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Research article

Macronutrient omission influences morphological parameters, growth, and yield in *Arracacia xanthorrhiza* Bancroft

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ABSTRACT

Mineral nutrition in arracacha is a critical production factor that conditions harvest yield. Few studies have been developed in nutrition and physiology, this does not allow to the design of ideal fertilization programs; consequences are increased production costs, soil degradation, and low-quality storage roots. Therefore, this study aimed to characterize the symptoms associated with macronutrient deficiency in arracacha plants and its effect on morphological parameters, the accumulation of fresh and dry biomass, and the distribution of dry matter in the different organs. Under greenhouse conditions, the experiment was conducted in Cajamarca, Tolima, Colombia. A completely randomized design was implemented, with seven treatments and six replicates (6 solutions lacking N, P, K, Ca, Mg, and S and Hoagland complete solution). Forty-two seedlings were transplanted, to which the complete solution was applied for 75 days, increasing the concentrations from 0.25 M to 1 M, and then nutritional deficiencies were induced. Deficiencies caused by macronutrients in arracacha plants exhibited visual symptoms and changes in their morphology. The omission of N, Ca, and S generated the most severe symptoms, drastically affecting plant height, leaf width, number of leaves, and plant mass accumulation. In the case of P, leaves became small and intense green with a violet margin. The Mg and K generated leaves with interveinal and margin chlorosis. Plants with the omission of macronutrients allocated dry mass in the following order: stem, storage roots, propagules, and leaves.

1. Introduction

Arracacha (*Arracacia xanthorrhiza* Bancr.) is a rustic herbaceous plant, typical of the Andean zone, adapted to different agroecological areas from 1500 to 3000 m a.s.l. and of great agro-food importance. It is grown mainly in Brazil, followed by Colombia, Venezuela, Peru, Bolivia, and Ecuador [1]. The production system is developed in 14 regions in Colombia with an average yield of 9.84

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t ha^{-1}. The Tolima region contributes about 72% of national production, with the municipality of Cajamarca contributing 93% of the region's production and an average yield of 12 t ha^{-1}. Around ten varieties are planted commercially in the country, with 'Amarilla común' occupying the largest planting area (95%) [2–4].

Mineral nutrients are essential to carry out all metabolic reactions in the plant and function as part of the organic structure or as activators of enzymatic reactions [5]. Nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S) were selected for the development of the research under the criteria proposed by Ref. [6]. They indicate that these are considered macronutrients because plant tissues contain them in high concentrations, are essential for their growth and development, and are essential in several fundamental metabolic processes [7].

The main production problems in the arracacha crop are associated with diseases, pests, and nutritional deficiencies. Nutrient deficiencies are an abiotic stress factor that impacts plant growth and can eventually generate significant agricultural yield losses [7]. If a nutrient is not present in the amount required by the plant to fulfill its functional roles, this will lead to a deficiency state, with nutrient-specific responses [8].

Leaf characterization and plant development, together with the symptoms of nutrient deficiencies, can aid in the diagnosis of nutrient disorders and imbalances [9]. When mineral nutrients are limited, plants reduce their growth and alter aspects of their morphology [10]. Nutrient deficiencies they affect the biomass distribution pattern between different plant organs and produce specific symptoms that can serve as indicators of nutritional status under field conditions [11] to distinguish them from other damages caused by inadequate environments, phytopathogens, insect pests, mites, chemical damage or phytotoxicity [12–14]. Recognition of these visible signs and symptoms is essential to carry out the relevant and necessary actions to mitigate the impacts on growth and yield [14]. To determine the role of chemical elements in plant metabolic functions, experiments evaluate these functions using soil and nutrient solutions [5]. Nutrient omission in experimental nutrient solutions has been widely used for nutritional diagnosis. Although this is an indirect approach, it can provide information on fertilizer requirements and improve plant quality [15].

Worldwide, little research has been done on arracacha in nutrition. Among these, those carried out in Brazil and related to the nutritional requirements for the crop stand out [16]. In addition, they identified symptoms associated with macronutrient deficiency, boron, and mineral nutrient concentration due to their deficit, but, did not identify the dynamics of fresh and dry biomass accumulation, and the distribution of dry matter in the different plant organs [17]. In the South American Andean countries, the response of N, P, and K doses on root yield and aerial growth variables has been mainly evaluated [4,18,19].

Considering the above, this research becomes the first study for Colombia with results that may have applicability in the arracacha-producing countries of the Andean zone, which provide tools for decision-making in the field by farmers and technical assistants and can be a crucial support in fertilization recommendations for the crop. The main objective of this study was to characterize the symptoms associated with macronutrient deficiencies, elucidate their effect on plant morphological parameters, fresh and dry biomass accumulation, and dry matter distribution in leaves, propagules, stock, and tuberous roots of A. xanthorrhiza plants.

2. Materials and methods

2.1. Study area

The experiment was conducted under greenhouse-type plastic cover conditions 60 m^2 for 270 days in Cajamarca, Tolima, Colombia, at coordinates N 04°23′25.4″, W 075°30′49.4″ at 2067 m.a.s.l. The average temperature recorded for the study was 18.7 °C, an average maximum of 28.7 °C, a minimum of 8.6 °C, and relative humidity of 82%. Climate data were measured with the automated weather station (Davis Vantage Pro2™).

2.2. Experimental design and set-up

A completely randomized design with seven treatments and six replications was used. The treatments were based on the complete nutrient solution Hoagland and Arnon [20], modified and used by Barrera et al. [21], and corresponded to six nutrient solutions, which were as follows: T1: nitrogen (-N); T2: phosphorus (-P); T3: potassium (-K); T4: calcium (-Ca); T5: magnesium (-Mg); T6: sulfur (-S) and T7: complete solution (control).

