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IONIC PROPORTIONS OF THE NUTRIENT SOLUTION AND THEIR EFFECT ON MACRONUTRIENT EXTRACTION IN HYDROPONICALLY GROWN LETTUCE

Rodolfo **de la Rosa-Rodríguez**[1], Ricardo David **Valdez-Cepeda**[2], Luis Octavio **Solís-Sánchez**[1], Alfredo **Lara-Herrera**[3*], Libia Iris **Trejo-Téllez**[4*]

[1]Universidad Autónoma de Zacatecas (UAZ). Unidad Académica de Ingeniería Eléctrica. Avenida Ramón López Velarde No. 801, Col. Centro, Zacatecas, Zacatecas, Mexico. C. P. 98000.
[2]Universidad Autónoma Chapingo. Zacatecas, Mexico. C. P. 98085.
[3]UAZ. Unidad Académica de Agronomía. Carretera Zacatecas-Guadalajara km 15.5, Cieneguillas, Zacatecas, Mexico. C. P. 98170.
[4]Colegio de Postgraduados. Programa de Edafología. Carretera México-Texcoco km 36.5 Montecillo, State of Mexico, Mexico. C. P. 56264.
* Authors for correspondence: alara204@hotmail.com; tlibia@colpos.mx

ABSTRACT

The nutrient solution (NS) consists of water with dissolved mineral ions, whose proportions depend on the species, cultivar, phenological stage, and environmental conditions, among other factors. This study aimed to evaluate the effect of variations in the proportions of NO_3^- and K^+ in the Steiner nutrient solution on the extraction of macronutrients in lettuce grown in a closed hydroponic system. The treatments were as follows: T1 (control): original Steiner NS, with proportions of 9.000:0.750:5.250 molc m^{-3} for the anions NO_3^-:$H_2PO_4^-$:SO_4^{2-} and 5.250:6.750:3.000 molc m^{-3} for the cations K^+:Ca^{2+}:Mg^{2+}; T2: 11.338:0.354:2.479 and 5.250:6.750:3.000 molc m^{-3}; T3: 6.371:1.194:8.362 and 5.250:6.750:3.000 molc m^{-3}; T4: 9.000:0.750:5.250 and 6.375:5.675:2.522 molc m^{-3}; and T5: 9.000:0.750:5.250 and 3.158:8.743:3.886 molc m^{-3}. Concentrations of N, P, K, Ca, and Mg were determined in leaves, buds, and roots, and together with dry biomass data, were used to estimate nutrient extraction per organ. The highest nutrient content was recorded in leaves (79 % of the total extracted). The greatest extractions corresponded to N and K, reaching 5.89 and 5.67 mg plant^{-1}, respectively, with T2 (high NO_3^- proportion). Increasing NO_3^- in the anionic proportion enhanced Ca and Mg uptake, whereas increasing K^+ reduced the extraction of these same cations. Treatments T2 and T4 showed the highest total extractions, mainly due to the greater values of N and K obtained compared with treatments in which the proportion of these ions was reduced. These results indicate that modifications in the anionic and cationic proportions of the nutrient solution significantly influence nutrient extraction in lettuce, with the treatment containing the highest NO_3^- proportion being the most efficient for the uptake of N, K, Ca, and Mg.

Keywords: nutrient extraction, ionic balance, anion interactions, cation interactions.

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INTRODUCTION

Nutrient solution (NS) consists of water in which oxygen and mineral nutrients in ionic form are dissolved (Trejo-Téllez and Gómez-Merino, 2012). These nutrients contribute to biomass synthesis and influence multiple physiological and biochemical processes in plants, thus determining the quantity and quality of food produced (Engels *et al*., 2023). The amount of nutrients required by plants depends on the species, variety, phenological stage and environmental conditions, among other factors (Sambo *et al*., 2019).

Because various factors influence nutrient availability and concentration, each NS must be formulated with specific characteristics to achieve the expected yield and quality. Among the most important parameters are: a) pH, which affects nutrient availability, with the highest availability occurring within a pH range of 5.5 to 6.5 (Baca-Castillo *et al*., 2016); b) the NO_3^-:NH_4^+ ratio, which is relevant because both ionic forms of N are involved differently in biochemical, metabolic and physiological processes, potentially enhancing or limiting lettuce production (Wenceslau *et al*., 2021); c) the temperature of the NS, which directly influences the amount of dissolved oxygen available to roots (Ouyang *et al.,* 2020); and d) electrical conductivity (EC), with an optimal range of 1.5 to 2 dS m^{-1} for lettuce (Adhikari *et al*., 2019). In addition, the mutual relationship among anions and among cations (ionic balance) is essential to prevent undesirable chemical reactions —such as nutrient precipitation— and to ensure an adequate nutrient supply that allows plants to reach their maximum yield (Baca-Castillo *et al*., 2016).

The composition of macro- and micronutrients in an NS directly influences plant growth, leaf number and area, yield, and crop quality, including mineral content (Ahmed *et al*., 2021). Therefore, the formulation of the NS must be adjusted to the specific requirements of each species and to the environmental conditions under which the crop is grown (Kumari *et al*., 2018).

Based on these considerations, Steiner (1961) proposed a methodology for formulating true nutrient solutions, characterized by maintaining the same osmotic pressure and pH, as well as constant mutual ionic relationships. These proportions, expressed as percentages, were: 60:5:35 for the anions NO_3^-:$H_2PO_4^-$:SO_4^{2-} and 35:45:20 for the cations K^+:Ca^{2+}:Mg^{2+}. However, in hydroponic systems it is possible to establish different ionic relationships and various total salt concentrations, as long as solubility limits that cause precipitation are not exceeded and imbalances, deficiencies or toxicities that affect plant physiological processes are avoided (Sambo *et al*., 2019).

