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Impact of potassium nutrition on vegetative growth, macronutrient content, and photosynthetic performance in seven cacao (*Theobroma cacao* L.) cultivars

Laura Michell Carmona-Rojas[1,2,3*], Valeria Sáenz-Gallego[1], Edwin Antonio Gutiérrez-Rodríguez[4], Ruby Alejandra Loaiza-Ruiz[5], Oscar de Jesús Córdoba-Gaona[5], Jean Rivoal[2] and Aura Inés Urrea-Trujillo[1*]

[1] *Grupo de Biotecnología, Facultad de Ciencias Exactas y Naturales, Universidad de Antioquia, Medellín 050010, Colombia*
[2] *Institut de Recherche en Biologie Végétale, Université de Montréal, 4101 Sherbrooke est, Montréal, Québec H1X 2B2, Canada*
[3] *Present address: Horticultural Sciences Department, University of Florida, Gainesville, FL 32611-0690, USA*
[4] *Tropical Research and Educational Center, University of Florida, Homestead, FL 33031-3314, USA*
[5] *Facultad de Ciencias Agrarias, Universidad Nacional de Colombia, Sede Medellín, Medellín 3840, Colombia*
* Corresponding authors, E-mail: laura.carmona@udea.edu.co; aura.urrea@udea.edu.co

Abstract

Limited progress has been made in developing potassium-efficient cultivars for agriculturally important crops due to a lack of knowledge about the biological mechanisms in tolerant cultivars. For *Theobroma cacao* L. (cacao) cultivars, the characterization of potassium use efficiency (KUE) has remained largely unexplored. This study aimed to characterize the effects of potassium (K) levels on cacao morphology, biomass production, macronutrient (K, N, Mg, and Ca) accumulation, and photosynthetic performance during the vegetative growth phase. Seven cacao cultivars (FEAR5, IMC67, CAU39, FSV85, FSV89, CCN51, and FSV4) were grown under different K regimes (0, 0.04, 0.4, and 4 mM). K deficiency (0 mM) significantly reduced leaf area and biomass production. Cultivar IMC67 exhibited lower leaf, stem, and root biomasses, while FEAR5 showed no significant differences, indicating a greater tolerance to K deficiency. In roots, the accumulation of K, N, and Mg did not change significantly across K treatments for most cultivars. However, in leaves, K deficiency significantly reduced K and N accumulation in IMC67 and FSV85, while no significant difference was observed in FEAR5. The daily integral of net photosynthesis was significantly affected by K deficiency in IMC67, FSV85, and FSV89, but not in FEAR5. Overall, our study indicates cultivar-specific responses in which FEAR5 exhibited resilience under low K conditions, while IMC67 and FSV85 were more sensitive. This study is the first to characterize K nutrition dynamics in these cacao cultivars, providing a foundation for future research to identify genes and pathways crucial for improving K nutrition in cacao and informing breeding programs.

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Introduction

In agriculture, the selection and the development of cultivars with high potassium (K) use efficiency (KUE) have received significant attention in recent years[1,2]. Cultivars with high KUE represent a climate-smart strategy to maximize the absorption and translocation efficiency of nutrients while minimizing production costs and environmental impacts from excess fertilizer application[2,3]. K is an essential macronutrient involved in numerous functions that influence plant metabolism, growth, and development[4,5]. It plays vital roles in protein synthesis, enzyme activities, anion-cation balance, and electrogenic transport, and it acts as a major osmolyte for turgor and cell expansion[4,5]. Additionally, K is crucial for physiological functions such as stomatal and mesophyll conductance, chloroplast ultrastructure, photoassimilate translocation, and internal water transport regulation[4−8]. Consequently, K deficiency can significantly reduce crop yields by affecting plants at cellular, biochemical, physiological, and morphological levels[7,9−11].