Propagules of variety "Amarilla común" pre-rooted for 30 days were used, with the following average morphoagronomic characteristics: 1 genuine leaf, seedling height 15.1 cm ± 0.7, seedling fresh mass 24.3 g ± 1.4, leaf 6.3 g ± 0.5 and rootlets 1.3 g ± 0.1. Before transplanting, the roots were washed with a 5% sodium hypochlorite solution; then pressurized water was applied to eliminate the residues of the germination substrate, and the seedlings were planted in 20 kg plastic pots spaced 0.50 m apart and 0.70 m between rows. As substrate, washed quartzite sand was used, with grain size 0.5 mm, pH 6.9, EC 0.09 dS m^{-1}, SOM 0.1 g/100 g soil, P (Bray II) 4.3 mg kg^{-1}, exchangeable bases (cmol kg^{-1}) Ca <0.5, Mg 0.2, K < 0.06, Na <0.1, ECEC 0.9 cmol kg^{-1}, S 3.4 mg kg^{-1} and micronutrients (Olsen) (mg kg^{-1}) Fe 8.6, B 0.07, Mn, Zn and Cu < 1, characteristics determined by physicochemical analysis of the substrate carried out by the Soil Physics and Chemistry Laboratory the Corporación Colombiana de Investigación Agropecuaria – AGROSAVIA.

The following methods analyzed soil chemical parameters: soil reaction or pH, was determined by potentiometric method, with 1:1 P/V ratio [22], organic matter-MO (%) Walkley-Black oxidation method [23]; phosphorus-P (mg kg^{-1}) modified Bray II extraction and quantification by reduction with ascorbic acid [24]; sulfur-S (mg kg^{-1}) extraction with calcium monophosphate 0.008 M and quantification turbidimetrically; potassium-K, calcium-Ca, magnesium-Mg, and sodium-Na (cmol(+) kg^{-1}) by atomic absorption and emission spectrophotometry [22,25], Colombian Technical Standard-NTC 5349 [26]; iron-Fe, manganese-Mn, zinc-Zn and copper-Cu (mg kg^{-1}) were determined by modified Olsen's method spectrophotometry and quantification by atomic absorption, NTC 5526:2007

[27] and boron-B (mg kg^{-1}) by extraction with monobasic calcium phosphate-azomethine H, NTC 5404:2011 [28].

During the first three days after transplanting (one per pot), irrigation was carried out with purified water with the following chemical composition: pH 7.8, EC 0.4 dS m^{-1}, Ca 2.3, Mg 0.7, K 0.06, Na 0.2, $CO_3^{=}$ 0.2, HCO_3^{-} 3.03, Cl^{-} 0.06 and $SO_4^{=}$ 0.9 (meq L^{-1}), B 0.04, $PO_4^{\equiv}$ and Fe < 0.5 (mg L^{-1}). Then, the complete solution was applied with increasing concentrations from 0.25 M to 0.5 M and 1 M every 25 days for 75 days and with a water volume of 250 mL per plant twice a week. The pH of the nutrient solutions was adjusted to 5.6 ± 0.1 and measured with the Thermo Scientific Orion™ 2-Star potentiometer following the methods described by Kirkby and Mengel [29]. Electrical conductivity had a mean value of 0.8 ± 0.2 dS m^{-1} and was taken at 25 °C with the Oakton® PC 700 conductivity meter [9,30].

2.3. Deficiency symptoms, morphological parameters, growth and production

Plants were randomized and assigned to the respective treatments to induce nutrient deficiencies. For 150 days, the nutrient solutions at 1 M corresponding to the treatments were applied with a water volume of 400 mL per plant twice a week for the first 60 days and 900 mL after that until harvest. Symptoms were described 135 days after applying the treatments when plants showed well-defined deficiencies [31]. Two hundred and seventy Days After Transplanting (DAT), direct measurements of growth parameters such as plant height (from the base to the apex of the central leaf), flag leaf petiole length, flag leaf length and width, the number of leaves and propagules were made. Fresh and dry mass of leaves, petioles, propagules, stem, storage roots, and whole plant were also determined using a 0.1 g precision digital balance.

To obtain the dry mass, the fresh material was washed with clean water and allowed to dry at room temperature, fragmented and placed in paper bags, to be taken to a drying oven at a temperature of 65 °C until a constant weight was reached. The dry samples were processed in a mill stainless steel (Thomas -Willey, Philadelphia, USA) and passed through a stainless-steel sieve with 2 mm mesh [32], and then sent to the Soil, Water, and Plant Chemistry Laboratory of AGROSAVIA.

Nutrient analysis was done for leaf tissue from four plants (leaves + petiole) by merging all leaves per plant [30] (Table 1). N was determined by the extraction and quantification method EPA 351.3 modified: Kjeldahl/Volumetry [33]. P by open digestion nitric: perchloric (5:2)/Spectrophotometry, K, Ca, and Mg with open digestion nitric: perchloric (5:2)/Inductively coupled plasma emission spectrometry and S with open digestion nitric: perchloric (5:2)/Turdibimetry [34].

2.4. Statistical analysis

The parameters of vegetative development and fresh and dry mass were subjected to classical analysis of variance. Variables that did not meet the assumptions of normality and homoscedasticity were transformed with Box-Cox of the MASS package. The dry mass data were used to determine the dry matter distribution of the arracacha plants subjected to induced nutrient deficiencies. Means were compared using the Multiple comparisons Tukey test ($p \leq 0.05$), using the R project software Version 4.2.0 [35].