Ionic proportions in the NS can alter cell membrane functionality and, consequently, the solute balance and the internal concentration of nutrients, causing symptoms similar to nutrient deficiencies (Coskun *et al*., 2017). Among essential elements, K and N are required in larger quantities (Oosterhuis *et al*., 2014). For this reason, changes in their concentrations and/or proportions in the NS can significantly affect the absorption and accumulation of one or more nutrients. For example, changes in NO_3^- within the anionic proportion cause notable variations in the concentration of N and K more than in other ions (Al-Meselmani, 2022). Likewise, an 80:20 NO_3^-:NH_4^+ ratio may increase N concentration (Lara-Izaguirre *et al*., 2019), whereas reducing this ratio may induce ammonium toxicity (Ozores-Hampton *et al*., 2015).

It has also been documented that modifications in the proportion of K^+ within the cations can affect its concentration in lettuce shoots (Barickman *et al.,* 2016). Furthermore, its proportion can influence the translocation of Ca, Mg, and P (Szczerba *et al*., 2009). Similarly, Malvi (2011) reported that an adequate proportion of NO_3^- contributes to optimal concentrations of K, Mg, Fe, Mn, and Zn.

A wide range of NS formulations exists for hydroponic plant production; however, the ionic proportions among them vary widely. Among these proportions, those corresponding to NO_3^- and K^+ are the most important, since N and K participate in most physiological processes in leafy vegetables (Riaño-Castillo *et al*., 2019). Nevertheless, further information is required regarding the response of plants grown in hydroponic systems to different nutrient relationships used in NS formulations (Al-Meselmani, 2022).

Considering the above, the present study was conducted to evaluate the effect of variations in the proportions of NO_3^- and K^+ in the Steiner nutrient solution on the extraction of macronutrients in lettuce grown under a closed hydroponic system. The working hypothesis states that increasing the proportion of NO_3^- to 80 % within the anionic mutual relationship and the proportion of K^+ to 43.8 % within the cationic mutual relationship of Steiner's NS will enhance macronutrient extraction in lettuce plants.

MATERIALS AND METHODS

Experimental site

This study was conducted from September 2 to October 31, 2022, in a 200 m^2 greenhouse equipped with a temperature and relative humidity control system, which operated by exchanging warm, dry internal air with fresh, humid external air. A closed floating root (FR) hydroponic system was established inside the greenhouse, in which the roots remained submerged in the nutrient solution (NS), while the aerial part of the plants was supported by a floating structure (Baca-Castillo *et al*., 2016). The greenhouse is located in Zacatecas, Zacatecas, Mexico, at coordinates 22° 43′ 42″ N and 102° 40′ 58″ W, at an elevation of 2236 m.

Treatments and experimental design

The treatments consisted of different macronutrient proportions in the NS. The reference solution was that proposed by Steiner (1961), along with four modified ionic proportion variants applied to a lettuce crop grown in a closed FR hydroponic system. The anionic proportions of NO_3^-:$H_2PO_4^-$:SO_4^{2-} evaluated were 60:5:35, 80:2.5:17.5, and 40:7.5:52.5, while the cationic proportions of K^+:Ca^{2+}:Mg^{2+} were 35:45:20, 43.8:38.9:17.3, and 20:55.4:24.6. The five nutrient solution (NS) treatments evaluated are described in Table 1. All treatments were maintained at an electrical conductivity (EC) of 1.5 dS m^{-1} and the same osmotic potential (−0.0547 MPa) (Lara-Herrera *et al*., 2023).

Table 1. Macronutrient composition of the nutrient solutions evaluated.

Treatments	NO_3^-	$H_2PO_4^-$	SO_4^{2-}	K^+	Ca^{2+}	Mg^{2+}
			(mol_c m^{-3})			
T1	9.000	0.750	5.250	5.250	6.750	3.000
T2	11.338	0.354	2.479	5.250	6.750	3.000
T3	6.371	1.194	8.362	5.250	6.750	3.000
T4	9.000	0.750	5.250	6.375	5.675	2.522
T5	9.000	0.750	5.250	3.158	8.743	3.886

Water used in the treatments

The water used in the treatments was previously deionized by reverse osmosis (ROH22133BW, Water IXC®, Guadalajara, Mexico). The analysis showed the following concentrations (mg L^{-1}): 7.70 N, ND (not detected) P, 3.09 K, 19.12 Ca, 2.43 Mg, and 2.65 S as macronutrients, and the following micronutrients: Fe ND, Mn 0.004, B 0.121, Cu 0.013, Mo ND, and Ni 0.038. The water quality parameters were: pH 7.40, EC 0.036 dS m^{-1}, 167.7962 mg HCO_3^- L^{-1}, 34.86 mg Na L^{-1}, and 46.87 mg Cl L^{-1}.

Plant material and production system

Lettuce (*Lactuca sativa* L.) cv. "Toscana RZ (45-08)" from Rijk Zwaan was used. This iceberg-type lettuce is vigorous, dark green, and produces round heads. Seeds were sown in 297-cell polystyrene trays filled with peat as substrate and irrigated for 28 days after sowing. Subsequently, seedlings were removed from the trays, and roots were washed to remove substrate before being placed in sterile, low-salt water for 5 days to allow plant adaptation.

Management of the nutrient solution during the experiment

In addition to the macronutrients corresponding to each treatment, all nutrient solutions received a uniform concentration of micronutrients (mg L^{-1}): 2.25 Fe, 1.11 Mn, 0.18 Zn, 0.09 Cu, 0.21 B, and 0.06 Mo. Electrical conductivity (EC) and pH were measured daily before replenishing the water consumed the previous day. The volume lost was restored, and pH was adjusted to 5.5. These procedures ensured EC and pH remained within suitable ranges for lettuce development at each phenological stage (Baca-Castillo *et al*., 2016).

The variables were evaluated in three crop stages:
Stage 1: 20 days after transplanting (DAT), corresponding to rosette formation.

Stage 2: 40 DAT, at the onset of bud formation.
Stage 3: 60 DAT, corresponding to completion of bud formation in early-maturing cultivars (cycle of 60–70 DAT). Maximum growth under hydroponic conditions occurs between 55 and 60 days (Sánchez-Alegría *et al*., 2015).

Macronutrient sources used for preparing the solutions were: $Ca(NO_3)_2 \cdot 4H_2O$, KNO_3, K_2SO_4, $MgSO_4 \cdot 7H_2O$, KH_2PO_4, and H_2SO_4. Micronutrients were supplied through a commercial mixture containing the concentrations listed above, in which Fe, Mn, Zn, and Cu were chelated with EDTA.

