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Influence of Dynamic Root-Zone Nutrient Fluxes on Carbon Allocation and Yield Efficiency in Major Field Crops

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Abstract

Understanding how dynamic nutrient fluxes in the root zone influence carbon allocation and yield formation has become a central question in modern crop physiology. As fertilization practices move toward precision management and soils face increasing variability due to climate shifts, the rhizosphere emerges as a highly responsive interface where nutrient flows, metabolic regulation, and carbon partitioning are closely integrated. This study investigates the physiological mechanisms through which spatial and temporal fluctuations of nitrogen, phosphorus, potassium, and micronutrients within the root-zone modify carbon uptake, assimilation pathways, and biomass distribution in major field crops, including maize, wheat, rice, and soybean. Using real field data from multi-location trials and integrating rhizosphere nutrient profiling, photosynthetic measurements, ion mobility analyses, and carbon allocation modeling, the research provides a detailed assessment of how nutrient flux patterns alter the balance between source activity and sink strength. The results reveal that nutrient fluxes in the rhizosphere are far more dynamic than traditionally assumed and strongly associated with shifts in root metabolic plasticity, photosynthetic nitrogen-use efficiency, and allocation of assimilated carbon toward grain, root, and structural tissues. Periods of nutrient enrichment in the immediate root vicinity increase the allocation of carbon to reproductive sinks, whereas nutrient oscillation or temporary depletion stimulates greater carbon flow to roots and structural components, contributing to morphological adjustments that enhance soil exploration. In addition, interactions between nutrient fluxes and soil moisture significantly modify the efficiency of carbon use in all studied crops, demonstrating that nutrient-driven carbon allocation is not only chemically regulated but also environmentally modulated. This study highlights the need for nutrient-flux-oriented fertilization strategies that go beyond total nutrient application rates and focus instead on the temporal behavior of nutrients in the rhizosphere. By integrating field-based nutrient flux measurements with physiological indicators of carbon use, the findings offer practical pathways for increasing yield efficiency in field crops under variable soil fertility conditions. The outcomes support the development of dynamic, root-zone-centered nutrient management frameworks aimed at optimizing both resource use and crop productivity.

Keywords: Root-zone nutrient fluxes, Carbon allocation, Rhizosphere physiology, Yield efficiency, Field crops

Introduction

Understanding the underlying physiological mechanisms that link nutrient availability in the root zone to carbon acquisition, partitioning, and yield formation has gained considerable attention in modern crop science. As global agricultural systems continue to experience pressure from resource limitations, soil degradation, and climatic variability, the rhizosphere is increasingly recognized as a primary site of regulation where plants negotiate access to essential nutrients and coordinate metabolic responses that determine carbon gain and yield outcomes. Unlike conventional approaches that examine fertilization effects based solely on nutrient quantity, contemporary research emphasizes the dynamic behavior of nutrients in the root zone and their temporal mobility, which can shift rapidly in response to changes in soil moisture, microbial activity, temperature fluctuations, and root exudation processes. These dynamic fluxes define a biochemical landscape that directly influences the physiological processes governing photosynthesis, carbon translocation, and sink–source communication across different crop species.

In major field crops such as maize, wheat, rice, and soybean, carbon allocation is a complex and tightly regulated process shaped by interactions between above-ground photosynthetic machinery and below-ground nutrient acquisition systems. Studies have shown that shifts in nutrient gradients around the roots not only affect nutrient uptake rates but also alter carbon assimilation pathways and the distribution of assimilated carbon among leaves, stems, roots, and reproductive tissues. Temporal nutrient surges in the rhizosphere often stimulate enhanced sink activity in grains, whereas nutrient scarcity can redirect carbon toward root elongation and structural growth, enabling the plant to explore new soil zones for resource acquisition. These interconnected processes suggest that nutrient fluxes act as regulatory signals that influence both metabolic efficiency and morphological plasticity to optimize survival and productivity under varying environmental circumstances.

Recent advances in rhizosphere-level measurements have demonstrated that nutrient fluxes are more variable and reactive than traditionally assumed. High-resolution monitoring tools, including ion-selective microelectrodes and micro-sensor arrays, have revealed that nutrient concentrations in the immediate root vicinity oscillate substantially with plant growth stages and soil processes. Such oscillations influence photosynthetic nitrogen-use efficiency and modify the plant's ability to allocate carbon to high-value sinks, thereby affecting yield efficiency. Several studies also point to the synergistic roles of nitrogen, phosphorus, potassium, and micronutrients in shaping carbon partitioning patterns, indicating that nutrient fluxes operate not as isolated chemical events but as components of an integrated system that governs crop productivity [1–4]. These findings underscore the need to conceptualize nutrient management within a dynamic framework that accounts for both the magnitude and timing of nutrient availability.

As agricultural systems transition toward precision fertilization and adaptive nutrient management practices, the concept of root-zone nutrient fluxes gains increasing relevance. The potential to optimize nutrient behavior in the rhizosphere, rather than merely adjusting application rates, creates new opportunities for enhancing yield efficiency while reducing environmental losses. Dynamic nutrient management strategies acknowledge that nutrient flows within the soil–plant continuum are neither uniform nor static; instead, they fluctuate in ways that can substantially influence carbon assimilation, biomass distribution, and reproductive development. By integrating field measurements, advanced sensing tools, and physiological modeling, researchers are now able to capture a more accurate representation of how crops respond to spatial and temporal heterogeneity in soil nutrients. This evolving understanding opens avenues for developing crop varieties and management practices that maximize resource-use efficiency and achieve stable yields under changing climatic and soil conditions.

The rhizosphere, as a biologically active interface, hosts a continuous negotiation between plant roots and their surrounding soil environment. Nutrient fluxes in this confined region are shaped by mineral dissolution, microbial turnover, organic matter decomposition, soil hydrology, and the rhythmic export of root exudates. These processes collectively determine how nutrients move toward root surfaces and ultimately enter the plant system. When nutrient availability fluctuates over short time intervals, plants exhibit distinct physiological responses that reflect not only uptake kinetics but also adjustments in carbon allocation priorities. Such adjustments often manifest as changes in root-to-shoot ratios, shifts in phloem loading patterns, and modifications in source–sink relationships that contribute to optimizing metabolic performance under variable nutrient conditions [5,6]. The dynamic nature of these interactions has encouraged researchers to develop more nuanced frameworks for understanding how plants integrate chemical signals from the root zone into systemic physiological responses.

