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Critical potassium concentrations for the initial cultivation of *Cedrela fissilis* Vell

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ABSTRACT: Providing nutrients in optimum quantities is essential for increasing the productivity of timber species. Despite this, we know little about the actual potassium (K) requirements of native Amazonian Forest species. This study aimed to determine the critical level of K deficiency and toxicity for the initial cultivation of cedar. We grew *Cedrela fissilis* seedlings in a nutrient solution under the effect of five concentrations of K (0, 1, 2, 5, and 8 mmol L^{-1}) in a completely randomized design with five replications. After 30 days, we evaluated the relative growth rate, dry mass production, proline content, symptomatology, macro and micronutrient content and accumulation, and K absorption and utilization efficiencies. Concentrations of K positively influence the growth, accumulation, and content of nutrients in the dry mass of the aerial part of young cedar plants. Providing varying amounts of potassium significantly affects the nutritional and growth parameters of *Cedrela fissilis* seedlings. Potassium doses of 3.5 - 4.00 mmol L^{-1} in the growing substrate led to better nutritional status (26.08 - 27.28 g kg^{-1} of K) and plant growth.

Keywords: cedar, nutrient deficiency, forest nutrition, phytotoxicity.

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INTRODUCTION

The vast majority (≈ 77 %) of the predominant soils in the dry land of the Amazon are *Latossolos* (Hapludox) and *Argissolos* (Kandiudults), which have low concentrations (<40 mg dm^{-3}) of available potassium (K) (Moreira and Fageria, 2009). However, for most plants to develop appropriately, K concentrations in the soil must be around 60 mg dm^{-3} (Gonçalves, 1995). Therefore, potassium fertilization of these soils is a recommended silvicultural practice and has been increasing in forestry crops (Battie-Laclau et al., 2016).

Plants require approximately 20 to 50 g kg^{-1} of K in dry matter for adequate growth (Marschner, 2012). Potassium is the most abundant cation in plant tissues (Luan et al., 2009) and the second most demanded nutrient by crops (Marschner, 2012). This nutrient plays a central role in plant physiological processes, influencing energy status, translocation and storage of assimilates, maintenance of water in tissues, and activator of more than 60 enzymes (Oosterhuis et al., 2014).

Potassium deficiency for the plant implies the regulation of water vapor loss through the stomata, a lower turgor pressure and cell expansion, decreased activation of the nitrate reductase enzyme, and irregular functioning of the stomata, which reduces the entry and assimilation of CO_2 in the plant, and consequently the photosynthetic performance and development of the crop (Wang et al., 2015). In addition, the stress caused by low K concentrations in plants stimulates an increase in proline production, which can play a protective and osmoregulatory role in plants under drought (Mukarram et al., 2020) and waterlogging (Ghosh et al., 2022) stress and nutritional deficiency (Mansour and Ali, 2017).

Excessive absorption of this element leads to a reduction in the absorption of nutrients such as phosphorus (P), calcium (Ca), magnesium (Mg), and nitrogen (N) in the form of ammonium ($N\text{-}NH_4^+$) due to the high mobility of K in the soil and plant and the competition of these nutrients for absorption, transport, and function with K (Fageria, 2001). This nutritional imbalance affects the plant metabolic processes, such as CO_2 absorption and assimilation, photosynthesis, and water use efficiency (Oosterhuis et al., 2014), and limits crop development (Reich, 2017). Thus, symptoms of K toxicity, expressed in the form of reduced growth of the aerial part and roots, are mainly due to deficiencies of other nutrients caused by the antagonistic effect of K on these (Reich, 2017).

Plants have a specific demand for K, which can vary among and within species and according to their growth stage (Marschner, 2012). However, there are few studies (Silva et al., 1997; Souza et al., 2009; Oosterhuis et al., 2014) evaluating the response of forest species to K fertilization, especially those native to the Amazon with commercial timber potential, among which *Cedrela fissilis* stands out.

This species has excellent potential for wood production in the tropical region. Its wood is of good quality and has significant economic and environmental importance to Brazil. On the other hand, the demand for timber products has exerted intense pressure on natural forests in the tropics, causing a reduction in native populations in recent years (Zeugin et al., 2010). *Cedrela fissilis* occurs in a region with a tropical climate, classified as Aw, with an average air temperature of between 24.6 and 26.9 °C and daily relative humidity ranging from 75 % during relatively dry days to 92 % during the rainy season, with an average annual rainfall of 2,362 mm (Peel et al., 2007).

Silva et al. (1997) observed a positive effect of K on the development of *Cedrela fissilis*. In this study, the authors evaluated the response of 14 forest species of different successional stages, including *Cedrela fissilis*, to the omission and supply of 84 mg dm^{-3} of K in a greenhouse, and observed that the K in the substrate led to an increase in plant growth. Souza et al. (2009) assessed the effect of omitting the nutrients N, P, K, Ca, Mg, sulfur (S), boron (B), and zinc (Zn) on the development of 30-day-old

Cedrela fissilis plants. Using the subtraction diagnosis technique, these researchers carried out the study for 80 days on a medium texture dystrophic *Latossolo Vermelho-Amarelo* (Red - Yellow Hapludox). They observed that K was the third element that most limited plant development. Freiberger et al. (2013), in a study with *Cedrela fissilis* in a greenhouse, without temperature and relative humidity control, using a medium texture *Latossolo Vermelho* (Red Hapludox) as a substrate, observed that the K content in the leaves was equal to 10.0 g kg^{-1}, with K being the second most demanded nutrient by the species. This study aimed to determine the critical level of K deficiency and toxicity for the initial cultivation of *Cedrela fissilis* Vell.

MATERIALS AND METHODS

Species, growing conditions, and experimental design

Thirty-day-old *Cedrela fissilis* seedlings at the stage of two to four pairs of leaves were grown in a greenhouse with natural light and semi-controlled environmental conditions, average temperature of 34.29 °C, relative humidity of 63 %, photoperiod of 12/12 h (day/night) and 612.3 μmol m^{-2} s^{-1} photosynthetic photon flux density, at the Federal University of Amazonas, Manaus-AM.

Plants were grown in a completely randomized design and exposed to five concentrations of K (0, 1, 2, 5, and 8 mmol L^{-1}), with five repetitions and one plant per experimental unit. The research results of Barrera-Aguilar et al. (2013) justified the choice of K concentrations.

Preparing the substrate, growing containers, and obtaining seedlings

River sand with particles between 0.5 and 2.0 mm in diameter, standardized through sieves, was used as a substrate. Substrate was washed in running water, submerged in a 0.5 mol L^{-1} HCl solution for 24 h, and then washed in tap water and deionized water until the drained water had an electrical conductivity (EC) ≤3 μS cm^{-1}. The substrate was then dried under natural conditions and placed in polyethylene plastic pots with 15, 18, and 12 cm of height, an upper internal diameter, and a lower inner diameter, respectively (volume of 2.7 dm^3), and with a controlled drainage pore.

Cedrela fissilis seeds from ten matrices were processed and disinfected externally with 1 % sodium hypochlorite and then washed with running water and deionized water. Treated seeds were sown in plastic trays measuring 0.60 × 0.40 × 0.10 m in length, width, and height, respectively. We used washed river sand as a germination substrate, saturated with a 0.1 mmol L^{-1} $CaCl_2$ solution until germination. After this stage, we irrigated daily with ≈ 200 mL of deionized water until 30 days after sowing (DAS).

