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Research Article

Macronutrient deficiencies in tomato plants: impacts on symptomatology, growth, physiology, fruit yield, and quality

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Abstract

In tomato production systems, nutrient limitations are a frequent abiotic challenge affecting plant development, yield, and marketable quality. This study evaluated the individual effects of macronutrient deficiencies-nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S)-on visual symptoms, vegetative development, physiological parameters, and fruit-related outcomes in tomato (*Solanum lycopersicum* L. cv. 'Kardelen F1') grown in a soilless greenhouse environment. A randomized experimental design with three replicates per treatment was applied. Visual deficiency symptoms were distinctive and element-specific, accompanied by marked alterations in leaf morphology and associated physiological functions. Nitrogen deficiency resulted in the most dramatic reductions in plant height (-52.67%), stem diameter (-37.73%), and leaf dry weight (-93.31%). Chlorophyll-a and total chlorophyll contents decreased by over 60% under N deficiency, whereas P and K deficiencies significantly increased these pigment levels by approximately 50–60% compared to the control. Nitrogen limitation caused the most substantial yield loss (-90.16%), followed by P (-61.39%) and K (-52.16%) shortages. Fruit weight declined by 59.6% with N deficiency, whereas Ca and S deficiencies had little impact on this trait. Potassium deficiency significantly decreased lycopene content (-51.11%), total soluble solids (-24.28%), and titratable acidity (-43.47%), along with increasing pH and contributing to a more yellowish skin color. The greatest reduction in fruit firmness was observed under Ca deficiency (-16.0%), while the lowest vitamin C content occurred under N deficiency (-36.77%). Moreover, total phenolic and flavonoid concentrations rose significantly under N and P deficiencies, indicating a possible stress-triggered antioxidant response. These findings highlight the distinct functions of individual macronutrients and emphasize the necessity of balanced nutrition to support optimal performance and quality in substrate-grown tomato crops.

Keywords: fruit yield and quality; macronutrient deficiency; mineral nutrition; physiological response; *Solanum lycopersicum* L.; symptomatology

Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most widely cultivated vegetable crops globally and plays a pivotal role in both agricultural production and human nutrition (Stein *et al.*, 2024). With an estimated production of 187 million metric tons in 2020, tomatoes remained one of the most important cultivated crops worldwide. China remains the leading producer, contributing approximately 65 million metric tons, followed

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by India with 20.5 million metric tons, and Türkiye with 13.2 million metric tons (FAOSTAT, 2020; Dasgan *et al*., 2024).

Tomatoes are highly valued for their nutritional composition, as they are rich in vitamins, minerals, dietary fiber, and phytochemicals, including essential antioxidants (Ali *et al*., 2020). Consequently, increased tomato consumption is encouraged as part of a healthy and balanced diet (Birgin *et al*., 2021; Amenu *et al*., 2023). Tomatoes are utilized either in their fresh state or processed into products like ketchup, purée, sauces, juice, paste, and tomato powder. Over the last few decades, their consumption has expanded significantly on a global scale (Chabi *et al*., 2024).

Proper mineral nutrition is essential for optimal plant growth and development. Nutrients are categorized as macronutrients (N, P, K, Ca, Mg, S) and micronutrients (B, Cl, Cu, Fe, Mn, Mo, Zn) based on the quantities required by plants (Tran *et al*., 2019). Among them, macronutrients are directly linked to key physiological processes, plant vigor, yield formation, and fruit quality (Kadyampakeni and Chinyukwi, 2021; Kumar *et al*., 2021). Nitrogen (N) is central to the synthesis of proteins, nucleic acids, chlorophyll, and enzymes, while phosphorus (P) is involved in energy metabolism and cell division (Jezek *et al*., 2023; Lopez *et al*., 2023; Wang *et al*., 2024). Potassium (K) regulates stomatal function, enzyme activation, and carbohydrate translocation, influencing both yield and quality (Akhtyamova *et al*., 2023; Uthman and Garba, 2023). Likewise, calcium (Ca), magnesium (Mg), and sulfur (S) contribute to cell wall stability, chlorophyll biosynthesis, and protein structure, respectively (Narayan *et al*., 2022; Navarro-León *et al*., 2022; Lamichhane *et al*., 2023).

When macronutrients are not available in sufficient amounts, plants exhibit specific deficiency symptoms, especially in the leaves, due to disrupted metabolic and physiological processes (Francis *et al*., 2023). These deficiencies not only restrict vegetative development but also reduce fruit yield and compromise marketable quality (Santiago *et al*., 2018; Kumari *et al*., 2022).

One reliable approach for studying nutrient deficiencies is the "diagnosis by subtraction" technique, in which plants are grown under a complete nutrient solution and compared with treatments where a single nutrient is omitted (Mauad *et al*., 2019). This method has been effectively applied to various crops, including fig (Garza-Alonso *et al*., 2019), cowpea (Santiago *et al*., 2018), and cucumber (Campos *et al*., 2021). However, comprehensive studies that simultaneously assess visual symptomatology, physiological performance, and detailed fruit quality parameters under individual macronutrient deficiencies in tomato remain limited. To address this gap, the present study investigates the effects of single macronutrient omissions (N, P, K, Ca, Mg, and S) on the morphological, physiological, and biochemical responses of tomato plants cultivated in a soilless system under greenhouse conditions. In addition to evaluating growth, yield, and quality-related traits, the study also documents the visual deficiency symptoms through systematic photographic records, enhancing the diagnostic utility of symptom-based nutrient assessment. These findings aim to provide practical insights into nutrient-specific stress responses, thereby contributing to the development of optimized fertilization strategies for improving tomato production and fruit quality.

Materials and Methods

Plant material and growth ***conditions***

Tomato (*Solanum lycopersicum* L. cv. 'Kardelen F1') was used as the plant material. Seedlings were obtained from a certified commercial nursery in Antalya (Türkiye). Thirty-day-old seedlings, approximately 10 cm tall and having developed their second set of true leaves, were transplanted individually into pots.

A sterile growing medium consisting of peat and perlite in a 2:1 (v/v) ratio was used. Peat moss (Klasmann), derived from the *Sphagnum* genus, has a high water-holding capacity with a pH of 5.5-6.0. Perlite is an inert, salt-free substrate with a neutral pH and high aeration. Each 3-L pot (16.5 cm diameter, 19.0 cm depth) was filled with 1500 g of this mixture. Drainage holes were made to ensure proper leaching.

The experiment took place in a controlled greenhouse at the Agricultural Research Station of Ondokuz Mayıs University (41°21' N, 36°11' E), Samsun, Türkiye. Environmental conditions were maintained at 29 ± 4 °C during the day and 22 ± 2 °C at night, with a 12-hour photoperiod and 55% ± 5% relative humidity. The greenhouse, with a metal structure of 6.0×16.0 m and a ceiling height of 4.5 m, was covered with a UV-stabilized plastic film to optimize light transmission while minimizing UV damage.

Experimental design and treatments

The experiment employed a completely randomized design with a single-factor scheme. The experimental setup included a complete nutrient solution as the control (NSc), along with treatments in which individual macronutrients were omitted: nitrogen (-N), phosphorus (-P), potassium (-K), calcium (-Ca), magnesium (-Mg), and sulfur (-S). Each treatment had three replicates, totaling 21 pots.

Macronutrient concentrations in the nutrient solutions (Table 1) were prepared following the method of Berry and Knight (1996). In the deficiency treatments, the ionic strength of the nutrient solutions was balanced by adjusting other ions to maintain equilibrium between cations and anions.

The fertilizers used as macronutrient sources in the preparation of nutrient solutions were potassium dihydrogen phosphate (KH_2PO_4), potassium nitrate (KNO_3), potassium sulfate (K_2SO_4), ammonium nitrate (NH_4NO_3), calcium nitrate tetrahydrate ($Ca(NO_3)_2{\cdot}4H_2O$), magnesium sulfate heptahydrate ($MgSO_4{\cdot}7H_2O$), magnesium nitrate hexahydrate ($Mg(NO_3)_2{\cdot}6H_2O$), calcium dihydrogen phosphate monohydrate ($Ca(H_2PO_4)_2{\cdot}H_2O$), sodium chloride (NaCl), magnesium chloride ($MgCl_2$), and calcium chloride ($CaCl_2$).