Beyond its fundamental role as a vital nutrient, K also influences the uptake and accumulation of other elements[12,13]. Plants adjust and regulate nutrient uptake based on external ion concentrations to maintain internal cation-anion balance[12]. For instance, K deficiency can reduce nitrogen transport from roots to shoots, as xylem nitrate (NO_3) transport relies on K as a counterion[11]. Similarly, disrupted K supply decreases K accumulation in plant tissues, potentially increasing calcium (Ca), magnesium (Mg), and sodium (Na) levels[13−15]. This shift helps maintain the osmotic potential for cell expansion[13−15]. Thus, K deficiency can alter the balance of various ions, affecting the uptake and accumulation of nutrients like nitrogen (N), Ca, and Mg in plant tissues.

Traditionally, agronomists address K deficiency by supplementing nutrient-poor soils with fertilizers. However, even with adequate soil nutrient levels, plants may exhibit inefficient K uptake, leading to excessive fertilizer application[3,16,17]. Conversely, many plant species have evolved adaptive mechanisms to tolerate low K concentrations, accumulating enough K to maintain vital functions and proper growth[1,17]. This variation highlights genetic differences between and within crop species[2]. Cultivars with greater K uptake efficiency (KUpE) may exhibit changes in root architecture, high root uptake capacity, and the ability to mobilize non-exchangeable K via root exudates[2]. Additionally, plants with high K utilization efficiency (KUtE) may maintain optimal K concentrations in metabolically active compartments, redistribute K from senescent to younger tissues, replace K in nonspecific roles, and maintain water relations and photosynthetic function[2]. These mechanisms depend on species nutrient requirements, K distribution, cultivar genetic background, and environmental conditions. For *Theobroma cacao* L.

(cacao) cultivars, the characterization and underlying mechanisms controlling K uptake and use remain largely unexplored[18].

Cacao is an economically important crop which has become a significant player in the agricultural sector of several tropical countries[19,20]. However, several technical and production challenges must be addressed to fully realize its potential in a sustainable system[21]. One challenge is improving crop nutritional status through sustainable systems, considering the exponential decrease in soil fertility[18,22]. For cacao trees, K is essential for various processes, such as physiological functions, growth, flowering, cherelle development, and pod formation[23,24]. Cacao pods require high amounts of K, exceeding other macronutrients such as N and phosphorus[25,26]. However, in many tropical countries, K is scarce in soils where cacao is cultivated, and soil K may be lost through leaching[27,28]. Additionally, the physical and chemical conditions of soils where cacao is grown may vary widely, presenting nutritional challenges[18,27]. Therefore, because of a high soil-to-plant K export rate, supplementary K fertilization is needed before harvest to sustain optimal growth and high yields[27]. Improving K nutrition in cacao through nutrient-efficient cultivar identification combined with rational soil fertilization programs may offer a promising nutrient management strategy for sustainable agriculture[18].

Most of the studies on K nutrition have primarily focused on major crops like maize, wheat, and rice[2], leaving a significant knowledge gap in other important crops such as cacao[18]. Despite the critical role of K in cacao plant health and fruit formation, our understanding of the mechanisms underlying K use efficiency is still scarce for this species. This study addresses this issue by exploring the morphophysiological responses of seven cacao cultivars to varying K levels, providing novel insights into potassium use efficiency (KUE). The specific objectives were to: (1) characterize the effect of K application on plant morphology and biomass production during vegetative growth in greenhouse conditions; (2) determine the effects of K application on nutrient accumulation (in leaves and roots) and interactions with N, Mg, and Ca; and (3) investigate the effects of K supply on various photosynthesis parameters. This study represents the first attempt to characterize parameters of K nutrition in these cultivars during the juvenile phase, focusing on evaluating this agronomic trait in rootstocks. Our findings set the stage for further investigations into the molecular and biochemical mechanisms underlying these responses, supporting breeding programs to develop new rootstocks with high KUE for cacao crops.