3. Results

3.1. Deficiency symptoms, morphological parameters, growth and production

Plants under Hoagland and Arnon's complete solution were characterized by average growth and absence of nutrient deficiency symptoms, indicating adequate EC and pH. The effect of macronutrient deficiency on variety 'Amarilla común' arracacha plants is shown below:

3.1.1. Nitrogen (N) deficiency

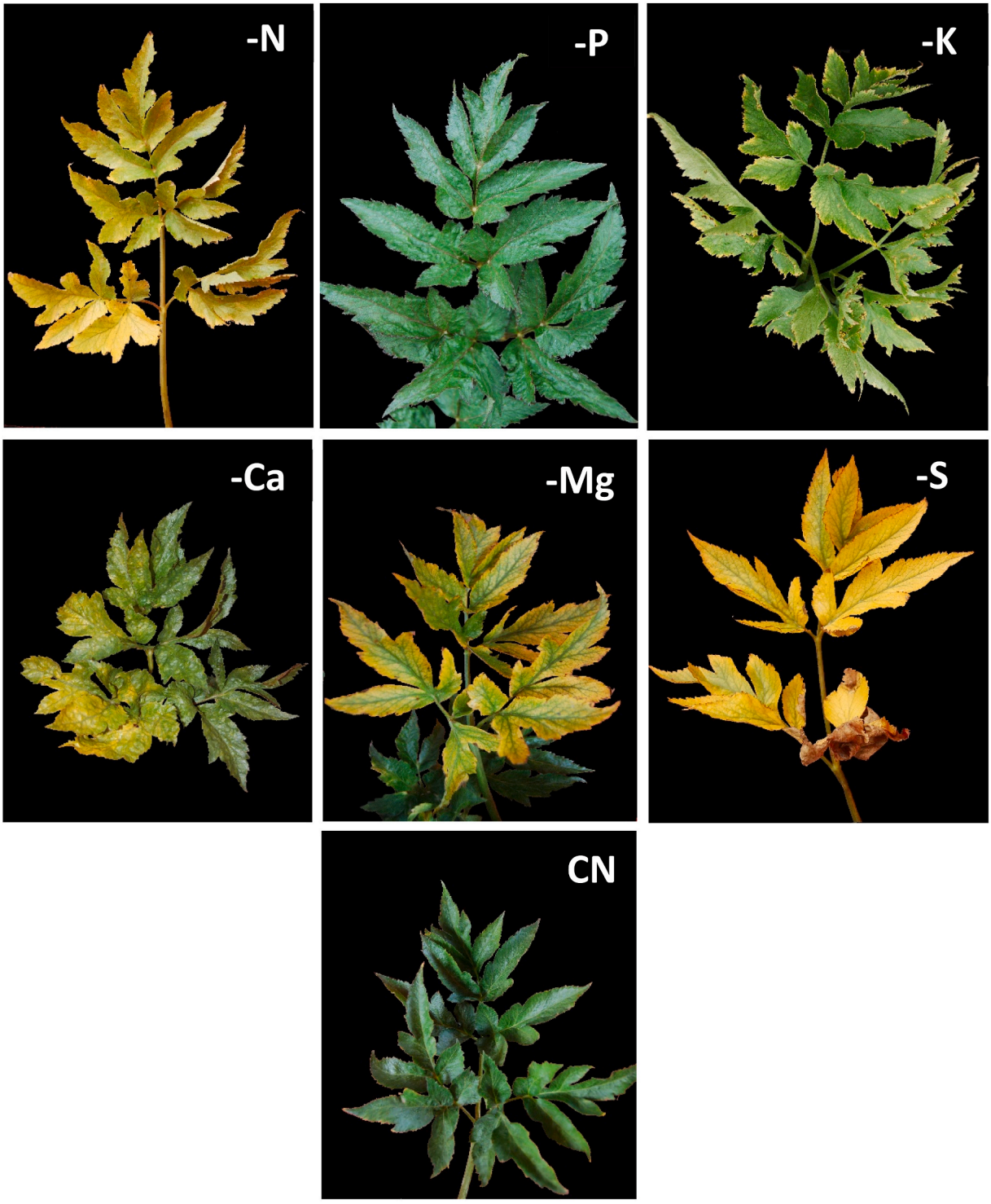
Plants showed a drastic decrease in size (dwarfism) (Fig. 1). The first symptoms were evident in adult leaves, which initially showed light green coloration, eventually showing generalized chlorosis wilt small leaflets with thin laminae and short petioles with low turgor (Fig. 2).

N deficiency reduced plant height by 29%, petiole length by 61.4%, leaf length by 31.1%, leaf width by 27%, and the number of leaves by 66.7% compared to the control plant (Table 2). Similarly, there was a decrease in the fresh and dry mass of the plant (36.8% and 45.3%, respectively) and in organs such as leaves (86.1% and 90.5%), petioles (92% and 94.7%), propagules (62.5% and 60.1%), and stem (32.6% and 35.7%), respectively. The fresh and dry mass of storage roots increased significantly on average by 47.3% and 13.7%, compared to plants receiving complete nutrition (Table 3).

Table 1
Initial macronutrient concentration in propagules used for the trial and final macronutrient concentration in leaves (leaflets + petioles) of 'Common Yellow' arracacha plants grown under macronutrient omission for 270 days.