Preparing solutions, supplying, and changing nutrient solutions

Pre-cultivation nutrient solutions and those for cultivation and treatments were made from stock solutions prepared with pure reagents for analysis (p.a.). To avoid the formation of precipitates, we prepared individual solutions of macronutrient sources [($NH_4H_2PO_4$; $Ca(NO_3)_2.4H_2O$; $Mg(NO_3)_2$. $6H_2O$ and $(NH_4)_2SO_4$)], a solution containing only Fe-EDTA and a solution composed of the other micronutrients ($MnSO_4.H_2O$; $ZnSO_4.7H_2O$; $CuSO_4.5H_2O$; H_3BO_3; $(NH_4)_6Mo_7O_{24}.4H_2O$ and $CaCl_2.2H_2O$). Nutrients were supplied every three days; on the other days, the plants were given deionized water with the pH adjusted to 5.8, with NaOH or HCl at 0.2 or 0.5 mol L^{-1}, both by supplying 50 mL $plant^{-1}$. Substrate saturation in the container was kept at around 65 % of its total saturation capacity (≈ 580 mL of nutrient solution). We carried out the renewal of the nutrient solution for desalination of the substrate every seven days, starting with monitoring the EC, cleaning the substrate by supplying deionized water until the water drained from the containers showed an EC ≤3 μS cm^{-1}, followed by renewal of the growing solution and reapplication of the treatments.

Pre-cultivation

Seedlings at 30 DAS were transplanted into the growing containers and pre-cultivated for 60 days, receiving essential fertilizer in the form of a nutrient solution equivalent to 1/10 and 1/4 of the standard Hoagland and Arnon (1950) solution in the first and last 30 days of pre-cultivation, respectively. During this phase, K was maintained at a concentration of 0.3 mmol L^{-1}, and the pH of the solution was kept at 5.8, using NaOH or HCl at 0.2 or 0.5 mol L^{-1}, respectively.

Cultivation

After the pre-cultivation phase, the plants were cultivated for 30 days, receiving the treatments (0, 1, 2, 5, and 8 mmol L^{-1} of K), using potassium sulfate (K_2SO_4) as the source of K. We did not balance the sulfur in the respective treatments to avoid the effect of antagonism between sulfate ions and phosphate, chloride, and molybdenum anions (Prado, 2021). Together with essential fertilization, in the form of a nutrient solution with an ionic strength equivalent to 1/4 of the standard solution of Hoagland and Arnon (1950), with a chemical composition corresponding to: 2.98 mmol L^{-1} of N-NO_3^-; 1.24 mmol L^{-1} of N-NH_4^+; 0.25 mmol L^{-1} of P; 1.0 mmol L^{-1} of Ca; 0.5 mmol L^{-1} of Mg; 0.5 mmol L^{-1} of S; 2.27 μmol L^{-1} of Mn; 0.2 μmol L^{-1} of Zn; 0.075 μmol L^{-1} of Cu; 11.65 μmol L^{-1} of B; 0.025 μmol L^{-1} of Mo; 8.0 μmol L^{-1} of Fe; 12.5 μmol L^{-1} of Cl, the pH of the solution was maintained at 5.8, using NaOH or HCl at 0.2 or 0.5 mol L^{-1}, respectively.

Relative growth rate

The height of the aerial part (H) was obtained from the base of the stem to the apical bud of the plant, and the diameter of the stem (D) was measured with a Starret 727 Digital 150 × 6 Inch Pachymeter (Brand Starrett USA), 0.5 cm from the surface of the sand. After removing the plants from the substrate, we measured the root length (RL). From the H, D, and RL data, the height relative growth rate (RGR_H), diameter relative growth rate (RGR_D), and root growth rate (GR_R) were calculated for each experimental unit as described by Bugbee (1996).

Dry mass production

After removing the plants from the substrate, we divided the plants into shoots (leaf + stem + petioles) and roots. They were then washed in deionized water and dried in a forced-air oven at 70 °C until they reached a constant mass. After drying, the shoot dry matter (SDM) and root dry matter (RDM) were determined using a balance with a precision of 0.001 g model XPR504S/A Mettler Toledo, USA.

Proline content

Proline was determined in the root dry mass (RDM) using a colorimetric method, according to Leite et al. (2000).

Symptomatology, content, and accumulation of macro and micronutrients

We used a Canon EOS REBEL T7+ S18-55 IS II BR camera to record the symptoms of nutritional status in the aerial part and roots of the plants with 120 DAS. Contents of K, Ca, Mg, P, sulfur (S), iron (Fe), manganese (Mn), zinc (Zn), and copper (Cu) were determined after grinding the SDM in a Willey-type stainless steel mill, following the extraction and determination methodology of Malavolta et al. (1997). We calculated the accumulation of nutrients in the plant shoots by multiplying the total nutrient content in SDM (g kg^{-1}) by the SDM (kg) mass.

Potassium absorption and utilization efficiency

Potassium absorption efficiency (KUpE) was calculated according to the expression: [(K absorbed in the applied dose - K absorbed in the control treatment)/applied dose] × 100

(Baligar et al., 2001). The efficiency of K utilization (KUtE) for SDM was obtained according to the expression: KUtE = $[(SDM)^2/(K\ accumulated\ in\ SDM)]$ (Siddiqi and Glass, 1981).

Data analysis

We previously submitted the data to outlier detection and test of normality (Shapiro and Wilk, 1965) and homogeneity of variances (Levene, 1960). The variables that did not meet these assumptions (root growth rate - RG_R, Proline, P, K, Ca, Mn, Cu, Fe content, AP, ACa, and KUtE) were transformed into a logarithmic function and then submitted to the tests again. Following the principles of normality and homoscedasticity, the data was submitted for analysis of variance. When the F was significant ($p<0.05$), the means of the dependent variables were tested and fitted to polynomial regression models. The criteria for choosing the regression models were the significance of the model and the highest coefficient of determination.

We considered the curve adjustment significant when p-values were ≤0.05 for the "x^2" and "x" parameters in the equation $Y = ax^2 + bx + c$ for the quadratic model. We estimated the critical K concentration in the shoot of *the Cedrela fissilis* plant from the nutrient content (g kg^{-1}) and accumulation (g $plant^{-1}$). Critical deficiency level (CDL) was considered 90 % of the maximum production (MP) (Parent et al., 1995) in height relative growth rate and shoot dry mass, while the critical toxicity level (CTL) corresponding to the dose above the maximum physical efficiency (MPE) sufficient to promote a 10 % reduction in the response variable (Dow and Roberts, 1982). We placed this variable of nutritional status on the ordinate (Y-axis) against the respective K concentration of substrate on the abscissa (X-axis). For the K critical levels (mmol L^{-1}) in the substrate, the applied K was plotted on the X axis against the nutrient content (g kg^{-1}), accumulation (g $plant^{-1}$), height relative growth rate, and shoot dry mass on the Y axis.

RESULTS

Nutrient accumulation, nutrient content, and symptoms

Potassium levels in the growing solution significantly influenced ($p<0.01$) the nutrient accumulation in the aerial part of the plants. We observed that the K, P, Ca, S, and Zn accumulation in *Cedrela fissilis* fitted the quadratic regression model (Figure 1). On the other hand, the accumulation of the elements Mg, Mn, Cu, and Fe held a linear regression model (Figures 1d, 1f, 1h, and 1i). The accumulation of K, P, Ca, S, and Zn increased linearly as a function of the supply of K in the growing substrate, ranging from 0 to 4.07, 2.80, 1.84, 3.33, and 2.78 mmol L^{-1} of K, respectively. Then there was stabilization in the accumulation values in the ranges of 2.55 and 5.60 g kg^{-1}, 1.03 and 4.56 g kg^{-1}, 0.21 and 4.00 g kg^{-1}, 1.52 and 5.14 mg kg^{-1}, and 0.94 and 4.62 mg kg^{-1} for K, P, Ca, S, and Zn, respectively (Figures 1a, 1b, 1c, 1f, and 1g).

Maximum accumulation values were K = 12.23, Ca = 1.87, S = 1.12, P = 0.99, and Zn = 131.77 mg $plant^{-1}$. Based on these values, there was a reduction in the absorption of these nutrients due to increasing doses of K in the substrate (Figures 1a, 1c, 1f, 1b, and 1g). The doses of K in the nutrient solution referring to CDL and CTL are in a range of 2.55 and 5.60, 0.21 and 4.00, 1.52 and 5.14, 1.03 and 4.56, and 0.94 and 4.62 mmol L^{-1} for K, Ca, S, P, and Zn uptake, respectively (Figures 1a, 1c, 1f, 1b, and 1g).