Table 1. Ion concentrations (mM) in the complete and deficient nutrient solutions applied in the experiment

Plant Nutrient Ions	Complete solution (mM)	Deficient solution (mM)					
		-N	-P	-K	-Ca	-Mg	-S
Cations							
Na^+	0.5	0.5	0.5	0.5	0.5	0.5	0.5
K^+	4	4	4	0	8	4	4
Mg^{2+}	1	1	1	1	1.5	0	1
Ca^{2+}	2.5	2.5	2.5	4.5	0	3.5	2.5
Anions							
NO_3^-	7	0	7	8	7	7	7
PO_4^{3-}	1	2	0	1	1	1	2
SO_4^{2-}	1.5	2.5	2	1	1.5	1.5	0
Cl^-	0.5	4.5	0.5	0.5	0.5	0.5	2.5

All treatments received a uniform micronutrient supply based on the concentrations recommended by Alpaslan *et al.* (1998). The solution included 5 µM Mn ($MnCl_2{\cdot}2H_2O$), 40 µM Fe (Fe-EDDHA), 30 µM B (H_3BO_3), 0.75 µM Cu ($CuSO_4{\cdot}5H_2O$), 4 µM Zn ($ZnSO_4{\cdot}7H_2O$), and 0.5 µM Mo ($(NH_4)_6Mo_7O_{27}{\cdot}4H_2O$)).

Tap water used in the preparation of nutrient solutions had an electrical conductivity of 0.05 dS m^{-1}. Chemical analyses confirmed the absence of any interfering mineral elements. The pH of the nutrient solutions was monitored daily and adjusted to 6.0 ± 0.5 using 0.1 mol L^{-1} NaOH or HCl, as needed. All nutrient solutions were prepared using analytical-grade reagents to ensure consistency and accuracy.

Based on their specific treatment conditions, tomato seedlings were supplied with a diluted nutrient solution at 25% of the recommended concentration for the first 3 days, followed by 50% concentration for the next 4 days to facilitate acclimatization. After this period, the nutrient solution was administered at full

strength (100%) until the end of the experiment. To maintain the substrate's moisture at 80% of its total porosity, the pots were weighed daily, and the nutrient solution was replenished accordingly.

Visual symptoms

To characterize the visual symptoms of macronutrient deficiencies, leaf color and shape were systematically examined throughout the experiment. Symptoms such as chlorosis and tissue necrosis were assessed through visual observation and documented using a Canon EOS 550D camera.

Measurement of plant growth parameters

Plant height and stem diameter were recorded at 75 days after transplanting (DAT). Plant height was measured from the stem base at the substrate surface to the apex of the youngest fully expanded leaf using a measuring tape. Stem diameter was measured 5 cm above the substrate surface using a digital caliper.

At 90 DAT, tomato plants were harvested and separated into roots, stems, and leaves for biomass determination. The plant parts were oven-dried at 72 °C for three days (Nüve, ES-500, Türkiye) until constant weight was achieved. The dry weights of each organ were measured using a precision balance (Precisa, XB-620M, Switzerland).

Measurement of leaf photosynthetic pigments

Chlorophyll a (Chl-*a*), chlorophyll b (Chl-*b*), total chlorophyll (Chl-*t*), and carotenoid (*Car*) contents were determined spectrophotometrically according to the method of Arnon (1949). Results were expressed as mg g^{-1} fresh weight (FW).

Leaf macronutrient analysis

Leaf macronutrient concentrations were analyzed in accordance with the procedures outlined by Kacar and Inal (2008). The leaves collected from tomato plants were washed in running water and then gently washed again with a 0.1% neutral detergent solution to remove surface contaminants, followed by thorough rinsing in deionized water. The washed leaves were blotted dry with paper towels, then dried in an air-circulating oven at 65 °C for 48 h, ground using a mill, and passed through a 1 mm sieve. Dried and ground leaf samples (0.5 g) were subjected to a wet digestion process using a nitric acid (HNO_3) and perchloric acid ($HClO_4$) mixture in a volume ratio of 4:1 (v/v) for the quantification of P, K, Mg, Ca, and S. The digested samples were filtered and diluted to a predetermined volume before analysis. Macronutrient concentrations were determined using appropriate analytical instruments: P and S were measured using a Jenway 7300 spectrophotometer, K and Ca were quantified using a flame photometer (BWB-XP, BWB Technologies, United Kingdom), and Mg was analyzed using an atomic absorption spectrophotometer (AAnalyst 400 AA Spectrometer, PerkinElmer, Inc., USA). Additionally, the total N content of the dried and ground tomato leaf samples was analyzed using the modified Kjeldahl digestion method, following the protocol outlined by Bremner and Mulvaney (1982). The macronutrient analyses were performed in triplicate and expressed as a percentage of dry weight (% dry matter basis).

Evaluation of fruit yield components

Fruit harvests were carried out six times in all treatments except for the nitrogen-deficient (-N) group, in which only two fruits were produced and collected in a single harvest. Total fruit yield per plant was calculated by summing the weights of all harvested fruits, and the mean fruit weight was obtained by dividing the total yield by the number of fruits. Yield measurements were performed using a precision scale (Precisa XB-620M, Switzerland).

Assessment of fruit biophysical quality traits

The height and diameter of intact tomato fruits were measured using a digital caliper (ASIMETO, Series 307). Fruit height was recorded from the blossom end to the apex, and diameter was measured at the widest equatorial region. The fruit shape index was calculated as the ratio of vertical to horizontal diameter. To ensure consistent accuracy, the caliper was rinsed with water every hour to remove any plant residues. Fruit firmness was determined using a digital penetrometer (PCE Instruments, PCE-FM 200) fitted with a cone-shaped probe (Φ8 mm), with measurements taken at the equatorial zone. Results were expressed as penetration resistance (kgf cm^{-2}).

Determination of fruit skin color parameters

Fruit skin color was measured using a CR-300 colorimeter (Konica Minolta, Tokyo, Japan), and the results were expressed in terms of L^* (lightness), a^* (red-green), and b^* (yellow-blue) values based on the CIELAB system (McGuire, 1992). Color readings were taken from the equatorial and distal regions of fully ripened tomato fruits. Chroma (C^*) and hue angle ($h°$) were calculated from the a^* and b^* values according to the method of Lancaster *et al.* (1997), using the formulas $C^* = \sqrt{(a^{*2} + b^{*2})}$ and $h° = \arctan(b^*/a^*)$.

Fruit sampling and analysis of physicochemical and nutraceutical quality traits

Fully ripened tomato fruits were harvested and immediately rinsed with tap water, then gently dried with paper towels. After removing the seeds, the pericarp and mesocarp tissues were homogenized into a uniform puree using a kitchen blender (Tefal MB450, Türkiye). A portion of the fresh puree was used for the determination of total soluble solids, titratable acidity, dry matter content, lycopene, and vitamin C. For pH measurements, the homogenate was filtered through 120 mm Whatman filter paper, and the clear juice was used for analysis. The remaining sample was stored at -18 °C until it was used for the quantification of total phenolics and flavonoids.

As a part of the physicochemical assessments, fruit juice pH, total soluble solids, titratable acidity, and fruit dry matter were analyzed. The pH of the filtered juice was measured using a pH meter SevenCompact S220 (Mettler Toledo, Switzerland), also equipped with automatic temperature compensation. For total soluble solids (TSS) determination, a drop of clear tomato juice was analyzed at room temperature using an Atago 3810 (PAL-1) digital pocket refractometer (ATAGO, Tokyo, Japan) and the obtained values were given in °Brix. Titratable acidity (TA) was quantified by titrating 10 mL of filtered tomato juice with 0.1 N standardized NaOH solution, using phenolphthalein as an indicator, until the endpoint at pH 8.1 was attained. The obtained results were expressed as the percentage (%) of citric acid, the predominant organic acid in tomatoes. The dry matter content (%) was determined gravimetrically by drying 5.0 g of tomato homogenate in a laboratory oven (Nüve, ES-500, Türkiye) at 70 °C until a stable weight was reached.

As part of the nutraceutical assessments, the contents of lycopene, vitamin C, total phenolics, and flavonoids were analyzed. Lycopene content was determined according to the method of Tremlove *et al.* (2021), using a solvent mixture of hexane, acetone, and ethanol (2:1:1, v/v/v). Fresh tomato puree was homogenized in the solvent, and the extraction was allowed to proceed for 15-30 minutes. To promote phase separation, distilled water (15 mL per 100 mL of solvent) was added. The upper hexane-rich phase, containing lycopene, was carefully collected. Absorbance was measured at 444 and 503 nm using a spectrophotometer calibrated with the extraction solvent as a blank. Lycopene concentration was expressed as mg per 100 g fresh weight (mg 100 g^{-1} FW). Vitamin C content was determined by titration with 2,6-dichlorophenolindophenol (DCPIP) according to Padayatt *et al.* (2001), and results were expressed as mg ascorbic acid per 100 g fresh weight (mg 100 g^{-1} FW). Total phenolic content was determined using the Folin-Ciocalteu colorimetric method as described by Spanos and Wrolstad (1990) and expressed as mg gallic acid equivalent (GAE) per kg fresh weight (mg GAE kg^{-1} FW). Flavonoid content was determined using the aluminum chloride colorimetric protocol described by Crozier *et al.* (1997) and expressed as mg quercetin equivalent (QE) per kg fresh weight (mg QE kg^{-1} FW).

