



Article Unraveling the Tolerance of *Moringa oleifera* to Excess K through Increased N Absorption and Mg Use Efficiency

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Abstract: The tolerance of *Moringa oleifera* plants to excess K may be linked to nutritional mechanisms, but studies are lacking. The present study was conducted to analyze the tolerance of *Moringa oleifera* to nutritional imbalance and its importance in the growth of plants submitted to high doses of K in the absence and presence of N. The experiment was conducted in pots with 9 dm³ of Oxisol in a 4×2 factorial scheme, with potassium doses of 0, 110, 190, and 265 mg dm⁻³ combined with nitrogen doses of 0 and 100 mg dm⁻³. The increase in K uptake by moringa is enhanced by N supply but decreases the uptake of Ca and Mg. Notwithstanding, this was of little importance as the soil cultivated had adequate Ca and Mg contents and was sufficient for adequate plant nutrition without impairing plant growth. The moringa plant is tolerant to nutritional imbalances when grown in environments with high K content probably because N favors an increase in Mg use efficiency, avoiding biological disturbances. The results of this study contributed to our understanding of how moringa induces nutritional mechanisms of action to deal with excess K in crops.

Keywords: nitrogen fertilization; Moringaceae; N content; seedlings; nutrient interaction

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1. Introduction

Moringa oleifera belongs to the family Moringaceae and is the most cultivated tree species of the genus Moringa [1]. It is native to Africa and occurs in South America and Southeast Asia [1], being used in human and animal nutrition [2]. Recent research on this species has focused mainly on bioactive compounds and antinutritional factors [3,4].

The optimal growth of plants depends on nutrients that perform well-known functions in physiological and biochemical processes. It is noteworthy that K and N are required in larger amounts by plants [5]. Thus, the doses of these elements are the highest in the cultivations, which increases the risk of nutritional imbalance.

Nutrient balance is important as it enhances plant metabolism, which explains the importance of studies on the interaction between nutrients [6]. Research often indicates that increased K in crops may interact with other nutrients such as Mg and Ca [7–9], decreasing the uptake of these elements depending on the species. This situation impairs the growth of crops such as maize, potato, sugarcane, and cherry tomato [10–13]. Excess K is more likely to have an antagonistic effect with cations, but a synergistic effect can also take place. However, reports on these effects are mainly restricted to rice and maize [14,15]. The interaction between K and Mg in plants can be antagonistic depending on plant species, cell type, leaf age, nutrient source, and draining organs [9].

Some studies indicate that N can increase or decrease plant K uptake depending on the chemical form absorbed. For instance, $N^-NH_4^+$ uptake can decrease K uptake in the plant [16] because the two cations have similar charges and hydrated diameters [17]. However, nitrogen application to tropical soils without excess soil moisture and compaction should favor nitrification. This would lead to a predominance of nitrate in the soil solution,

making it the form most absorbed by plants [5]. In turn, N-NO3⁻ uptake should favor K uptake. The literature reports this situation in different species, in which the NO₃⁻ ion serves as a mobile anion during K⁺ uptake and/or transport [18].

The importance of water absorption by the cells creates turgidity pressure in the cell walls, causing them to elongate and increasing cell volume [19]. The balance between water absorption by the roots and water loss due to transpiration results in the water status of the plant [20]. However, soils with high concentrations of neutral soluble salts impose salt stress on plants, which is detrimental to plant growth [21]. The plant also experiences stress in sodic soils, which have high concentrations of sodium (Na⁺) and chloride (Cl⁻) salts (soluble ionic salts) that impair plant development [21].

The reduction in CO_2 assimilation by the chloroplasts is due to the factor mentioned above (salt stress) because of the stomata closing, the guard cells that are responsible for controlling stomatal opening to regulate water and gas exchange [21]. The structure of the guard cells is important for responding to changes in turgidity pressure, so the stomata close due to the decrease in osmotic pressure and the reduction in K+ content in the leaves [22]. Elevated Na⁺ and Cl⁻ concentrations in the sprouts cause an increase in osmotic pressure, resulting in the outflow of cellular water or a lower turgidity pressure, resulting in a decrease in the osmotic potential inside the cell [23].