In general, the absence of K (0 mmol L^{-1} of K) resulted in accumulations of 0.79 g $plant^{-1}$, 38.88 mg $plant^{-1}$, 7.43 mg $plant^{-1}$, and 266.19 mg $plant^{-1}$ of Mg, Mn, Cu, and Fe, respectively. There was a reduction in the accumulation of Mg = 0.082 g $plant^{-1}$, Mn = 3.224 mg $plant^{-1}$, Cu = 0.702 mg $plant^{-1}$, and Fe = 22.003 mg $plant^{-1}$ in the aerial part of the plants for each mmol of K supplied in the growing substrate (Figures 1d, 1f, 1h, and 1i).

Potassium uptake (KUpE) and utilization (KUtE) efficiency

Increasing levels of K in the growing medium significantly affected ($p<0.01$) the KUpE and KUtE values. The data of plants' KUpE fitted to a quadratic reduction (Figure 2a) in the function of the increase of the concentration of K in the growing substrate. The decrease in KUpE was approximately 3.184 mg g^{-1} for each rise of one mmol L^{-1} of K in the nutritive solution up to a dose of ≈ 5 mmol L^{-1} of K in the solution, with a slight stabilization in the reduction from this dose onwards.

Concerning KUtE, the results fitted a U-shaped curve model (Figure 2b), with the values decreasing as the concentration of K in the growing medium increased from zero to ≈ 4.0 mmol L^{-1} and then increasing as the concentration of K increased (>4.0 mmol L^{-1} of K).

Nutrient content

The levels of K significantly influenced ($p<0.01$) the content of K, P, Ca, Mg, S, Mn, Zn, Cu, and Fe in the aerial part of the cedar plants. The nutrient contents fitted a quadratic model, except for the Ca content, which decreased linearly as the levels of K in the growing substrate increased (Figure 3c).

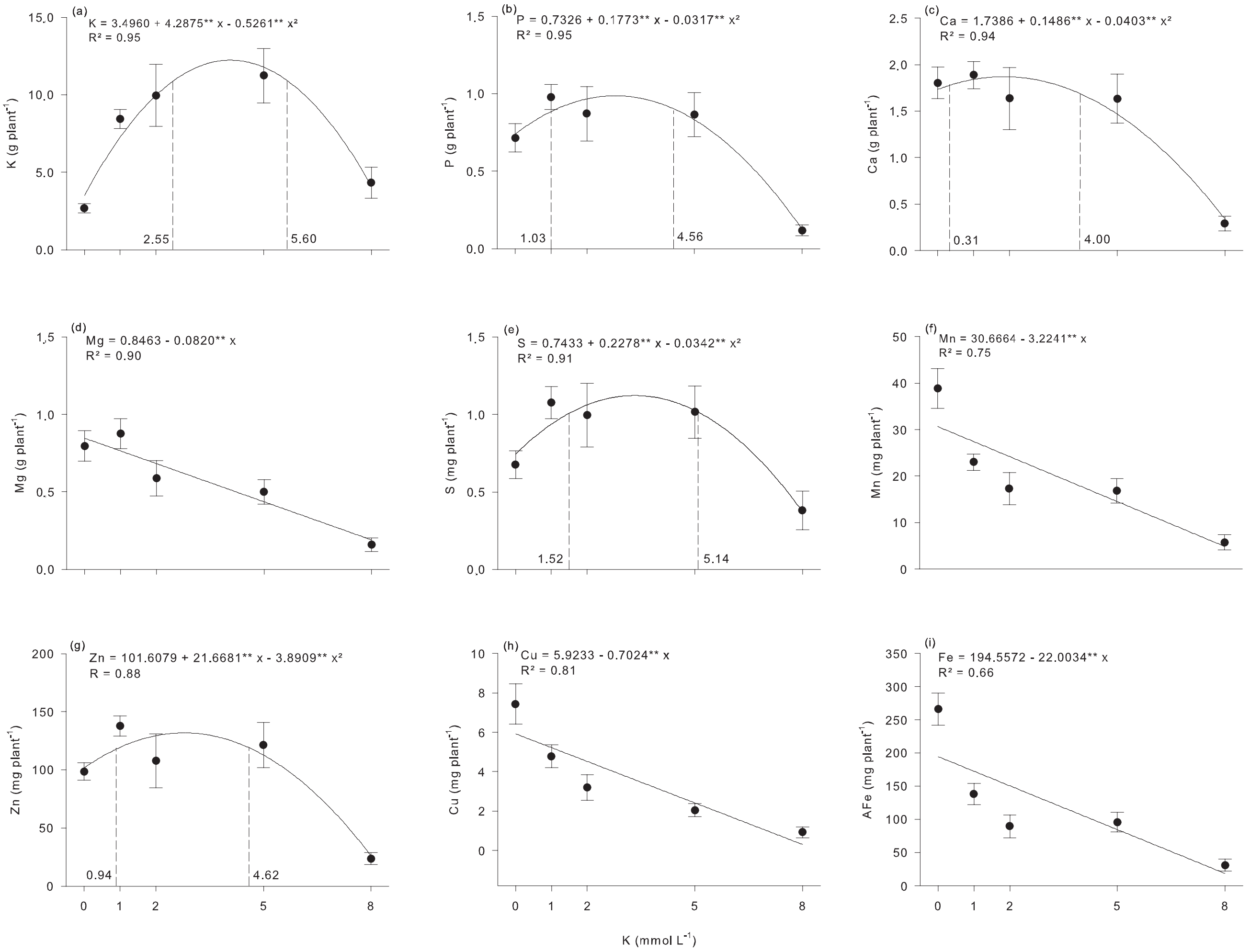

Figure 1. Accumulation of potassium (K) (a), phosphorus (P) (b), calcium (Ca) (c), magnesium (Mg) (d), sulfur (S) (e), manganese (Mn) (f), zinc (Zn) (g), copper (Cu) (h), and iron (Fe) (i) in the shoot of *Cedrela fissilis* plant (n = 5), fertilized with varying rates of K, for 30 days. ** Indicate significant difference at $p<0.01$ (Regression test).

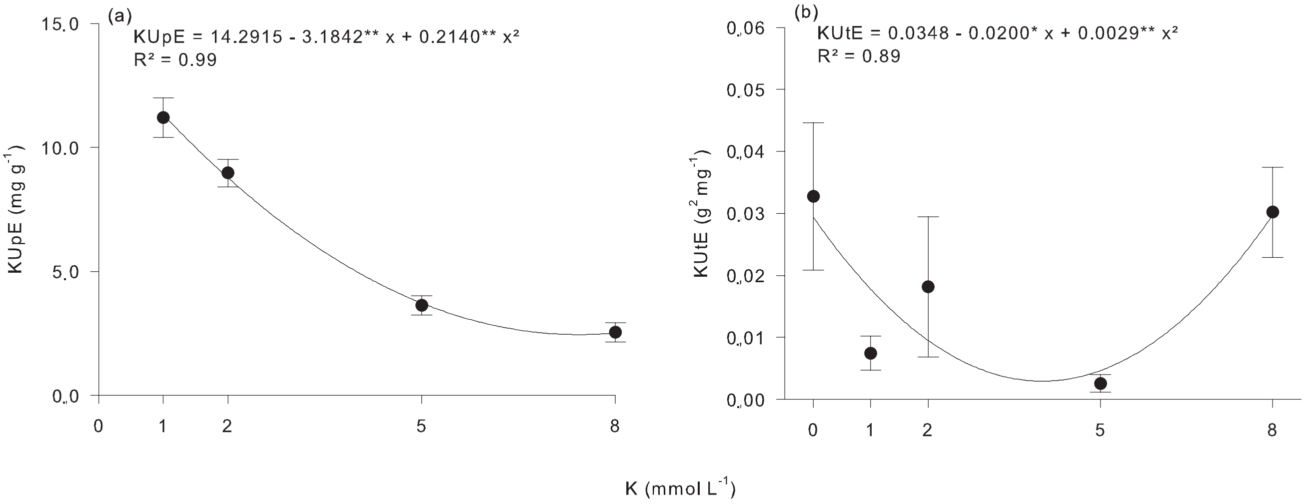

Figure 2. Potassium absorption efficiency (KUpE) (a) and potassium use efficiency (KUtE) (b) in *Cedrela fissilis* plant (n = 5) fertilized with varying rates of K, for 30 days. ** Indicate significant difference at p<0.01 (Regression test).