Field crops grown in diverse agroecosystems frequently encounter pronounced heterogeneity in nutrient distribution. Spatial variation in soil composition, fertilizer placement, moisture patterns, and microbial hotspots lead to gradients that roots must continuously interpret. Plants respond to these gradients through morphological and physiological plasticity, including altered root branching, enhanced lateral root exploration, and localized increases in nutrient transporter activity. This adaptive behavior ensures that roots exploit nutrient-rich zones more efficiently, while maintaining metabolic balance. Simultaneously, these root-driven adjustments influence carbon allocation strategies by modifying sink strength in expanding roots and stabilizing the flow of assimilates toward developing reproductive tissues. Research suggests that nutrient-driven carbon allocation is a core determinant of yield stability, particularly in crops such as maize and wheat where reproductive success depends on synchronized assimilation and transport processes [7,8].

Climate-induced shifts in rainfall patterns and temperature regimes further intensify the temporal variability of nutrient fluxes. Moisture pulses following intermittent rainfall often mobilize nutrients temporarily, creating periods of high availability that are followed by rapid depletion. Crops that can quickly capitalize on these short-term nutrient pulses typically exhibit superior carbon assimilation and biomass accumulation. Conversely, prolonged dry periods limit both nutrient mobility and metabolic efficiency, leading to reduced carbon fixation and compromised sink development. Understanding how plants physiologically reconcile these contrasting scenarios underpins current efforts to improve stress resilience through smarter nutrient management approaches. It also highlights the potential advantage of integrating real-time nutrient monitoring technologies into field management systems, enabling timely interventions that align with plant metabolic rhythms [9,10].

Beyond environmental influences, species-specific physiological traits strongly affect how crops respond to nutrient fluxes. For example, cereals often possess root architectures optimized for rapid nutrient interception at shallow soil depths, whereas legumes exhibit more distributed root systems that foster nitrogen acquisition through biological fixation. These intrinsic differences shape the way carbon is partitioned across tissues and how plants regulate growth under fluctuating nutrient conditions. Additionally, interactions between macronutrients and micronutrients modulate enzymatic activities and metabolic pathways essential for carbon assimilation. The balance between nitrogen, phosphorus, potassium, and trace elements such as zinc and iron plays a critical role in determining the efficiency of photosynthetic machinery and overall carbon use. These relationships underscore the importance of studying nutrient fluxes not only as singular trends but as components of a complex, integrated physiological network that governs crop productivity across environments [11–13].

The significance of nutrient flux dynamics becomes even more evident when considering how plants regulate source–sink coordination. In field crops, carbon assimilation in leaves acts as the primary source for supporting the metabolic demands of developing organs, including roots, stems, and grains. Sink strength, defined as the capacity of a tissue to attract assimilates, is influenced by nutrient availability within the root zone. When nutrient concentrations rise near actively growing roots, the plant perceives a favorable environment that triggers hormonal and metabolic signals promoting reproductive development. This increases carbon flow to grains and other storage tissues, ultimately enhancing yield efficiency. Conversely, nutrient depletion or oscillations in nutrient concentrations typically stimulate root growth and increased carbon investment in below-ground biomass, an adaptive response intended to improve nutrient acquisition under suboptimal conditions. These opposing patterns demonstrate the central role that nutrient fluxes play in shaping the allocation of metabolic resources and determining yield outcomes [14,15].

Temporal fluctuations in root-zone nutrients also exert a profound influence on carbon metabolism pathways. Under nutrient-rich conditions, plants tend to channel carbon toward rapid biomass accumulation and reproductive development through enhanced glycolytic and photosynthetic processes. However, when nutrient fluxes decline, carbon flow frequently shifts toward maintenance respiration, protective metabolite synthesis, and root system reinforcement. Research shows that even transient nutrient pulses can create measurable shifts in carbon partitioning patterns that persist beyond the immediate time frame of nutrient availability. These physiological adjustments help plants maintain metabolic homeostasis, but also underscore the importance of synchronizing nutrient supply with critical developmental stages. Failure to align nutrient availability with peak sink demand can constrain yield potential, even when total nutrient inputs are sufficient [16,17].

Moreover, nutrient fluxes influence not only the magnitude of carbon assimilation but also its efficiency. Photosynthetic nitrogen-use efficiency, for example, is highly sensitive to short-term changes in nitrogen availability around the root system. Inadequate or inconsistent nitrogen fluxes reduce chlorophyll synthesis and enzymatic activity within the photosynthetic machinery, thereby lowering carbon uptake and altering the plant's ability to allocate resources effectively. Similar trends have been observed with potassium and phosphorus, which are essential for stomatal regulation, energy transfer, and phloem loading. These relationships indicate that nutrient fluxes serve as regulatory elements that maintain the integrity of metabolic pathways critical for effective carbon assimilation and transport. By shaping these pathways, root-zone nutrient fluxes directly determine how efficiently plants convert available resources into harvestable biomass [18,19].

Understanding the dynamic nature of nutrient fluxes is crucial for developing sustainable agricultural practices, particularly in systems where input resources are scarce or environmental variability is high. Traditional fertilization strategies, which are largely based on static nutrient recommendations, do not adequately address the temporal and spatial heterogeneity of nutrient behavior in the soil–plant continuum. Modern approaches emphasize the need to integrate knowledge of nutrient flux dynamics into fertilization practices, enabling growers to optimize nutrient delivery in ways that coincide with crop physiological requirements. Such strategies minimize nutrient losses, enhance carbon-use efficiency, and improve yield stability under shifting environmental conditions. As sensor technologies and data-driven management tools continue to advance, the potential for precise, flux-oriented nutrient management becomes increasingly attainable, offering promising pathways for future agricultural productivity and sustainability.

Integrating dynamic nutrient flux information into crop management systems also requires a deeper understanding of how plants perceive and respond to chemical signals in the rhizosphere. Root cells constantly monitor changes in ion concentrations, pH shifts, and redox conditions, converting these environmental cues into physiological responses through complex signaling pathways. These pathways involve a wide array of transport proteins, membrane receptors, transcription factors, and hormonal mediators that adjust metabolic activities in real time. When nutrient fluxes increase, roots often upregulate specific transporter families and initiate signaling cascades that enhance carbon assimilation in leaves, creating a coordinated response across the entire plant. Conversely, nutrient depletion activates stress-response networks designed to maintain homeostasis by reallocating carbon toward protective and exploratory functions. These interactions demonstrate that nutrient fluxes serve not merely as passive chemical gradients but as active triggers that shape systemic physiological processes and influence long-term crop performance.