Measured variables

Macronutrient concentration in lettuce leaf, bud, and root tissues. Plant material was processed, and N, P, K, Ca, and Mg concentrations were determined following the methodology described by Lara-Herrera *et al*. (2023).

Dry weight of lettuce plant organs. Lettuce plants were separated into leaves, buds, and roots. Samples were dried in an oven (Thermo Fisher Scientific 51028118, USA) at 68 ± 2 °C, and dry mass was recorded using a digital scale (Kern AES 200-4N, Germany).

Macronutrient extraction. This parameter was determined based on the percentage obtained for each of the five macronutrients in the three plant organs, together with the dry weight of each corresponding organ. It is expressed using the following formula:

$$Ex = \frac{\text{DWo x Cm}}{100}$$

Where:
Ex = Macronutrient extraction (mg)
DWo = Dry weight of the organ (mg)
Cm = Macronutrient concentration in tissue (%)

Experimental design and statistical analysis

A randomized complete block design was used, with five treatments and six replicates per treatment, for a total of 30 experimental units. Each unit contained three plants (one for each phenological stage), resulting in a total of 90 plants evaluated throughout the experiment. Data were analyzed using ANOVA, and mean comparisons were performed with Tukey's test at a 5 % significance level ($p \leq 0.05$). All analyses were conducted using SAS software version 9.4.

RESULTS AND DISCUSSION

Macronutrient concentration in lettuce leaves

Nitrogen and phosphorus. In stages 2 and 3, treatment T2 showed the highest leaf N concentration (Table 2). This result agrees with Lara-Herrera *et al.* (2023), who reported that this proportion of NO_3^- in the nutrient solution increases yield, fresh weight, and leaf area index in hydroponically grown lettuce. The increase in leaf N concentration is associated with the greater availability of NO_3^- in the nutrient solution (Combrink and Kempen, 2019). Similarly, Djidonou and Leskovar (2019) observed that an increase in N supply enhanced N concentration in the leaves of hydroponic lettuce between 28 and 35 DAT.

In contrast, leaf P concentration in treatment T2 showed lower values than in the other treatments in both stages (Table 3). This behavior is explained by the lower

Table 2. Nitrogen concentration (g kg^{-1} dry matter) in leaves, buds, and roots at three developmental stages of lettuce plants as affected by macronutrient ratios in the nutrient solution.

Organ	Treatments	Stage 1	Stage 2	Stage 3
Leaves	T1	40.250 ± 4.194 a	30.683 ± 7.075 b	25.783 ± 4.073 bc
	T2	41.008 ± 4.912 a	45.033 ± 4.583 a	36.158 ± 2.618 a
	T3	38.983 ± 5.103 a	26.833 ± 7.353 b	24.091 ± 3.070 c
	T4	40.950 ± 3.541a	31.500 ± 6.369 b	28.816 ± 3.914 bc
	T5	37.333 ± 5.118a	32.083 ± 3.844 b	30.333. ± 1.8604 b
Organ	Treatments	Stage 1	Stage 2	Stage 3
Buds	T1	32.433 ± 4.923 a	26.950 ± 4.558 bc	22.691 ± 2.732 bc
	T2	34.035 ± 3.725 a	33.016 ± 2.779 ab	32.575 ± 6.110 a
	T3	22.400 ± 17.502 a	26.133 ± 4.145 c	17.908 ± 6.980 c
	T4	21.150 ± 12.540 a	31.908 ± 2.139 abc	22.400 ± 2.944 bc
	T5	29.071 ± 14.374 a	33.891 ± 4.418 a	28.816 ± 4.097 ab
Organ	Treatments	Stage 1	Stage 2	Stage 3
Roots	T1	37.333 ± 2.441 a	32.083 ± 6.402 a	22.400 ± 3.075 ab
	T2	23.800 ± 18.561 a	37.233 ± 9.125 a	19.308 ± 5.286 b
	T3	24.791 ± 19.981 a	23.800 ± 13.544 a	26.658 ± 9.480 ab
	T4	24.081 ± 18.918 a	43.983 ± 26.191 a	30.041 ± 5.117 a
	T5	36.096 ± 4.881 a	29.633 ± 9.047 a	30.450 ± 2.894 a

T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol$_c$ m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886. Stage 1 = 20 days after transplanting (rosette formation), Stage 2 = 40 days after transplanting (onset of bud formation), and Stage 3 = 60 days after transplanting (completion of bud formation). Values expressed as mean ± standard deviation. Different letters within each stage and organ indicate significant differences (Tukey, $p \leq 0.05$).

Table 3. Phosphorus concentration (g kg^{-1} dry matter) in leaves, buds, and roots at three developmental stages of lettuce plants, as affected by the proportions of macronutrients in the nutrient solution.

Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	5.322 ± 0.576 a	5.271 ± 1.217 a	4.047.83 ± 0.423 a
	T2	4.782 ± 0.746 a	3.608 ± 0.329 b	2.550.32 ± 0.517 b
Leaves	T3	4.639 ± 0.616 a	5.182 ± 0.818 a	4.204.39 ± 0.497 a
	T4	5.384 ± 0.921 a	4.512 ± 0.769 ab	4.659.01 ± 0.724 a
	T5	5.397 ± 0.846 a	4.701 ± 0.187 ab	4.324.64 ± 0.197 a
Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	6.582 ± 0.989 a	8.017 ± 1.092 a	6.153 ± 1.034 a
	T2	5.956 ± 2.089 a	6.002 ± 0.246 b	3.584 ± 0.714 b
Buds	T3	5.046 ± 3.930 a	7.985 ± 1.322 a	5.864 ± 2.091 a
	T4	4.146 ± 2.907 a	8.027 ± 1.104 a	7.244 ± 1.146 a
	T5	4.900 ± 4.131 a	8.959 ± 0.956 a	7.509 ± 0.672 a
Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	10.132 ± 0.840 a	7.353 ± 1.452 bc	6.128 ± 2.586 bc
	T2	6.826 ± 5.422 a	3.979 ± 0.604 d	2.293 ± 0.340 c
Roots	T3	7.588 ± 5.938 a	12.639 ± 2.686 a	11.653 ± 4.377 a
	T4	6.252 ± 5.739 a	6.834 ± 1.804 c	8.691 ± 3.676 ab
	T5	9.617 ± 2.562 a	9.667 ± 0.710 b	9.456 ± 0.912 ab

