Salguero J. Auxin-cytokinin balance shapes maize root architecture by controlling primary root elongation and lateral root development—frontiers in Plant Science,2022:13:836592.
21. Schlüter U, Colmsee C, Scholz U, Bräutigam A, Weber APM, Zellerhoff N. *et al*. Adaptation of maize source leaf metabolism to stress-related disturbances in carbon, nitrogen, and phosphorus balance. BMC Genomics,2013:*14*:442-442.
22. Shrestha J, Subedi S, Acharya R, Sharma S, Subedi M. Grain Yield Stability of Maize (*Zea mays* L.) Hybrids using Ammi Model and GGE Biplot Analysis. SAARC Journal of Agriculture,2022:19(2):107-121. https://doi.org/10.3329/sja.v19i2.57675
23. Souza L, Miranda G, Galvão J, Eckert F, Mantovani É, Lima RO. *et al*. Genetic control of grain yield and nitrogen use efficiency in tropical maize. Pesquisa Agropecuária Brasileira,2008:43:1517-1523. https://doi.org/10.1590/s0100-204x2008001100010
24. Sun X-c, Chen H, Wang P, Chen F, Yuan L, Mi G. *et al*. Low nitrogen induces root elongation via auxin-induced acid growth and auxin-regulated target of rapamycin (TOR) pathway in maize. Journal of plant physiology,2020:254:153281.
25. Varga B, Grbeša D, Kljak K, Horvat T. Nitrogen Uptake and Utilization Efficiency of Maize Hybrids under High and Limited Nutrient Supply. Cereal Research Communications,2008:36:463-466. https://doi.org/10.1556/CRC.36.2008.Suppl.1
26. Vicente EJ, Dean DR. Keeping the nitrogen-fixation dream alive. Proceedings of the National Academy of Sciences,2017:114(12):3009-3011.
27. Wang X, Miao Y, Dong R, Chen Z, Kusnierek K, Mi G. *et al*. Economic Optimal Nitrogen Rate Variability of Maize in Response to Soil and Weather Conditions: Implications for Site-Specific Nitrogen Management. Agronomy, 2020.
28. Wang Z, Yu X, Gao J, Sun J-Y, Su Z-J, Yu S. *et al*. Physiological Basis of Heterosis for Nitrogen Use Efficiency of Maize. Scientific Reports, 2019, *9*. https://doi.org/10.1038/s41598-019-54864-x
29. Wani SH, Vijayan R, Choudhary M, Kumar A, Zaid A, Singh V. *et al*. Nitrogen use efficiency (NUE): elucidated mechanisms, mapped genes and gene networks in maize (Zea mays L.). Physiology and Molecular Biology of Plants,2021:27(12):2875-2891.
30. Wilkinson SR, Ohlrogge AJ. Mechanism for Nitrogen-increased Shoot/Root Ratios. Nature,1964:204:902-904.
31. Yang T, Zhang W, Cui Y, Wang Y, Qin H, Lv X. *et al*. Genome-Wide Association Studies for Wheat Height Under Different Nitrogen Conditions. Agriculture,2024:14(11):1998. https://www.mdpi.com/2077-0472/14/11/1998
32. Ying S, Webster B, Gomez-Cano L, Shivaiah K-k, Wang Q, Newton L. *et al*. Multiscale physiological responses to nitrogen supplementation of maize hybrids. Plant Physiology,2023:195:879-899.
33. Ying S, Webster B, Gomez-Cano L, Shivaiah KK, Wang Q, Newton L. *et al*. Multiscale physiological responses to nitrogen supplementation of maize hybrids. Plant Physiol,2024:195(1):879-899. https://doi.org/10.1093/plphys/kiad583
34. Zhang L, Zhang X, Gao Q, Yan L. Nitrogen Application Effect on Maize Yield, NH3, and N2O Emissions in Northeast China by Meta-Analysis. Agronomy,2023:13(6):1479. https://www.mdpi.com/2073-4395/13/6/1479
35. Zheng-rui W, Yu-kui R, Jian-bo S, Fu-suo Z. Effects of N fertilizer on root growth in Zea mays L. seedlings. Spanish Journal of Agricultural Research,2008:6(4):677-682.