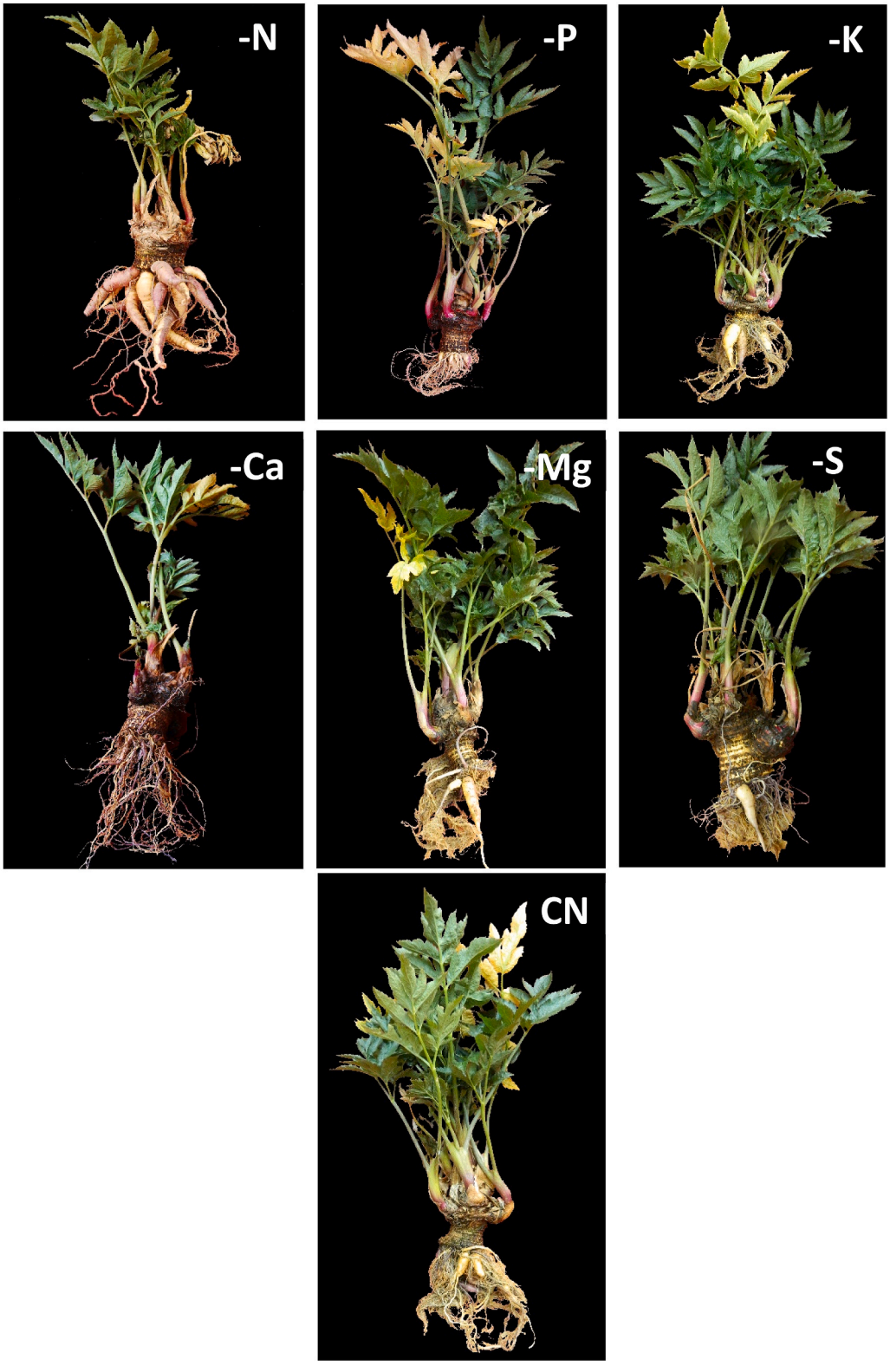
Macronutrient concentration in tissue	Unit (%)					
	- N	- P	- K	- Ca	- Mg	- S
Initial concentration in propagules	1.21	0.33	1.79	0.91	0.27	0.31
Final concentration in leaves	3.62	0.23	1.46	0.69	0.2	0.19

DAP: days after planting.



Source: *Jose Jamir Londoño*

Fig. 1. Symptoms and morphological changes in leaves of arracacha plants subjected to deficiency of: –N: nitrogen, -P: phosphorus, -K: potassium, -Ca: calcium, -Mg: magnesium, –S: sulfur and CN: Hoagland complete nutrition.



Source: *Jose Jamir Londoño*

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Fig. 2. Morphological changes in the canopy and storage roots of arracacha plants subjected to deficiency of: –N: nitrogen, -P: phosphorus, -K: potassium, -Ca: calcium, -Mg: magnesium, –S: sulfur and CN: Hoagland complete nutrition.

3.1.2. Phosphorus (P) deficiency

Plants showed reduced growth (Fig. 2). First symptoms were observed in adult leaves which became small and intense green with a violet margin (Fig. 1). The leaves curled towards the beam and broke as the days passed, showing a light green color with violet veins and a violet laminar margin.

P deficit reducted leaf width on average by 29.7%, the number of leaves by 45.5% (Table 2), fresh and dry mass of leaves by 78.6% and 81.8%, petioles by 59.3% and 56.8%, propagules by 46.5% and 37.4%, stem by 35.6% and 43.8%, storage roots by 31.9%, and 41.4%, and whole plant by 46.1% and 48.6%, respectively (Table 3).

3.1.3. Potassium (K) deficiency

Symptoms develop on adult leaves with yellow tones from the margin to the midrib, burning at the edges, and green veins (Fig. 1). Young leaves tended to be corrugated and rolled towards the upper side. This treatment made the plants highly susceptible to attack by thrips and aphids.

K deficient plants registered lower height with an average of 2.5% (Table 2), fresh and dry mass of leaves 5% and 27.3%, petioles 28.4% and 24%, storage roots 48.8% and 10.7% and fresh mass for the whole plant 14.7%. The dry mass of propagules and stem were also affected by reducing their development by 26.5% and 3.3%, respectively (Table 3).

3.1.4. Calcium (Ca) deficiency

Symptoms are present in young leaves and leaf lamina with evident wrinkles, chlorosis, and turgor loss. Occasionally chlorotic areas were found in with death of growing points and marginal leaf necrosis (Fig. 1). Susceptibility to sanitary problems such as stem

Table 2
Effect of macronutrient nutrient deficiency on plant height (PH), flag leaf petiole length (PL), flag leaf length (LL), flag leaf width (AW), number of leaves (NL), and number of propagules (NPR) in arracacha plants.