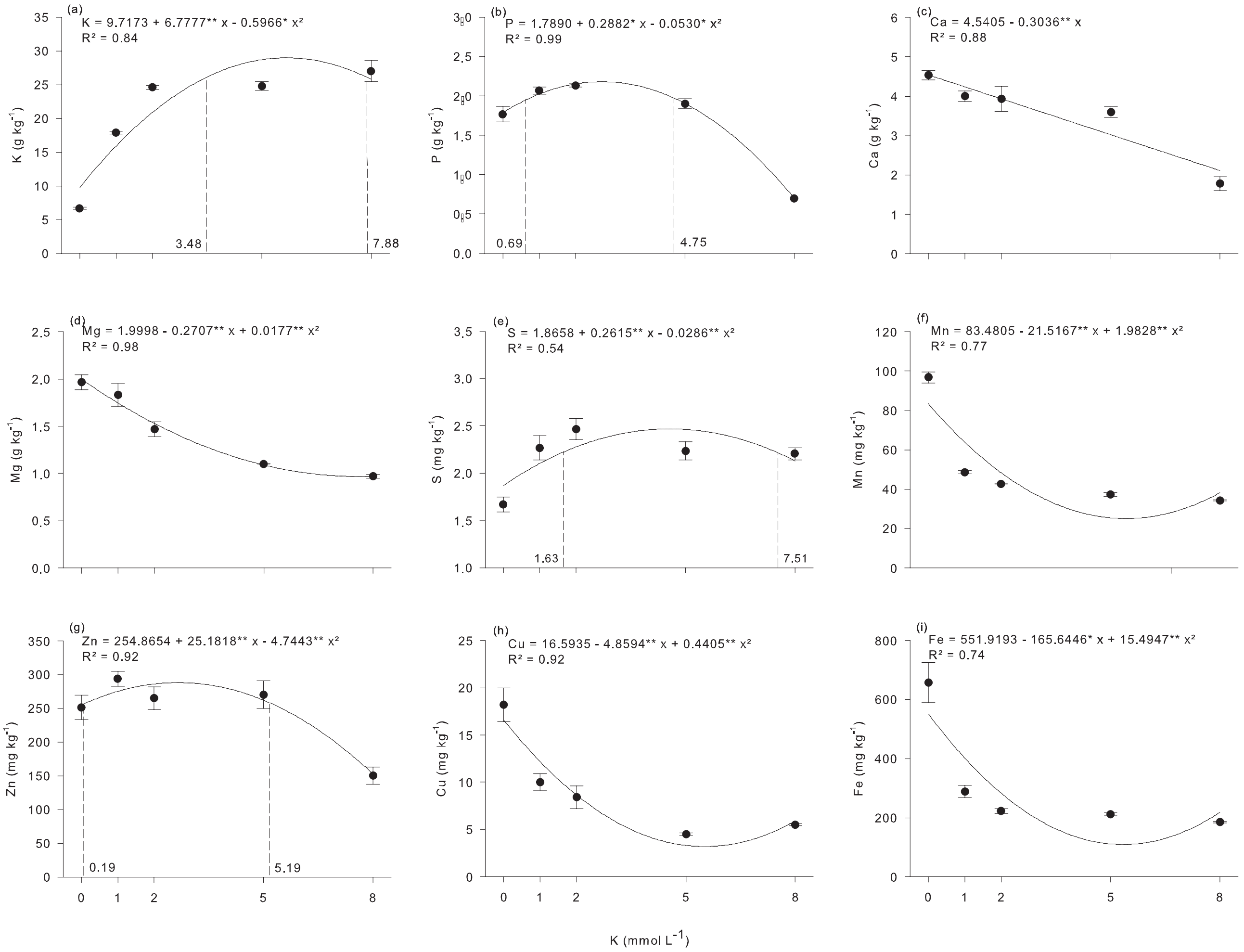

Figure 3. Concentration of potassium (K) (a), phosphorus (P) (b), calcium (Ca) (c), magnesium (Mg) (d), sulfur (S) (e), manganese (Mn) (f), zinc (Zn) (g), copper (Cu) (h) and iron (Fe) (i) in shoot of *Cedrela fissilis* plant (n = 5), fertilized with varying rates of K, for 30 days. ** Indicate significant difference at p<0.01 (Regression test).

The K, P, S, and Zn contents in the shoot of the plants fitted a positive quadratic regression model (Figures 3a, 3b, 3e, and 3g) as a function of the levels of K available in the growing substrate. The maximum content values (K = 28.97 g kg^{-1}, P = 2.18 g kg^{-1}, S = 2.47 mg kg^{-1}, and Zn = 288.28 mg kg^{-1}) were reached at levels of 5.58, 2.72, 4.47 and 2.65 mmol L^{-1} of K, respectively. We estimated the doses of K corresponding to the CDL and CTL in the growing substrate; these situated in a range between 3.48 - 7.88, 0.69 - 4.75, 1.63 - 7.51, and 0.19 - 5.19 mmol L^{-1} of K, corresponding to the contents of the elements of 3.49 - 7.88 g kg^{-1}, 0.69 - 4.75 g kg^{-1}, 1.63 - 7.51 g kg^{-1} and 0.19 - 5.19 mg kg^{-1} of K, P, S, and Zn, respectively (Figures 3a, 3b, 3e, and 3g).

On the other hand, there was a reduction in the levels of cationic elements (Ca, Mg, Mn, Cu, and Fe) in the plant aerial part as the K levels in the growing substrate increased (Figures 3c, ed, 3f, 3h, and 3i). Except for Ca, which fitted a linear regression model (R^2 = 0.88) (Figure 3c), the others held a quadratic mathematical model with, in general, a reduction up to the level of 5 mmol L^{-1} of K and a slight increase at the highest dose (Figures 3d, 3f, 3h, and 3i).

Without K in the growing substrate, the highest Mg, Mn, Cu, and Fe contents were around 1.96, 96.76, 10.03, and 657.66 mg kg^{-1}, respectively (Figures 3d, ef, 3h, and 3i). Concerning the Ca content in the aerial part of the plants, the highest value (4.43 g kg^{-1}) was observed in the treatment without the supply (0 mmol L^{-1}) of K, with a reduction of 0.3036 g kg^{-1} for each increase of one mmol of K in the growing substrate (Figure 3c).

Proline content

The levels of K in the growing substrate significantly influenced ($p<0.05$) the proline content in young *Cedrela fissilis* plants. Increasing the doses of K led to a linear reduction in the proline content in the root of the plants (Figure 4). We observed the highest (17.05) and lowest (8.95 mg RDM^{-1}) values of proline concentration in the leaves of *Cedrela fissilis* seedlings with 0 and 8 mmol L^{-1} of K, respectively. In general, for each increase of 1 mmol L^{-1} of K in the nutrient solution, there was a decrease of 0.1022 mg g^{-1} in the proline concentration in the dry matter of the leaves of *Cedrela fissilis* plants.