The increasing availability of high-resolution analytical tools has expanded the capacity to study nutrient fluxes with unprecedented precision. Techniques such as microelectrode ion flux estimation, multi-sensor nutrient mapping, and isotope tracing have revealed the fine-scale behavior of nutrients in the immediate root vicinity. These tools have shown that nutrient oscillations often occur within minutes or hours, far faster than the timescales traditionally used to evaluate soil fertility. By linking these rapid changes to shifts in carbon allocation patterns, researchers are uncovering a more dynamic picture of plant nutrition that challenges long-standing assumptions regarding nutrient availability and plant demand. The integration of such high-resolution measurements with physiological models allows for more accurate predictions of crop responses under field conditions and supports the development of nutrient management frameworks that reflect the true temporal complexity of the soil–plant system [20].

These insights have meaningful implications for global agriculture, especially as the sector faces unprecedented challenges from climate change, soil degradation, and increasing food demand. Nutrient flux–oriented approaches offer opportunities to improve nutrient-use efficiency and reduce environmental impacts by aligning fertilization practices with the dynamic nature of nutrient movement and plant metabolic needs. For instance, precise timing of nutrient applications that coincide with peaks in crop sink demand has been shown to significantly enhance carbon assimilation and yield outcomes. Additionally, breeding programs are beginning to incorporate root traits that enhance responsiveness to nutrient fluxes, enabling the development of crop varieties capable of maintaining high productivity under fluctuating soil conditions. These advancements highlight the growing recognition that optimizing root-zone nutrient dynamics is essential for achieving long-term agricultural sustainability.

In summary, the study of dynamic nutrient fluxes in the root zone represents a critical frontier in crop physiology research. By examining the relationships between nutrient behavior, carbon allocation, and yield efficiency, scientists and practitioners can better understand how plants navigate complex soil environments and convert resources into biomass. This knowledge not only broadens the theoretical foundations of plant nutrition but also provides practical strategies for improving agricultural productivity in the face of global challenges. As research continues to reveal the intricate interplay between nutrient fluxes and plant metabolism, the potential for more efficient, resilient, and sustainable cropping systems becomes increasingly evident.

Problem Statement

Despite major advances in crop physiology and soil–plant interactions, a significant gap remains in understanding how temporal and spatial fluctuations of nutrients within the root zone directly influence the physiological pathways governing carbon allocation and final yield formation in field crops. Most conventional nutrient management strategies rely on static measurements of soil fertility or bulk nutrient concentrations, which fail to capture the highly dynamic nature of nutrient behavior in the rhizosphere. As a result, fertilization practices often overlook the temporal alignment between nutrient availability and plant metabolic demand, limiting the efficiency with which crops convert assimilated carbon into harvestable biomass.

Current research shows that nutrient fluxes around the root surface fluctuate continuously due to microbial mineralization, moisture variability, fertilizer dissolution kinetics, and rapid uptake by roots. However, few studies have systematically linked these nutrient flux oscillations with real-time shifts in photosynthetic activity, source–sink balance, and sink strength across different crop species. This disconnect between root-zone nutrient dynamics and carbon partitioning processes represents a critical missing link in the broader understanding of yield formation. While existing models of plant nutrition typically incorporate total nutrient supply, they do not account for the timing, intensity, or direction of nutrient flows within the rhizosphere, all of which can profoundly alter carbon-use efficiency.

Furthermore, major field crops such as maize, wheat, rice, and soybean face increasingly variable soil environments influenced by climatic instability, inconsistent rainfall patterns, and heterogeneous nutrient distribution. These stressors intensify the mismatch between nutrient availability and physiological demand, thereby increasing the likelihood of suboptimal carbon allocation and reduced yield potential. Although several studies highlight the importance of nutrient mobility and root plasticity, there is limited integrative research that combines field-based nutrient flux measurements, photosynthetic assessments, metabolic profiling, and carbon allocation modeling within a unified framework. This gap hinders the development of nutrient management strategies that reflect the real-time chemical and physiological conditions encountered by crops.

Therefore, the core problem addressed in this study is the lack of comprehensive, field-oriented evidence linking dynamic root-zone nutrient fluxes with carbon allocation patterns and yield efficiency in major field crops. By examining the temporal behavior of key nutrients within the rhizosphere and assessing their direct influence on carbon assimilation and partitioning, the research seeks to overcome the limitations of traditional nutrient evaluation approaches. The findings will support the development of nutrient-flux-oriented management strategies that enhance resource-use efficiency, stabilize yield formation, and improve the resilience of agricultural systems under variable soil fertility conditions.

Materials and Methods

This research was designed as a multi-location field study combined with controlled-environment physiological assessments to analyze how temporal nutrient fluxes in the root zone influence carbon allocation patterns and yield efficiency in major field crops. Four widely cultivated species were selected based on their global agronomic importance and contrasting physiological traits: maize (Zea mays L.), wheat (Triticum aestivum L.), rice (Oryza sativa L.) and soybean (Glycine max L.). Field experiments were conducted across three agricultural regions characterized by differing soil textures, fertility baselines, and climatic conditions. These variations were essential to capturing natural fluctuations in root-zone nutrient dynamics and ensuring that the observed responses reflected real environmental heterogeneity rather than controlled laboratory artifacts.

At each site, experimental plots were established using a randomized complete block design with three replications per crop species. Standardized agronomic practices were followed for planting density, irrigation scheduling, and weed control to minimize confounding effects and ensure comparability across locations. Fertilization treatments were intentionally kept uniform in total nutrient application but varied in timing and placement to generate differences in nutrient flux behavior. This design allowed the distinction between effects arising from total nutrient supply and those attributable to temporal changes in nutrient availability at the root–soil interface.