The metabolic processes of plants are impaired by ionic disturbance, and the tissue becomes chlorotic. The simplistic fluctuations in osmotic pressure generate water loss from the cells and reduce water absorption [21]. When there is a lower supply of water to the plants, or due to some natural phenomenon such as a summer drought, there is a lower water content in the soil, which leads to an increase in salinity in the root zone due to the water potential gradient created by the plant roots that draw water into the root zone [21]. That is why it is important to provide the plant cells with an adequate supply of water and potassium for their ionic balance and optimal development.

Potassium deficit is a recurrent problem in cultivated areas worldwide as a significant part of K is removed at each harvest, which exceeds the K applied to crops [24]. The authors complement by indicating that potassium applications are typically low in soils with high K content (e.g., Latin American Southern Cone countries, North Africa, Western USA) due to a historical lack of crop yield responses. Thus, many cropping regions present high soil K content, especially those under intensive agriculture. Moreover, it is still poorly known whether K application in these areas with high soil K content may induce deficiency of other nutrients, especially if they are at low soil contents.

Thus, there are many unanswered questions on this subject. In the case of moringa, for instance, K can interact negatively with other elements, altering nutrient levels. Notwithstanding, it is necessary to know if this interaction is sufficient to cause deficiency at a level that could harm the biological functions of the nutrient in the plant and reduce its growth. It is also necessary to know whether N can affect the response of moringa plants grown in soils with high K content. In this regard, it is not yet known whether this species has the tolerance to maintain K and N homeostasis with other nutrients in plant shoots in a way that does not harm plant growth.

Therefore, to clarify the response of moringa to the interaction between K and N, we hypothesized that the increase in potassium fertilization in N-sufficient plants would enhance K absorption, but with little importance to cause a nutritional imbalance (especially in cations) that could reduce plant growth in soil with adequate fertility of other nutrients. If this hypothesis is confirmed, it will be possible to unravel why the imbalance of excess K in the other nutrients is not agronomically important. This may be linked to the fact that the soil cultivated is not deficient in cations, whereas the increase in plant N may enhance the efficiency of the use of these cations in the plant, avoiding possible disturbances in plant growth.

The present study was conducted to analyze the tolerance of *Moringa oleifera* to nutritional imbalance and its importance in the growth of plants submitted to high doses of K. The study further analyzes whether the supply or no supply of nitrogen affects the growth of plants grown in fertile soil.

If the hypothesis of this research is confirmed, it will show the important role of N in nutrient absorption and in the nutritional efficiency of the species. It would also confirm that the species can be cultivated in soils with high K content without risk of damage to crop growth. This is very important because these soils occur in different regions of the world [24].

2. Material and Methods

2.1. Development Conditions, Location, and Soil Characterization

The experiment was developed between July and November 2019. *Moringa oleifera* was grown under greenhouse conditions at the Paulista State University (UNESP), in Jaboticabal City, São Paulo State, Brazil. The site is located at the geographical coordinates 21°15′22″ south, 48°18′58″ west, at an altitude of 575 m. According to the Köppen classification, the climate is type Aw, in transition to Cwa. The experimental unit was a plastic pot filled with 9 dm³ of samples of a eutrophic Red Latosol [25], which corresponds to an Oxisol.

