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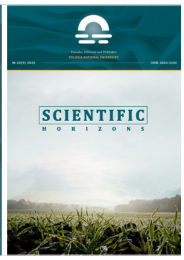

Balanced plant nutrition: From functional deficiency to a systematic strategy for increasing crop yields: Literature review

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Abstract. The aim of this study was to substantiate the functional hierarchy of nutrients and develop an applied biochemical model for optimising nutrient management in plants. The research methodology combined a comprehensive analysis of international and national scientific sources with systematisation of biochemical interactions among macro- and microelements. It was found that nutrient uptake and activation in plants follow a specific biochemical sequence, in which sulphur, boron, silicon, and calcium serve as initiating elements that activate metabolic pathways, enabling efficient nitrogen, magnesium, phosphorus, carbon, and potassium assimilation. The study analysed the physiological and biochemical mechanisms of nutrient interrelations and demonstrated that this sequential activation ensures a balance between structural development, photosynthetic activity, and stress tolerance. It was established that the efficiency of metabolic processes directly depends on the synchronisation of elemental uptake according to plant growth phases. The research generalised experimental and theoretical data on the role of calcium in transport and signalling, sulphur in protein synthesis, silicon in cell strengthening, and boron in reproductive development. Based on these findings, a functional biochemical model was developed, showing how consistent nutrient activation improves crop productivity and enhances resilience under environmental stress. The model was

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applied to analyse nutrient dynamics in Sorghum bicolor and Triticum spelta, revealing that maintaining this sequence ensures metabolic stability and sustainable soil fertility. The practical significance of the study lies in its applicability for agronomists, soil scientists, and researchers in plant physiology, as well as for agricultural enterprises seeking to improve nutrient management efficiency, optimise fertilisation strategies, and increase crop productivity under sustainable farming systems

Keywords: biochemical sequence; plant nutrition; sulphur; boron; silicon; calcium; nitrogen; photosynthesis; metabolism; agroecosystem

INTRODUCTION

The rational organisation of plant mineral nutrition is one of the central priorities of modern agriculture, as the biochemical sequence of nutrient assimilation determines both yield quality and ecosystem stability. Imbalanced application of fertilisers, without taking into account the functional order of macro- and microelements, often leads to the accumulation of nitrates, protein synthesis disruption and weakening of plant immunity. Consequently, contemporary agronomic research increasingly focuses on the interdependence and metabolic hierarchy of mineral elements that regulate photosynthesis, enzymatic activity, and antioxidant defence.

Sulfur is considered the initiating element of metabolic activation. According to R.K. Sharma *et al.* (2024), sulfur plays a fundamental role in amino acid synthesis, chlorophyll formation and oxidative stress control, and its deficiency disrupts the assimilation of nitrogen into proteins, causing metabolic imbalance. The authors emphasise that optimal sulfur supply improves both yield and the nutritional quality of crops. In turn, C. Boubakry *et al.* (2023) experimentally confirmed that the agronomic efficiency of elemental sulfur depends on particle size and soil microbial activity, which determine oxidation rates and the availability of sulfates to plants. This work substantiates the need for complex sulphur-nitrogen management strategies. Complementary findings were obtained by T. Bruulsema and R. Olson (2024), who demonstrated that sulfur management following the 4R stewardship concept – "right source, right rate, right time, and right place" – enhances crop productivity and contributes to sustainable soil fertility. These studies collectively highlight sulfur as the starting point in the biochemical sequence of nutrient activation.

Equally important is the synergistic interaction between boron and silicon. H. Sheng *et al.* (2024) established that these elements share structural and physiological roles in cell wall stability, membrane integrity and assimilate transport. Their analogy in plant nutrition reveals that silicon partially compensates for boron deficiency by maintaining turgor and mechanical strength. E. Réthoré *et al.* (2023) experimentally verified this relationship in *Brassica napus*, showing that silicon enhances tolerance to boron deficiency by stimulating the remobilisation of boron and the expression of its transporter genes. A.C. Buchelt *et al.* (2020) further proved that the inclusion of silicon in nutrient solutions mitigates nitrogen, potassium, calcium, magnesium, and sulfur deficiencies, normalising ionic balance and improving enzymatic activity. These findings position silicon as a biochemical catalyst that stabilises metabolic processes and reinforces other nutrients' functions. Calcium, traditionally perceived as a structural component, has recently been identified as a signalling regulator in nutrient transport. T. Wang *et al.* (2023) showed that calcium ions mediate the transmission of stress and nutrient uptake signals, linking cellular transport systems and metabolic feedback. O. Sahin *et al.* (2024) complemented this view by demonstrating that ecological nano-calcium derived from eggshells increases lettuce tolerance to salinity and boron toxicity, reducing oxidative stress and stabilising antioxidant enzymes. Thus, calcium serves as both a mediator and modulator in the biochemical sequence of mineral nutrition.

Another critical relationship concerns the interaction between sulfur and nitrogen. A.A. Rahman *et al.* (2025) established, through multi-site field trials on soybean, that the combined application of these elements increases the content of sulfur-containing amino acids and improves seed quality. This reinforces the hypothesis that nitrogen utilisation efficiency depends on prior sulfur activation. M.I.R. Khan *et al.* (2023) extended this concept theoretically, asserting that plant nutrition efficiency is determined not only by the quantity of elements but by their chronological participation in metabolic cycles. Such a sequence ensures homeostatic balance and resilience under environmental fluctuations.