Statistical analysis

Statistical evaluation was performed using JMP version 5.1. Data were presented as mean values (n = 3). A one-way analysis of variance (ANOVA) was employed to assess the overall treatment effects at a significance threshold of $p < 0.05$. Comparisons among treatment means were conducted using Fisher's Least Significant Difference (LSD) test.

Results

Symptomatology

Photographs of representative leaves at various growth stages were taken to document and compare the symptoms that developed under the different nutrient deficiency treatments (Figure 1).

Figure 1. Representative visual symptoms of tomato (cv. 'Kardelen F1') leaves under individual macronutrient deficiencies. (**A**) N deficiency; (**B**) P deficiency; (**C**) K deficiency; (**D**) Ca deficiency; (**E**) Mg deficiency; (**F**) S deficiency; (**G**) Control

Symptoms of N deficiency became noticeable 20 days after the experiment commenced, primarily affecting mature leaflets on the lower part of the stem. The affected leaflets appeared small, with a pale green to yellow coloration, and exhibited interveinal chlorosis. As the deficiency progressed, irregularly shaped necrotic spots developed, particularly along the leaflet margins, indicating increased physiological stress. Additionally, some leaflets showed curling and drying (Figure 1A). Symptoms of P deficiency became evident 25 days after the start of the experiment, again affecting mature leaves in the lower part of the plant. Affected leaves developed a deep green hue with a slight bluish tint, which is characteristic of P deficiency. As symptoms advanced, necrotic spots appeared on the leaf tips and margins, leading to tissue deterioration. Leaf expansion was limited, and the leaves became rigid. In some cases, a purplish pigmentation was observed due to anthocyanin accumulation, a typical physiological response to P deficiency (Figure 1B). Symptoms of K deficiency were detected 25 days after the start of the experiment. Initially, interveinal chlorosis developed, followed by necrotic spots along the leaf margins and lamina. This led to dry, scorched edges and tissue death. Leaf curling was also observed, especially in older leaves, which were more severely affected due to the mobile nature of K (Figure 1C). Symptoms of Ca deficiency became evident 35 days after the experiment commenced, primarily affecting young leaves. Necrosis was observed at the leaf tips, along with tip curling. Leaf edges became distorted, and localized necrotic lesions developed (Figure 1D). Symptoms of Mg deficiency were observed 35

days after the experiment began, mainly in the older leaves near the stem base. These leaves exhibited pronounced interveinal chlorosis and brown necrotic lesions along the margins (Figure 1E). Symptoms of S deficiency appeared around 45 days after the experiment began. Chlorosis was the dominant symptom, initially visible in younger leaves, which turned light green to yellow. Unlike N deficiency, which affects older leaves first, S deficiency symptoms were prominent in young foliage. Affected leaves also became smaller and stiffer (Figure 1F). In contrast, tomato plants grown under a complete nutrient solution (NSc) exhibited healthy leaf morphology with no deficiency symptoms (Figure 1G).

Vegetative growth

Macronutrient deficiencies significantly affected ($p < 0.05$) vegetative growth parameters of tomato plants, including plant height, stem diameter, and the dry weights of stem, roots, and leaves (Table 2).

Table 2. Vegetative growth of tomato (cv. 'Kardelen F1') under individual macronutrient deficiencies

Treatments	Plant height (cm)	Stem diameter (mm)	Dry weight		
			Stem (g)	Roots (g)	Leaves (g)
NSc (Control)	186.66 a	15.69 a	45.94 a	5.30 ab	51.46 a
-N	88.35 e	9.77 c	4.75 e	1.79 e	3.44 e
-P	174.00 bc	12.74 b	20.48 d	4.07 c	17.78 d
-K	178.00 ab	12.71 b	19.06 d	3.29 d	35.10 c
-Ca	163.32 d	14.62 a	40.17 b	5.14 b	40.92 b
-Mg	168.35 cd	15.46 a	37.00 c	5.10 b	45.21 b
-S	176.30 bc	15.49 a	35.23 c	5.66 a	44.55 b
$LSD_{0.05}$	9.21*	1.51*	1.83*	0.50*	4.43*

Each value represents mean (n = 3); Means followed by the same letter within a column are not significantly different at $p < 0.05$ according to the LSD test. *Significant at 5% level

Plant height was significantly reduced under N, P, Ca, Mg, and S deficiencies compared to the complete nutrient solution (NSc), while K deficiency did not lead to a statistically significant decrease. Among all treatments, N deficiency caused the most severe reduction in plant height. Similarly, stem diameter decreased significantly under N, P, and K deficiencies, whereas Ca, Mg, and S deficiencies did not result in notable changes (Table 2).

The most dramatic decline in stem, root, and leaf dry weights was observed under N deficiency. Compared to the NSc, stem dry weight was reduced by 89.66%, 55.42%, 58.51%, 12.55%, 19.46%, and 23.31% under N, P, K, Ca, Mg, and S deficiencies, respectively. P and K deficiencies also caused substantial reductions, while the least effect was observed under Ca deficiency. For root dry weight, significant reductions occurred under N, P, and K deficiencies. Interestingly, root dry weight under S deficiency was slightly higher than the control, though this difference was not statistically significant. The reductions compared to NSc were 66.23% (-N), 23.21% (-P), 37.93% (-K), 3.02% (-Ca), and 3.78% (-Mg). All macronutrient deficiencies significantly decreased leaf dry weight. The most pronounced reduction was again observed under N deficiency (93.32%), followed by P (65.45%) and K (31.80%) deficiencies. Reductions under Ca, Mg, and S deficiencies were less severe, ranging from 12.55% to 20.49%.

Leaf photosynthetic pigments

Macronutrient deficiencies significantly affected ($p < 0.05$) the levels of leaf photosynthetic pigments, including chlorophyll-a (Chl-*a*), chlorophyll-b (Chl-*b*), total chlorophyll (Chl-*t*), and carotenoids (*Car*), as illustrated in Figure 2.

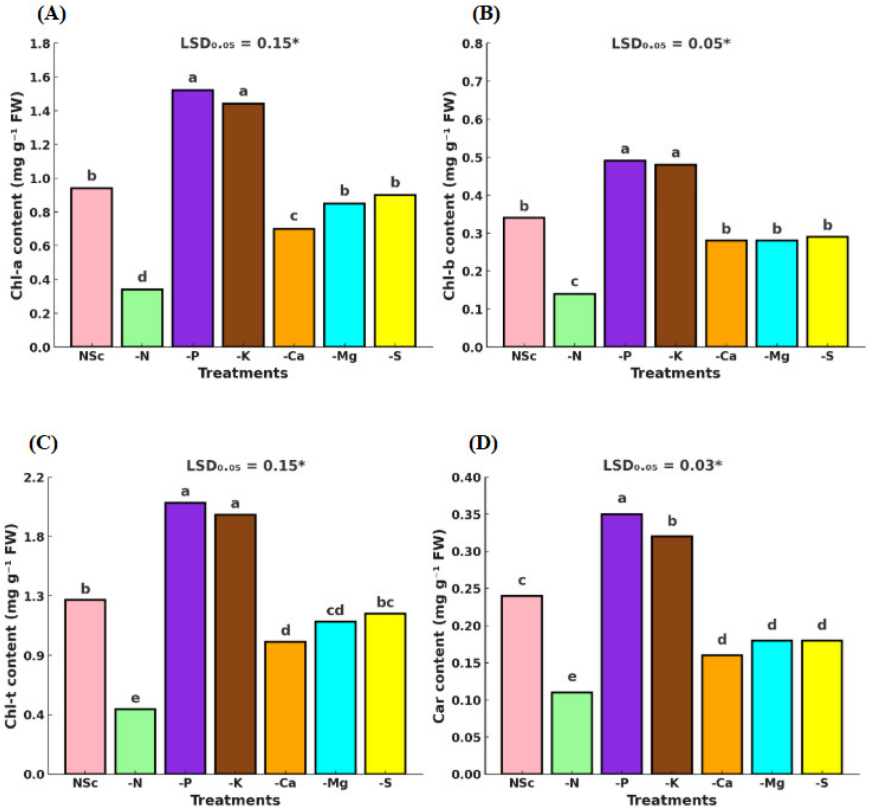

Figure 2. Chlorophyll-a (**A**), chlorophyll-b (**B**), total chlorophyll (**C**), and carotenoids (**D**) content in the leaves of tomato (cv. 'Kardelen F1') grown under varying nutrient regimes
Each value represents mean (n = 3); Means followed by the same letter within a column are not significantly different at $p < 0.05$ according to the LSD test. *Significant at 5% level