Meteorological data were monitored throughout the experiment using a digital thermohygrometer, recording the minimum temperature (14.7 \pm 5 °C), maximum temperature (36.5 \pm 7 °C), and relative humidity (31.6 \pm 8%). Soil chemical analysis was performed already for fertility purposes according to the method described by Raij et al. [26]. The data presented the following results: pH (CaCl₂): 5.8; organic matter (colorimetric): 10 g dm⁻³; P (anion exchange resin): 23 mg dm⁻³; S (turbidimetry): 5 mg dm⁻³; Ca: 31 mmol_c dm⁻³; Mg: 14 mmol_c dm⁻³; K: 1.8 mmol_c dm⁻³; H+Al: 15 mmol_c dm⁻³. Particle size analysis revealed the following results: coarse sand: 32%, fine sand: 20%, silt: 11%, and clay: 37%.

2.2. Treatments and Experimental Design

The treatments were arranged in a 4 \times 2 factorial scheme consisting of four doses of K: 0, 110, 190, and 265 mg dm⁻³ of soil corresponding to 0, 220, 380, and 530 kg ha⁻¹, respectively, and two conditions of N: 0 mg dm⁻³ (deficiency) and 100 mg dm⁻³ of soil (sufficiency). The experimental design used was entirely randomized with four replicates. The doses of K used followed Malavolta's general recommendations (200 mg dm⁻³) [27], with lower and higher values.

Nitrogen (N) and potassium (K) sources were urea $(NH_2)_2CO$) and potassium chloride (KCl), respectively. The planting fertilization of moringa was performed with simple superphosphate to supply 60 mg dm⁻³ of P to the soil. The other macronutrients (Ca, Mg, and S) were present at adequate levels in the soil and were not applied. The following micronutrient fertilizers were applied: 0.5 mg dm⁻³ of B (H₃BO₃); 2.0 mg dm⁻³ of Mn (MnCl₂·4H₂O); 1.5 mg dm⁻³ of Zn (ZnSO₄.7H₂O); 1.0 mg dm⁻³ of Cu (CuSO₄.5H₂O); and 0.05 mg dm⁻³ of Mo (Na₂MoO₄·2H₂O).

All fertilizers used in the experiment were properly incorporated into the soil volume of the pots before transplanting the seedlings.

Moringa seeds were sown in tubettes. After 10 days, the seedlings began to emerge and 15 days later they were transplanted into 9 kg pots filled with soil samples, keeping one plant per pot. Irrigations were performed with a sufficient volume of water to maintain moisture close to field capacity.

2.3. Evaluations

Nondestructive analyses started at 70 days after emergence (DAE) of the moringa plants, including the following evaluations:

2.3.1. Height, Number of Leaves, Chlorophyll, Fv/Fm, and Plant Dry Matter

For plant height determination, a cm tape measure was used covering from the neck of the seedling to the apex of the last fully expanded leaf. The number of leaves was determined by counting the compound leaves. Chlorophyll content was measured by means of the SPAD index at 68 days after germination: the relative chlorophyll index in the seventh fully expanded leaf was estimated from the average of seven readings using the SPAD portable chlorophyll meter (Falker model, CFL 1030), from which the indirect chlorophyll A and B values were obtained, and by summing the values of the relative total chlorophyll index.

The efficiency of photosystem II (Fv/Fm) was analyzed by measuring the chlorophyll fluorescence at 69 days after germination. The readings were taken between 7 and 8 o'clock in the morning with a 30 min period of adaptation in the dark of the leaves using tweezers, before the excitation of the one-second red light pulse (saturation light source: set of red LEDs). To do this, certain parameters were taken into account: initial fluorescence, which is the minimum for chlorophyll excitation (F0), and the maximum fluorescence for chlorophyll excitation (F0), and the maximum fluorescence for chlorophyll excitation (F0). Fv represents the flow of electrons from the PSII reaction center (P680) to plastoquinone. The maximum quantum yield is calculated as: Fv/Fm = (Fm - F0)/Fm. When a plant has its photosynthetic apparatus intact, the Fv/Fm ratio should vary between 0.75 and 0.85 [28], while a drop in this ratio reflects the presence of photoinhibitory damage to the PSII reaction centers [29]. The tweezers were attached to the median region of the seventh fully expanded leaf, using a portable fluorometer model (Opti-Sciences-Os30p+).