Ukrainian research supports these findings in a regional context. V. Gamayunova and O. Sydiakina (2023) analysed the nitrogen imbalance in Ukrainian agroecosystems, noting that excessive nitrogen fertilisation without sulfur or calcium supplementation reduces soil microbiological activity and leads to nutrient leaching. L. Harbar *et al.* (2021) confirmed that fertiliser efficiency in sunflower cultivation depends on the coordination of calcium, boron and sulfur supply during the reproductive phase, which directly influences productivity. Collectively, these studies outline a coherent scientific paradigm: effective plant growth and productivity result from the biochemical sequence of nutrient interaction, not from isolated fertiliser application. The synchronised supply of sulfur, boron, silicon, calcium, nitrogen, magnesium and phosphorus forms a metabolic chain that activates enzymatic systems, enhances stress resistance and ensures sustainable yield formation. Purpose of the study – to substantiate the biochemical sequence of plant mineral nutrition and define the functional interaction of key macro- and microelements in metabolic activation.

This review is based on a systematic analysis of international and Ukrainian scientific publications from 2020 to 2025, focusing on biochemical mechanisms and functional interactions of sulfur, boron, silicon, calcium, nitrogen, magnesium, and phosphorus in plant metabolism. The methodological framework included comparative and analytical synthesis of peer-reviewed studies indexed in Scopus, Web of Science, and leading agronomic journals such as Frontiers in Plant Science, Physiologia Plantarum, Agronomy Journal, and Journal of Agriculture and Food Research. Priority was given to works combining physiological, biochemical, and agroecological approaches. The sources were critically evaluated for methodological transparency, reproducibility, and consistency of results. This integrative analysis allowed the identification of functional hierarchies among nutrients, establishing the conceptual model of a biochemical sequence of mineral nutrition as the foundation for sustainable crop production. This publication proposes a generalised model of biochemical sequence that takes into account both classical scientific approaches and empirical data from field studies. The aim is to create a structured view of the interaction of the main elements – sulphur, boron, silicon, calcium, nitrogen, magnesium, phosphorus, carbon and potassium – and their functional inclusion in plant metabolic processes. Such a model is not absolute, but it can serve as a guideline for planning crop nutrition in different agroecological conditions.

FUNCTIONAL HIERARCHY OF NUTRIENTS AND BIOCHEMICAL SEQUENCE OF ACTIVATION

In international scientific literature, particularly in the works of foreign researchers, the complexity of nutrient interactions at the level of cellular metabolism and plant anatomical and physiological responses is emphasised. Their studies highlight the importance of maintaining an optimal balance between nutrients and their mutual influence on uptake efficiency (Hernandez *et al.*, 2024). At the same time, some authors focus on the molecular-genetic mechanisms of nutrient transport as well as species-specific sensitivity to deficiencies of particular elements. A practical approach to structuring the sequence of nutrient uptake was proposed by Hugh Lovel, whose concept suggests that nutrients are incorporated into metabolic processes not simultaneously but according to the plant's functional needs at different developmental stages. This allows the design of agrotechnologies not only by growth phase but also by considering the biochemical logic of plant development. Such a model is widely applied in biological farming systems (Bruulsema & Olson, 2024). In the Ukrainian agrochemical and plant physiology research tradition, the interdependence of nutrients and their sequential activation has been actively studied, particularly within the research of specialised academic institutions. Works by scientists affiliated with the National Scientific Centre "O.N. Sokolovsky Institute for Soil Science and Agrochemistry" and the Institute of Plant Physiology and Genetics of the National Academy of Sciences of Ukraine examine issues of calcium bioactivation, the role of silicon in enhancing tolerance to abiotic stress factors, and the physiological and biochemical mechanisms of nitrogen and phosphorus uptake. Special attention is devoted to the regional specificity of nutrient balance in the agroecosystems of the Forest-Steppe and Steppe zones of Ukraine, especially in the context of organogenesis (Trembitska *et al.*, 2020).

The study of mechanisms regulating nutrient functioning in soil and their influence on plant growth indicates the existence of a clear hierarchy or "biochemical sequence" of nutrients (Sharma *et al.*, 2024). This sequence determines which elements must act first to create favourable conditions for the efficient assimilation of subsequent nutrients. It is based on the complex interaction of chemical and biological processes in the soil that form the foundation of plant vitality. The fundamental idea of this hierarchy is that elements participating in reactions at the early stages establish the basis for soil biological activity and, consequently, for effective plant growth. Sulphur, boron, silicon, and calcium are critical initiating elements, while nitrogen, phosphorus, and potassium – despite their conventional prominence in crop nutrition – occupy the final stages of this biochemical sequence (Sheng *et al.*, 2024; Sahin *et al.*, 2024) (Fig. 1).