Under N deficiency, Chl-*a* content declined markedly, reaching only 36.17% of the NSc value. In contrast, Chl-*a* levels increased significantly under P and K deficiencies. Calcium (Ca) deficiency caused a moderate but statistically significant reduction, whereas Mg and S deficiencies led to slight, statistically non-significant decreases (Figure 2A). Similarly, Chl-*b* content dropped significantly under N deficiency, falling to 41.18% of the NSc value. Conversely, P and K deficiencies induced significant increases in Chl-*b*, by 144.12% and 141.18%, respectively. Deficiencies of Ca, Mg, and S led to moderate decreases, retaining 82.35%, 82.35%, and 85.29% of the NSc value, respectively (Figure 2B). Total chlorophyll (Chl-*t*) content showed a significant decline under N deficiency, reaching 37.21% of the NSc. However, it significantly increased under P and K deficiencies by 155.81% and 148.84%, respectively. Ca deficiency resulted in a moderate reduction (75.97% of NSc), while Mg and S deficiencies led to smaller decreases (87.60% and 92.25%, respectively) (Figure 2C). Carotenoid (*Car*) content followed a similar trend, decreasing sharply under N deficiency to 45.83% of the NSc value. On the other hand, P and K deficiencies caused increases of 145.83% and 133.33%, respectively. Ca deficiency led to a decrease to 66.67% of NSc, while *Car* contents under Mg and S deficiencies remained at 75.00% of the NSc value (Figure 2D).

Leaf macronutrients

Macronutrient concentrations in tomato leaves varied significantly ($p < 0.05$) under different macronutrient deficiency treatments (Table 3).

Table 3. Leaf N, P, K, Ca, Mg, and S concentrations in tomato (cv. 'Kardelen F1') grown under varying nutrient regimes

Treatments	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)
NSc	3.38 c	0.24 d	2.62 a	1.60 a	0.79 b	0.51 ab
-N	0.33 e	0.36 b	2.51 b	1.17 e	0.67 d	0.48 bc
-P	3.74 a	0.08 e	2.30 d	1.22 d	0.79 ab	0.43 d
-K	3.55 b	0.40 a	0.31 e	1.45 c	0.79 ab	0.54 a
-Ca	3.70 a	0.30 c	2.39 c	0.52 f	0.83 a	0.48 bc
-Mg	3.44 c	0.30 c	2.52 b	1.23 d	0.22 e	0.47 c
-S	3.01 d	0.23 d	2.64 a	1.52 b	0.75 c	0.13 e
$LSD_{0.05}$	0.07*	0.03*	0.05*	0.04*	0.04*	0.03*

Each value represents mean (n = 3); Means followed by the same letter within a column are not significantly different at $p < 0.05$ according to the LSD test. *Significant at 5% level

The most pronounced reduction in leaf N content occurred under the -N treatment, where it dropped to 0.33%, representing a drastic decline compared to the control (NSc, 3.38%). Phosphorus content reached its lowest level (0.08%) under -P treatment. Likewise, K concentration decreased significantly in the -K treatment, dropping to 0.31%. A sharp decline in Ca content was observed in the -Ca treatment, with values falling to 0.52%, while Mg concentration was lowest under -Mg treatment at 0.22%. Sulfur concentration decreased to 0.13% under the -S treatment, marking the most significant reduction for this element. Interestingly, some compensatory increases were also observed: in the -K treatment, P concentration rose to 0.40%, the highest among all treatments. Similarly, in the -Ca treatment, Mg content increased to 0.83%, surpassing the control and other treatments (Table 3).

Yield and its components in tomato

Macronutrient deficiencies had a significant effect ($p < 0.05$) on total fruit yield, number of fruits per plant, and average fruit weight in tomato plants (Figure 3).

Total fruit yield was markedly reduced under all deficiency treatments compared to the complete nutrient solution (NSc) (Figure 3A). Among the deficiencies, nitrogen deficiency (-N) caused the most severe yield reduction, with a relative yield of only 9.83% compared to NSc. Relative yields under other deficiencies were as follows: phosphorus (-P) 38.60%, potassium (-K) 47.84%, magnesium (-Mg) 63.71%, calcium (-Ca) 70.25%, and sulfur (-S) 79.70%.

Plants under N deficiency produced only two fruits, the lowest among treatments, whereas NSc produced 22 fruits. P and K deficiencies also significantly reduced fruit numbers, while Ca and Mg deficiencies had a moderate impact. Notably, S deficiency resulted in a relatively higher fruit count, second only to the control (Figure 3B). Mean fruit weight varied significantly across treatments (Figure 3C).

The highest values were recorded under Ca and S deficiencies, which were statistically similar to the control. In contrast, N, P, and K deficiencies led to the lowest fruit weights. Mg deficiency caused a moderate decline but still yielded significantly heavier fruits than N, P, and K-deficient plants (Figure 3C).

Biophysical quality characteristics

Macronutrient deficiencies led to notable variations in fruit size, diameter, and firmness ($p < 0.05$), while the fruit shape index remained largely unchanged ($p > 0.05$) (Figure 4A-D).

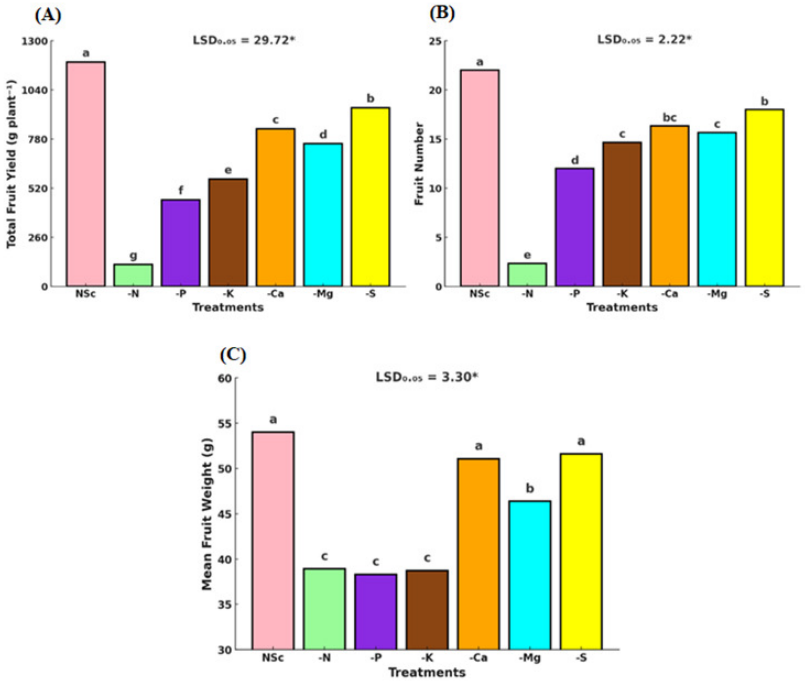

Figure 3. Total fruit yield (**A**), fruit number (**B**), mean fruit weight (**C**) of tomato (cv. 'Kardelen F1') grown under different nutrient regimes.