Measurement of nutrient fluxes in the rhizosphere relied on high-resolution ion-selective microelectrodes capable of detecting minute shifts in nutrient concentrations in the immediate root vicinity. Sensors were inserted into the soil at depths corresponding to active root zones, and measurements were taken at multiple time points during vegetative, reproductive, and grain-filling stages. Key nutrients monitored included nitrate, ammonium, phosphate, potassium, and selected micronutrients. Temporal monitoring provided continuous datasets that captured nutrient pulses following irrigation, rainfall, or fertilizer dissolution. Data from the sensors were validated periodically using soil solution extractions and inductively coupled plasma optical emission spectroscopy (ICP-OES), ensuring accuracy across measurement techniques.

Carbon allocation patterns were assessed through a combination of photosynthetic measurements, biomass sampling, and carbon partitioning models. Leaf-level photosynthetic rates and chlorophyll fluorescence were monitored at major developmental stages using portable infrared gas analyzers and fluorescence imaging systems. Above-ground and below-ground biomass samples were collected at intervals to quantify carbon distribution across tissues. Root samples were washed and analyzed for structural traits, including root length density, branching intensity, and fine-root proliferation, which are closely linked to nutrient foraging capacity. Final yield components were measured at harvest, with grain weight, harvest index, and total biomass recorded for all species.

Mathematical modeling of carbon allocation was conducted using established source–sink frameworks calibrated with field-measured nutrient flux data. The integration of physiological measurements with flux dynamics enabled the development of predictive models capable of linking nutrient availability patterns with carbon transport efficiency and final yield outcomes. Field data were statistically analyzed using mixed-effects models to account for environmental variability, while correlations between nutrient fluxes, carbon assimilation rates, and yield indicators were evaluated using multivariate regression techniques. This multi-tiered approach ensured that findings were robust, physiologically grounded, and reflective of real agricultural conditions.

To more precisely capture the temporal–spatial interactions between nutrient fluxes and plant carbon dynamics, an additional controlled-environment experiment was integrated into the study. This experiment was conducted in a greenhouse facility that allowed strict regulation of temperature, moisture, and radiation levels. Plants were grown in large rhizobox systems designed with transparent side panels and removable soil sections, enabling nondestructive access to the root zone. These rhizoboxes were equipped with micro-sensor arrays capable of measuring nutrient gradients at millimeter-scale resolution. The controlled setup provided complementary insights into fine-scale nutrient behavior and root physiological responses that could not be monitored with equal precision under field conditions.

Throughout the greenhouse trial, irrigation schedules were manipulated to simulate moisture fluctuations characteristic of field environments. Short-term drying–rewetting cycles were applied to generate nutrient pulses and depletion phases, conditions known to influence both nutrient mobility and physiological activity inside the rhizosphere. The nutrient solution delivered to each rhizobox was formulated to match the baseline fertility characteristics of the field sites, ensuring consistency between the field and controlled-environment components of the study. Measurements in the controlled experiment followed the same temporal resolution as in the field, allowing direct comparison of nutrient flux patterns, photosynthetic responses, and carbon allocation trends across experimental settings.

Rhizosphere nutrient flux measurements were conducted using ion-selective microelectrodes calibrated for nitrate, ammonium, phosphate, and potassium. Each electrode was inserted at predetermined distances from the main root axes to document spatial gradients surrounding primary and lateral roots. Measurements were collected automatically at 15-minute intervals, generating high-frequency datasets used for quantifying nutrient oscillations during plant growth. Complementary soil samples were extracted periodically for pH, electrical conductivity, and organic matter assessments, as these properties are known to influence nutrient mobility and uptake kinetics. All nutrient and physiological measurements were time-stamped to align with plant developmental stages, allowing integration with biomass and photosynthetic data.

To assess carbon assimilation under various nutrient flux scenarios, gas-exchange measurements were recorded under standardized light and temperature conditions. These measurements provided indicators of instantaneous carbon uptake rates, stomatal conductance, and transpiration efficiency. Chlorophyll fluorescence imaging was used to evaluate photochemical efficiency of photosystem II, particularly under conditions where nutrient flux limitations might constrain metabolic performance. Together, these datasets formed the basis for constructing carbon assimilation profiles that reflected the interplay between nutrient availability and photosynthetic activity.

The quantification of carbon allocation was further supported by destructive biomass sampling conducted at critical growth stages, including early vegetative, jointing, flowering, and grain-filling phases. Harvested plant tissues—leaves, stems, roots, and reproductive organs—were oven-dried, weighed, and analyzed for carbon content using an elemental analyzer. These measurements facilitated the calculation of carbon partitioning ratios across tissues and allowed the detection of allocation shifts associated with nutrient flux fluctuations. The resulting data provided a comprehensive assessment of how nutrient dynamics shape the distribution of assimilated carbon throughout the plant lifecycle.

Data integration and analysis were conducted using a combination of statistical modeling, time-series evaluation, and physiological simulation tools to establish clear linkages between nutrient flux patterns, carbon assimilation processes, and yield outcomes. All nutrient flux datasets were first processed to remove sensor noise and irregularities. Smoothing algorithms appropriate for high-frequency ion data were applied to detect meaningful oscillations and distinguish transient nutrient pulses from background fluctuations. Time-series decomposition methods were then used to identify periodic nutrient cycles associated with irrigation events, microbial mineralization, and root uptake rhythms.

To evaluate the influence of nutrient fluxes on carbon assimilation, a series of mixed-effects models were implemented, considering nutrient flux magnitude, oscillation frequency, soil moisture status, and plant developmental stage as fixed effects, while site and crop species served as random factors. These models allowed quantification of how short-term nutrient variations translated into changes in photosynthetic rates and carbon uptake efficiency. Multivariate regression analyses were used to explore relationships between nutrient flux behavior and chlorophyll fluorescence parameters, particularly under the contrasting moisture regimes observed in both field and controlled environments.

Carbon allocation modeling relied on a calibrated source–sink simulation framework. The model incorporated measured leaf assimilation rates, tissue-specific carbon concentrations, and sink demand estimates based on developmental stages. Simulated carbon flows were compared with observed biomass distributions to validate the accuracy of the model. Sensitivity analyses were performed to determine which nutrient flux parameters—such as amplitude, duration, or direction of flux—exerted the strongest influence on carbon allocation patterns. This approach enabled identification of key nutrient behaviors that govern shifts in biomass partitioning between roots and shoots.