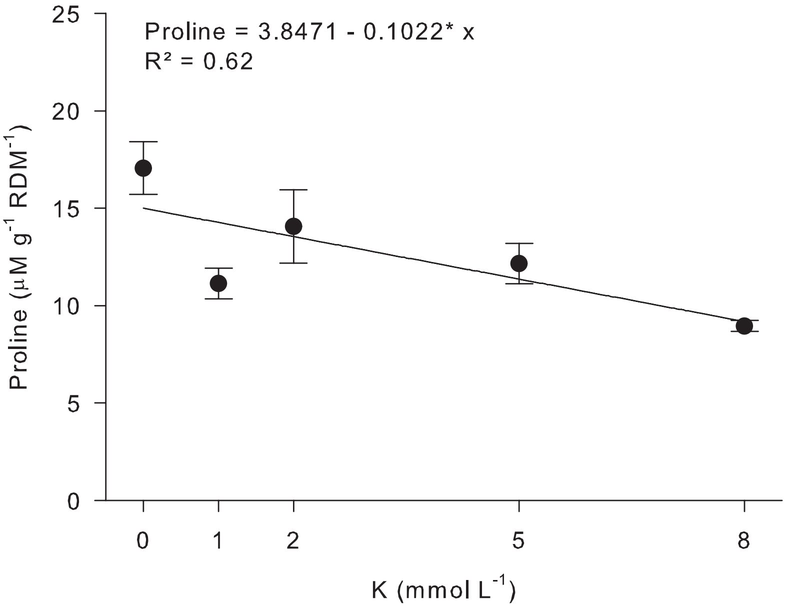

Figure 4. Proline concentration in the root of *Cedrela fissilis* plants (n = 5), fertilized with varying rates of K, for 30 days. * Indicate significant difference at $p<0.05$ (Regression test).

Visual symptoms of potassium deficiency and excess in plants

We observed a reduction in the growth of the aerial part, roots, and new leaves (Figure 5) in *Cedrela fissilis* plants supplied with 8.0 mmol L^{-1} of K. These symptoms are like those reported for K toxicity and appeared after 20 days of contact between the plants and this treatment. However, no characteristic K deficiency symptoms were observed in plants grown without this nutrient (0 mmol L^{-1} of K) during the 30 days. These symptoms would appear as chlorosis, browning, and necrosis from the leaf apex towards the edges in older leaves.

Plant growth and development

Potassium levels in the growing solution had a significant influence ($p<0.05$) on RGR_H, RGR_D, SDM, and RDM but did not significantly affect RG_R and total dry matter (TDM) (data not shown). The RGR_H and SDM data fitted a positive quadratic model with the increasing levels of K in the growing solution (Figures 6a and 6c). The RGR_H and SDM increased almost linearly when the K concentration in the growing solution varied from 0.0 to ≈ 2.5 mmol L^{-1}. Between the concentration of 2.5 and 5.0 mmol L^{-1} of K, there was a stabilization in the gains of these two variables. Finally, between ≈ 5.0 mmol L^{-1} and the highest dose of K (8.0 mmol L^{-1}), there was an almost linear reduction in RGR_H and SDM values.

We found the maximum values for RGR_H (0.13 cm^{-1} cm^{-1} $month^{-1}$) and SDM (0.48 g) at doses of 3.67 and 2.72 mmol L^{-1} of K, respectively, and from this point onwards, for each increase of one unit of K in the nutrient solution, there was a decrease of 0.0035 cm^{-1} cm^{-1} $month^{-1}$ for RGR_H and 0.0114 g for SDM (Figures 6a and 6c). On the other hand, the RGR_H and SDM values for 90 % of maximum production are 0.11 cm^{-1} cm^{-1} $month^{-1}$ for RGR_H and 0.48 g for SDM, corresponding to maximum economic efficiency doses of 1.77 and 0.68 mmol L^{-1} of K, respectively. Meanwhile, the CTL values for K in the growing solution were 5.77 and 4.77 mmol L^{-1} for RGR_H and SDM, respectively (Figures 6a and 6c), indicating that a K concentration above 4.77 mmol L^{-1} causes a reduction in the dry matter production of the plant aerial part. The results suggest that the CDL and CTL values change according to the variable studied, meaning there is no single value but a critical range for both K deficiency and toxicity in plants.

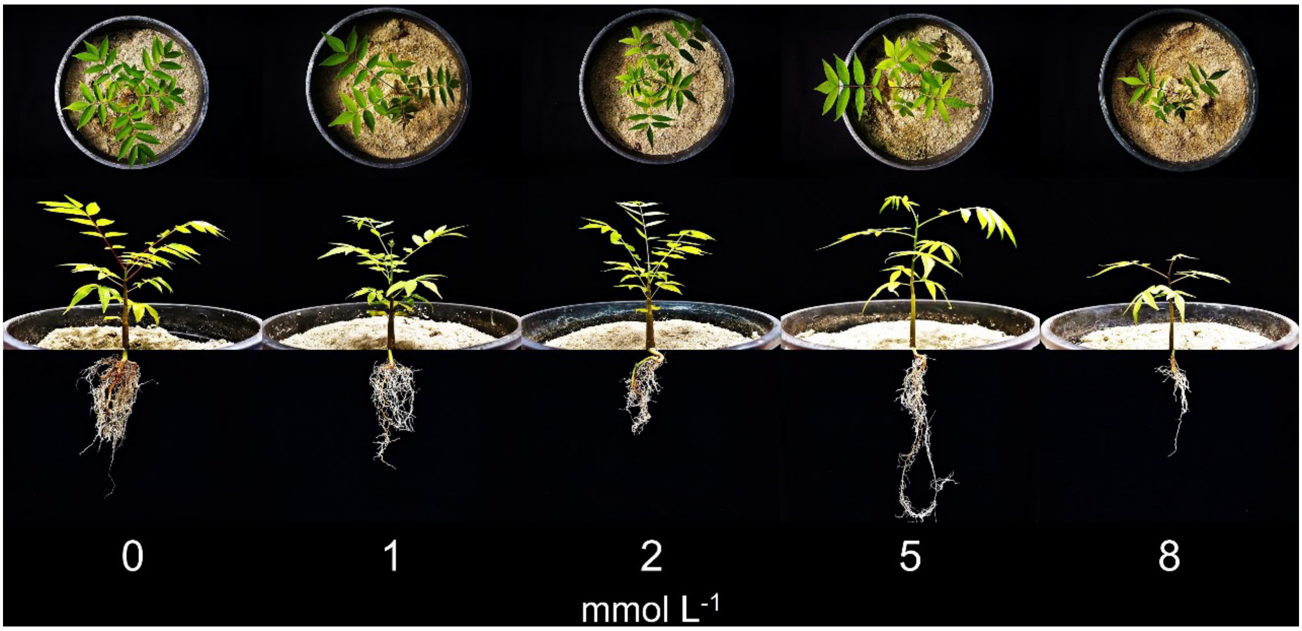

Figure 5. Digital image showing the effect of different doses of K on *Cedrela fissilis* seedlings during 30 days of cultivation.

The increase in K levels in the growing solution reduced RGR_D and RDM values. Concerning the RGR_D variable, the data fitted a quadratic mathematical model ($R^2 = 0.84$) (Figure 6b), with the highest growth rate (0.13 mm mm^{-1} $month^{-1}$) observed without the supply of K, and the values decreased linearly until the presence of 5.48 mmol L^{-1} of K, where they stabilized at ≈ 5.0 mmol L^{-1} of K in the nutrient solution and showed a slight increase until the highest dose of K. Similarly, the RDM results fitted a linear mathematical model ($R^2 = 0.90$) (Figure 6d). For each increase of one mmol of K in the growing solution, there was a decrease of 0.0419 g of RDM in young *Cedrela fissilis* plants.

DISCUSSION

Several studies have shown the positive effects of K on the growth, development, and production of agronomic species. Still, there needs to be more knowledge about the impact of K on forest species, especially for species from the Amazon biome with great timber potential and in the early stages of growth. We tried to understand the effect of potassium doses on the initial development of *Cedrela fissilis*, and we observed that the increasing levels of K in growing substrate positively influence the growth of young *Cedrela fissilis* plants, and there is an adequate range of potassium in the substrate that promotes better plant development.