Each value represents mean (n = 3); Means followed by the same letter within a column are not significantly different at $p < 0.05$ according to the LSD test. *Significant at 5% level

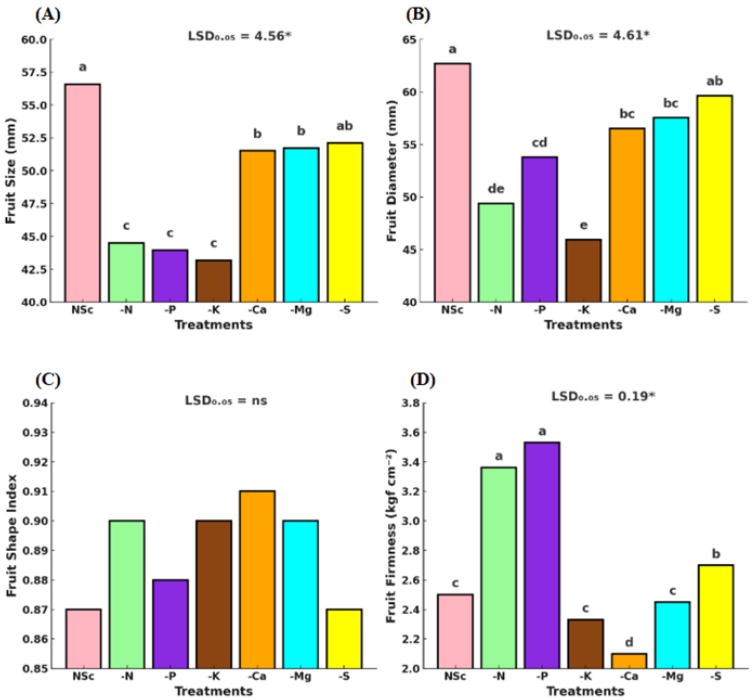

Figure 4. Fruit size (**A**), fruit diameter (**B**), fruit shape index (**C**), fruit firmness (**D**) of tomato (cv. 'Kardelen F1') grown under different nutrient regimes

Each value represents mean (n = 3); Means followed by the same letter within a column are not significantly different at $p < 0.05$ according to the LSD test. ns: non-significant; *significant at 5% level

The largest fruit size and diameter were recorded in the NSc, while N, P, and K deficiencies significantly reduced both parameters (Figure 4A-B). Among these, K deficiency had the most severe impact on both fruit size and diameter. In contrast, Ca, Mg, and S deficiencies resulted in intermediate fruit sizes, which were statistically similar to each other but lower than NSc (Figure 4A). The fruit shape index was not significantly affected by nutrient deficiencies (Figure 4C). However, fruit firmness varied considerably, with the highest values recorded under N and P deficiencies. Conversely, Ca deficiency caused the most substantial reduction in firmness, while Mg and S deficiencies also led to moderate decreases (Figure 4D).

Along with these changes, the fruit appearances of tomato plants grown under stress induced by macronutrient deficiencies were also presented (Figure 5).

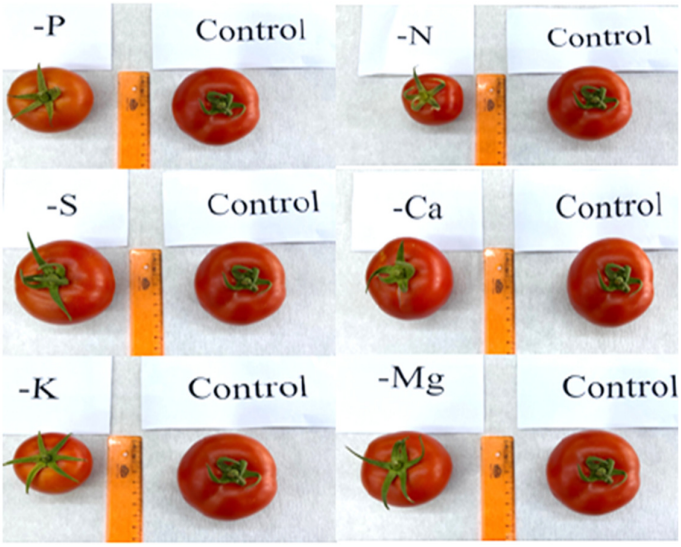

Figure. 5. Appearance of tomato fruits under individual macronutrient deficiencies

Fruit skin color parameters

Macronutrient deficiencies significantly influenced ($p < 0.05$) tomato fruit skin color characteristics, including a^*(red-green), b^*(yellow-blue), L^*(brightness), and h°(hue angle) (Table 4).

Table 4. Fruit skin color parameters of tomato (cv. 'Kardelen F1') grown under different nutrient regimes

Treatments	a^*	b^*	L^*	h°	C^*
NSc	19.58 b	25.53 bc	44.73 c	52.08 c	32.22
-N	19.79 ab	29.93 ab	48.24 ab	56.40 b	35.92
-P	18.87 bc	28.82 bc	49.00 a	56.72 b	34.45
-K	17.33 c	33.77 a	48.49 a	60.93 a	37.34
-Ca	19.84 ab	28.77 bc	47.30 abc	53.80 bc	32.37
-Mg	21.52 a	29.33 abc	45.75 bc	51.76 c	36.44
-S	20.13 ab	24.76 c	44.86 c	50.83 c	31.93
$LSD_{0.05}$	1.90*	4.93*	2.72*	4.15*	ns

Each value represents mean (n = 3); Means followed by the same letter within a column are not significantly different at $p < 0.05$ according to the LSD test. ns: non-significant; *significant at 5% level

Among treatments, Mg deficiency produced the highest a^* value (21.52), indicating enhanced redness in the fruit skin compared to other treatments, including the NSc. The highest b^* value (33.77), reflecting intense yellowness, was observed under K deficiency, while the lowest was recorded under the S deficiency treatment (24.76). Fruit brightness (L^*) increased significantly under P and K deficiencies, with values of 49.00

and 48.49, respectively-higher than the NSc (44.73). The hue angle ($h°$) was highest under K deficiency (60.93), suggesting a more yellow hue, in contrast to the redder tones seen in other treatments. No statistically significant differences ($p > 0.05$) were observed among treatments for chroma (C^*), indicating similar levels of color saturation across treatments (Table 4).

Physicochemical quality characteristics

Macronutrient deficiencies significantly influenced ($p < 0.05$) the physicochemical attributes of tomato fruits, including juice pH, total soluble solids (TSS), titratable acidity (TA), and dry matter content (Figure 6).

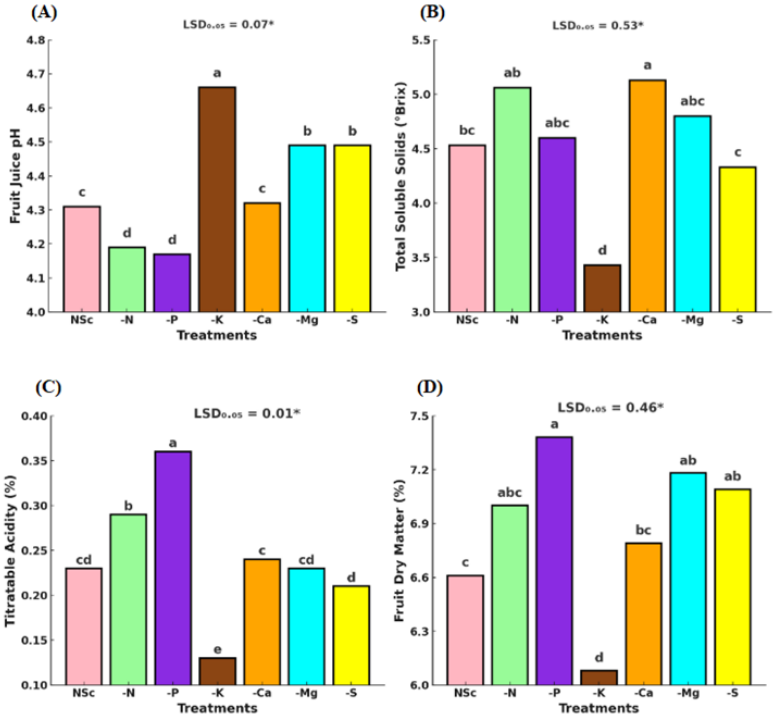

Figure 6. Fruit juice pH (**A**), total soluble solids (**B**), titratable acidity (**C**), fruit dry matter (**D**) of tomato (cv. 'Kardelen F1') grown under different nutrient regimes

Each value represents mean (n = 3); Means followed by the same letter within a column are not significantly different at $p < 0.05$ according to the LSD test. *Significant at 5% level

Fruit juice pH varied across treatments, with the highest value (4.66) recorded under K deficiency, significantly exceeding that of the control. Conversely, N and P deficiencies resulted in the lowest pH values, both being significantly lower than NSc. Moderate increases in pH were observed under Mg and S deficiencies, while Ca deficiency showed no statistically significant effect (Figure 6A). Total soluble solids (TSS) content peaked in the Ca-deficient treatment (5.13 °Brix), although values in -N and -Mg were statistically similar. K deficiency resulted in the most severe reduction in TSS (3.43 °Brix). The -P and -Mg treatments did not significantly affect TSS compared to the NSc, while -S treatment resulted in a moderate decrease (Figure 6B). The highest titratable acidity (0.36%) was observed under P deficiency, whereas K deficiency caused the lowest acidity (0.13%). N deficiency also increased TA significantly compared to the control, while Ca and S deficiencies did not result in significant changes. The response under Mg deficiency was statistically comparable to that of NSc (Figure 6C). Fruit dry matter content was highest under P deficiency (7.38%), followed by Mg and S deficiencies, both showing significant increases over the NSc. In contrast, K deficiency led to the lowest

dry matter accumulation (6.08%). No significant change was observed in the -N treatment compared to NSc, while Ca deficiency caused a moderate decline (Figure 6D).