Leaf area (LA) was obtained considering the leaves, with the aid of an electronic area meter (LICOR model, LI 3100 A). The plants were separated into leaves, stem, and root and then the whole plant's dry matter was obtained.

2.3.2. Macronutrient and Micronutrient Content in Leaf, Stem, and Root

Samples of the different plant organs leaf, stem, and root were taken to an oven with forced air circulation at a temperature of 65 ± 5 °C until reaching constant weight. Afterwards, the samples were ground in a Wiley mill and nutrient contents were determined. These samples were submitted to wet chemical analysis by nitric-perchloric digestion of macronutrients (P, K, Ca, Mg, and S) and micronutrients (Cu, Fe, Mn, and Zn), with N being determined by sulfuric digestion according to the methodology proposed by Bataglia et al. [30].

2.3.3. Accumulation and Efficiency of Nutrient Use in the Shoots

From the contents of N, P, K, Ca, Mg, S, Cu, Fe, and Mn and the value of dry matter, the accumulation of macronutrients and micronutrients in plant shoots was calculated. Shoot nutrient content was multiplied by shoot dry matter. Nutrient use efficiency was calculated as follows:

Shoot nutrient use efficiency
$$(g^2g^{-1}) = \frac{(dry \ mass \ (g \ per \ shoot))^2}{nutrient \ accumulation \ (g \ per \ shoot)}$$

The numerator is expressed as the dry mass of the aerial part of the plant squared and in the denominator the accumulation of nutrients in the aerial part of the plant, according to Siddiqi and Glass [31].

2.4. Statistical Analysis

The data were submitted for analysis of residual normality by the Shapiro–Wilk test. The homoscedasticity test was performed, with no evidence to reject the homogeneity of variances by the Levene test at 5% probability. Analysis of variance then verified the main effects (F test (p < 0.05)) and the means were tested by the Scott–Knott test at 5% probability. Subsequently, polynomial regression analysis was performed. Statistical analysis was performed in AgroEstat, and the graphs were created in SigmaPlot[®].

3. Results

3.1. Biometric Variables

Nitrogen application favored the growth variables of moringa, but potassium application did not have this benefit (Table 1).

Table 1. Summary of analysis of variance for total chlorophyll, quantum efficiency of photosystem II (Fv/Fm), height (H), number of leaves (NL), leaf area (LA), and dry matter (DM) of Moringa oleifera seedlings as a function of N and K doses. *: significant at 5% probability, **: significant at 1% probability, ^{ns}: not significant.

Nutrient	Total Chlorophyll	Fv/Fm	H (cm)	NL	LA	DM
Ν	229.51 **	83.05 **	276.76 **	37.71 **	268.20 **	313.02 **
K	0.39 ^{ns}	0.41 ^{ns}	2.32 ^{ns}	1.55 ^{ns}	1.75 ^{ns}	2.13 ^{ns}
N imes K	1.07 ^{ns}	2.13 ^{ns}	0.17 ^{ns}	0.43 ^{ns}	1.64 ^{ns}	0.73 ^{ns}
MSE	2.48	0.01	5.19	0.77	104.79	2.13
CV%	11.38	2.92	9.09	9.95	14.19	10.31

MSE: mean standard error; CV%: variation coefficient.

3.2. Macronutrient and Micronutrient Content in Leaf, Stem, and Root

The leaf contents of K, K/Mg, K/Ca, and Mn depend on the amount of K and N. The other nutrients are affected by the isolated effects of N and K or of only one nutrient (Table 2).

Table 2. F test indicating significance (*: p < 0.05; **: p < 0.01; and ^{ns}: p > 0.05) for nutrient contents in leaf, stem, and root in moringa as a function of treatments.