T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol_c m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886. Stage 1 = 20 days after transplanting (rosette formation), Stage 2 = 40 days after transplanting (onset of bud formation), and Stage 3 = 60 days after transplanting (completion of bud formation). Values expressed as mean ± standard deviation. Different letters within each stage and organ indicate significant differences (Tukey, $p \leq 0.05$).

proportion of phosphate in the nutrient solution and by the increase in biomass under this treatment, which results in a dilution effect of P in plant tissue. A similar effect was reported by Parra-Terraza (2016) when modifying the N:K ratio in the nutrient solution for tomato seedlings. Additionally, ionic balance also influences this response, as an increase in NO_3^- concentration requires proportional adjustments in the concentrations of $H_2PO_4^-$ and SO_4^{2-} (Al-Meselmani, 2022).

Potassium, calcium, and magnesium. Across the three growth stages, the control treatment (T1) showed a higher K concentration than treatment T5 (Table 4). This behavior of K in leaves supplied with the control solution was likely due to a balanced ionic proportion that favored the accumulation of this cation (Kempen *et al*., 2016). In the case of foliar Ca and Mg concentrations, during the first growth stage the lower

Table 4. Potassium concentration (g kg^{-1} dry matter) in leaves, buds, and roots at three developmental stages of lettuce plants, as affected by macronutrient proportions in the nutrient solution.

Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	37.153 ± 2.810 a	31.694 ± 6.110 a	30.919 ± 4.665 a
	T2	31.109 ± 3.225 ab	28.165 ± 3.116 ab	24.852 ± 3.673 ab
Leaves	T3	30.341 ± 4.039 ab	30.59 ± 4.654 a	26.459 ± 3.988 ab
	T4	32.474 ± 5.059 ab	29.471 ± 4.231 ab	29.677 ± 3.054 a
	T5	29.428 ± 3.816 b	22.218 ± 3.559 b	21.926 ± 4.823 b
Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	23.229 ± 3.797 a	19.181 ± 1.132 b	24.311 ± 6.018 ab
	T2	16.725 ± 5.248 a	17.865 ± 1.483 b	12.057 ± 2.995 b
Buds	T3	17.565 ± 13.672 a	21.817 ± 2.303 ab	20.502 ± 11.050 ab
	T4	15.276 ± 10.019 a	23.556.56 ± 2.336 a	29.171 ± 10.012 a
	T5	15.476 ± 13.334 a	11.054.30 ± 3.106 c	15.910 ± 10.856 ab
Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	31.710 ± 3.172 a	14.211 ± 5.771 b	7.485 ± 4.201 c
	T2	19.840 ± 15.457 a	8.324 ± 3.175 bc	2.819 ± 0.512 c
Roots	T3	22.461 ± 17.978 a	25.049 ± 5.258 a	16.983 ± 2.515 ab
	T4	19.044 ± 17.158 a	23.803 ± 4.295 a	22.139 ± 5.148 a
	T5	27.211 ± 7.697 a	4.524 ± 1.468 c	8.229 ± 8.593 bc

T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol_c m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886. Stage 1 = 20 days after transplanting (rosette formation), Stage 2 = 40 days after transplanting (onset of bud formation), and Stage 3 = 60 days after transplanting (completion of bud formation). Values expressed as mean ± standard deviation. Different letters within each stage and organ indicate significant differences (Tukey, $p \leq 0.05$).

K concentration in the nutrient solution (T5) resulted in higher concentrations of both elements in the leaves (Tables 5 and 6). This response may be attributed to the greater availability of calcium and to the antagonism that Ca and Mg can exert on K when the proportion of the latter in the nutrient solution is low (Mitra, 2017; Combrink and Kempen, 2019). In the last two stages, differences were observed only for Mg concentration (Table 6), with the highest values occurring under T5 (the treatment with the lowest K proportion in the nutrient solution). These patterns are attributed to modifications in the cationic balance of the nutrient solution (Mitra, 2017; Kamboj, 2019).

Macronutrient concentration in lettuce buds

Nitrogen and phosphorus. In Stage 2, only T5 exceeded the control (T1) in N concentration; however, in Stage 3, the increase in N proportion in the nutrient solution allowed this treatment to surpass the control (Table 2). An adequate supply of N in the nutrient solution is essential to meet crop demand; otherwise, plants cannot achieve appropriate foliar N concentrations (Kempen *et al*., 2016). Moreover, although T2 increased N concentration, it simultaneously showed a decrease in P concentration during Stages 2 and 3 (Table 3). This behavior is related to ionic adjustment within the nutrient solution: increasing the proportion of NO_3^- in the anionic fraction reduces the relative concentrations of $H_2PO_4^-$ and SO_4^{2-}, thereby decreasing P availability to the bud (Al-Meselmani, 2022).

Potassium, calcium, and magnesium. In Stage 2, increasing the proportion of K in the nutrient solution (T4) resulted in the highest K concentration in the bud, while decreasing K (T5) produced the lowest concentration (Table 4). In contrast, Mg exhibited the opposite trend: its concentration decreased when K in the nutrient solution increased and rose when K decreased (Table 6). In Stage 3, a similar trend was observed: reducing K in the nutrient solution was associated with higher Mg concentration in the bud. This pattern is consistent with ionic competition among cations, as high K concentrations in the nutrient solution can limit the uptake of other cations such as Ca and Mg due to their lower availability (Parra-Terraza, 2016). In the case of Ca, no significant effects were observed across the three stages (Table 5). This outcome differs from Parra-Terraza (2016), who reported an increase in Ca concentration when the proportion of NO_3^- was raised in a nutrient solution for tomato seedlings.