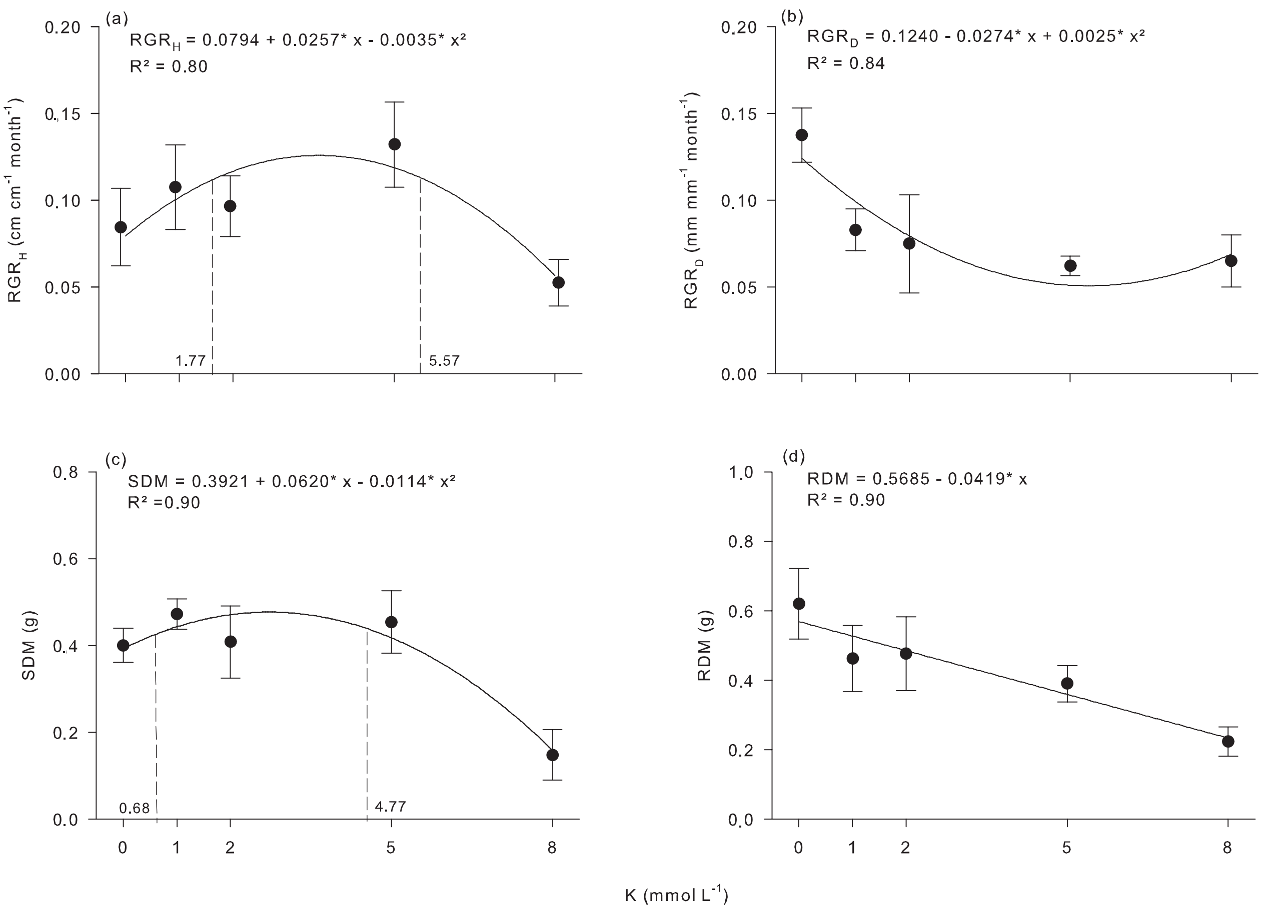

Figure 6. Height relative growth rate (RGR_H) (a), diameter relative growth rate (RGR_D) (b), shoot dry mass (SDM) (c), and root dry mass (RDM) (d) of *Cedrela fissilis* plants (n = 5), fertilized with varying rates of K for 30 days. * Indicate significant difference at $p<0.05$ (Regression test).

These results show *Cedrela fissilis* is responsive to the supply of K when found in low or medium quantities in the growing substrate and corroborate the results found by Silva et al. (1997) and Souza et al. (2009), who observed a positive effect of potassium supply on the growth of *Cedrela fissilis* seedlings.

Potassium deficiency mainly affects the physical processes of cell elongation in plants, mainly through a reduction in turgor (Leigh and Jones, 1984). When we expose the plants to these conditions for long periods, there will be a reduction in growth and the appearance of chlorosis in the older leaves (Malavolta et al., 1997). This response is because K ion performs specific plant functions, such as regulating water use, transpiration, stomatal movement, membrane permeability, cell osmoregulation, cell expansion, and enzyme activity (Kusaka et al., 2021). In addition, a reduction in K availability hurts the absorption and assimilation of other essential elements in plants (Réthoré et al., 2021). Low K availability causes severe morphological, physiological, biochemical, and molecular changes, culminating in a reduction in plant development and yield.

Accumulation values of K, P, Ca, S, and Zn stabilized in the ranges of 2.55 and 5.60 g kg^{-1}, 1.03 and 4.56 g kg^{-1}, 0.21 and 4.00 g kg^{-1}, 1.52 and 5.14 mg kg^{-1}, and 0.94 and 4.62 mg kg^{-1} for K, P, Ca, S, and Zn, respectively. These nutrient accumulation values in these ranges signify luxury consumption, which corresponds to the absorption of nutrients in quantities more significant than that required for maximum plant growth (Hommels et al., 1989) and is a characteristic more associated with slower-growing species (Chapin, 1980). Then, there was a reduction in the absorption of these nutrients due to increasing doses of K in the substrate. Potassium doses in the nutrient solution referring to CDL and CTL are in a range of 2.55 and 5.60, 1.03 and 4.56, 0.21 and 4.00, 1.52 and 5.14 and 0.94 and 4.62 mmol L^{-1} for K, P, Ca, S, and Zn, respectively.

This negative effect of K on the absorption of these cationic elements is possibly related to antagonism (Walker and Peck, 1975; Jakobsen, 1993), especially in the case of Mg and Ca. However, this effect was less pronounced in the present study for Ca. Several studies (Fageria, 2001) have shown an inhibitory effect of K on Ca absorption. However, the result seems specific to the plant species (Robson and Pitman, 1983). The antagonistic interaction between K and Mg is commonly found in crops and constitutes one of the leading causes of Mg deficiency in cultivated plants (Xie et al., 2021). Experimental results such as those of Seggewiss and Jungk (2010) have shown the antagonistic effect occurs from 20 µmol L^{-1} of K, and the negative impact can occur during root absorption, translocation, and redistribution in the plant aerial part (Xie et al., 2021).

Concerning micronutrients, these interactions are primarily physiological and occur during the process of absorption by the roots and in translocation processes (Fan et al., 2021). Alam et al. (2005), evaluating the role of K rates in alleviating Mn toxicity in rice and barley, observed that high doses of K reduced Mn absorption by plants. Similarly, Rietra et al. (2017), reviewing different scientific articles, noted that in several studies, there was an antagonistic effect between the cations K, Cu, Fe, Mn, and Zn. According to Dibb and Thompson (1985), several non-ionic factors also influence the interaction of K with other ions, such as exposure time, sampling time, environmental conditions, cultivated species, and cultivars. In the case of Fe, Panda et al. (2012) observed that higher K doses increase rice root oxidizing power, resulting in the oxidation of Fe^{2+} to Fe^{3+} and a consequent decrease in the absorption of this ion.

The positive effect of concentration and accumulation of nutrients in the growth and development of the aerial part of the plants of *Cedrela fissilis* indicate that K levels are associated with the accumulation (Figure 1) and content of other nutrients in the plant (Figure 3), as observed by Oosterhuis et al. (2013). These results show the positive effect of K on the absorption of P, S, and Zn and the negative impact of K supply on the absorption of Ca, Mg, Mn, Cu, and Fe. Thus, even though *Cedrela fissilis* plants grown in the absence of K showed levels below those considered ideal for the species (Souza et al., 2009; Freiberger et al., 2013), the lack of characteristic symptoms of K deficiency in the plants may be related to the species adaptability to soils with low availability of this nutrient or hidden hunger. Similarly, we did not observe any visual symptoms of K toxicity in the plants grown at the highest levels of K in the substrate. However, the adverse effects on plant development were likely due to nutritional imbalance, such as reduced absorption of other essential elements, mainly P, Ca, and Mg (Fageria, 2001).