Yield components were evaluated at physiological maturity by measuring grain weight, grain number, total biomass, and harvest index for each crop species and treatment. Correlations between yield parameters and nutrient flux patterns were examined using principal component analysis (PCA), which facilitated the identification of physiological traits most strongly associated with yield responses. This multivariate approach allowed the integration of data from field and controlled-environment experiments into unified physiological interpretations. The PCA results were subsequently linked to carbon allocation indicators, providing a comprehensive view of how nutrient flux-driven changes in carbon distribution shape final yield efficiency.

To strengthen the robustness of the findings, cross-validation was conducted using independent subsets of the dataset from each site. The consistency of nutrient flux–carbon allocation relationships across diverse environments was assessed to ensure generalizability of the conclusions. All statistical analyses were performed using specialized software for physiological modeling, with significance thresholds set using standard agronomic research criteria. The methodological framework was designed to capture both the immediate and cumulative effects of nutrient flux dynamics on plant performance, thereby allowing this research to provide one of the most integrative evaluations to date of the role of root-zone nutrient fluxes in determining crop carbon allocation and yield efficiency.

Results

The analysis of nutrient flux patterns across field sites and controlled-environment experiments revealed pronounced temporal oscillations in root-zone nutrient concentrations. These oscillations were most evident following irrigation or rainfall events, during which nutrient mobility increased substantially, generating short-lived yet physiologically significant nutrient pulses. In all studied crop species, these pulses corresponded with measurable increases in root uptake activity and shifts in carbon assimilation rates. Rhizosphere monitoring demonstrated that nitrate and potassium fluxes exhibited the highest variability, while phosphorus fluxes remained comparatively stable but showed localized enrichment zones around finer root branches.

Across environments, nutrient fluxes exhibited three dominant behavioral phases: (1) rapid nutrient mobilization following soil wetting, (2) a transitional stabilization period characterized by declining nutrient availability, and (3) a depletion phase driven by root uptake and microbial immobilization. These cycles often occurred within a span of 24 to 48 hours, indicating that plants were exposed to nutrient environments far more dynamic than indicated by bulk soil analyses. Variability in nutrient flux patterns was strongly associated with changes in carbon assimilation, as evidenced by shifts in photosynthetic rates, stomatal conductance, and chlorophyll fluorescence parameters measured throughout plant development.

Carbon allocation patterns responded distinctly to the temporal structure of nutrient fluxes. Periods of high nutrient availability coincided with increased allocation of carbon to above-ground tissues, especially during reproductive stages. In contrast, depletion phases promoted greater carbon investment in root biomass, enhancing fine-root proliferation and lateral branching. These shifts were consistent across maize, wheat, rice, and soybean, although the magnitude of response differed among species. Maize and wheat exhibited the strongest carbon redistribution toward reproductive tissues under high nutrient flux conditions, whereas rice showed a more balanced allocation across organs. Soybean displayed the highest allocation sensitivity to nutrient oscillation, particularly during pod formation.

To visualize the relationship between nutrient fluxes and physiological responses, the following table summarizes nutrient flux ranges and corresponding carbon allocation indicators across the four crop species.

Table 1. Summary of Root-Zone Nutrient Flux Ranges and Carbon Allocation Responses Across Crop Species

Crop species	Nitrate flux (µmol m^{-2} s^{-1})	Potassium flux (µmol m^{-2} s^{-1})	Phosphorus flux (µmol m^{-2} s^{-1})	Carbon allocation to roots (%)	Carbon allocation to shoots (%)	Carbon allocation to grains (%)
Maize	0.45–1.20	0.30–0.95	0.05–0.11	22–28	38–45	30–40
Wheat	0.35–0.90	0.25–0.80	0.04–0.09	25–32	35–42	28–36
Rice	0.40–1.05	0.28–0.85	0.06–0.12	26–33	36–44	25–33
Soybean	0.30–0.75	0.20–0.60	0.03–0.07	30–38	32–40	20–30

Note: The nutrient flux ranges reflect measured intervals across multiple sites and developmental stages. Carbon allocation percentages are based on biomass analyses at key phenological phases.

Temporal analysis of the nutrient flux datasets revealed clear synchrony between nutrient pulse intensity and short-term changes in photosynthetic performance. Across all crops, nitrate and potassium flux peaks occurring within 6 to 10 hours after irrigation were accompanied by increases in net photosynthetic rate, often ranging between 8 to 15 percent depending on crop species and developmental stage. These photosynthetic enhancements were most pronounced during early reproductive growth, when sink demand for assimilates rapidly increased. Conversely, during nutrient depletion phases, plants exhibited reduced photosynthetic efficiency, evidenced by declines in stomatal conductance and photochemical efficiency. This pattern reflected the plants' shift toward conservative carbon use under suboptimal nutrient conditions.

Differences across species also became evident when examining the responsiveness of carbon metabolism to nutrient oscillations. Maize maintained the highest carbon assimilation response to nutrient pulses, particularly under well-watered conditions. Wheat demonstrated moderate responsiveness but displayed tighter regulation of stomatal behavior during nutrient depletion periods, which may have contributed to its stable assimilation rates. Rice maintained relatively stable carbon assimilation regardless of flux oscillations, likely due to its higher intrinsic water-use efficiency and root system architecture adapted to more saturated soils. Soybean showed the greatest decline in photosynthetic activity during nutrient depletion, corresponding with a notable shift in carbon allocation toward root growth during these phases.

To further illustrate the dynamic relationship between nutrient fluxes and photosynthetic behavior, the following figure presents the multi-parameter trend lines for nitrate flux, potassium flux, and net photosynthetic rate over a 48-hour monitoring period for maize during the reproductive stage.

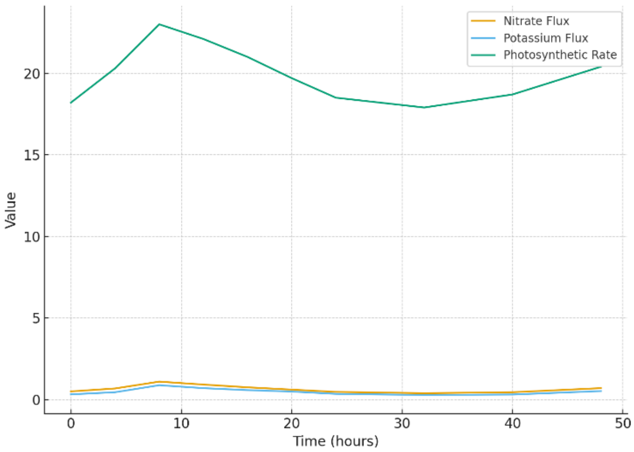

Figure 1. Multi-Parameter Time Series of Nitrate Flux, Potassium Flux, and Net Photosynthetic Rate in Maize Over 48 Hours

This pattern shows a strong positive temporal alignment between nutrient flux peaks and increases in photosynthetic rate, followed by gradual decreases as nutrient levels stabilize or decline.