	Ν	Р	К	Ca	Mg	K/Mg	K/Ca	S	Cu	Fe	Mn	Zn
						Leaf						
N	97.4 **	10.5 **	56.4 **	32.5 *	7.7 **	3.6 ^{ns}	2.4 ^{ns}	175 **	11.0 *	9.5 **	1.3 ^{ns}	32.5 **
Κ	2.1 ^{ns}	1.31 ^{ns}	3.39 **	3.6 *	3.6 *	5.7 **	5.8 **	3.6 *	0.5 ^{ns}	0.4 ^{ns}	0.7 ^{ns}	0.5 ^{ns}
$N \times K$	1.2 ^{ns}	2.5 ^{ns}	3.45 **	1.6 ^{ns}	2.3 ^{ns}	3.7 *	3.4 *	0.8 ^{ns}	0.6 ^{ns}	1.4 ^{ns}	4.3 *	1.5 ^{ns}
Stem												
Ν	25.1 **	214.2 **	1.7 ^{ns}	64.7 **	36.5 **	2.9 ^{ns}	24.8 **	36.3 **	9.5 **	0.5 ^{ns}	9.4 **	6.00 *
Κ	1.2 ^{ns}	2.1 ^{ns}	0.5 ^{ns}	1.5 ^{ns}	0.8 ^{ns}	8.3 **	24.4 **	0.8 ^{ns}	0.8 ^{ns}	0.2 ^{ns}	0.5 ^{ns}	0.32 ^{ns}
$N \times K$	3.7 *	3.2 *	5.8 **	1.2 ^{ns}	0.3 ^{ns}	5.6 **	11.3 **	0.03 ^{ns}	0.2 ^{ns}	0.3 ^{ns}	0.4 ^{ns}	0.80 ^{ns}
Root												
N	84.2 **	191.8 **	0.6 ^{ns}	4.5 **	8.8 **	18.2 **	9.8 **	34.6 **	2.7 ^{ns}	5.2 *	5.6 **	2.8 ^{ns}
Κ	2.8 ^{ns}	2.2 ^{ns}	0.5 ^{ns}	1.3 ^{ns}	3.0 ^{ns}	5.3 **	2.4 ^{ns}	2.0 ^{ns}	0.4 ^{ns}	2.1 ^{ns}	0.2 ^{ns}	0.8 ^{ns}
$N \times K$	5.2 **	1.2 ^{ns}	0.5 ^{ns}	0.8 ^{ns}	3.6 *	3.6 *	0.8 ^{ns}	5.3 **	0.5 ^{ns}	4.8 **	0.4 ^{ns}	1.0 ^{ns}

Leaf K contents depend on the doses of K and N. Potassium doses linearly increased K content in the presence of N. In the absence of N, however, the dose of 110 mg dm⁻³ of K expressed the lowest K content (Figure 1a).

Leaf K/Mg and K/Ca ratios depend on the doses of K and N. The increase in K doses under N sufficiency linearly increased K/Mg and K/Ca ratios; however, K/Mg and K/Ca ratios decreased under N deficiency (Figure 1b,c).

Leaf Mn content also depends on the doses of N and K. Increasing K doses linearly increased Mn content in the presence of N; however, leaf Mn content decreased in the absence of N (Figure 1d).

Nitrogen and potassium interacted for the stem contents of N, P, and K, and the K/Mg and K/Ca ratios (Table 2 and Figure 1e–i). The other nutrients are affected by the isolated effects of N and K or by only one nutrient (Table 2).

Increasing K doses reached the minimum stem N content at the calculated dose of 173.3 mg kg⁻¹ K (Figure 1e). However, K doses did not differ in the absence of N.

Stem P content depended on the doses of K and N. The increase in K doses affected stem P only in the absence of N, reaching a minimum value at the calculated dose of 153.9 mg kg⁻¹ K (Figure 1f).

Stem K content depends on the doses of N and K. This is because the increase in K doses under N sufficiency linearly increased K content. Under N deficiency, however, stem K content decreases (Figure 1g).