The decrease in KUpE was approximately 3.184 mg g^{-1} for each rise of one mmol L^{-1} of K in the nutritive solution up to a dose of ≈ 5 mmol L^{-1} of K in the solution, with a slight stabilization in the reduction from this dose onwards. This response pattern is possibly associated with the principle of the law of decreasing increments (Ferreira et al., 2017) and the plant metabolic demand (Amtmann and Armengaud, 2009), which leads to a reduction in KUpE as the availability of K in the growing substrate increases. According to Chapin (1980), slow-growing species adapted to infertile soils, characteristics that may apply at least in part to the species studied, generally have a low rate of nutrient absorption per plant and a slight increase in the absorption rate due to the rise in external concentration.

The results indicate that the plant KUtE response pattern is dependent on the availability of K in the growing substrate. As the K in the growing medium increases, there is a more outstanding production of dry matter and accumulation of K. However, this increase is non-linear, especially at the higher doses. Consequently, K utilization efficiency tends to decrease at K doses above maximum economic efficiency (Benincasa et al., 2011), which in this study corresponds to amounts above the CDL of K in the growing medium.

Despite this response pattern, plants generally are more efficient at using nutrients when their availability is low (Mi et al., 2007), a fact that must be associated with the dilution and saturation of the plant metabolic demand. Oliveira et al. (2022), evaluating the effect of different P levels on different sunflower cultivars, observed that the lowest dose promoted the best efficiency indices in the other cultivars, indicating that this response pattern is independent of the element tested. However, in certain situations, factors such as the species, cultivar, and the methodology used to obtain these indices influence the response pattern (White et al., 2021).

In general, despite the higher KUpE and KUtE in *Cedrela fissilis* plants grown without the supply of this nutrient (Figure 2), the plants are in a situation of mineral stress due to the low concentration of K absorbed (Figure 1a). These results suggest that these efficiency indices must be associated with an adequate concentration of K that does not limit plant yields.

In addition, the data indicates that both K deficiency and excess inhibit *Cedrela fissilis* plant height development and SDM production (Figure 6c). Between the concentration of 2.5 and 5.0 mmol L^{-1} of K, there was a stabilization in the gains of these two variables, which is associated with luxury consumption. Finally, between ≈ 5.0 and the highest dose of K (8.0 mmol L^{-1} of K), there was an almost linear reduction in TCR_H and SDM values, which is associated with a toxic effect of K on the plants. Luxury consumption of nutrients occurs when plant growth or yield does not increase in proportion to nutrient absorption (Oyarzabal and Oesterheld, 2009), and, in this study, luxury consumption was higher for the RGR_H variable than the SDM variable.

Regarding the toxic effect of K at the highest doses, 5.57 (RGR_H) and 4.77 (SDM), this possibly is associated with the impact of direct toxicity, where excess K causes osmotic stress in the plant cell (Zhao et al., 2020) and, in addition, there is also the effect of indirect toxicity of excess K causing lower absorption of essential elements as observed for the details Ca, Mg, Mn, Cu and Fe in this study. Meanwhile, the CTL values for K in the growing solution were 5.77 and 4.77 mmol L^{-1} for RGR_H (Figure 6a) and SDM (Figure 6c), respectively, indicating that a K concentration above 4.77 mmol L^{-1} causes plant toxicity and consequently a reduction in the dry matter production of the aerial part. According to Ragel et al. (2019), there is a sharp curvilinear response pattern between K content in plant tissue and plant growth, and a critical concentration supports 90 % of maximum plant growth. On the other hand, plant growth does not correlate with the K content in the plant tissue above this concentration. The results indicate that the CDL and CTL values change according to the variable studied, meaning there is no single value but a critical range for both K deficiency and toxicity in plants.

Considering that the production of the amino acid proline acts as one of the plant response mechanisms to stress (Shuyskaya et al., 2020), these results indicate that K deficiency acts with greater magnitude as a source of abiotic stress for plants compared to K excess. In general, an increase in the proline content in plant leaves was expected as a function of the rise in K concentration in the growing substrate, especially at higher doses, as observed by Weimberg et al. (1982) in Sorghum bicolor leaves. Our results show that this response pattern must be associated with K role in proline biosynthesis, which depends on the interaction between K and the amino acid arginine. This interaction may depend on the plant species (Rao et al., 1981). According to Mansour and Ali (2017), proline accumulation is specific to each species and depends on the strength and time of exposure to salt stress. Thus, a correlation between proline accumulation and the species sensitivity to salt stress is not a rule.

Because of this, the research results do not yet support the hypothesis that proline biosynthesis is closely associated with salt adaptation. Concentration of K above 5 mmol L^{-1} (a concentration considered medium to high for the cultivation of most species) led to a reduction in the growth variables RGR_H and SDM; P, S, and Zn content (Figures 3b, 3e, and 3g) and the accumulation of K, P, Ca, S, and Zn (Figures 1a, 1b, 1c, 1e, and 1g), suggesting that the plants were under stress. In this case, there should be an increase in the concentration of this amino acid, a response pattern that was not confirmed in this study (Figure 4).

Given the role of K in the osmotic adjustment process of plants (Wang et al., 2015), plants with the highest K supply showed lower proline production when compared to plants with no K supply. These results corroborate the premise of Rao et al. (1981), who stated that high proline production helps the osmoregulation process by restricting water loss to the atmosphere and preventing further dehydration of leaf tissues. Proline accumulates in a wide variety of plant species in response to stress caused by K deficiency, acting as a protective mechanism activated in response to adverse conditions related to the irregular functioning of stomata (Mansour and Ali, 2017).

About the nutritional status of the plants, as there is no reference for the nutrient concentrations in the dry mass of the aerial part of *Cedrela fissilis* plants as a function of the variation in K levels, the nutrient content in this species obtained in the SDM at 110 days (Souza et al., 2009) and the leaf tissue at 120 days (Freiberger et al., 2013) after germination, both grown in a medium texture dystrophic *Latossolo Vermelho - Amarelo* (Yellow-Red Hapludox) and in a greenhouse, were used for comparison.

In this study, the maximum values for the K, P, and S contents in the SDM were above (Souza et al., 2009; Freiberger et al., 2013), while the Zn content was below (Freiberger et al., 2013) and above (Souza et al., 2009) of the value considered ideal for the development of the species. We estimated the doses of K corresponding to the CDL and CTL in the growing substrate; these situated in a range between 3.48 - 7.88, 0.69 - 4.75, 1.63 - 7.51, and 0.19 - 5.19 mmol L^{-1} of K, corresponding to the contents of the elements of 3.49 - 7.88 g kg^{-1}, 0.69 - 4.75 g kg^{-1}, 1.63 - 7.51 g kg^{-1}, and 0.19 - 5.19 mg kg^{-1} of K, P, S and Zn, respectively.

Without K, the highest Mg, Mn, Cu, and Fe content values were around 1.96, 96.76, 10.03, and 657.66 mg kg^{-1}, respectively, and these values were above the concentration considered ideal for Mn and Cu (Souza et al., 2009; Freiberger et al., 2013) and Fe (Freiberger et al., 2013), while Mg was below (Souza et al., 2009; Freiberger et al., 2013). This response pattern is likely associated with the fact that this study assessed the plants at a younger age (90 days) while the others were 110 (Souza et al., 2009) and 210 (Freiberger et al., 2013) days old. This hypothesis corroborates the results found by Rehmus et al. (2015) for the elements Cu and Fe in the control treatment (optimum growth condition); however, these authors worked with the *Cedrela odorata* species. Concerning the Ca content in the aerial part of the plants, the highest value (4.43 g kg^{-1}) was observed in the treatment without the supply (0 mmol L^{-1}) of K, with a reduction of 0.3036 g kg^{-1} for each increase of 1 mmol of K in the growing substrate (Figure 3c). Calcium content remained below the species requirement for good growth (Souza et al., 2009; Freiberger et al., 2013), regardless of the level of K in the growing substrate. Reducing the content of cationic elements may be associated with the dilution effect. Considering that the elemental composition of a plant, at a given time, is a result of the interaction between the nutrient supply and the plant growth (Jarrell and Beverly, 1981), with the supply of K, there is a more excellent production of plant biomass, contributing to the dilution of the concentration of these elements. These results indicate the need to establish these reference levels for different stages of development for these forest tree species with timber potential.