Materials and methods

Plant material and growth conditions

Seven cacao genotypes were selected: FEAR5, IMC67, CAU39, FSV85, FSV89, CCN51, and FSV41. Controlled self-pollinated seeds were obtained from The Nacional Federation of Cacao (Fedecacao) experimental farms (Villa Monica, San Vicente de Chucurí, Santander, Colombia). IMC67 and, less commonly, CAU39 are among the most widely used rootstocks for cacao crops despite limited evidence supporting their agronomic traits[29,30]. These two cultivars were selected as reference rootstocks due to their traditional use. Additionally, FEAR5, FSV41 (regional cultivars), and CCN51 (universal cultivar) were included in the study due to their widespread use in Colombia and Latin America. FEAR5 and FSV41 are particularly valued for their high yields, disease tolerance, and exceptional flavor and aroma profiles[31]. FSV89 and FSV85 are currently under consideration by Fedecacao for potential use as rootstocks based on preliminary studies[32].

Seeds were germinated in an inert substrate (60:20:20 % v/v of coco peat : peat : perlite). At day 9, seedlings with straight radicles (5–7 cm in length) were transferred to 5 L plastic bags (40 cm × 15 cm) containing washed sand as a substrate. The plants were irrigated daily with deionized water. Then, at 42 d the plants were fertilized four times a day with 40 mL of a nutrient solution providing essential nutrients and specific K levels (Supplementary Table S1). Four K concentrations were tested: sufficient (4 mM), intermediate (0.4 mM), low (0.04 mM), and deficient (0 mM), using KCl as the source. The sufficient K concentration and source were determined in a previous study[33]. Cotyledons were removed at day 55 to avoid uncontrolled additional nutrient transfer. The experiment was performed for a total of 130 d (Fig. 1). Phytosanitary control was performed using Lannate® (Methomyl) when needed. Greenhouse conditions were as follows: 12 h light/12 h dark cycle at 200–300 $m^{-2} \cdot s^{-1}$ PAR with 12 h daylight (6:00 am to 6:00 pm), a temperature of 28 ± 3 °C in the light and 21 ± 3 °C at night, and a relative humidity of 40%–60%.

Determination of photosynthetic and chlorophyll fluorescence parameters

During the last four days of the experiment, net photosynthesis (*A*), transpiration rate (*E*), and intracellular CO_2 concentration (*Ci*) were recorded using the second fully expanded leaf with a portable infrared gas analyzer (LCi Portable Photosynthesis System - ADC BioScientific Ltd., Herts, UK). The photosynthetic photon flux density (PPFD) inside the measurement chamber was set to 650 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with an ambient CO_2 concentration of approximately 500 ppm. Stomatal conductance (g_s) was calculated based on *A* and *E* parameters. Gas exchange parameters were recorded eight times per leaf at different times of the day: 8:00, 10:00, 12:00, 14:00, and 16:00 to estimate the daily integral for *A*, *E*, and g_s[34].

Additionally, water use efficiency (WUE) was calculated as the A/E ratio, intrinsic water use efficiency (WUE*i*) as the A/g_s ratio, and instantaneous carboxylation efficiency in leaves as the A/C_i ratio. Chlorophyll fluorescence was measured for the same leaf using two protocols. Initially, the maximum quantum yield of photosystem II (F_v/F_m) was determined with a Pocket PEA fluorometer (Hansatech Instruments Ltd., King's Lynn, UK). Subsequently, several quenching parameters (quantum photosynthetic yield of PSII (Y(II)), electron transport rate (ETR), photoprotective non-photochemical quenching Y(NPQ), non-photo-protective non-photochemical quenching Y(NO), and non-photochemical quenching (NPQ)) were obtained using a modulated chlorophyll fluorometer (OS1p, Opti-Sciences, Inc., Hudson, USA).