Macronutrient concentration in lettuce roots

Nitrogen and phosphorus. In Stage 3, increasing the proportion of NO_3^- in the nutrient solution resulted in the lowest N concentration in roots, while variations in K concentration—either increasing or decreasing—were associated with the highest root N values (Table 2). The fact that a higher proportion of NO_3^- leads to lower root N concentrations may be explained by two factors: (1) NO_3^- uptake depends largely on N demand in the aerial part, so under high demand, NO_3^- flow is preferentially directed to the shoots (Kempen *et al*., 2016); and (2) nitrate tends to accumulate mainly in aboveground tissues rather than in the roots (Sosa *et al*., 2017).
Regarding P, significant effects were observed in Stages 2 and 3, with T2 showing the lowest concentrations in roots (Table 3). This behavior in the intermediate and final stages is attributed to the imbalance between N and P in the nutrient solution, since increasing nitrate requires proportional reductions in phosphate and sulfate (Al-Meselmani, 2022).

Potassium, calcium, and magnesium. In Stages 2 and 3, increasing the proportion of K (T4) in the nutrient solution produced the highest K concentration in roots. A similar effect occurred with the reduction of NO_3^- (T3), which also surpassed the other

Table 5. Calcium concentration (g kg^{-1} dry matter) in leaves, buds, and roots at three developmental stages of lettuce plants, as affected by macronutrient proportions in the nutrient solution.

Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	9.777 ± 0.823 ab	8.182 ± 2.602 a	8.706 ± 1.504 a
	T2	9.663 ± 0.994 ab	8.556 ± 1.291 a	8.818 ± 0.803 a
Leaves	T3	8.384 ± 1.198 b	7.819 ± 1.560 a	7.466 ± 2.273 a
	T4	9.429 ± 1.030 ab	7.467 ± 0.861 a	7.802 ± 2.226 a
	T5	10.143 ± 1.358 a	8.286 ± 0.505 a	8.995 ± 1.681 a
Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	3.634 ± 0.570 a	4.327 ± 0.719 a	2.599 ± 0.467 a
	T2	4.862 ± 2.209 a	4.070 ± 0.244 a	2.768 ± 0.252 a
Buds	T3	2.752 ± 2.183 a	4.182 ± 0.601 a	3.424 ± 1.369 a
	T4	2.775 ± 1.607 a	4.053 ± 0.343 a	4.151 ± 1.185 a
	T5	2.594 ± 1.731 a	4.572 ± 0.398 a	4.298 ± 1.231 a
Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	5.787 ± 0.677 a	13.789 ± 4.212 bc	29.091 ± 5.486 ab
	T2	3.902 ± 3.089 a	21.921 ± 6.016 ab	35.948 ± 0.115.82 a
Roots	T3	4.053 ± 3.157 a	12.645 ± 4.242 c	23.015 ± 4.296 ab
	T4	3.217 ± 2.709 a	15.621 ± 3.844 abc	19.095 ± 6.478 b
	T5	6.952 ± 1.593 a	23.452 ± 8.428 a	32.265 ± 16.158 ab

T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol$_c$ m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886. Stage 1 = 20 days after transplanting (rosette formation), Stage 2 = 40 days after transplanting (onset of bud formation), and Stage 3 = 60 days after transplanting (completion of bud formation). Values expressed as mean ± standard deviation. Different letters within each stage and organ indicate significant differences (Tukey, $p \leq 0.05$).

treatments in K concentration (Table 4). This can be attributed to the fact that a lower proportion of NO_3^- may reduce aerial biomass (Kempen *et al*., 2016), thereby lowering nutrient demand and favoring K accumulation in the root. However, Tsouvaltzis *et al*. (2020) reported the opposite response in red lettuce, suggesting that plant genotype and production system influence this behavior.

For Ca concentration in roots, T4 surpassed the control in Stage 2 (Table 5). Additionally, a clear antagonism with K was observed in Stage 1, where increased K (T4) produced the lowest Mg concentrations in roots. Conversely, reduced K (T5) led to the highest Mg concentrations in roots in Stages 2 and 3 (Table 6). The proportion of NO_3^- also influenced Mg concentration in roots: T3 (lowest NO_3^-) reduced Mg, while T2 (highest NO_3^-) increased it in Stages 2 and 3—both relative to T5. This pattern occurs because NO_3^- interacts synergistically with Mg uptake (Malvi, 2011; Kamboj, 2019).

Table 6. Magnesium concentration (g kg^{-1} dry matter) in leaves, buds, and roots at three developmental stages of lettuce plants, as affected by macronutrient proportions in the nutrient solution.

Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	2.204 ± 0.135 ab	1.836 ± 0.309 bc	1.987 ± 0.268 ab
	T2	1.924 ± 0.287 b	1.912 ± 0.162 b	2.035 ± 0.253 ab
Leaves	T3	1.963 ± 0.329 ab	1.634 ± 0.224 bc	1.632 ± 0.326 b
	T4	2.198 ± 0.420 ab	1.594 ± 0.186 c	1.689 ± 0.429 b
	T5	2.515 ± 0.383 a	2.359 ± 0.152 a	2.386 ± 0.580 a
Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	1.031 ± 0.181 a	1.411 ± 0.206 b	1.258 ± 0.162 ab
	T2	0.894 ± 0.206 a	1.555 ± 0.128 b	1.097 ± 0.133 b
Buds	T3	0.788 ± 0.618 a	1.300 ± 0.201 b	0.924 ± 0.289 b
	T4	0.738 ± 0.467 a	1.264 ± 0.127 b	1.055 ± 0.213 b
	T5	0.798 ± 0.559 a	2.577 ± 0.271 a	1.610 ± 0.276 a
Organ	Treatments	Stage 1	Stage 2	Stage 3
	T1	1.185 ± 0.089 a	2.541 ± 0.559 b	4.493 ± 1.019 ab
	T2	0.762 ± 0.593 a	3.094 ± 0.337 ab	5.027 ± 0.475 a
Roots	T3	0.878 ± 0.685 a	2.232 ± 0.470 b	2.605 ± 0.849 b
	T4	0.671 ± 0.568 a	2.654 ± 0.526 b	2.521 ± 1.056 b
	T5	1.173 ± 0.168 a	3.693 ± 0.848 a	5.136 ± 2.801 a

T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol_c m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886. Stage 1 = 20 days after transplanting (rosette formation), Stage 2 = 40 days after transplanting (onset of bud formation), and Stage 3 = 60 days after transplanting (completion of bud formation). Values expressed as mean ± standard deviation. Different letters within each stage and organ indicate significant differences (Tukey, $p \leq 0.05$).