Treatment	*PH (cm)	PL (cm)	LL (cm)	AW (cm)	NL (un)	NPR (un)
- N	21.1 ± 0.7 e	6.7 ± 0.2 e	11.4 ± 0.5 bc	13.3 ± 0.6 b	9.0 ± 0.6 d	8.5 ± 0.3 abc
- P	29.6 ± 0.7 ab	15.0 ± 0.6 c	14.1 ± 0.8 ab	12.8 ± 0.7 b	14.2 ± 0.6 c	7.8 ± 0.1 bc
- K	29.0 ± 0.6 bc	15.3 ± 0.4 b	14.2 ± 0.4 ab	18.3 ± 0.7 a	27.3 ± 1 a	10.2 ± 0.5 a
- Ca	25.7 ± 1.8 cd	15.0 ± 0.8 c	13.6 ± 0.6 b	14.9 ± 1 ab	8.8 ± 0.7 d	1.6 ± 0.3 d
- Mg	32.5 ± 1.6 ab	17.7 ± 1.3 a	14.0 ± 0.7 ab	18.5 ± 1.2 a	21.3 ± 1 b	9.3 ± 0.5 ab
- S	24.3 ± 0.9 de	9.6 ± 0.7 d	10.3 ± 0.6 c	12.2 ± 0.7 b	11.5 ± 0.8 cd	8.5 ± 0.2 abc
Complete	29.7 ± 0.4 ab	17.8 ± 0.4 a	16.5 ± 0.6 a	18.2 ± 0.5 a	27.0 ± 1.5 a	8.8 ± 0.4 ab
CV (%)	9.10	12.52	11.90	12.98	15.05	15.30

Different letters indicate significant differences according to Tukey's mean comparison test ($p \leq 0.05$). *Data transformed by Box-Cox. ±Standard error (n = 6).

Table 3
Effect of macronutrient nutrient deficiency on fresh mass (FM) and dry mass (DM) of leaves, petioles, propagules, stem, storage roots, and whole plant in arracacha.

Treatment	Leaf		Petiole		Propagules	
	*FM	*DM	*FM	*DM	FM	*DM
- N	7.7 ± 0.6 g	1.1 ± 0.04 f	2.3 ± 0.18 g	0.2 ± 0.02 e	34.8 ± 2.3 bc	6.4 ± 0.1 e
- P	11.9 ± 1.5 f	2.1 ± 0.2 e	11.6 ± 1.3 d	1.4 ± 0.1 c	49.7 ± 5.2 b	10.0 ± 0.6 c
- K	52.8 ± 3.5 b	8.3 ± 0.2 b	20.5 ±1.7 b	2.4 ± 0.1 b	84.7 ± 5.4 a	11.8 ± 0.9 b
- Ca	12.5 ± 1.4 ef	2.2 ± 0.2 e	4.2 ± 0.9 f	0.8 ± 0.1 d	18.4 ± 2.1 c	4.6 ± 0.3 f
- Mg	42.4 ± 2.5 c	6.6 ± 0.2 c	19.2 ± 1.5 c	1.7 ± 0.2 c	87.4 ± 6.6 a	16.8 ± 0.7 a
- S	20.2 ± 2.9 d	2.0 ± 0.2 e	3.3 ± 0.9 fg	0.2 ± 0.03 e	30.7 ± 4.3 bc	6.8 ± 0.6 e
Complete	55.5 ± 1.6 a	11.4 ± 0.4 a	28.5 ± 1.1 a	3.2 ± 0.1 a	92.8 ± 2.1 a	16.0 ± 1 a
CV (%)	17.09	19.35	19.84	18.85	18.54	15.74
Treatment	Stem		Storage roots		Whole plant	
	FM	*DM	*FM	*DM	FM	DM
- N	97.3 ± 5.6 b	20.0 ± 0.9 g	91.3 ± 10.7 a	11.7 ± 1.4 a	233.4 ± 10.8 c	39.3 ± 1.8 c
- P	92.9 ± 9.1 b	17.5 ± 1.3 h	32.8 ± 3.2 c	5.9 ± 0.6 e	198.9 ± 10.8 cd	36.9 ± 1.9 c
- K	132.3 ± 12 ab	30.0 ± 2.7 b	24.7 ± 1.5 d	9.0 ± 0.6 c	314.9 ±11.9 b	61.6 ± 3.4 ab
- Ca	117.8 ± 6.7 ab	22.7 ± 1 e	8.7 ± 0.9 g	2.4 ± 0.4 f	161.5 ± 7.3 d	32.6 ± 1.4 c
- Mg	128.8 ± 13.9 ab	23.3 ± 0.8 d	22.4 ± 1.7 f	6.7 ± 0.8 d	300.1 ± 17 b	55.1 ± 2.1 b
- S	96.6 ± 6.6 b	22.3 ± 0.4 f	23.8 ± 1.9 e	2.9 ± 0.3 f	174.7 ± 7.6 d	34.1 ± 0.8 c
Complete	144.3 ± 10.7 a	31.1 ± 2.5 a	48.1 ± 2 b	10.1 ± 0.6 b	369.3 ± 10.8 a	71.8 ± 3.1 a
CV (%)	19.45	14.23	18.05	17.29	19.39	19.85

Different letters indicate significant differences according to Tukey's mean comparison test ($p \leq 0.05$). *Data transformed by Box-Cox. ±Standard error (n = 6).

rot, propagules, and storage roots (*Pectobacterium* spp.) produced less productive plants, with short, highly branched roots and a shorter phenological cycle (±20 days) concerning the other macronutrients, which finally led to their death (Fig. 2).