Plant growth parameters and mineral composition

The plants were harvested at day 130. Morphological parameters, including primary root length, plant height, number of leaves, and stem base diameter, were recorded. Leaf area was measured using a portable area meter (LI-COR 3000C, USA). For biomass, leaves, stems, and roots were dried in an oven for 72 h at 65 °C to obtain dry weight (DW) for each organ. K, Ca, and Mg were quantified from dried samples by atomic absorption spectroscopy, while the Kjeldahl method was used for total N determination. These analyses were performed at the Soil Laboratory of the Universidad Nacional (Medellin, Colombia). Nutrient efficiency parameters were determined using the following equations:

$$\mathrm{UA} = \mathrm{U}_{\mathrm{L\ or\ R}} \times \mathrm{DW}_{\mathrm{L\ or\ R}}$$

$$\mathrm{U\ transfer\ efficiency\ \%} = \frac{\mathrm{DW}_{\mathrm{L}} \times \mathrm{U}_{\mathrm{L}}}{\mathrm{UA}_{\mathrm{L}} + \mathrm{UA}_{\mathrm{R}}}$$

where, U: Content of any given element K, Mg, N or Ca ($mg \cdot g^{-1}$); UA: U accumulation; L: Leaves; R: Roots; DW: dry weight (g).

Statistical analysis

A completely randomized design was used. In the figures and tables representing morphological analyses, growth, and element content, data were analyzed using a one-way analysis of variance (ANOVA) for each cultivar, with analyses conducted separately for each tissue (roots and leaves). Measurements of leaf gas exchange and chlorophyll fluorescence parameters were performed on 28 plants daily for 4 d, totaling 112 plants. Data were analyzed with one-way ANOVA for each cultivar in a randomized complete block design, using the day of measurement as a block. When significance was detected, means were compared using Fisher's LSD post hoc test ($\alpha = 0.05$). All statistical evaluations were performed using the R programming language, version 4.4[35], with the Doebioresearch package (version 0.1.0).

Results

Effect of K concentration on plant growth and development

The morphology of the shoot and root architecture of the cacao cultivars is shown in Fig. 2 and Supplementary Fig. S1. A strong change in the phenotype of aerial parts was not observed across cultivars subjected to different K treatments. However, a visible reduction was observed in the root system under K deficiency, mainly for IMC67 and FSV85 (Fig. 2). Overall growth and morphology revealed that under sufficient K conditions, FEAR5, IMC67, and, to a lesser extent, FSV85 exhibited the highest values, while FSV41 and CCN51 yielded the lowest values (Fig. 3; Supplementary Table S2). For plants grown under K deficiency conditions, the leaf area was significantly reduced in three cultivars, IMC67, FSV85, and CAU39 (Fig. 3). For FSV41, leaf area was slightly higher under K deficiency (Fig. 3). However, this cultivar also had the lowest leaf number of all cultivars used in this experiment (Supplementary Table S2).

Biomass production in all organs (roots, stems, and leaf dry weight) was significantly reduced by K deficiency in some of the cultivars. For instance, IMC67 exhibited a reduction in leaf, stem, and root biomasses of 41%, 39% and 40%, respectively (Fig. 4; Supplementary Fig. S2). Similarly, FSV85 showed a reduction in leaf, stem, and root biomass of 36%, 47%, and 42%, respectively (Fig. 4; Supplementary Fig. S2). These trends were also reflected in the whole-plant dry weight, which showed a similar pattern of reduction (Supplementary Fig. S3).

Effect of K nutrition on K, N, Mg, and Ca accumulation in vegetative organs.