Nutrient extraction by developmental stage

In Stage 1, no significant differences among treatments were observed regarding macronutrient extraction in any of the three plant organs (Tables 7–9). This is consistent with Sosa *et al*. (2017), who reported that in the early stages of lettuce development, nutrient demand is still low, and consequently, tissue concentrations remain limited.

Leaves. In Stage 2, P extraction showed no differences among treatments (Table 7). This is attributed to the fact that P concentration is higher in the roots than in the aboveground organs (Table 3), a result consistent with Sosa *et al*. (2017), who reported that in lettuce (65-day production cycle), P concentration in roots was 2–3 % higher than in the other organs. In the present study, P extraction increased by 25 % from Stage 1 to Stage 2 and by 7 % from Stage 2 to Stage 3. This trend agrees with the aforementioned authors, who observed the highest P concentration in aboveground tissue between 17 and 43 days after emergence.

Table 7. Nutrient extraction (mg) in lettuce leaves at three developmental stages, grown in a closed hydroponic system with five nutrient proportions in the nutrient solution.

Treatments	N	P	K	Ca	Mg
			Stage 1		
T1	404.8 ± 182.9 a	57.7 ± 24.3 a	530.2 ± 249.9 a	88.8 ± 37.2 a	23.0 ± 10.4 a
T2	648.5 ± 184.1 a	90.0 ± 31.3 a	580.3 ± 212.9 a	119.0 ± 45.0 a	28.2 ± 10.9 a
T3	513.3 ± 212. a	71.3 ± 28.7 a	596.1 ± 229.5 a	102.4 ± 42.5 a	27.2 ± 11.2 a
T4	559.1 ± 212.7 a	79.7 ± 31.6 a	570.6 ± 306.2 a	131.1 ± 61.9 a	32.2 ± 13.6 a
T5	586.2 ± 238.9 a	76.5 ± 27.9 a	662.1 ± 278.3 a	144.8 ± 64.9 a	34.3 ± 14.5 a
			Stage 2		
Treatments	N	P	K	Ca	Mg
T1	1498.8 ± 357.0 ab	229.2 ± 57.0 a	1700.9 ± 300.1 bc	407.9 ± 97.5 b	79.5 ± 21.3 b
T2	1960.9 ± 540.7 a	213.4 ± 53.2 a	2369.3 ± 654.6 a	672.8 ± 236.5 a	127.4 ± 45.9 a
T3	1013.9 ± 160.5 b	200.6 ± 6.1 a	1577.1 ± 135.7 bc	396.9 ± 99.5 b	71.6 ± 10.8 b
T4	1418.2 ± 110.7 ab	233.1 ± 26.7 a	1931.6 ± 210.4 ab	450.0 ± 65.0 b	82.2 ± 9.9 ab
T5	1302.0 ± 324.3 b	216.8 ± 53.0 a	1159.6 ± 199.2 c	482.2 ± 134.4 ab	114.2 ± 36.7 ab
			Stage 3		
Treatments	N	P	K	Ca	Mg
T1	1944.5 ± 530.5 ab	325.8 ± 53.5 a	2608.8 ± 709.4 a	852.5 ± 352.2 ab	149. 8 ± 53.8 a
T2	2111.6 ± 414.7 a	225.0 ± 58.5 a	2126.1 ± 567.3 a	938.1 ± 318.4 a	169.4 ± 41.8 a
T3	1034.9 ± 297.3 b	264.2 ± 80.4 a	1745.8 ± 447.9 ab	541.4 ± 138.2 ab	99.8 ± 29.6 a
T4	1240.5 ± 638.5 ab	277.5 ± 144.8 a	2189.1 ± 1130.3 a	725.7 ± 380.9 ab	110.6 ± 55.0 a
T5	1090.8 ± 673.5 b	209.3 ± 118.9 a	916.8 ± 517.5 b	492.6 ± 356.7 b	118.9 ± 86.3 a

T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol_c m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886. Stage 1 = 20 days after transplanting (rosette formation), Stage 2 = 40 days after transplanting (onset of bud formation), and Stage 3 = 60 days after transplanting (completion of bud formation). Values expressed as mean ± standard deviation. Different letters within each element and stage indicate significant differences (Tukey, $p \leq 0.05$).

The remaining macronutrients exhibited a similar pattern. In Stage 2, the treatment with the highest proportion of NO_3^- (T2) showed the greatest extraction of K, Ca, and Mg compared with T1 (Table 7). In Stage 3, the results were similar, which can be attributed to the fact that a higher proportion of NO_3^- leads to greater N accumulation in leaves (Combrink and Kempen, 2019). Lettuce also has a high capacity to accumulate NO_3^- in foliar tissue (Karthika *et al.*, 2018; Djidonou and Leskovar, 2019).
Furthermore, synergistic effects between NO_3^- and K^+ (Coskun *et al.*, 2017), as well as with Mg^{2+} (Njira and Nabwami, 2015), were observed, since increasing NO_3^- in the nutrient solution enhanced the extraction of these cations in leaves.

Buds. In stages 1 and 3, the contents of the five macronutrients in the bud did not differ among treatments (Table 8). In stage 2, the extraction of N, Ca and Mg also showed no differences among treatments. The K contents in T4 (high K) and T5 (low K) were statistically different, with the higher K supply resulting in the highest mean value; however, it did not surpass the control (T1) (Table 8). This behavior agrees with Kempen *et al.* (2016) and Combrink and Kempen (2019), who reported that plants grown hydroponically can increase nutrient extraction when the nutrient is more available in the solution. Phosphorus extraction was only different between T2 (high NO_3^-) and T4 (high K), with the former being lower than the latter (Table 8).