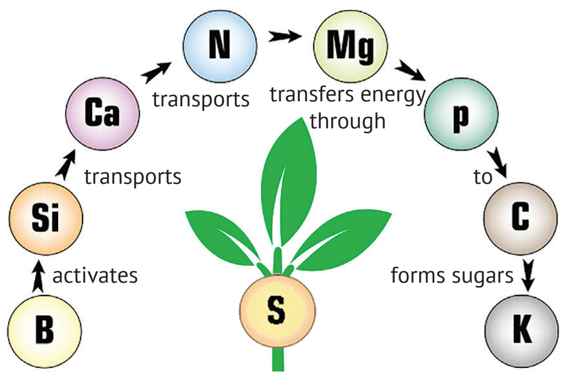

***Figure 1**. Biochemical foundation of nutrient sequence*
***Source:** developed by the authors based on H. Sheng et al. (2024) and O. Sahin et al. (2024)*

Sulphur is a key catalyst of biochemical reactions occurring on the surface of soil particles. It interacts with essential compounds of carbon, hydrogen, oxygen, and nitrogen, activating the surfaces where chemical reactions take place. However, its role extends far beyond the soil environment. In plants, sulphur is an indispensable component of amino acids such as methionine and cysteine, as well as of vitamins (biotin and thiamine) and enzymes that regulate metabolism. Sulphur participates in protein synthesis, chlorophyll formation, stimulates photosynthetic activity, and enhances nitrogen assimilation. Without sufficient sulphur, nitrogen cannot be converted into amino acids, leading to nitrate accumulation in plant tissues and impaired protein metabolism. Therefore, sulphur and nitrogen must act synergistically – sulphur opens the pathway for the full incorporation of nitrogen into biochemical chains. In this context, sulphur is not merely a nutrient but a trigger mechanism for protein synthesis (Sharma *et al.*, 2024). Furthermore, sulphur plays a crucial role in plant resistance to stress factors – it is involved in the synthesis of glutathione, one of the key cellular antioxidants that protects the plant against oxidative stress, diseases, and toxic substances. In rhizobial bacteria, sulphur is essential for the synthesis of enzymes responsible for nitrogen fixation, making it particularly critical for leguminous crops. Under sulphur deficiency, plants display symptoms similar to nitrogen shortage: chlorosis of young leaves, growth inhibition, reduced protein content, and decreased yield. However, unlike nitrogen, sulphur is poorly redistributed within the plant, so its deficiency appears primarily in young tissues (Buchelt *et al.*, 2020). Thus, sulphur is not only a structural element but a true metabolic "switch" that regulates nitrogen metabolism, energy balance, and plant defence mechanisms. Its presence is a prerequisite for proper growth, development, and the formation of high-quality yields.

Boron plays a vital role in the formation of cellular structures and tissue differentiation processes, ensuring mechanical strength and elasticity. It facilitates the effective uptake of nutrients by the root system and improves the synthesis, transport, and distribution of carbohydrates from photosynthetic organs to meristematic zones, roots, and generative organs. One of boron's important functions is its involvement in calcium uptake, the formation of the primary root system, and the development of nodules in leguminous crops. Adequate boron supply promotes the formation of generative organs, stimulates flowering, and improves fertilisation by enhancing pollen viability and germination quality. This, in turn, positively affects seed productivity and quality parameters (Vera-Maldonado *et al.*, 2024). Boron is an essential element in the plant's metabolic processes, and its deficiency leads to physiological and biochemical imbalances. Unlike many other mineral nutrients, boron cannot be remobilised within the plant – it does not move from senescing or older organs to younger tissues. Therefore, its supply must be continuous throughout the growing season, with special attention during critical growth and development phases (Réthoré *et al.*, 2023). In addition, boron increases plant resistance to phytopathogens of both fungal and bacterial origin and enhances tolerance to abiotic stresses, including extreme temperature conditions.

Silicon is also one of the most important mineral nutrients that positively influences the physiological and biochemical processes in plants. It participates in the formation of cell walls, strengthening their structure and increasing tissue mechanical stability. Accumulating in epidermal cells, silicon creates a protective barrier that reduces water loss, lowers pathogen and pest damage, and enhances tolerance to adverse environmental conditions such as drought, temperature stress, and soil salinity (Calero Hurtado *et al.*, 2019; 2020). Silicon contributes to the enhancement of photosynthetic efficiency by improving the plant's water balance, ensuring balanced uptake of macro- and microelements, and stabilising chloroplast structures. Adequate silicon supply increases the activity of enzymatic systems involved in nitrogen, phosphorus, and potassium metabolism. It also promotes root growth, stimulates the development of root hairs, improves nutrient uptake from the soil, and reduces the toxic effects of heavy metals and excessive concentrations of ions such as sodium and aluminium. Through its role in metabolic processes, silicon indirectly affects plant generative development – improving fruit and seed setting, increasing quality and storage potential. In cereals, silicon contributes to the formation of full ears, reduces stem brittleness, and minimises yield losses during ripening (de Melo Peixoto *et al.*, 2022; de Farias Guedes *et al.*, 2022).

Boron and silicon together form the basis of the plant's transport system. Boron, in combination with silicon, is responsible for the functionality of the plant's vascular system – it increases cell wall permeability and facilitates the movement of nutrients through vascular tissues. When boron or silicon are deficient, especially under hot conditions, plants wilt rapidly even with sufficient soil moisture, indicating nutrient transport failure rather than water deficit (Sheng *et al.*, 2024). Boron is also essential for maintaining sap pressure within plant tissues, influencing active growth, particularly in crops with branched venation systems (e.g., beans, tomatoes, courgettes). In contrast, crops with parallel vascular structures (e.g., cereals) tolerate boron deficiency better due to their higher silicon content (Réthoré *et al.*, 2023). Modern agricultural practices – particularly "clean farming" and the excessive use of soluble nitrogen fertilisers – can accelerate the depletion of boron and silicon reserves. This occurs because microbial activity decreases, and humus-clay complexes that retain these elements are destroyed. As a result, nutrients are easily leached, and soil biological activity declines.