Ca deficient plants' growth and yield parameters showed an average height loss of 13.6%, leaves of 67.3%, and the number of propagules of 81.1% were observed compared to the control (Table 2). The average accumulation of fresh and dry biomass decreased compared to the control in the storage roots by 82% and 76.8%, in the stem by 27% for dry mass, propagules by 80.2% and 71.1%, petioles by 85.3% and 76.9%, leaves 77.5% and 81%, and whole plant 56.3% and 54.7%, respectively (Table 3).

3.1.5. Magnesium (Mg) deficiency

The plants showed adult leaves with interveinal chlorosis in primary and secondary veins (Fig. 1). With the evolution of the degree of deficiency, the same symptoms occurred in new leaves, while the adults showed sporadic necrotic areas.

Mg deficiency influenced leaf number by causing an average decrease of 21% (Table 2), fresh and dry matter of leaves 23.7% and 41.8%, petioles 33% and 46.7%, stem 25% for dry mass, storage roots 53.5% and 33.6% and whole plant 18.7% and 23.2% respectively (Table 3).

3.1.6. Sulfur (S) deficiency

The plants showed poor and slow growth similar to that observed in N deficiency. Symptoms were associated with undersized young leaves and generalized chlorosis, short, stiff, and brittle petioles. Some leaves eventually showed leaf lamina rolling (Fig. 1).

S deficiency significantly limited plant growth and yield parameters compared to the control. Plant height was reduced on average 18.2%, petiole length 46.2%, leaf length 37.8%, leaf width 32.8%, number of leaves 57.4% (Table 2), fresh and dry mass of leaves 63.7% and 82.8%, petioles 88.5% and 94.5%, propagules 66.9% and 57.4%, stem 33% and 28.3%, storage roots 50.4% and 71.5%, and whole plant 52.7% and 52.5%, respectively (Table 3).

3.2. Dry matter distribution

Under good water and nutrient conditions, arracacha plants distributed their dry biomass in 20.3% to leaves (leaflets + petioles), 22.4% to propagules, 43.3% to stem, and 14.1% to storage roots (Figs. 2 and 3). From this pattern, the partitioning of photoassimilates in arracacha due to macronutrient deficiencies can be compared.

N deficiency induced a greater translocation of carbohydrates to the stem (50.9%) and to the storage roots (29.7%) and caused a decrease in the percentage of dry biomass in propagules (16.2%) and leaves (3.2%). On the other hand, P and K deficiency reduced dry mass accumulation in leaves by 9.4% and 17.4%, respectively, and concentrated them in the stem by 47.4% and 48.8%, in propagules with 27.2% for P deficiency, and storage roots with 16% for P and 14.6% for K, respectively (Figs. 2 and 3).

The treatments with Ca, Mg, and S deficiencies were those that most affected the accumulation of dry mass towards the storage roots, which was reflected in the lowest values of biomass translocated towards this organ with 7.2%, 12.2%, and 8.4%, respectively, of the total dry biomass of the plant (Fig. 2). This physiological disorder was associated with a reduction in the distribution of photoassimilates to the Ca (14.2%) and S (20%) deficient propagules and the leaves with 8.9%, 15.1%, and 6.3%, respectively, as well as a greater allocation to the stem with 69.9%, 42.3%, and 65.3%, respectively (Fig. 3).

4. Discussion

4.1. Deficiency symptoms, morphological parameters, growth and production

The arracacha plant achieves optimum storage roots production at pH 5.5 to 6.3 and EC < 0.8 dS m^{-1} [4], which corresponds to the ranges used in this study.

4.1.1. Nitrogen (N) deficiency

The observed symptoms are consistent with Souza de Miranda et al. [31] reported in cowpea and Buitrago et al. [14] in feijoa. The generalized chlorosis in adult leaves and the pale green coloration of the leaves are due to the mineral element's high mobility and the loss of chlorophyll that requires N as an essential constituent [36,37]. This deficiency affects the leaf formation and development and thus growth parameters, possibly due to low production rates of amino acids and proteins essential for cell division and elongation [31,38].

The fresh and dry biomass was affected in a more significant proportion in petioles and leaves for being specific organs in photosynthesis [39], followed by propagules, whole plant, and stem, while the biomass of storage roots presented a substantial gain in weight. This has been seen in *Stevia rebaudiana* by registering a poorer growth in aerial organs [40].

Under N deficiency stress, plants tend to allocate more biomass to the root system as a consequence of metabolic changes in aerial tissues and an adjustment of carbohydrate partitioning to the root [41], thus maintaining relatively better root growth and function to optimize N acquisition from the growing medium [42].

The arracacha plant comprises four principal organs: compound leaves, asexual seeds, modified stems, and tuberous roots, which are very succulent tissues due to their high-water content. In general terms, the tuberous root is the organ of preference for human consumption and accumulates the highest moisture content with about 70% [1,43], which gives it a short shelf life in postharvest. Tuberous roots lose the highest mass values during the first three days of storage, and in the following nine days, there is an increase in respiratory intensity. Firmness is probably affected by the degradation of pectins due to the increase in polygalacturonase activity, generating softening in the plant material [44].

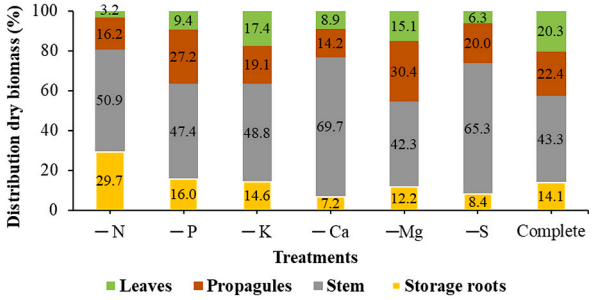

Fig. 3. Distribution of dry biomass in organs of arracacha plants subjected to macronutrient nutrient deficiencies. Complete: Plants that received all nutrients.