Nutraceutical quality characteristics

Macronutrient deficiencies had a significant effect ($p < 0.05$) on the nutraceutical quality of tomato fruits, including lycopene, vitamin C, total phenolic, and flavonoids content (Figure 7).

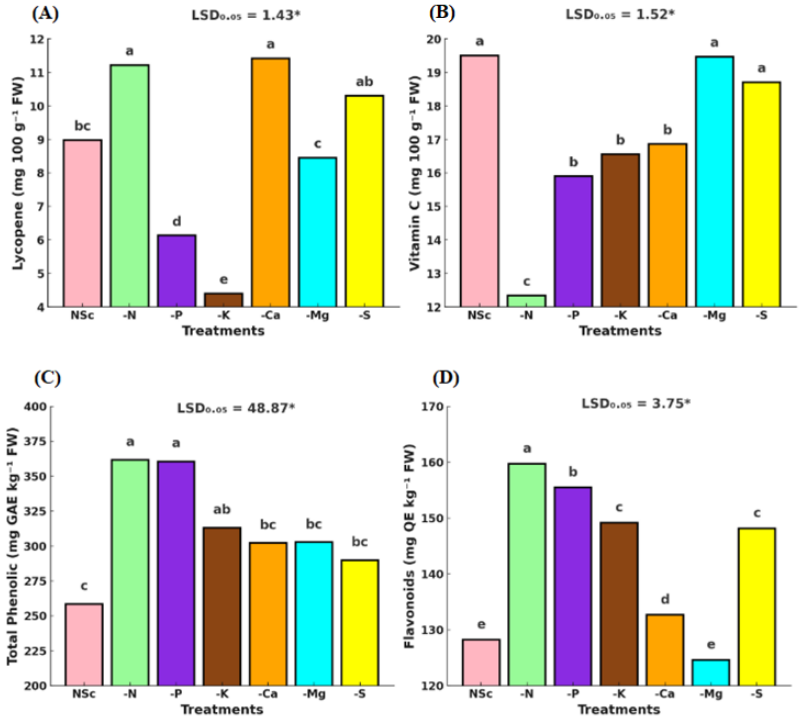

Figure 7. Lycopene (**A**), vitamin C (**B**), total phenolic (**C**), flavonoids contents (**D**) of tomato (cv. 'Kardelen F1') grown under different nutrient regimes

Each value represents mean (n = 3); Means followed by the same letter within a column are not significantly different at $p < 0.05$ according to the LSD test. *Significant at 5% level

Lycopene content increased markedly under Ca (11.41 mg 100 g^{-1} FW) and N (11.21 mg 100 g^{-1} FW) deficiencies compared to the NSc. In contrast, K deficiency resulted in the lowest lycopene content (4.39 mg 100 g^{-1} FW). Additionally, P deficiency led to a substantial decrease, while Mg and S deficiencies did not significantly differ from the NSc, although Mg showed a slight reduction (Figure 7A). Vitamin C content was highest in fruits from the NSc, -Mg, and -S treatments (19.50, 19.46, and 18.70 mg 100 g^{-1} FW, respectively), showing no statistical differences among them. The lowest vitamin C level (12.33 mg 100 g^{-1} FW) was recorded under N deficiency. Moderate reductions were also observed under P, K, and Ca deficiencies (Figure 7B). Total phenolic content peaked under N and P deficiencies (361.63 and 360.55 mg GAE kg^{-1} FW), while the lowest value was recorded in the NSc (258.40 mg GAE kg^{-1} FW). K deficiency resulted in a moderate increase, whereas Ca, Mg, and S deficiencies produced values statistically comparable to the control (Figure 7C). Flavonoid content was highest under N deficiency (159.73 mg QE kg^{-1} FW), significantly exceeding all other treatments. P, K, Ca, and S deficiencies also elevated flavonoid levels to varying degrees, while Mg deficiency did not significantly affect this trait. The lowest flavonoid content was found in fruits from the NSc and -Mg treatments (Figure 7D).

Heatmap of Pearson correlation analysis

The Pearson correlation analysis identified significant linear relationships among growth parameters, physiological traits, yield, and fruit quality traits in tomato plants subjected to different nutrient regimes, including individual macronutrient deficiency (-N, -P, -K, -Ca, -Mg, -S) and sufficient (NSc) conditions (Figure 8). The results revealed significant relationships between the analyzed parameters at the $p < 0.01$ level.

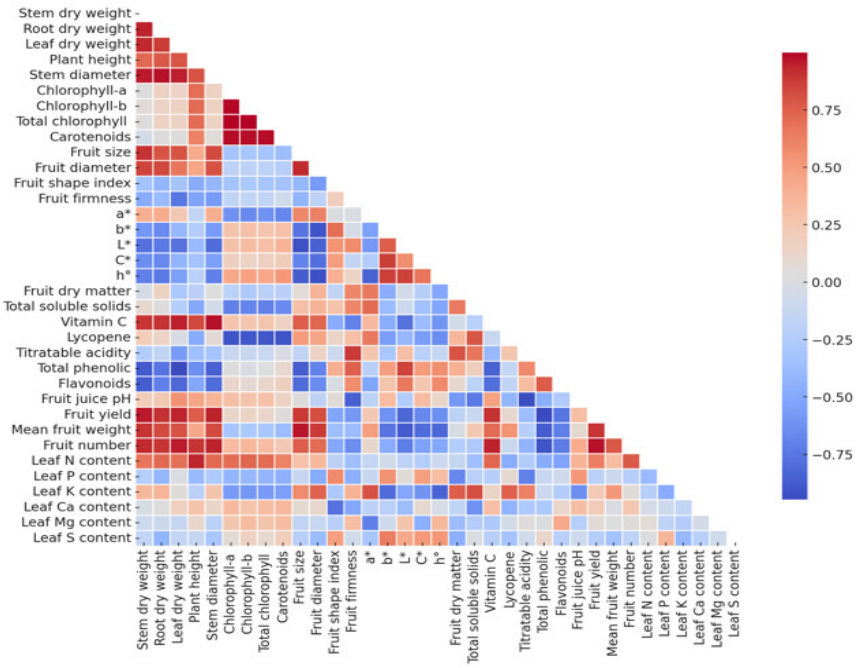

Figure 8. Heatmap of Pearson's correlation coefficients among growth, physiological, yield, and fruit quality traits in tomato plants grown under varying nutrient regimes

A strong positive correlation was observed between root dry weight and stem diameter ($r = 0.904$; $p < 0.01$). Additionally, leaf dry weight showed strong positive correlations with fruit number ($r = 0.940$; $p < 0.01$) and stem diameter ($r = 0.900$; $p < 0.01$). Among the photosynthetic pigments, Chl-*t* exhibited high correlations with Chl-*a* ($r = 0.996$; $p < 0.01$) and Chl-*b* ($r = 0.963$; $p < 0.01$). A strong positive association was also detected between fruit number and total fruit yield ($r = 0.967$; $p < 0.01$), while mean fruit weight correlated strongly with fruit size ($r = 0.844$; $p < 0.01$). Furthermore, leaf N content displayed a significant positive correlation with plant height ($r = 0.928$; $p < 0.01$), whereas leaf K content was positively associated with total soluble solids ($r = 0.741$; $p < 0.01$).

Conversely, a strong negative correlation was observed between titratable acidity and fruit juice pH ($r = -0.91$; $p < 0.01$). Likewise, Chl-*a* and lycopene content exhibited a strong negative correlation ($r = -0.87$; $p < 0.01$). Similarly, Chl-*t* and lycopene content ($r = -0.87$; $p < 0.01$) showed a strong negative correlation. Additional negative correlations were detected between fruit firmness and fruit juice pH ($r = -0.808$; $p < 0.01$), as well as leaf K content and hue angle ($h°$) ($r = -0.720$; $p < 0.01$).