Calcium is another key element, acting as a major transport agent in plant nutrition systems, working in combination with magnesium, potassium, and sodium. It provides structural stability to cells and is crucial for cell division processes, which are necessary for fruit and seed formation. Calcium plays a special role in its interaction with nitrogen for the synthesis of amino acids – the basis of the protein structure that governs enzyme and hormone function. Calcium is also a vital component of cell walls, particularly of pectic substances, where it forms calcium-pectate bonds, ensuring tissue integrity and mechanical strength. Its presence supports normal growth of meristematic tissues, especially root and shoot tips where metabolic activity is high (Wang *et al.*, 2023). In addition, calcium has a regulatory function in intracellular signal transduction, participating in stress signalling, stomatal regulation, and plant adaptation to adverse environmental conditions. Calcium also reduces cell membrane permeability, limiting pathogen invasion and thus enhancing disease resistance. Calcium deficiency, especially during active growth phases, leads to impaired development of growth points, tissue deformation, necrosis of young parts, disrupted water balance, and reduced productivity. Continuous calcium supply, particularly during critical phases of development (growth spurts and reproductive organ formation), is essential for stable growth, normal metabolism, and high-quality yields (Sahin *et al.*, 2024).

Above all, calcium interacts with nitrogen to form amino acids, which are the basis of DNA, RNA, and proteins. These nitrogen compounds, in turn, sustain the complex chemistry of enzymes and vital hormones involving all elements from sulphur and silicon to magnesium, iron, phosphorus, zinc, manganese, and copper. Most importantly, nitrogen provides amino acids in chlorophyll, which is crucial for photosynthesis – the highly efficient mechanism of energy capture (Rahman *et al.*, 2025). For instance, in maize (*Zea mays*), calcium deficiency results in incomplete kernel formation, while in soybean (*Glycine max*), adequate calcium levels prevent pod abscission. Overall, calcium is a critically important element for normal plant growth and development. It provides structural stability to cells, supports enzymatic function, participates in cell division and the formation of reproductive organs, and enhances stress and pathogen resistance. Its interaction with nitrogen underpins the synthesis of proteins and chlorophyll. Continuous calcium supply throughout the vegetation period is the key to high-quality yields.

FUNCTIONAL INTERRELATIONS OF NITROGEN, MAGNESIUM, PHOSPHORUS, CARBON AND POTASSIUM

Nitrogen: the driving factor of biochemical activity. As mentioned above, where calcium goes, nitrogen follows. Nitrogen is the foundation for amino acid formation, protein chemistry, and the replication and expression of DNA. Once nitrogen becomes active, all types of proteins, enzymes, and hormones are produced, initiating highly complex processes that involve micronutrients (Sharma *et al.*, 2024). Unfortunately, soluble nitrogen fertilisers stimulate only the final part of this process, disregarding the priority of sulphur, boron, silicon, and calcium. Such fertilisers accelerate vegetative growth, but they act similarly to stimulants, providing weak yields dependent on high weed competition, pest infestation, and disease pressure (Bruulsema & Olson, 2024). All parts of plant protein chemistry require amino acid-based nitrogen. Nitrogen lies at the intersection between chemically neutral silicon and calcium, with a large portion of amino acids being utilised for chlorophyll formation – the key to energy capture. Energy accumulation is vital, as without photosynthesis, plant life would cease to exist (Alves *et al.*, 2020). Nitrogen is not merely a growth source but a trigger for synchronising metabolic pathways that ensure full functionality of cellular structures. In agrobiological terms, nitrogen initiates the biosynthesis of nucleotides, alkaloids, vitamins, and secondary metabolites that play a critical role in plant defence mechanisms and adaptation to environmental stressors (Hernandez *et al.*, 2024).

Furthermore, nitrogen bioavailability influences the equilibrium between vegetative and generative development. Excessive nitrogen results in the overaccumulation of green biomass at the expense of fruit and seed formation. Conversely, nitrogen deficiency causes growth retardation, chlorosis, protein synthesis inhibition, and general physiological suppression. Therefore, efficient nitrogen nutrition must not rely solely on the quantity of applied compounds but should be balanced with elements that ensure full expression of its metabolic function – specifically sulphur (for amino acid synthesis), boron (for sugar transport and growth regulation), silicon (for tissue resilience), and calcium (for cellular stability). Only under such a system does nitrogen truly become the viable foundation of a productive and resilient plant organism (Boubakry *et al.*, 2023). Hence, nitrogen is a key element of protein and energy metabolism that activates the primary biochemical processes in plants. Its effectiveness, however, depends on balanced interactions with calcium, sulphur, boron, and silicon. Under such conditions, nitrogen supports not only growth but also crop resistance and productivity (Bruulsema & Olson, 2024).