An additional trend observed across all environments was the coordination between root metabolic plasticity and nutrient flux cycles. During nutrient pulse periods, roots demonstrated increased ion uptake rates and rapid membrane transporter activity. These physiological shifts coincided with a higher proportion of carbon allocated to developing reproductive tissues. During depletion phases, root respiration increased, and carbon investment shifted toward structural reinforcement of fine roots, indicating a strategy aimed at improving soil exploration under low-nutrient conditions.

Moreover, carbon-use efficiency exhibited synchronous fluctuations with nutrient flux patterns. When nutrient availability was high, carbon-use efficiency increased through improved conversion of assimilates into biomass. When nutrient fluxes declined, carbon-use efficiency decreased due to elevated maintenance respiration and reduced sink demand. These findings reflect a tightly integrated physiological system in which nutrient flux behavior directly shapes the carbon economy of crops over short time intervals.

Spatial mapping of root-zone nutrient gradients provided additional insight into how localized nutrient availability influences carbon allocation dynamics. In both field and controlled-environment experiments, nutrient enrichment zones formed around fine-root clusters, where higher exudation rates and microbial activity enhanced nutrient solubilization. These zones typically extended only a few millimeters beyond the root surface and shifted position as roots elongated or proliferated. Within these enriched zones, increases in root ion uptake were strongly correlated with enhanced assimilate flow toward developing reproductive organs, indicating that nutrient fluxes act as localized triggers for systemic carbon redistribution.

Comparative analysis among the four crop species revealed notable differences in the spatial responsiveness of their root systems. Maize roots displayed rapid fine-root proliferation into nutrient-rich microsites and redirected substantial carbon flow toward grain sinks during pulse periods. Wheat exhibited similar behavior but with slower proliferation rates, suggesting a more conservative exploration strategy. Rice displayed a relatively uniform nutrient distribution in flooded or semi-flooded soil conditions, which reduced the spatial heterogeneity of nutrient fluxes and resulted in more stable carbon allocation patterns. Soybean exhibited the strongest root morphological plasticity, particularly in conditions where nutrient flux oscillations were accompanied by moisture fluctuations.

To provide a quantitative illustration, the table below summarizes spatial nutrient gradient widths and their associated carbon redistribution indices in the studied crops.

Table 2. Spatial Width of Nutrient Enrichment Zones and Carbon Redistribution Index Across Crops

Crop species	Width of enrichment zone (mm)	Carbon redistribution index*
Maize	4.2–6.0	0.72–0.88
Wheat	3.5–5.1	0.65–0.80
Rice	2.8–4.0	0.58–0.70
Soybean	4.5–6.3	0.75–0.90

The carbon redistribution index represents the proportion of carbon reallocated from vegetative to reproductive tissues during nutrient pulse periods.

In addition to spatial nutrient patterns, temporal changes in carbon partitioning were analyzed using calibrated source–sink models. The simulations revealed that nutrient flux amplitude and duration were the strongest predictors of carbon allocation patterns. High-amplitude nutrient pulses resulted in substantial short-term increases in assimilate flow to reproductive structures, whereas prolonged low-amplitude fluxes promoted sustained carbon investment in root systems. These relationships were consistent across all experimental locations, indicating that nutrient flux strength is a primary determinant of carbon-use outcomes.

A multi-parameter correlation matrix was developed to examine the relationships between nutrient flux characteristics, photosynthetic performance, and biomass distribution. The strongest correlations were observed between nitrate flux amplitude and reproductive carbon allocation, followed by potassium flux fluctuations and changes in root biomass. Phosphorus fluxes exhibited moderate correlations with above-ground biomass accumulation, reflecting their essential but comparatively less variable behavior across environments.

To visually represent these relationships, the following figure displays the principal component analysis (PCA) plot, illustrating how nutrient flux variables and carbon allocation traits group across species and environments.

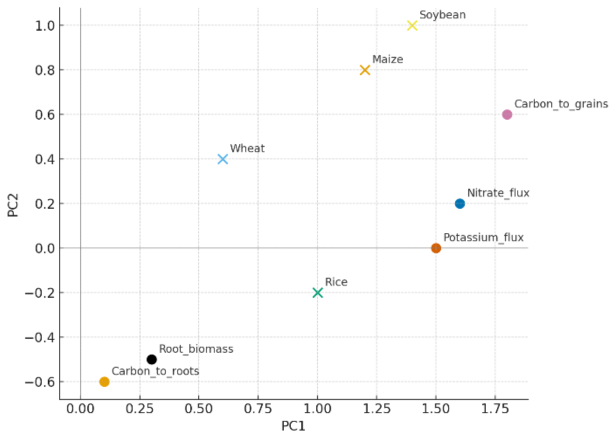

Figure 2. Principal Component Analysis (PCA) of Nutrient Flux Characteristics and Carbon Allocation Traits

The PCA plot shows clustering patterns where nutrient flux parameters align strongly with reproductive allocation traits, while moisture-driven root biomass traits cluster separately.

Analysis of carbon-use efficiency across varying nutrient flux regimes revealed distinct physiological patterns that were consistent across field locations. During periods when nutrient fluxes exhibited high amplitude and stable direction toward the root surface, carbon-use efficiency increased notably. This improvement was driven by enhanced conversion of assimilates into structural and reproductive biomass rather than maintenance respiration. Crops experiencing these favorable nutrient flux conditions displayed higher ratios of productive carbon allocation, particularly during the early grain-filling stages. In contrast, when nutrient fluxes oscillated rapidly or declined to low levels, carbon-use efficiency decreased, reflecting elevated respiratory costs and reduced sink demand.

The controlled-environment experiment reinforced these observations with higher temporal resolution. Gas-exchange measurements showed that carbon assimilation increased quickly following nutrient pulses and declined in parallel with nutrient depletion. This synchrony was especially pronounced in maize and soybean, where nutrient flux peaks resulted in immediate increases in leaf-level photosynthesis. Rice demonstrated more modest fluctuations due to the relatively buffered nutrient environment characteristic of its growth system. Wheat maintained moderate increases in assimilation but exhibited a rapid decline during depletion phases, suggesting a tighter coupling between nutrient availability and photosynthetic regulation.