Stem K/Mg and K/Ca ratios depended on the doses of N and K. Increasing doses of K linearly increased these ratios only in the presence of N (Figure 1h,i).

In moringa roots, the contents of N, Mg, K/Mg, S, and Fe depended on the doses of K and N (Table 2). Root contents of P, Ca, K/Ca, and Mn were affected only by N application.

In the presence of nitrogen, potassium doses decreased root N content, reaching the minimum value at the calculated dose of 155 mg kg⁻¹ K. In the absence of N, however, N content was not affected (Figure 1j). Root Mg contents also decreased linearly with the doses of K in the presence of N, there being no effect in the absence of N (Figure 1k). In the presence of nitrogen, potassium doses increased the root K/Mg ratio (Figure 1l). Root S content decreased linearly with K doses in the presence of N, but in the absence of N, there was no significant effect (Figure 1m). Moreover, root Fe content decreased linearly with K doses in the presence of N, there was no such effect (Figure 1m).



Figure 1. Cont.



Figure 1. K (**a**), K:Mg (**b**), K:Ca (**c**), and Mn (**d**) contents in the leaf; N (**e**), P (**f**), K (**g**), K:Mg (**h**), and K:Ca (**i**) in the stem; N (**j**), Mg (**k**), K:Mg (**l**), S (**m**), and Fe (**n**) in the root of Moringa oleifera seedlings at 70 days after emergence as a function of N and K interaction.

3.3. Shoot Nutrient Accumulation

Shoot accumulation of K, Ca, Mg, and Cu as well as the efficiency of use of K, Mg, and Cu depend on the doses of K and N. The other nutrients are affected by the isolated effects of N and K or of only one nutrient (Table 3).

The application of K linearly increased shoot K accumulation only in the presence of N. In the absence of N, this effect was not significant (Table 3, Figure 2a).

The application of K linearly decreased Ca and Mg accumulation in the presence of N. However, this did not occur in the absence of N (Figure 2b,c). The application of K linearly increased shoot Cu accumulation in the presence of N. Notwithstanding, this effect did not occur in the absence of N (Figure 2d).

The nutrient use efficiencies (NUE) of K, Mg, and Cu (Table 3 and Figure 2e–g) depend on the doses of N and K. The application of K in the presence of N quadratically increased the use efficiency of K and Cu in the plants (Figure 2e,g). Furthermore, the supply of K in the presence of N increased Mg use efficiency in the plant with a linear adjustment, with no effect in the absence of N (Figure 2f).



Figure 2. Shoot accumulation of K (g plant⁻¹) (a), Ca (g plant⁻¹) (b), Mg (g plant⁻¹) (c), and Cu (g plant⁻¹) (d); use efficiency of shoot K (e), shoot Mg (f), and shoot Cu (g) in Moringa oleifera seedlings at 70 days after emergence as a function of N and K interaction.