Since photosynthesis requires magnesium, it ranks fifth in the biochemical sequence, preceding all other less critical microelements. Photosynthesis is not merely the accumulation of energy in chlorophyll; this energy must be transferred from chlorophyll to silicon to produce sugars from carbon dioxide and water, a process that demands phosphorus for energy transport. Without sufficient phosphorus, chlorophyll becomes unstable, leading to leaf discolouration and premature senescence (Buchelt *et al.*, 2020). If phosphorus is available, carbon is released from carbon dioxide to combine with water, producing sugars and releasing oxygen. Magnesium acts as the central atom of the chlorophyll molecule – without it, light absorption and its conversion into chemical energy would be impossible. Yet the role of magnesium extends beyond photosynthesis. It activates more than 300 enzymatic systems, including those responsible for the synthesis of nucleic acids, proteins, carbohydrates, and lipids. Magnesium maintains ribosomal stability, participates in ATP synthesis, and facilitates phosphate transport within the plant (Wang *et al.*, 2023). In addition, magnesium is essential for carbohydrate mobilisation, particularly for transporting assimilates from leaves to growing points, generative organs, and the root system. Magnesium deficiency leads to carbohydrate accumulation in leaves, premature ageing, disrupted nitrogen metabolism, and reduced overall productivity. It also exhibits antagonistic interactions with calcium and potassium, so overapplication of one without balancing magnesium can disturb ionic equilibrium and cause secondary deficiencies (Hernandez *et al.*, 2024). Thus, magnesium is indispensable for photosynthesis and general plant metabolism, as it forms part of chlorophyll and activates numerous enzymes. It enables ATP synthesis, phosphate and carbohydrate transport, and maintains the balance of nutrient elements. Its deficiency disrupts energy exchange, reduces photosynthesis, and limits plant productivity.

Phosphorus. Photosynthesis is not only the capture of light energy by chlorophyll – this energy must be converted into sugars from carbon dioxide and water, a process requiring phosphorus. Otherwise, chlorophyll "burns out", and leaves acquire a reddish hue. Phosphorus is a key element in cellular energy transfer and storage since it forms part of ATP – the main energy carrier in biochemical reactions. It allows energy captured during photosynthesis to be used for synthesising carbohydrates, proteins, nucleic acids, and other organic compounds (Wang *et al.*, 2023). Phosphorus is also an essential component of phospholipids forming cell membranes and of RNA and DNA, ensuring genetic information transfer and regulation of cell division. It participates in coenzyme and regulatory molecule synthesis, coordinating primary metabolic pathways, including nitrogen and carbohydrate metabolism. Phosphorus is particularly crucial in early plant development, stimulating root system growth, accelerating establishment, enhancing water efficiency, and improving the uptake of other nutrients. During the generative phase, phosphorus ensures full flowering, fruit set, and seed filling. Hence, phosphorus is critical for energy metabolism, synthesis of nucleic acids, proteins, carbohydrates, and cell structures. Its deficiency results in energy depletion and metabolic disturbances (Bolokhovsky *et al.*, 2024).

Carbon. When phosphorus levels are adequate, carbon participates as carbon dioxide, and energy is transferred from chlorophyll through phosphorus to bind CO_2 with water, forming sugar and releasing oxygen. Carbon is the fundamental building block of all organic molecules in plants – from simple sugars to complex proteins, lipids, nucleic acids, and cell wall structures. About 45% of plant dry matter consists of carbon, assimilated from the atmosphere as CO_2 through stomata. Using photosynthetic energy, this carbon dioxide is converted into glucose, the primary molecule for synthesising structural and storage compounds (Khan, 2025). Carbon is also a key component of cellulose, hemicellulose, and lignin – materials that form cell walls and vascular tissues. In the form of organic acids, it participates in pH buffering, mineral transport, and osmotic regulation. The accumulation of carbon compounds such as sugars and starch provides plants with energy and affects root development, stress adaptation, and yield quality. Furthermore, the carbon-to-nitrogen balance determines the growth direction – vegetative or generative – and directly influences resistance to diseases and drought (Khan *et al.*, 2023). Thus, carbon is not merely a passive element absorbed from the air but an active regulator and structural component of all vital plant processes. Its assimilation and utilisation are closely linked to the efficient functioning of the photosynthetic apparatus, phosphorus and magnesium availability, and optimal water balance. Carbon underlies organic plant life, forming structures, energy reserves, and metabolic compounds. Its assimilation through photosynthesis drives the synthesis of sugars, proteins, nucleic acids, and cell walls. The carbon balance with other nutrients defines plant growth direction, stress resistance, and yield quality.

Potassium. At this stage, sugars move into plant sap, where potassium – as an electrolyte – directs them to where they are most needed. Potassium plays a crucial role in regulating osmotic pressure, stomatal opening, and the transport of assimilates, particularly sugars, from photosynthetic leaves to growth points, roots, and reproductive organs. Through potassium, the efficient movement of nutrients through the phloem is ensured, which is particularly critical during grain filling or fruit development (Bolokhovsky *et al.*, 2024). Potassium activates more than 60 enzyme systems, including those responsible for protein synthesis, carbohydrate metabolism, and energy accumulation. Although it does not form part of organic molecules, it is indispensable for their biochemical activity. Potassium also regulates starch synthesis, water balance, and membrane integrity, enhancing resistance to mechanical stress and pathogen attack (Hernandez *et al.*, 2024). Adequate potassium levels strengthen plant tissues, improve tolerance to drought and low temperatures, and enhance resistance to fungal and bacterial diseases. It also plays a vital role in stress adaptation by maintaining turgor and reducing damage under unfavourable conditions. Thus, potassium is a critical element for sugar transport, water balance regulation, and enzymatic activity in plants. While not part of organic compounds, it ensures their effective functioning, promoting growth, energy accumulation, stress resistance, and yield formation.