We observed that the K content (6.66 g kg^{-1}) in the SDM of *Cedrela fissilis* plants grown without K supply and the Ca (1.78 - 4.53 g kg^{-1}), Mg (0.97 - 1.96 g kg^{-1}) and S (1.66 - 2.46 mg kg^{-1}) content in *Cedrela fissilis* plants grown with K supply were below the range considered adequate for the best growth of the species (Souza et al., 2009; Freiberger et al., 2013). With the supply of 1, 2, 5, and 8 mmol L^{-1} of K in the substrate, the K concentrations in the aerial part of the plants were around 17.86, 24.60, 24.80, and 27.01 g kg^{-1}, respectively. Considering the range of values of the contents found between the CDL and CTL for P (0.70 - 2.13 g kg^{-1}), Mn (34.25 - 96.76 mg kg^{-1}), Zn (150.46 - 293.7 mg kg^{-1}), Cu (4.50 - 10.03 mg kg^{-1}) and Fe (184.68 - 657.66 mg kg^{-1}), we note that the values corresponding to the CTL remained above the range considered ideal for the excellent growth of the species (Souza et al., 2009; Freiberger et al., 2013), except for Fe in the study by Souza et al. (2009), which was higher than the value found in this study.

The decrease in the levels of Ca and Mg in the aerial part of the plants as the levels of K in the growing substrate increased is possibly related to the similarity of the chemical properties of K and these elements, the high mobility of K to cross the plasma membrane, reducing the absorption of slower cations and the competition for the place of adsorption, absorption, transport and function with K (Wang et al., 2013). Although the concentrations of Ca, Mg, and S were below (Freiberger et al., 2013) and adequate for Mg and S (Souza et al., 2009), while Ca was below (Souza et al., 2009) the ideal for the growth of seedlings of this forest species, we did not observe symptoms of deficiency of these elements in the plants (Figure 5). According to Dwivedi and Randhawa (1974), plant mineral deficiency in the initial phase may not show any visual symptoms (hidden hunger) but is limiting plant growth and development. In this study, the absence of deficiency symptoms of Ca, Mg, and S indicates that only low concentrations of these nutrients meet the metabolic demands of the plants.

Regarding micronutrients, there are records of a competitive interaction (cation-cation) between K and Mn (Alam et al., 2005). In the present study, we observed an antagonistic response regarding the levels of these nutrients due to the increase in K levels (Figure 2). However, at all the K levels tested, the concentration of Mn (mg kg^{-1}) in the aerial part of the *Cedrela fissilis* plants was above the range considered optimal for the growth of forest essences at seven months of cultivation (Freiberger et al., 2013), regarding the reduction in Cu and Fe levels in the aerial part of the plants due to the increase in K doses in the substrate. There are few reports on the interaction between these two elements and K, and the results are contradictory (Van Brunt and Sultenfuss, 1998). Smith (1975), evaluating the effect of potassium top dressing, observed a reduction in Cu levels in alfalfa plants, possibly due to the dilution effect. Juang et al. (2021) noted that K had little impact on alleviating Cu-induced oxidative toxicity in grapevine roots, except at the highest dose of K. While lower amounts of K contributed to increasing root Cu content. Despite reports of Fe interaction (Van Brunt and Sultenfuss, 1998), it is uncertain whether K availability increases or decreases Fe levels in the plant.

Potassium positive effect on growth and biomass production in the aerial part of *Cedrela fissilis* was between 0.0 and 5.57 and 0.0 and 0.68 mmol L^{-1} of K for height and SDM, respectively, with growth values stabilizing and then decreasing. These results corroborate those observed by Silva et al. (1997) in a study of *Cedreila fissilis* Vell. and 13 other forest species with timber potential. However, although *Cedrela fissilis* shows efficient absorption and utilization under conditions of low K supply, the highest concentrations tested increased the plant stress level in the present study. This observation indicates that an excess supply of K to the species harms its plant nutritional status (Figures 1 and 3) and growth (Figure 6).

Cedrela fissilis plants cultivated with levels of 1, 2, 5, and 8 mmol L^{-1} of K at the end of the experimental period showed K contents in the SDM above those considered ideal by Souza et al. (2009) Freiberger et al. (2013) but only in plants supplied with 8.0 mmol L^{-1} of K did we observe symptoms, which are similar to those reported for K toxicity and these appeared after 20 days of contact between the plants and this treatment. These symptoms manifested as a reduction in the growth of the aerial part, roots, and new leaves. However, no characteristic K deficiency symptoms were observed in plants grown without this nutrient (0 mmol L^{-1} of K) (Figure 5) during the 30 days. These symptoms would appear as chlorosis, browning, and necrosis from the leaf apex towards the edges in older leaves.

Thus, by relating the K levels in the growing substrate for the lowest (CDL) and highest (CTL) values with the K content in the SDM, we can see that the optimum K concentration in the SDM for 90 % of the maximum production is 26.08 g kg^{-1} in the SDM and the K content in *Cedrela fissilis* plants corresponding to the dose above the maximum production sufficient to promote a 10 % reduction in production is 27.28 g kg^{-1} in the SDM, both values being above the range considered ideal for good growth and development of the species (Souza et al., 2009; Freiberger et al., 2013). The concentrations of the variables tested between the CDL and CTL were considered luxury consumption and, on the other hand, concentrations of K in the cultivation solution above the CTL that caused a reduction in the variables evaluated were considered toxic concentrations, mainly due to the competition of K with other essential elements (Yeo, 2007). According to Berry and Wallace (1981), a chemical element becomes toxic when an increase in its dose causes a reduction in plant growth/yield without the imbalance of any other essential element being the cause.

Despite the adaptation of *Cedrela fissilis* to the natural conditions of nutritional deficit that prevail in most dryland soils in the Amazon, we observed that the availability of K affects the nutritional demand, biochemical parameters, and development of *Cedrela fissilis* plants. Plant species native to nutrient-poor habitats tend to have lower CDL inside the cells (~50 mmol) (Hommels et al., 1989) in the aerial part compared to species from nutrient-rich habitats (~100 mmol) (Römheld, 2012). In principle, this lower CDL would reflect greater nutrient use efficiency and is one of the mechanisms to separate more efficient genotypes from more efficient ones.

The results obtained at 120 after germination, in addition to establishing an optimum interval for the supply of K in the initial phase of *Cedrela fissilis* plants, have important implications for the proper management of potassium fertilization, the conscious use of fertilizers and increasing the productivity of forest species, especially in the seedling production phase.

CONCLUSIONS

This study focuses on the impact of potassium on the initial growth of *Cedrela fissilis plants*. It is the first attempt to identify the critical doses of potassium deficiency and toxicity in the growing substrate and the essential levels of potassium deficiency and toxicity in the aerial part of the plants. The study demonstrates that providing varying amounts of potassium significantly affects the nutritional and growth parameters of *Cedrela fissilis* seedlings. Providing 3.5 - 4.00 mmol L^{-1} of K in the growing substrate led to better nutritional status (26.08 - 27.28 g kg^{-1} of K) and plant growth.

However, it is essential to approach these findings with caution due to certain limitations of the study. Specifically, the short duration of the study (30 days) and the testing of only one potassium source, potassium sulfate, indicate the need for further research in this area.

DATA AVAILABILITY

All data was generated or analyzed in this study.

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