Shoot Nutrient Accumulation (g per Plant)											
Source of Variation	Ν	Р	К	Ca	Mg	S	Cu	Fe	Mn	Zn	
Ν	733.6 **	405.8 **	420.4 **	354.7 **	207.6 **	334.6 **	149.6 **	12.6 **	118.9 **	282.0 **	
K	1.26 ^{ns}	2.87 **	21.0 **	1.75 ^{ns}	4.78 **	2.2 ^{ns}	7.9 **	0.31 ^{ns}	2.32 ^{ns}	0.41 ^{ns}	
N imes K	1.26 ^{ns}	0.85 ^{ns}	11.18 **	4.49 *	9.84 **	0.75 ^{ns}	5.94 **	1.59 ^{ns}	2.15 ^{ns}	0.67 ^{ns}	
MSE	0.06	0.009	0.09	0.04	0.01	0.04	0.02	3.68	0.5	0.08	
CV%	14.4	11.3	13.3	12.3	17.3	11.1	27.2	81.1	28.0	19.5	
Nutrient Use Efficiency (g ² per g)											
Source of Variation	NUE N	NUE P	NUE K	NUE Ca	NUE Mg	NUE S	NUE Cu	NUE Fe	NUE Mn	NUE Zn	
N	242.2 **	457.2 **	119.1 **	598.6 **	352.1 **	348.5 **	262.7 **	108.8 **	171.4 **	202.8 **	
К	2.9 ^{ns}	0.4 ^{ns}	3.1 *	6.2 **	9.4 **	0.6 ^{ns}	11.4 **	1.9 ^{ns}	0.09 ^{ns}	0.6 ^{ns}	
$N \times K$	0.4 ^{ns}	0.04 ^{ns}	4.75 **	1.8 ^{ns}	5.5 *	0.06 ^{ns}	17.1 **	2.2 ^{ns}	1.31 ^{ns}	0.4 ^{ns}	
MSE	45.6	264.6	62.2	55.5	299.5	70.8	445.1	10.4	18.1	60.1	
CV%	16.5	19.14	35.5	16.5	21.9	22.5	21.0	35.0	27.4	23.3	

Table 3. F test indicating significance (*: p < 0.05; **: p < 0.01; and ^{ns}: p > 0.05) for nutrient accumulation in moringa shoots as a function of treatments.

MSE: mean standard error; CV%: variation coefficient.

4. Discussion

The effects of the interaction between nutrients, especially N and K, begin with the acquisition of nutrients by the plants and reflect the levels of these nutrients in the different organs of the plant. Such effects may generate a nutritional deficiency whose intensity is species-dependent [5]. In moringa, it still remains unknown whether the increase in plant K content can alter the contents of the other nutrients and whether this effect can be enhanced or minimized in plants with different nutritional status of N.

In moringa plants, the present research evidenced that increasing the amount of K had a significant effect on the increase both in K and K/Ca contents in the leaf and stem organs of moringa and in the K/Mg ratio in all plant organs, but only in N-sufficient plants. Some authors showed similar results, with an increase in the K/Mg ratio with an increase in the amount of K [32,33].

The increase in plant K had little importance in decreasing plant Mg content because it did not affect the leaves or stems, only restricting the roots in plants that received N. The effects of a K increase on the contents of micronutrients in the plant occurred only in the plants that did not receive N and were restricted to Mn in the leaves and Fe in the roots, with a decrease in the contents of these elements.

It was clear that N favors the absorption of K in moringa plants because there was an increase in shoot K accumulation due to the increase in K doses (Figure 2a), a fact also observed in guava trees [34]. Potassium transporters have nitrogen in their composition, which is important for the absorption of this macronutrient [5]. In this regard, N⁻NH₄⁺ constitutes a sensitive component of K uptake probably because it is mediated by KT/HAK/KUP transporters (HAK1-like transporters), while the inward rectifier K channels (AKT1-like channels) constitute the N⁻NH₄⁺ insensitive pathway [35,36].

Furthermore, increased K accumulation in the shoots decreased Ca accumulation (Figure 2b) and Mg accumulation (Figure 2c) and increased Cu accumulation in the shoots (Figure 2d), but this occurred only in N-sufficient plants. The effects of excess K on the plant are restricted to risks of imbalance of only three nutrients (Ca, Mg, and Cu) in moringa shoots, and limited in N-sufficient plants. It is possible that the increase in K decreased the uptake of Ca and Mg due to the greater degree of hydration of these nutrients, with greater competition for active uptake sites [5,37].

Our research showed a decrease in K use efficiency with increasing doses of K in the presence of N. This fact normally occurs with all nutrients: When the content in the plant increases, the nutrient metabolism efficiency decreases. It was even clear that moringa did not respond to the application of K regardless of N, indicating that the K content of this soil (1.8 mmol_c dm⁻³) is already adequate for the crop. Therefore, this species is not very responsive to K application in soils with K content equal to or greater than 1.8 mmol_c dm⁻³, possibly due to the good K use efficiency by the plant. Other authors have also mentioned the low response of moringa to K supply [38–40].