APPLIED BIOCHEMICAL MODEL FOR SORGHUM BICOLOR AND TRITICUM SPELTA

All these processes unfold only when the biochemical sequence is activated by the initiating elements. To sustain this biochemical sequence, it is crucial to use mineral supplements such as gypsum, silicate rock powders, lime, and dolomite, which help restore and maintain elemental balance in the soil. In addition, organic methods of soil enrichment – such as composting with the addition of rock powders – contribute to the restoration of natural soil biology and increase fertility (Drobitko & Kachanova, 2023). Considering the interrelations of elements in plant nutrition and their functional sequence, a diagram of biochemical interactions among macro- and microelements was constructed. Using two crops – common sorghum (*Sorghum bicolor*) (Table 1) and spelt wheat (*Triticum spelta*) (Table 2) – the dynamics of nutrient incorporation into metabolic processes were illustrated, allowing observation of the stages of productivity formation and plant adaptive stability (Khan *et al.*, 2023; Bruulsema & Olson, 2024).

***Table 1**. Functional role of key elements in the biochemical nutrition system of common sorghum*

Element	Function	Critical period
Sulphur (S)	Activates protein metabolism, stimulates photosynthesis, reduces nitrate accumulation	Early vegetation, tillering stage
Boron (B)	Forms the vascular system, increases pollen viability	Before stem elongation
Silicon (Si)	Strengthens cell walls, reduces moisture loss	Throughout vegetation
Calcium (Ca)	Forms cell membranes, improves nitrogen uptake	Tillering – stem elongation
Nitrogen (N)	Ensures growth and protein synthesis	Vegetation, grain filling
Magnesium (Mg)	Central atom of chlorophyll, energy metabolism	All photosynthetic phases
Phosphorus (P)	Root system growth, energy metabolism	Early development, reproductive phase
Carbon (C)	Forms organic matter, photosynthesis	Constantly
Potassium (K)	Assimilate transport, drought resistance	Grain filling, ripening

***Source:** authors' data based on T. Bruulsema and R. Olson (2024), M. Khan et al. (2023)*

***Table 2**. Biochemical activity of major elements during key ontogenetic phases of spelt wheat*

Element	Function	Critical period
Sulphur (S)	Stimulates protein and gluten synthesis, enhances disease resistance	Spring regrowth
Boron (B)	Ear formation, pollen fertility improvement	Stem elongation – heading
Silicon (Si)	Stem strengthening, lodging reduction	Throughout vegetation
Calcium (Ca)	Increases cell wall stability, nutrient transport	Tillering – heading
Nitrogen (N)	Growth, protein formation, ear and grain development	Spring – grain filling
Magnesium (Mg)	Chlorophyll formation, photosynthesis	Vegetation
Phosphorus (P)	Root system development, energy supply	Autumn vegetation – spring regrowth
Carbon (C)	Organogenesis, energy potential	All phases
Potassium (K)	Resistance to lodging, frost, and disease	Tillering – grain filling

***Source:** authors' data based on T. Bruulsema and R. Olson (2024), M. Khan et al. (2023)*

The analysis of the biochemical nutrient sequence in *Sorghum bicolor* and *Triticum spelta* showed that the efficiency of metabolic processes in these crops directly depends on the sequential and balanced supply of macro- and microelements. A key role in initiating biochemical activity is played by sulphur, boron, silicon, and calcium, which create the prerequisites for the full assimilation of nitrogen, magnesium, phosphorus, carbon, and potassium. This sequence determines the stability of growth processes, photosynthetic activity, and crop quality. Applying this model not only enhances the efficiency of mineral nutrition but also ensures the ecologically balanced functioning of agroecosystems (Sun *et al.*, 2024).

In general, the results of the study confirmed that the effectiveness of plant growth and productivity is determined by the sequence and balance of nutrient supply. The active interaction of sulphur, boron, silicon and calcium creates conditions for the absorption of nitrogen, magnesium, phosphorus, carbon and potassium, ensuring metabolic stability and crop resilience.

CONCLUSIONS

The conducted analytical study confirmed that the functional hierarchy of nutrients and their biochemical sequence of activation form the physiological basis of effective plant growth and productivity. The research summarised both classical and modern concepts of nutrient interactions, emphasising the critical role of sulphur, boron, silicon, and calcium as initiating elements that activate metabolic pathways and prepare the biochemical environment for the effective utilisation of nitrogen, magnesium, phosphorus, carbon, and potassium. These primary elements not only initiate enzymatic and photosynthetic activity but also enhance structural integrity, transport processes, and stress resistance in plants. The analysis of the applied biochemical model for Sorghum bicolor and Triticum spelta demonstrated that the balanced and sequential uptake of macro- and microelements directly determines the metabolic stability and adaptive potential of crops. In both species, the functional order of nutrient activation ensures a synergistic relationship between energy metabolism and protein synthesis, maintaining photosynthetic efficiency and reproductive success. The implementation of this sequence in agronomic practice contributes to the optimisation of fertilisation systems, reduces nutrient losses, and supports sustainable soil fertility. The results also highlight the importance of integrating mineral and organic soil amendments such as gypsum, dolomite, silicate powders, and composts enriched with rock dusts. These materials restore the natural balance of nutrient elements, enhance soil microbial activity, and promote the development of biologically active agroecosystems. The proposed model provides a universal framework for adapting biochemical nutrient sequences to specific crop requirements and regional agroecological conditions.