Discussion

Macronutrient deficiencies in tomato plants induced characteristic visual symptoms, each reflecting the physiological role and phloem mobility of the deficient element. These symptoms, shown in Figure 1, serve as key diagnostic markers for the early detection of nutrient imbalances and stress responses (Sales *et al.*, 2021;

Muneer *et al*., 2024). N deficiency symptoms appeared earliest, primarily on mature leaves, which turned pale yellow and developed marginal necrotic lesions (Figure 1A). These signs reflect nitrogen's high mobility and central role in chlorophyll and protein synthesis. The degradation of chloroplast proteins in aging leaves under N-limiting conditions enables nitrogen redistribution to younger tissues, sustaining plant vigor (Sakuraba, 2022). This pattern of leaf yellowing is a classic response linked to declining chlorophyll stability and loss of photosynthetic capacity. P deficiency led to the formation of dark green, rigid leaves with restricted expansion, marginal necrosis, and, in some cases, purple pigmentation due to anthocyanin accumulation (Figure 1B). This response represents a photoprotective mechanism under P stress, as anthocyanins counteract oxidative damage and delay senescence (He *et al*., 2021; Li *et al*., 2023). These symptoms align with phosphorus's limited mobility and its pivotal role in energy transfer, nucleic acid synthesis, and membrane formation. K deficiency symptoms were characterized by interveinal chlorosis, progressing to marginal necrosis and leaf curling, especially in older leaves (Figure 1C). These features are attributed to potassium's role in protein synthesis, osmoregulation, and enzyme activation. Reduced K uptake leads to putrescine accumulation, which exacerbates oxidative stress by promoting reactive oxygen species (ROS) production and resulting in cellular damage (Pathak *et al*., 2014; Chen *et al*., 2016). This explains the scorched appearance of leaf margins under prolonged K stress. Ca deficiency affected younger leaves, as Ca is phloem-immobile. Tip necrosis, marginal curling, and distortion were common symptoms (Figure 1D). These anomalies reflect calcium's function in maintaining cell wall rigidity and membrane stability. Disruption of Ca-mediated pectin crosslinking leads to abnormal cell expansion and disorganized tissue growth, particularly in rapidly dividing regions (Hepler and Winship, 2010; Proseus and Boyer, 2012). Mg deficiency manifested in older leaves as interveinal chlorosis with necrotic spots along the margins (Figure 1E). Mg, being highly mobile in the phloem, is redistributed from mature to developing tissues. Its deficiency disrupts chlorophyll biosynthesis and thylakoid structure, explaining the degradation of green pigmentation while leaving the veins green longer (Hawkesford *et al*., 2011; Silva *et al*., 2011). Sulfur (S) deficiency developed last, presenting with uniform chlorosis in young leaves, which also became smaller and stiffer in texture (Figure 1F). Unlike N, S has low phloem mobility, hence symptoms appear in developing tissues. S is crucial for amino acid and protein synthesis, and its deficiency impairs chlorophyll formation, particularly by limiting the synthesis of functional groups such as iron-sulfur clusters and heme groups (Malavolta, 2006). In contrast, plants supplied with a complete nutrient solution (NSc) exhibited normal leaf morphology, robust expansion, and intense green coloration, indicating balanced nutrition (Figure 1G). Collectively, these results confirm that each macronutrient deficiency triggers visually distinct and physiologically interpretable symptoms in tomato leaves, reinforcing their diagnostic value in controlled cultivation systems.

Nutrient deficiency alters key physiological processes, adversely affecting plant growth and architecture (Song *et al*., 2024). In the present study, N deficiency had the most severe impact, significantly reducing plant height, stem diameter, and biomass accumulation (Table 2). This outcome aligns with the findings of Jing *et al*. (2020), who reported that crops generally exhibit greater sensitivity to N deficiency than to P or K. As an essential component of amino acids, nucleic acids, proteins, and chlorophyll, N supports core metabolic pathways and photosynthesis, both of which drive vegetative growth and fruit development (Zhang *et al*., 2020; Fan *et al*., 2022). P deficiency also caused considerable reductions in biomass and shoot growth (Table 2), due to its role in ATP and NADPH synthesis, nucleic acid production, and membrane formation (Calderón-Vázquez *et al*., 2011; Sun *et al*., 2016). Inadequate P disrupts cell division and elongation, resulting in stunted growth (Mengel and Kirkby, 2004). Similarly, K deficiency led to reduced dry matter accumulation and structural development (Table 2). As a key osmoticum and enzyme activator, K regulates carbohydrate metabolism, protein synthesis, and cellular water balance (Hawkesford *et al*., 2011). Although some physiological compensation may occur through the uptake of other cations (e.g., Ca^{2+}, Mg^{2+}, Na^{+}), it is often insufficient to maintain optimal growth under K-limiting conditions (Winkler and Zotz, 2010). In contrast, Ca, Mg, and S deficiencies had milder effects on vegetative parameters, though some growth impairment was still evident (Table 2). Notably, Ca deficiency resulted in the least reduction in stem dry weight, emphasizing

its role in cell wall integrity and structural stability (Veazie *et al*., 2020). As a non-mobile element, Ca is critical for meristem development and cell expansion, especially in young tissues. Interestingly, root dry weight under S deficiency slightly increased compared to the control, although the difference was not statistically significant (Table 2). This suggests a more nuanced interaction between S availability and root growth. Supporting this, Santiago *et al*. (2018) observed that sulfur-deficient plants maintained shoot and root biomass at levels comparable to the control, potentially due to atmospheric S deposition. Leal and Prado (2008) similarly reported that S omission did not significantly impact most growth parameters in common bean. In contrast, Narayan *et al*. (2023) demonstrated that S deficiency may reduce biomass and alter plant morphology, highlighting species-specific responses.

Photosynthetic pigments are essential for light harvesting and energy conversion in plants (Kume *et al*., 2018). In the present study, macronutrient deficiencies significantly altered pigment profiles in tomato leaves, particularly affecting chlorophyll and carotenoid content (Figure 2). Among all treatments, N deficiency resulted in the most pronounced reductions in Chl-*a*, Chl-b, Chl-t, and carotenoids (*Car*), reflecting N's central role in pigment synthesis and stability. These findings are consistent with those of Huang *et al*. (2021), who reported drastic pigment loss under N starvation, and Xu *et al*. (2021), who estimated that N constitutes approximately 75% of leaf chlorophyll content. Interestingly, P and K deficiencies led to increased pigment concentrations compared to the control (Figure 2). This response may represent a compensatory mechanism aimed at maximizing light capture under nutrient stress. Similar patterns have been reported in *Brassica rapa*, where chlorophyll levels were maintained under P deficiency to preserve photosynthetic function (Veazie *et al*., 2020). These results suggest that moderate P and K stress may induce adaptive strategies that sustain pigment synthesis and light-use efficiency despite metabolic constraints.

A notable outcome of this study is that the omission of any specific macronutrient consistently resulted in a significant decline in its corresponding leaf concentration, confirming nutrient-specific uptake limitations (Table 3). This pattern aligns with previous observations in tomato and other crops under controlled nutrient regimes (Campos *et al*., 2021). Interestingly, leaf magnesium concentration was elevated in Ca-deficient plants, suggesting a nutrient antagonism between calcium and magnesium. This inverse relationship is attributed to competition at the root uptake sites, where excess or limited availability of one divalent cation can influence the transport efficiency of the other (René *et al*., 2017). Such interactions underscore the complexity of nutrient dynamics in plant systems and highlight the importance of maintaining ionic balance in fertigation programs to optimize nutrient use efficiency.

Tomato (*Solanum lycopersicum* L.) is among the most widely grown vegetable crops worldwide, valued for its high nutritional content, including vitamins, dietary fiber, antioxidants, and pigments (Liu *et al*., 2022). However, like many horticultural species, its productivity is frequently limited by abiotic stresses-most notably, nutrient deficiencies in the growing medium (Rai *et al*., 2023). The findings of the present study reveal that macronutrient deficiencies significantly reduce tomato fruit yield, number, and average fruit weight, although the severity of the impact varied depending on the omitted nutrient (Figure 3). N deficiency exerted the most drastic reduction, with yield falling to only 9.83% of the complete nutrient control (NSc), underscoring nitrogen's pivotal role in vegetative growth, chlorophyll biosynthesis, and reproductive development. Similarly, the absence of phosphorus and potassium led to pronounced yield losses (38.60% and 47.84%, respectively), likely due to their essential functions in energy metabolism, root growth, and assimilate transport. These results reinforce the importance of a balanced N-P-K supply for sustaining tomato productivity. As previously reported by Rahman and Zhang (2018), nutrient imbalances-particularly among N, P, and K-can impair uptake efficiency and disturb physiological processes, leading to suboptimal yield outcomes.