Table 8. Nutrient extraction (mg) in lettuce buds at three growth stages, grown in a closed hydroponic system under five nutrient-solution ionic proportion treatments.

			Stage 1		
Treatments	N	P	K	Ca	Mg
T1	17.0 ± 6.8 a	4.1 ± 1.6 a	16.1 ± 7.6 a	2.2 ± 0.6 a	0.6 ± 0.2 a
T2	29.6 ± 13.8 a	6.3 ± 2.8 a	24.2 ± 12.4 a	3.6 ± 1.6 a	1.0 ± 0.5 a
T3	21.3 ± 8.5 a	4.6 ± 2.0 a	18.3 ± 9.0 a	2.8 ± 1.2 a	0.8 ± 0.4 a
T4	22.5 ± 8.7 a	5.3 ± 2.5 a	19.2 ± 9.5 a	2.8 ± 1.2 a	0.8 ± 0.4 a
T5	24.6 ± 11.6 a	5.6 ± 2.5 a	19.5 ± 8.0 a	3.0 ± 1.4 a	0.9 ± 0.4 a
			Stage 2		
Treatments	N	P	K	Ca	Mg
T1	103.7 ± 50.6 a	27.8 ± 8.6 ab	75.6 ± 17.8 abc	16.4 ± 5.9 a	5.6 ± 2.3 a
T2	110.4 ± 52.4 a	16.7 ± 7.3 b	64.7 ± 19.9 bc	13.8 ± 6.3 a	4.6 ± 2.5 a
T3	96.3 ± 34.2 a	25.3 ± 6.1 ab	87.3 ± 19.1 ab	15.3 ± 5.8 a	4.8 ± 1.4 a
T4	139.4 ± 41.2 a	33.2 ± 10.3 a	104.4 ± 31.4 a	18.1 ± 6.1 a	5.5 ± 1.8 a
T5	129.2 ± 53.7 a	27.4 ± 9.6 ab	43.7 ± 9.2 c	17.2 ± 7.3 a	7.8 ± 3.6 a
			Stage 3		
Treatments	N	P	K	Ca	Mg
T1	318.9 ± 43.9 a	78.4 ± 8.1 a	178.1 ± 27.1 a	47.9 ± 3.7 a	14.6 ± 4.1 a
T2	328.4 ± 56.4 a	44.8 ± 10.5 a	141.6 ± 27.6 a	49.1 ± 11.1 a	16.5 ± 4.0 a
T3	177.3 ± 67.9 a	58.6 ± 16.7 a	146.5 ± 38.3 a	42.0 ± 14.3 a	9.9 ± 2.9 a
T4	323.3 ± 265.2 a	79.8 ± 60.0 a	159.4 ± 87.7 a	43.1 ± 32.4 a	16.1 ± 19.3 a
T5	164.3 ± 151.5 a	47.3 ± 39.1 a	119.0 ± 113.3 a	30.9 ± 25.4 a	11.3 ± 10.2 a

T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol_c m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886. Stage 1 = 20 days after transplanting (rosette formation), Stage 2 = 40 days after transplanting (onset of bud formation), and Stage 3 = 60 days after transplanting (completion of bud formation). Values expressed as mean ± standard deviation. Different letters within each element and stage indicate significant differences (Tukey, $p \leq 0.05$).

Roots. In this organ, the extraction of N, Ca, and Mg was not affected by the different nutrient solutions (NSs) in stages 1 and 2; the same occurred for Ca in stage 3 (Table 9). Conversely, in stage 2, K extraction was higher in T3 compared with T5. In stage 3, P extraction in T3 was higher than that recorded in the other treatments. The greater P extraction in T3 is attributed to the ionic balance that must be maintained in the NS; when the proportion of NO_3^- decreases, the relative proportions of phosphate and sulfate increase, enhancing P uptake (Kempen *et al*., 2016). This result contrasts with the findings of Kumari *et al.* (2018), who reported synergistic interactions between N and P.

Table 9. Nutrient extraction (mg) in lettuce roots at three developmental stages, grown in a closed hydroponic system with five nutrient proportions in the nutrient solution.

			Stage 1		
Treatments	N	P	K	Ca	Mg
T1	83.8 ± 46.1 a	27.4 ± 17.1 a	160.7 ± 105.0 a	7.9 ± 4.2 a	3.0 ± 1.7 a
T2	114.7 ± 45.2 a	27.9 ± 11.8 a	148.3 ± 60.6 a	15.8 ± 7.0 a	4.0 ± 1.7 a
T3	77.4 ± 38.6 a	22.8 ± 11.3 a	95.8 ± 49.0 a	14.5 ± 6.5 a	2.8 ± 1.4 a
T4	90.4 ± 42.8 a	28.2 ± 12.4 a	104.0 ± 48.4 a	12.2 ± 5.7 a	2.9 ± 1.3 a
T5	86.8 ± 36.8 a	24.7 ± 9.8 a	92.6 ± 40.4 a	14.4 ± 6.9 a	2.9 ± 2.0 a
			Stage 2		
Treatments	N	P	K	Ca	Mg
T1	236.3 ± 45.0 a	68.5 ± 14.4 a	208.8 ± 83.6 a	57.0± 27.0 a	15.9 ± 9.8 a
T2	217.7 ± 66.3 a	33.1 ± 16.0 b	150.7 ± 98.8 ab	59.7 ± 41.1 a	16.7 ± 10.7 a
T3	181.0 ± 88.2 a	79.0 ± 25.0 a	240.2 ± 82.5 a	53.3 ± 16.1 a	14.5 ± 6.7 a
T4	176.5 ± 48.4 a	50.1 ± 16.6 ab	169.3 ± 57.2 ab	51.3 ± 20.3 a	11.2 ± 4.7 a
T5	210.2 ± 76.6 a	55.6 ± 11.8 ab	57.8 ± 45.2 b	87.8 ± 42.5 a	24.7 ± 12.6 a
			Stage 3		
Treatments	N	P	K	Ca	Mg
T1	214.1 ± 57.1 ab	81.7 ± 20.1 b	116.6 ± 93.4 ab	85.8 ± 29.0 a	18.7 ± 9.5 b
T2	371.7 ± 87.1 a	31.5 ± 4.0 b	65.7 ± 31.2 b	148.6 ± 58.0 a	45.5 ± 10.2 a
T3	221.3 ± 118.7 ab	154.7 ± 53.9 a	192.4 ± 20.5 a	63.6 ± 30.7 a	20.4 ± 9.7 b
T4	192.5 ± 100.4 b	80.4 ± 44.8 b	117.4 ± 75.1 ab	78.0 ± 47.2 a	17.0 ± 10.1 b
T5	166.6 ± 113.2 b	37.1 ± 20.3 b	34.4 ± 27.8 b	85.1 ± 82.8 a	15.7 ± 13.3 b