Future investigations should focus on quantitative modelling of nutrient activation kinetics under varying climatic and soil conditions, as well as on identifying molecular mechanisms that regulate the biochemical synchronisation of nutrient uptake. Special attention should be given to the integration of this model into precision agriculture technologies, which would allow for dynamic adjustment of fertilisation regimes and real-time monitoring of plant physiological responses. This direction of research will ensure the practical application of biochemical nutrient hierarchy principles in the development of resilient, high-yield, and environmentally sustainable crop production systems.

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CONFLICT OF INTEREST

The authors of this study declare that there is no conflict of interest.

REFERENCES

[1] Alves, R.C., Nicolau, M.C.M., Checchio, M.V., da Silveira Sousa Junior, G., de Assis de Oliveira, F., Melo Prado, F., & Lupino Gratão, P. (2020). Salt stress alleviation by seed priming with silicon in lettuce seedlings: An approach based on enhancing antioxidant responses. *Bragantia,* 79(1), 19-29. doi: 10.1590/1678-4499.20190360.

[2] Bolokhovsky, V., Bolokhovska, V., Khomenko, T., Datsko, A., & Litvinova, O. (2024). Optimisation of plant nutrition under the influence of biopreparations in integrated sunflower cultivation technologies. *Plant and Soil Science,* 15(4), 64-75. doi: 10.31548/plant4.2024.64.

[3] Boubakry, C., Agyin-Birikorang, S., Adu-Gyamfi, R., Chambers, R.A., Tindjina, I., & Angzenaa, A.B. (2023). Improving agronomic effectiveness of elemental sulfur to increase productivity in sulfur-deficient soils. *Agronomy Journal*, 115(6), 3131-3143. doi: 10.1002/agj2.21458.

[4] Bruulsema, T., & Olson, R. (2024). The role of sulfur in meeting 4R nutrient stewardship goals. *Crops & Soils*, 57(3), 34-39. doi: 10.1002/crso.20360.

[5] Buchelt, A.C., Teixeira, G.C.M., Oliveira, K.S., Souza Rocha, A.M., de Mello Prado, R., & Caione, G. (2020). Silicon contribution via nutrient solution in forage plants to mitigate nitrogen, potassium, calcium, magnesium, and sulfur deficiency. *Journal of Soil Science and Plant Nutrition,* 20, 1532-1548. doi: 10.1007/s42729-020-00245-7.

[6] Calero Hurtado, A., Chiconato, D.A., de Mello Prado, R., da Silveira Sousa Junior, G., & Felisberto, G. (2019). Silicon attenuates sodium toxicity by improving nutritional efficiency in sorghum and sunflower plants. *Plant Physiology and Biochemistry,* 142, 224-233. doi: 10.1016/j.plaphy.2019.07.010.

[7] Calero Hurtado, A., Chiconato, D.A., de Mello Prado, R., da Silveira Sousa Junior, G., & Felisberto, G. (2020). Silicon application induces changes in C:N:P stoichiometry and enhances stoichiometric homeostasis of sorghum and sunflower plants under salt stress. *Saudi Journal of Biological Sciences,* 27(12), 3711-3719. doi: 10.1016/j.sjbs.2020.08.017.

[8] de Farias Guedes, V.H., de Mello Prado, R., José Frazão, J., Silva Oliveira, K., & Osvaldo Cazetta, J. (2022). Foliar-applied silicon in sorghum (*Sorghum bicolor* L.) alleviates zinc deficiency. *Silicon,* 14, 281-287. doi: 10.1007/s12633-020-00825-3.

[9] de Melo Peixoto, M., Alves Flores, R., do Couto, Ch.A., Pacheco, H.D.N., de Mello Prado, R., Souza-Junior, J.P., Castro-Netto, J.A., & Graciano-Ribeiro, D. (2022). Silicon application increases biomass yield in sunflower by improving the photosynthesizing leaf area. *Silicon,* 14, 275-280. doi: 10.1007/s12633-020-00818-2.

[10] Drobitko, A., & Kachanova, T. (2023). Agroecological substantiation of technologies for growing grain crops in the conditions of the Southern Steppe of Ukraine. *Ukrainian Black Sea Region Agrarian Science*, 27(4), 9-17. doi: 10.56407/bs.agrarian/4.2023.09.