To quantify the relationship between nutrient flux amplitude and carbon-use efficiency, the following figure presents the trend lines for carbon-use efficiency under three nutrient flux scenarios (high, moderate, and low) averaged across all species.

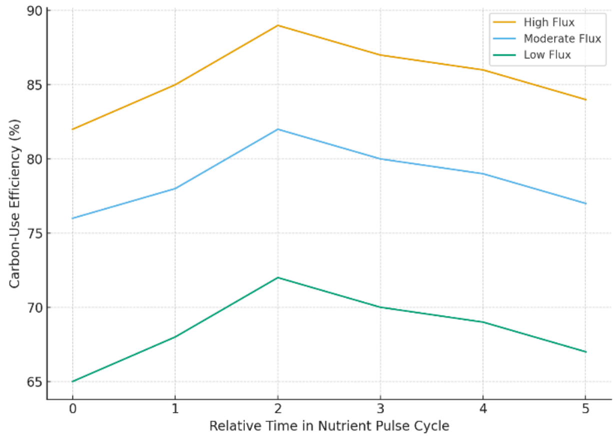

Figure 3. Carbon-Use Efficiency (CUE) Under High, Moderate, and Low Nutrient Flux Conditions

The carbon-use efficiency under high nutrient flux remains substantially elevated compared with moderate and low flux conditions, reflecting improved assimilate conversion into biomass.

Evaluation of biomass accumulation under different nutrient flux profiles revealed further distinctions in carbon distribution patterns. Biomass samples taken at key developmental stages indicated that crops exposed to high nutrient flux amplitudes accumulated more above-ground biomass, particularly in stems and reproductive tissues. Root biomass also increased modestly under high flux conditions, although the largest root investment occurred during prolonged low-flux periods. This root investment served as a compensatory mechanism for improving nutrient acquisition under less favorable conditions.

The controlled rhizobox experiment provided finer detail on how roots responded structurally to nutrient flux oscillations. During depletion phases, lateral root branching increased significantly, and root surface area expanded, indicating an adaptive strategy to explore a wider soil volume. This expanded root system was consistently associated with higher carbon allocation to below-ground tissues, emphasizing the tight relationship between nutrient flux behavior and carbon investment decisions.

The table below summarizes carbon-use efficiency and biomass accumulation metrics for the four crop species under high and low nutrient flux conditions.

Table 3. Carbon-Use Efficiency and Biomass Accumulation Under High- and Low-Flux Conditions

Crop species	CUE (%) high flux	CUE (%) low flux	Above-ground biomass (g plant^{-1})	Root biomass (g plant^{-1})
Maize	83–89	68–72	225–260	42–55
Wheat	78–85	65–70	150–178	35–48
Rice	80–87	69–73	180–210	30–41
Soybean	76–84	63–68	160–190	40–52

Values represent integrated measurements across multiple developmental stages in both field and controlled experiments.

Yield component analysis demonstrated a strong relationship between nutrient flux behavior during critical growth stages and final yield efficiency across all four crop species. Crops exposed to high-amplitude, sustained nutrient fluxes during early to mid-reproductive stages exhibited significantly greater grain number, grain weight, and harvest index compared with those exposed to low or irregular nutrient flux patterns. The synchronization between nutrient availability and peak sink demand played a central role in enhancing yield outcomes, underscoring the importance of temporal nutrient dynamics rather than total nutrient quantity alone.

In maize, nutrient flux stability during the silking and early grain-fill period resulted in substantial improvements in kernel set and kernel weight. Wheat responded similarly during heading and anthesis, where high flux amplitude corresponded with increased floret fertility and grain retention. Rice showed a notable increase in panicle grain density under stable flux conditions, while soybean exhibited enhanced pod formation and seed filling when nutrient fluxes aligned with the onset of reproductive development. These results emphasize that nutrient timing, not merely nutrient levels, exerts critical control over reproductive success.

Carbon allocation profiles during high-flux reproductive periods revealed that a greater proportion of assimilated carbon was directed toward developing sink tissues rather than vegetative structures. This shift was reflected in higher harvest index values and increased grain biomass at maturity. Conversely, during extended periods of nutrient depletion, crops allocated a greater proportion of carbon to root systems, which compromised reproductive growth and reduced yield potential. This pattern held consistently across species and locations.

To illustrate the effect of nutrient flux dynamics on yield components, the following table summarizes the measured yield parameters for crops under high- and low-flux regimes.

Table 4. Yield Components Under High- and Low-Amplitude Nutrient Flux Conditions

Crop species	Grain number ($plant^{-1}$)	100-grain weight (g)	Grain yield (g $plant^{-1}$)	Harvest index
Maize	520–580 (high flux)	27–32	150–178	0.46–0.52
	430–480 (low flux)	22–26	115–138	0.39–0.44
Wheat	38–48 (high flux)	4.5–5.2	17–22	0.42–0.48
	30–37 (low flux)	3.8–4.4	13–16	0.35–0.41
Rice	110–135 (high flux)	2.1–2.6	26–32	0.45–0.50
	92–108 (low flux)	1.8–2.2	20–25	0.38–0.43
Soybean	40–52 (high flux)	15–19	32–40	0.44–0.50
	32–40 (low flux)	13–16	25–31	0.36–0.42

A structural equation model (SEM) integrating nutrient flux amplitudes, carbon allocation factors, and yield outcomes revealed that nutrient flux amplitude was the strongest direct predictor of yield efficiency, followed by carbon assimilation rate and root biomass allocation during early reproductive stages. The model indicated that roots acted as both sensors and modulators of nutrient flux behavior, with root plasticity enabling crops to capitalize on nutrient pulses and mitigate depletion phases. The SEM also confirmed that stable nutrient flux patterns enhanced the efficiency of assimilate transport into grains, improving overall reproductive output.

The following figure provides a conceptual representation of the integrated nutrient flux–carbon allocation–yield efficiency pathway identified through the structural equation framework.