Macronutrient deficiencies markedly influenced the biophysical characteristics of tomato fruits, particularly size and firmness (Figure 4). Among the treatments, N deficiency caused the most substantial reduction in fruit size and diameter, highlighting nitrogen's central role in cell expansion and tissue development. Similarly, the omission of P and K significantly reduced fruit size, likely due to their involvement in energy transfer, phloem loading, and osmotic regulation-processes critical for cell enlargement and assimilate

transport. Ca deficiency resulted in the lowest fruit firmness, reflecting its essential function in stabilizing cell walls through the formation of calcium pectate. Adequate Ca availability enhances fruit texture by maintaining membrane integrity and strengthening pectic structures, thereby improving resistance to mechanical damage and postharvest decay (Thor, 2019; Zhang *et al*., 2019). Interestingly, fruits from the -N and -P treatments exhibited increased firmness compared to the control, which may be associated with stress-induced modifications in cell wall metabolism or reduced cell expansion. In contrast, S deficiency had a relatively minor impact on fruit size and diameter, suggesting that while S is crucial for protein synthesis and enzymatic function, it plays a less prominent role in determining the physical dimensions of tomato fruits. However, its involvement in metabolic processes may still influence textural attributes.

Color is a key quality attribute in tomatoes, closely associated with their sensory appeal and nutritional value (Lin *et al*., 2014). As a primary visual cue for consumers, fruit color is largely determined by pigment accumulation-especially carotenoids, which are responsible for red, orange, and yellow hues in tomato fruits (Llorente *et al*., 2017; Shin *et al*., 2019). In the present study, macronutrient deficiencies significantly influenced fruit color parameters (Table 4), indicating disruptions in pigment biosynthesis and ripening physiology. Among the treatments, Mg deficiency yielded the highest a^* value (21.52), reflecting enhanced red pigmentation, likely due to its involvement in chlorophyll and carotenoid metabolism. In contrast, K deficiency produced the highest b^* (33.77) and h° (60.93) values, resulting in a more yellowish hue-suggesting impaired lycopene accumulation and altered pigment profiles. These findings are consistent with previous reports linking K availability to lycopene synthesis and color uniformity in tomato (Fracchiolla *et al*., 2021). Furthermore, increased L^* values under -P and -K treatments suggest delayed or incomplete pigment development, potentially resulting from impaired energy transfer and sugar metabolism. Despite these hue and brightness shifts, chroma (C^*) values remained statistically unchanged, indicating stable overall color intensity across treatments. These observations reinforce the importance of balanced macronutrient supply-particularly potassium—for promoting uniform pigmentation and optimal fruit quality in tomato production systems.

The perception of fruit and vegetable quality is influenced by the interaction between their physicochemical properties and consumer expectations. Agro-environmental influences play a crucial role in shaping intrinsic quality traits (Kyriacou and Rouphael, 2018). In this study, macronutrient deficiencies significantly affected the pH, TSS, TA, and dry matter content of tomato fruits (Figure 6). In particular, K deficiency resulted in the highest pH (4.66) and the lowest TSS and TA values, suggesting impaired acid-base regulation, sugar transport, and ionic homeostasis. Being predominantly present in the form of K^+, it is essential for multiple physiological functions, such as regulating photosynthesis, carbohydrate transport, enhancement of source carbohydrate synthesis, and cytoplasmic pH stability (Oosterhuis *et al*., 2013; Wu *et al*., 2021). This suggests that K is essential for maintaining acidity and optimizing carbohydrate accumulation, which directly affects flavor and fruit quality. The acidity of fleshy fruits is primarily determined by the composition and concentration of organic acids, particularly malic and citric acids, which play a key role in pH regulation. Besides their involvement in pH regulation, organic acids serve as essential carbon reservoirs and contribute to various stress response mechanisms (Etienne *et al*., 2013; Batista-Silva *et al*., 2018; Walker and Famiani, 2018). The current study demonstrates that the -P treatment lowered pH, likely due to elevated organic acid content. These findings are in agreement with Li *et al*. (2021), who reported that key organic acids associated with tomato fruit sourness were over-accumulated under low P conditions, while soluble sugar content was significantly reduced. Furthermore, TA levels increased under P deficiency (Figure 6C), indicating enhanced organic acid accumulation and altered acid metabolism. These metabolic shifts were largely attributed to changes in enzyme activities within relevant pathways, further supporting the role of P in balancing sugar-acid metabolism and maintaining fruit flavor. Generally, TSS primarily consist of soluble sugars, which directly influence fruit ripeness and quality (Sun *et al*., 2022). The present study indicates that TSS content increased under Ca deficiency (Figure 6B), likely due to altered sugar partitioning. These results align with those of Sun *et al*. (2022), who reported that Ca-deficient apples exhibited significantly higher TSS content, further supporting the role of Ca in sugar accumulation. Notably, the present study reveals that fruit dry matter

accumulation declined with K deficiency, reinforcing potassium's role in water retention and carbohydrate metabolism. This is consistent with Hasanuzzaman *et al.* (2018), who emphasized that K is involved in key physiological processes requiring water, such as stomatal function, enzyme activation, and the movement of photoassimilates. These results underscore the complex interactions between macronutrients in determining fruit composition and quality. Maintaining adequate K, N, and P levels is particularly crucial for ensuring optimal acidity, sweetness, and structural integrity in tomatoes.

Tomato is an important dietary source of natural antioxidants such as vitamin C, phenolic compounds (including flavonoids), and lycopene-an effective antioxidant with nutritional and health-promoting properties (Khan *et al.*, 2021; Rosa-Martínez *et al.*, 2021). The concentration of these bioactive compounds is influenced by environmental conditions, cultivar selection, and nutrient management strategies (Balestrini *et al.*, 2021). The present study shows that macronutrient deficiencies significantly affected the nutraceutical profile of tomato fruits by altering the contents of lycopene, vitamin C, total phenolic, and flavonoids (Figure 7). Notably, the highest lycopene concentrations were observed under N and Ca deficiency, possibly due to enhanced carotenoid biosynthesis triggered by abiotic stress. In contrast, K deficiency led to a significant decrease in lycopene levels, reinforcing K's role in pigment formation and ripening processes. Vitamin C content was highest in the NSc, as well as in Mg- and S-deficient treatments, while the most pronounced decline occurred under -N. This reduction suggests that N is vital for ascorbate biosynthesis and recycling, possibly through its effect on enzyme systems linked to the ascorbate-glutathione pathway (Zhang *et al.*, 2016). Additionally, P deficiency was associated with significant increases in total phenolics and flavonoids (Figure 7C-D), likely reflecting a stress-induced upregulation of antioxidant metabolism. Similar trends have been observed in pak choi, where low P conditions promoted flavonoid accumulation as part of the plant's adaptive response to oxidative stress (Wagas *et al.*, 2024). Collectively, these findings highlight the complex interplay between nutrient availability and the accumulation of antioxidant compounds in tomato fruits. Strategic nutrient management is therefore essential not only for yield but also for enhancing the nutraceutical value of tomatoes.

Conclusions

The present study reveals that each macronutrient plays a distinct and critical role in the physiological performance, growth dynamics, and fruit development of tomato cultivated in a soilless greenhouse system. N deprivation produced the most drastic outcomes, with over 90% reduction in total yield and more than 93% decline in leaf biomass, highlighting its central role in both vegetative and reproductive stages. P and K shortages also led to pronounced yield penalties, reducing fruit production by approximately 61% and 52%, respectively.

In addition to yield suppression, K deficiency substantially deteriorated several quality-related traits, notably diminishing lycopene accumulation, total soluble solids, and titratable acidity, while concurrently increasing fruit pH and altering coloration. N stress caused significant depletion of chlorophyll a and total chlorophyll content, whereas P and K deficiencies triggered increases in leaf pigment levels-likely reflecting stress-induced adjustments in photosynthetic machinery. Ca scarcity primarily affected fruit texture by weakening structural stability, and N deficiency resulted in the sharpest drop in vitamin C, indicating disruption of antioxidant pathways. Furthermore, elevated levels of phenolic compounds and flavonoids under N and P limitation imply a shift toward secondary metabolite biosynthesis in response to nutrient-induced oxidative stress. Correlation analysis underscored the close association between chlorophyll content, biomass accumulation, nutrient status, and yield performance, offering valuable insights into trait-based indicators of productivity.

Overall, the data affirm that precise nutrient management-particularly of N, P, and K is vital to sustain tomato growth, yield, and fruit nutritional quality. Future research should prioritize the development of

targeted fertigation protocols aimed at alleviating nutrient stress and enhancing plant resilience under soilless and controlled-environment production systems.

Authors' Contributions

Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing – original draft, and writing – review and editing: GA.

The author read and approved the final manuscript.

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Conflict of Interests

The author declares that there are no conflicts of interest related to this article.

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