[11] Gamayunova, V., & Sydiakina, O. (2023). The problem of nitrogen in modern agriculture. *Ukrainian Black Sea Region Agrarian Science*, 27(3), 46-61. doi: 10.56407/bs.agrarian/3.2023.46.
[12] Harbar, L., Lishchuk, U., Dovbash, N., & Knap, N. (2021). Fertiliser efficiency in the formation of sunflower productivity. *Plant and Soil Science*, 12(1), 28-38. doi: 10.31548/agr2021.01.0028.
[13] Hernandez, L.E., Ruiz, J.M., Espinosa, F., Alvarez-Fernandez, A., & Carvajal, M. (2024). Plant nutrition challenges for a sustainable agriculture of the future. *Physiologia Plantarum,* 176(6), article number e70018. doi: 10.1111/ppl.70018.
[14] Khan, A.L. (2025). Silicon: A valuable soil element for improving plant growth and CO_2 sequestration. *Journal of Advanced Research,* 71, 43-54. doi: 10.1016/j.jare.2024.05.027.
[15] Khan, M.I.R., Nazir, F., Maheshwari, Ch., Chopra, P., Chhillar, H., & Sreenivasulu, N. (2023). Mineral nutrients in plants under changing environments: A road to future food and nutrition security. *The Plant Genome,* 16(4), article number e20362. doi:10.1002/tpg2.20362.
[16] Rahman, A.A., Brooks, K., Conley, S.P., Gaska, J.M., Irby, T., Knott, C., Lee, C., Lindsey, L.E., Mourtzinis, S., Naeve, S., Ross, W.J., Singh, M.P., Vann, R.A., & Matcham, E.G. (2025). Impact of sulfur and nitrogen fertilization on seed composition of soybean. *Frontiers in Sustainable Food Systems*, 9, article number 1572255. doi: 10.3389/fsufs.2025.1572255.
[17] Réthoré, E., Ali, N., Pluchon, S., & Hosseini, S. A. (2023). Silicon enhances *Brassica napus* tolerance to boron deficiency by the remobilisation of boron and by changing the expression of boron transporters. *Plants,* 12(13), article number 2574. doi: 10.3390/plants12132574.
[18] Sahin, O., Yagcioglu, K.D., Kadioglu, Y.K., & Gunes, A. (2024). Evaluating ecological nano-calcium from eggshells: Effects on calcium nutrition and oxidative stress in lettuce under saline and boron toxicity. *Journal of Plant Growth Regulation,* 43, 4416-4425. doi: 10.1007/s00344-024-11407-7.
[19] Sharma, R.K., Cox, M.S., Oglesby, C., & Dhillon, J.S. (2024). Revisiting the role of sulfur in crop production: A narrative review. *Journal of Agriculture and Food Research,* 15, article number 101013. doi: 10.1016/j.jafr.2024.101013.
[20] Sheng, H., Lei, Y., Wei, J., Yang, Z., Peng, L., Li, W., & Liu, Y. (2024). Analogy of silicon and boron in plant nutrition. *Frontiers in Plant Science,* 15, article number 1353706. doi: 10.3389/fpls.2024.1353706.
[21] Sun, T., *et al.* (2024). Unlocking the potential of nanoscale sulfur in sustainable agriculture. *Chemical Science*, 15, 4709-4722. doi: 10.1039/D3SC06122A.
[22] Trembitska, O., Kovalov, V., Klymenko, T., Zhuravel, S., & Fedorchuk, S. (2020). *Agroecological state of the Zhytomyr Polissia and the impact of fertilization systems on the fertility of soils contaminated with by radionuclides*. Zhytomyr: ZhNAEU.
[23] Vera-Maldonado, P., Aquea, F., Reyes-Díaz, M., Cárcamo-Fincheira, P., Soto-Cerda, B., Nunes-Nesi, A., & Inostroza-Blancheteau, C. (2024). Role of boron and its interaction with other elements in plants. *Frontiers in Plant Science,* 15, article number 1332459. doi: 10.3389/fpls.2024.1332459.
[24] Wang, T., Chen, X., Ju, C., & Wang, C. (2023). Calcium signaling in plant mineral nutrition: From uptake to transport. *Plant Communications*, 4(6), article number 100678. doi: 10.1016/j.xplc.2023.100678.

Збалансоване живлення рослин: від функціонального дефіциту до системної стратегії підвищення врожайності: огляд літератури

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Анотація. Метою даного дослідження було обґрунтування функціональної ієрархії поживних речовин та розробка прикладної біохімічної моделі для оптимізації управління поживними речовинами в рослинах. Методологія дослідження поєднувала комплексний аналіз міжнародних та національних наукових джерел із систематизацією біохімічних взаємодій між макро- та мікроелементами. Було встановлено, що поглинання та активація поживних речовин у рослинах відбувається за певною біохімічною послідовністю, в якій сірка, бор, кремній і кальцій виступають ініціаторами, що активують метаболічні шляхи, забезпечуючи ефективне засвоєння азоту, магнію, фосфору, вуглецю та калію. У дослідженні проаналізовано фізіологічні та біохімічні механізми взаємозв'язків між поживними речовинами та продемонстровано, що така послідовна активація забезпечує баланс між структурним розвитком, фотосинтетичною активністю та стресостійкістю. Було встановлено, що ефективність метаболічних процесів безпосередньо залежить від синхронізації поглинання елементів відповідно до фаз росту рослин. Дослідження узагальнило експериментальні та теоретичні дані про роль кальцію в транспорті та сигналізації, сірки в синтезі білків, кремнію в зміцненні клітин та бору в репродуктивному розвитку. На основі цих висновків було розроблено функціональну біохімічну модель, яка показує, як послідовна активація поживних речовин покращує врожайність та підвищує стійкість до екологічного стресу. Модель була застосована для аналізу динаміки поживних речовин у Sorghum bicolor та Triticum spelta, що дозволило виявити, що дотримання цієї послідовності забезпечує метаболічну стабільність та стійку родючість ґрунту. Практичне значення дослідження полягає в його застосовності для агрономів, ґрунтознавців та дослідників у галузі фізіології рослин, а також для сільськогосподарських підприємств, які прагнуть підвищити ефективність управління поживними речовинами, оптимізувати стратегії удобрення та збільшити врожайність культур у рамках систем сталого землеробства

Ключові слова: біохімічна послідовність; живлення рослин; сірка; бор; кремній; кальцій; азот; фотосинтез; метаболізм; агроекосистема