T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol_c m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886. Stage 1 = 20 days after transplanting (rosette formation), Stage 2 = 40 days after transplanting (onset of bud formation), and Stage 3 = 60 days after transplanting (completion of bud formation). Values expressed as mean ± standard deviation. Different letters within each element and stage indicate significant differences (Tukey, $p \leq 0.05$).

Interestingly, in stage 3, Mg extraction was not higher in the treatment with reduced NO_3^- (T3), but rather in T2, which had the highest proportion of this anion. This suggests that, in this developmental stage, greater NO_3^- availability favored Mg uptake, which aligns with the interaction reported between anion and cation absorption in hydroponic systems (Kempen *et al*., 2016). Finally, the increased extraction of K under a low NO_3^- proportion agrees with Weil *et al*. (2020), who indicate that elevated concentrations of NO_3^- can reduce K uptake in roots.

Total nutrient extraction. Total macronutrient extraction showed that the largest proportion accumulated in the aerial part of the plant, particularly in the leaves, which accounted for nearly 80 % of the total extracted by the plant (Figure 1). This value is slightly lower than that reported by Sosa *et al.* (2017), who found 88.9 % foliar extraction in 'Coolguard' lettuce at 65 days after transplanting. Among the macronutrients evaluated, K exhibited the highest total extraction, followed by N, whereas Mg was the least extracted nutrient, as shown in Figure 1. This pattern agrees with Weil *et al*. (2020) and Hong *et al.* (2022), who indicate that both K and N tend to accumulate preferentially in leaves due to their high mobility.

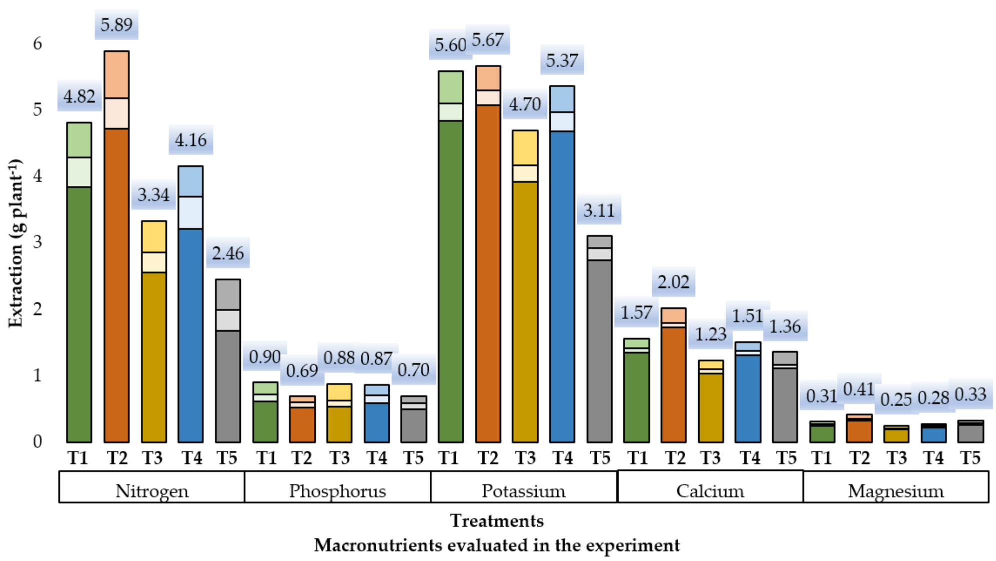

Figure 1. Total macronutrient extraction per treatment in lettuce leaves (basal section of each bar), buds (middle section of the bar), and roots (upper section of the bar) grown in a closed hydroponic system, as affected by five proportions of anions and cations in the nutrient solution. T1 = Ionic proportions in the nutrient solution: NO_3^- = 9.000, $H_2PO_4^-$ = 0.750, SO_4^{2-} = 5.250, K^+ = 5.250, Ca^{2+} = 6.750, Mg^{2+} = 3.000 mol_c m^{-3}. T2 = 11.338, 0.354, 2.479, 5.250, 6.750, 3.000. T3 = 6.371, 1.194, 8.362, 5.250, 6.750, 3.000. T4 = 9.000, 0.750, 5.250, 6.375, 5.675, 2.522. T5 = 9.000, 0.750, 5.250, 3.158, 8.743, 3.886.

In this study, P extraction was also highest in leaves, which contrasts with the findings of Hong *et al.* (2022), who reported greater P concentrations in the bud. Finally, the bud was the organ with the lowest overall extraction, contributing an average of 7 % of total nutrients, and showed significant differences only in Stage 2 for K, when its proportion in the nutrient solution was increased (Table 8).

CONCLUSIONS

The largest proportion of nutrients accumulated in the leaves, which accounted for approximately 79.5 % of the total extracted during the crop cycle; roots ranked second, with more than 13 %. The highest extractions corresponded to N and P, reaching 5.89 and 5.67 g plant^{-1}, respectively, under treatment T2 (highest proportion of NO_3^-). Treatments T2 and T4 showed the greatest extraction of N and K compared with the treatments in which the proportion of these ions was reduced. Increasing K^+ in the cationic proportion decreased the concentration of Ca^{2+} and Mg^{2+} in all three organs evaluated. Similarly, increasing NO_3^- in the anionic proportion reduced P extraction but enhanced the uptake of Ca^{2+} and Mg^{2+}.

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