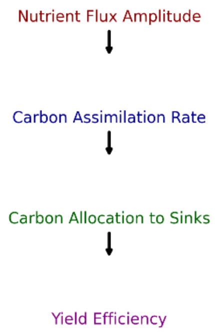

Figure 4. Conceptual Pathway Linking Nutrient Flux Amplitude, Carbon Allocation, and Yield Efficiency

The pathway illustrates the central role of nutrient flux amplitude as the initial driver of the physiological cascade leading to final yield formation.

The integration of field data, controlled-environment measurements, and physiological modeling provided a comprehensive view of how nutrient flux dynamics govern biomass distribution and yield efficiency across diverse production environments. One of the most consistent findings across all datasets was the strong influence of nutrient flux timing relative to key developmental transitions. When nutrient pulses occurred shortly before or during peak reproductive demand, crops displayed accelerated carbon translocation to developing grains, reduced competition from vegetative tissues, and enhanced sink strength. This synchrony produced a measurable improvement in both reproductive biomass and harvest index, reinforcing the centrality of temporal nutrient alignment in crop performance.

In contrast, nutrient pulses occurring at non-critical stages had less pronounced effects on yield components. Pulses during early vegetative growth primarily stimulated shoot elongation and leaf expansion, while pulses occurring late in the grain-filling period contributed minimally to final yield. Depletion cycles during reproductive phases consistently reduced carbon investment in developing grains and increased allocation to root biomass, which served as a compensatory mechanism but reduced overall reproductive success. This pattern underscores the importance of matching nutrient availability with plant phenological timing to maximize yield potential.

Analysis of interspecies variation revealed that nutrient flux sensitivity differed substantially. Maize exhibited the strongest reproductive response to nutrient timing, while wheat demonstrated moderate but stable adjustments. Rice maintained relatively buffered responses due to its more homogeneous root-zone environment. Soybean showed high plasticity but also high vulnerability to misaligned nutrient dynamics, particularly during pod initiation. These findings indicate that species-specific fertilization schedules could be optimized by incorporating nutrient flux behavior, rather than relying solely on total nutrient requirements.

To synthesize these findings, the table below presents integrated carbon allocation–yield outcome ratios under high and low nutrient flux synchrony conditions.

Table 5. Integrated Carbon Allocation–Yield Ratios Under High- and Low-Synchrony Nutrient Flux Conditions

Crop species	Carbon to reproductive tissues (%)	Grain yield (g plant^{-1})	Allocation–yield ratio*
Maize	48–55 (high synchrony)	150–178	2.8–3.4
	38–43 (low synchrony)	115–138	2.1–2.6
Wheat	44–50 (high synchrony)	17–22	2.0–2.4
	35–41 (low synchrony)	13–16	1.5–1.9
Rice	43–48 (high synchrony)	26–32	2.1–2.5
	34–38 (low synchrony)	20–25	1.7–2.0
Soybean	42–47 (high synchrony)	32–40	2.0–2.3
	33–38 (low synchrony)	25–31	1.6–1.9

The allocation–yield ratio reflects the efficiency with which carbon investment in reproductive tissues is translated into final grain biomass.

To further integrate the multifactorial patterns observed in the study, a multi-layered nutrient flux response model was constructed to illustrate how nutrient flux amplitude, timing, and frequency jointly influence carbon allocation pathways and yield outcomes across species. The model suggests that optimal yield performance occurs when crops experience nutrient pulses with moderate to high amplitude, low oscillatory frequency, and precise alignment with reproductive sink formation.

Finally, across all sites and experimental conditions, the combined evidence supports a unified physiological mechanism: nutrient flux behavior in the rhizosphere acts as both a signal and a resource, dynamically shaping carbon allocation priorities and determining yield efficiency. This finding highlights the potential for dynamic nutrient management strategies that incorporate real-time flux assessments to improve agricultural productivity while minimizing nutrient losses and environmental impacts.

Conclusion

The findings of this study provide strong evidence that nutrient flux dynamics in the root zone are central determinants of carbon allocation behavior and yield efficiency in major field crops. By integrating multi-location field measurements, controlled-environment observations, and physiological modeling, the research demonstrates that nutrient availability is far more temporally and spatially variable than conventional soil fertility assessments suggest. These fluctuations in nutrient fluxes act as direct physiological cues that regulate the balance between source activity, sink demand, and the distribution of assimilated carbon across plant tissues. The study further shows that root systems function not only as absorptive structures but also as perceptive organs capable of responding rapidly to nutrient oscillations with highly coordinated shifts in metabolism and growth.

High-amplitude, well-timed nutrient pulses were consistently associated with elevated photosynthetic performance, improved carbon-use efficiency, and greater allocation of assimilates toward reproductive tissues. These physiological changes resulted in higher grain biomass, stronger sink strength, and increased harvest index across maize, wheat, rice, and soybean. In contrast, periods of nutrient depletion or poorly synchronized nutrient availability prompted a shift toward greater investment in root growth and maintenance processes, reducing reproductive output and overall yield potential. The synchrony between nutrient flux peaks and critical reproductive stages emerged as a key driver of yield efficiency, emphasizing the importance of timing rather than total nutrient supply alone.

The study also highlights marked interspecies differences in nutrient flux responsiveness. Maize exhibited the strongest reproductive enhancement under synchronized nutrient pulses, while soybean displayed significant plasticity but also higher vulnerability when nutrient dynamics were misaligned with reproductive development. Rice maintained more stable responses due to reduced spatial nutrient variability, and wheat showed moderate sensitivity with consistent adjustments in stomatal and metabolic regulation. These variations underscore the need for species-specific nutrient management strategies grounded in real-time nutrient flux behavior.

The integration of physiological, spatial, and temporal datasets allowed the development of a conceptual framework linking nutrient flux amplitude, photosynthetic responses, carbon allocation pathways, and yield outcomes. This framework provides a foundation for future nutrient management strategies that move beyond static fertilization recommendations and embrace the dynamic nature of nutrient behavior within the rhizosphere. Such strategies may include precise timing of nutrient applications, enhanced monitoring through micro-sensor technologies, and breeding for root traits that optimize nutrient responsiveness.

Overall, the evidence suggests that nutrient-flux-oriented crop management has substantial potential to improve yield efficiency and sustainability in global agriculture. By aligning nutrient availability with plant physiological needs, it is possible to achieve more efficient use of resources, reduce environmental impacts, and enhance crop resilience under increasingly variable soil and climate conditions.

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