N deficiencies alter root system morphology substantially. It is possible that an increased sugar supply to the root affects root morphology through sugar signals. Sucrose is thought to promote cell differentiation and maturation, whereas hexoses favour cell division and expansion [45]. Furthermore, changes in hormonal balance in the root tissue might orchestrate changes in root morphology [46]. At the whole plant level, two types of response are activated. The first depends on external ion concentration and involves local signals. The second depends on whole plant mineral status and involves long-distance signalling. When plants are N-deficient, root growth accelerates and augmented lateral root (LR) branching further increases the foraging capacity of the root system. Interestingly, when roots of N-deficient plants contact nitrate, lateral rooting is stimulated further. Long-distance signals mediating the shoot response to nitrate perception in roots seem to involve cytokinins. It is possible that the reduction in cytokinins observed during N deficiency relieves a general inhibition of root growth by this hormone, and that an increase in auxin stimulates cell division and LR development. This process seems to be promoted by increased sucrose concentrations in the roots, suggesting that sucrose signals from the shoot could set the magnitude of morphological responses to N deficiency [41,46–48].

4.1.2. Phosphorus (P) deficiency

Kochhar and Gujral [49] described the similar symptoms in this experiment. Excess anthocyanins in some plant species give rise to a slightly purplish color in leaves [50,51], and the dark green color occurs because leaf expansion is inhibited to a greater extent than chlorophyll formation [52]; Meanwhile, malformations are due to the lack of energy to complete mitosis, thus limiting the correct formation of photosynthetic organs [14]. When P levels are low in foliar tissues, cell division rates are reduced, affecting tissue expansion, which restricts aerial sprouting and causes a rearrangement in the distribution of photoassimilates to the different plant organs [38].

Deficiency P influenced leaf width and leaf number. Fresh and dry biomass yield was reduced mainly in leaves and petioles, followed by propagules, whole plant, stem, and storage roots. Documented reduction of the leaf area in plants of *Passiflora mollisima* [38], in cowpea bean leaf length, leaf area, and whole plant biomass [31], in *Stevia rebaudiana*, loss of biomass in leaves and aerial tissues [40] and in arracacha decrease in dry matter of absorbent roots.

4.1.3. Potassium (K) deficiency

Morphological alterations due to K are detailed by Buitrago et al. [14] in feijoa, Fernandez-Escobar et al. [53] in olive, and Taiz et al. [39] in monocots. Symptoms in adult leaves are due to K moving through the phloem from mature to juvenile organs, favored by its solubility. Susceptibility to attack by pests such as mites is reported by Câmara Araujo [17] in arracacha. Chlorosis and leaf necrosis can be related to chloroplast collapse [53]. Also, Martinez et al. [54] indicate that K deficiency occurs mainly in adult leaves and their edges, where perimeter necrosis begins to appear, progressively increasing until it reaches the entire leaf lamina.

K did not significantly influence growth parameters. The most significant loss of fresh mass occurred in storage roots, followed by petioles, whole plant, and leaf, which agrees with [54]. who reported a 98.9% decrease in the fresh weight of cape gooseberry fruits, and with Souza et al. [31], who observed a decrease in 50% of the total fresh mass of cowpea bean plants. The reduction in the percentage of dry mass was in the following order: leaves, propagules, petioles, storage roots, and stem. In this regard, Falesi et al. [55] observed a decrease in the dry mass of leaves, stems, roots, and whole plant of *Tabebuia serratifolia* and Câmara Araujo [17] in absorbent roots of arracacha. Small reduction in the dry mass of arracacha storage roots (10.7%) is possible, because the K requirement in species with storage roots is lower because they can efficiently replace K by Ca, Mg, or Na for osmotic purposes in the vacuole, as is the case of sugar beet that replaces K by Na by up to 60% [56,57].

4.1.4. Calcium (Ca) deficiency

The visual symptoms in the plant as a result of Ca restriction coincide with those recorded in arracacha by Câmara Araujo [17]. Roots damaged by Ca limitation are susceptible to fungal and bacterial infection [58]. Necrotic islands and spots in the leaf lamina are associated with peculiarities of Ca^{2+} transport in the plant [59]. The evidence of symptoms in young tissues and meristematic zones of roots, stems, and leaves is explained by the fact that cell division is affected by Ca deficiency, and in these tissues, the mitotic index is normally high. Additionally, the middle lamina that forms between two daughter cells, one of whose main components is calcium pectate may be altered [36].

According to Câmara Araujo [17], Ca deficiency in arracacha reduced the number of propagules and the dry mass of stem, absorbing roots and petioles. Carvalho et al. [60] found that Ca deficit for 50 days in tomatoes caused a reduction of 82% in height, 93% in leaf area, and 86% of total plant dry mass. These data coincide with Sturião et al. [59] who reported cherry tomato stunted plant growth and lowered dry mass production in aerial tissues, fruits, and roots. These can be explained by the fact that when plant growth is restricted by Ca suppression, there is reduced production of photoassimilates. Ca plays a structural role in cells and serves secondary messenger functions, stimulating plant physiological responses to environmental or developmental disturbances [39,52].

4.1.5. Magnesium (Mg) deficiency

The symptomatology described is in agreement with that observed by Afrousheh et al. [61] in *Pistacia vera*, and Souza et al. [31] in *Vigna unguiculata* L. Mg is easily translocated; therefore, visual symptoms of Mg deficiency are noticed in adult leaves. Mg deprivation did not significantly limit plant structure because Mg^{2+} ions have a specific role in activating enzymes involved in respiration, photosynthesis, and DNA and RNA synthesis. It is also part of the ring structure of the chlorophyll molecule [39]. Interveinal chlorosis is due to chlorophyll depletion, which causes rapid chloroplast destructuring, affecting the photosynthetic allocation of C and N [36].