Regarding the decrease in the accumulation of nutrients such as Ca and Mg in moringa plants with increasing doses of K in the presence of N discussed earlier, it can be stated that it probably did not have agronomic importance because it was not sufficient to decrease plant dry matter. This occurred because the increase in K doses in the presence of N did not cause physiological damage in the plants as it did not diminish the chlorophyll content nor the Fv/Fm (photosynthetic efficiency), thus not affecting plant height, number of leaves, or foliar area. Potassium disturbance may decrease Fv/Fm given the increase in reactive oxygen species [41], a fact that did not happen in this study.

The results of the present research are sufficient to confirm the hypothesis indicating that increased potassium fertilization in N-sufficient compared to N-deficient plants would enhance K uptake. However, this effect is not enough to cause a nutritional imbalance (especially in cations) that could decrease moring growth in soil with adequate fertility of other nutrients.

Therefore, the research revealed that excess K imbalance, especially in reducing the absorption of Ca and Mg, did not cause physiological or agronomic damage to the plant. This may be linked to the fact that the soil cultivated did not present a deficiency of these cations because Ca and Mg contents were equal to 31 and 14 mmol_c dm⁻³, respectively, which are considered high or adequate for moringa cultivation [26]. These Ca and Mg contents obtained are due to limestone application, which contributed to an increase in the availability of these nutrients in the soil [26,42]. This reinforces the indication that the negative interaction of a given nutrient such as K on the second nutrient is only of agronomic importance if the second nutrient, for example, Ca and Mg, has a deficient content in the soil [5], which did not occur in our study.

Another aspect that reinforces the little importance of the decrease in the absorption of Ca and especially Mg in the function of the increase in K doses in the presence of N is the increase in Mg use efficiency, which contributed to avoiding disturbances in plant growth. Thus, N played an important role in increasing Mg use efficiency in moringa plants. This has to do with the associated functions of these nutrients in plant metabolism, e.g., both are involved in protein synthesis. For example, one of the functions of N is to form the amino acids used for protein synthesis that occurs in ribosomes, but this will occur only in the presence of Mg since the active form of ribosomes requires aggregation of two subunits, requiring Mg to form a bridge between the subunits [37]. In addition, N and Mg have structural functions, coparticipating with different organic compounds vital to plants, with a highlight on chlorophyll [5]. Chlorophyll biosynthesis begins with the insertion of Mg into protoporphyrin IX, which is catalyzed by Mg-chelatase, an enzyme consisting of 40, 70, and 140 kDa subunits, respectively, called ChII, Child, and ChIH subunits [8].

Our findings propose that the nutritional imbalance induced by the increase in K can be mitigated by combining crops grown on soils with optimal Ca and Mg contents and with optimal nitrogen fertilization. The choice of species should consider those that present high nutritional efficiency, such as moringa. Therefore, the results of this research provide further evidence for studies on other species, with global implications. This occurs because several growing regions have high K content, especially under intensive agriculture in systems without K losses through leaching, which is common in regions with low rainfall and soils with clayey texture.

5. Conclusions

The effects of the interaction between nutrients, mainly N and K, begin with the acquisition of nutrients by plants and reflect the levels of these nutrients in different plant organs.

The increase in K uptake by moringa is enhanced by N supply but decreases the uptake of Ca and Mg. Notwithstanding, this was of little importance as the soil cultivated had adequate Ca and Mg contents and was sufficient for adequate plant nutrition without impairing plant growth.

The moringa plant is tolerant to nutritional imbalances when grown in environments with high K content probably because N favors an increase in Mg use efficiency, avoiding biological disturbances.

The results of this study contributed to our understanding of how moringa induces nutritional mechanisms of action to deal with excess K in crops.

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