Mg deficiency in the arracacha plants caused a decrease in the fresh biomass of storage roots, followed by petioles, leaves, and the whole plant, which is in line with Hermans et al. [62], who found a reduction in the fresh biomass of shoots, absorbing roots, storage roots and whole plant of Beta vulgaris, with Verbruggen and Hermans [63], reporting a decrease in the fresh weight of petioles, stems and the entire plant of Pisum sativum and Souza et al. [31] in writing a reduction in the fresh mass of plants of Vigna unguiculata L. Meanwhile, the arracacha plant lost dry mass mainly in petioles, leaves, storage roots, stalk, and whole plants. Mg depletion reduced the dry mass of roots and stems of Pisum sativum [63], leaves, stems, roots, and whole plant of Tabebuia serratifolia [55], absorbing roots of A. xanthorrhiza [17] and total dry mass of Vigna unguiculata L. plants [31].

In Mg deficiency, adult leaves have the highest starch and sucrose contents and the lowest Mg concentration among all plant organs. These leaves provide fewer carbon resources to the young leaves; consequently, the total aboveground biomass is reduced. With the evolution of Mg deficiency, the intermediate and lower leaves also accumulate a higher amount of starch, and finally, the growth of the primary root is affected [61,64].

4.1.6. Sulfur (S) deficiency

The omission of S critically limited the growth parameters in the arracacha plant. It caused less accumulation of fresh and dry mass; this coincides with Souza et al. [31], who indicated a decrease in the fresh mass of *V. unguiculata* L. plants, and with Siddiqui et al. [65]. They recorded a decrease in the fresh and dry mass of shoots and roots in S. *lycopersicum* L. plants. Similar results have been reported in *S. rebaudiana* [66] and *S. lycopersicum* L. with reduced shoot length (47.86%) and root length (54.07%) [65].

The decrease in growth parameters under S-limited conditions may be due to the depression of root hydraulic conductivity and altered N metabolism [67]. After N, P, and K, S is essential to plant growth and development and is involved in the activity of photosynthetic enzymes RuBisco and CA and other photosynthetic parameters such as photosynthetic rate (Pn), stomatal conductance (Gs) and internal CO2 concentration (Ci). S starvation produces deleterious effects on S assimilation that cannot be dissociated from overall plant metabolism and is strongly related to the availability of other nutrients and carbohydrate metabolism [65].

4.2. Dry matter distribution

The distribution pattern of dry matter in arracacha plants at 270 days showed that aerial organs, comprised more than 50% of the total dry weight, which coincides with that reported by Câmara Araujo [17] in Brazil. Generally, in this species, it is the storage roots are consumed [1], so the plant has aerial organs that develop the first 180 days to ensure the allocation of photoassimilates to the storage roots between 120 and 180 days after planting [4].

Nutritional stress caused by N deficiency largely determines plant biomass distribution, sucrose synthesis, and degradation rates of sucrosa. N deficiency can stimulate sucrose synthesis, and due to higher activities of fructose-1,6-bisphosphatase and sucrose phosphate synthase can increase its translocation to roots [68]. N deficiency in arracacha allowed more significant carbohydrate accumulation in the stem and storage roots than in the rest of the plant. Similar results have been reported in *Phaseolus vulgaris* L., which accumulates photosynthates in shoots and roots [68], and in nursery *Psidium guajava* L. plants, in which 65% of dry matter was accumulated in the root [10].

In this study, P and K deficiencies concentrated carbohydrate accumulation in the stem. They reduced them in the leaves, while P deficiency substantially increased photoassimilates in the storage roots, agreeing with Dussán et al. [10] and Cabezas and Sanchez [38]. Low amounts of inorganic phosphate in the cytosol can reduce ATP synthesis and affect rubisco synthesis, leading to decreased carboxylation rates and lower carbohydrate production in the leaf. A more significant accumulation of dry matter in the roots favows P uptake and thus mitigates the deficiency effect of this nutrient [69]. In addition, in K-deficient plants, the translocation pattern of photoassimilates to growing organs is altered, and the photosynthesis process is affected due to its role in stomatal regulation [52].

Regarding the distribution of dry matter in arracacha plants with Ca, Mg, and S deprivation, less accumulation was observed in leaves and storage roots, similar to that reported by Hermans et al. [62] in sugar beet, He et al. [70] in banana and Falesi Bittencourt et al. [55]. in *Handroanthus chrysanthus*. Mg is associated with symplastic transport, which is a determinant in the distribution of photoassimilates to the different plant organs [71]. The lowest root dry mass gain was found in the treatment without Ca, possibly because Ca stimulates cell division in the meristematic apices, facilitating cell division, a response associated with its role in auxin synthesis [52]. The omission of S disrupts N metabolism, which, in turn, reduces photosynthetic rates as a direct consequence of the accumulation of sugars, which exceeds the amount needed to achieve the metabolic balance between leaves and demand organs [72].

5. Conclusions

Deficiencies of P, Mg, and K induced a change in the color and number of leaves without affecting plant growth to a greater degree. The most severe deficiency symptoms in arracacha plants of the common yellow variety were manifested by a marked decrease in N, Ca, and S in the nutrient solution, where, in addition to effects on the leaf lamina, there was a drastic change in plant height and accumulation of mass in the organs evaluated. The description of symptoms in the arracacha plant and the photographic material presented in this study facilitate the recognition of these nutritional deficiencies and the taking of corrective measures in the crop by the farmer.

Author contribution statement

Jorge Enrique Villamil Carvajal: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Johanna Paola Garnica Montaña: Conceived and designed the experiments; Performed the experiments; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Elberth Hernando Pinzón Sandoval: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Liliana Margarita Atencio Solano, Pedro José Almanza Merchán: Conceived and designed the experiments; Performed the experiments; Wrote the paper.[1]

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Data availability statement

The authors do not have permission to share data.

Declaration of interest's statement

The authors declare no competing interests.

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