We next quantified the final accumulation of the macronutrients K, N, Mg, and Ca in both leaves and roots when the plants were grown under different K concentrations (Figs 5, 6; Supplementary Figs S4 & S5). Our findings reveal distinct responses to K deficiency across different cultivars. Additionally, similar patterns were observed for K and N accumulation in roots and leaves (Figs 5 & 6). For all cultivars, root K accumulation did not significantly change across K treatments (Fig. 5). It was also the case for root N accumulation for most cultivars (Fig. 6). Considering all cultivars under sufficiency conditions, K accumulation ranged from 11 to 30 mg·g^{-1} organ DW (Fig. 5). Meanwhile, N accumulation ranged from 18 to 39 mg·g^{-1} organ DW (Fig. 6). Under K deficiency, K root accumulation ranged from 10 to 20 mg·g^{-1} organ DW whereas N accumulation ranged from 17 to 29 mg·g^{-1} organ DW. Overall, these results show that K deficiency does not affect the accumulation of root K and N for *T. cacao* under the vegetative growth phase.

In contrast to root, K deficiency significantly affected leaf K and N accumulation in some cultivars. For instance, a significant reduction in K was found for IMC67 and FSV85 (Fig. 5). Similarly, there was a significant decrease in N accumulation for IMC67, FSV85, and CAU39 (Fig. 6). In contrast, K deficiency did not have a significant impact on FEAR5, for either K or N accumulation (Figs 5 & 6, respectively).

The accumulation of Mg was quantified in roots and leaves subjected to K deficiency (Supplementary Fig. S4). In both organs, we did not observe a strong trend in Mg accumulation in relation to K treatments, suggesting that there was no clear synergy between these two nutrients. Finally, for Ca accumulation, K deficiency had significant effects for FSV85 on both the roots and leaves, for roots in IMC67 and leaves for CAU39 (Supplementary Fig. S5). In these cases, Ca levels were negatively impacted by K nutrition, suggesting a disruption in the balance of this element in response to K deficiency. Overall, the nutrient accumulation data indicate that FEAR5 and IMC67 have a greater capacity to uptake available nutrients, resulting in increased dry matter accumulation. However, under K deficiency, FEAR5 was less affected than IMC67 and FSV85,

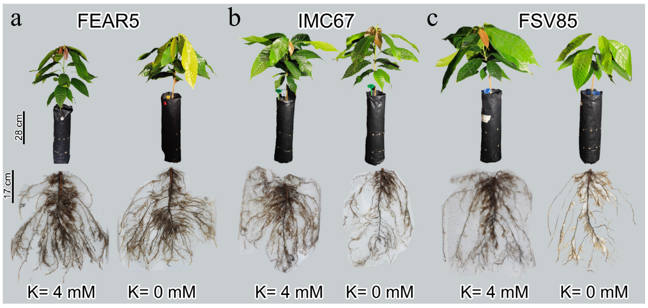

Fig. 2 Plant architecture of shoot and root system configurations for 130-day-old plants of three *T. cacao* cultivars. Plantlets of (a) FEAR5, (b) IMC67, and (c) FSV85 were grown under sufficient (4 mM) or deficient (0 mM) K conditions.

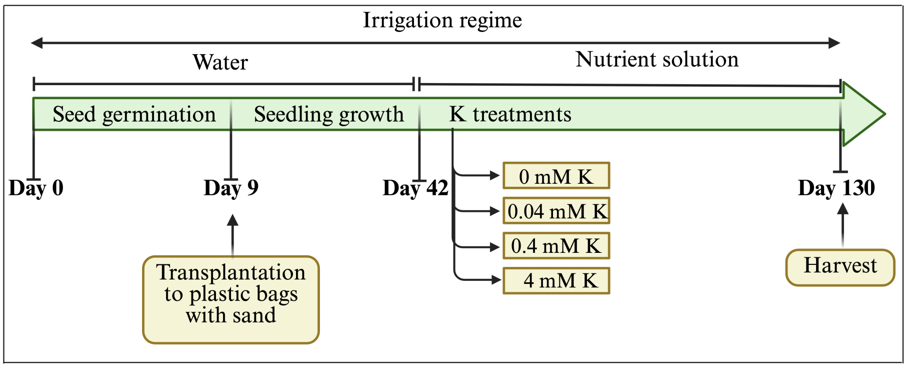

Fig. 1 Timeline of the experiment.

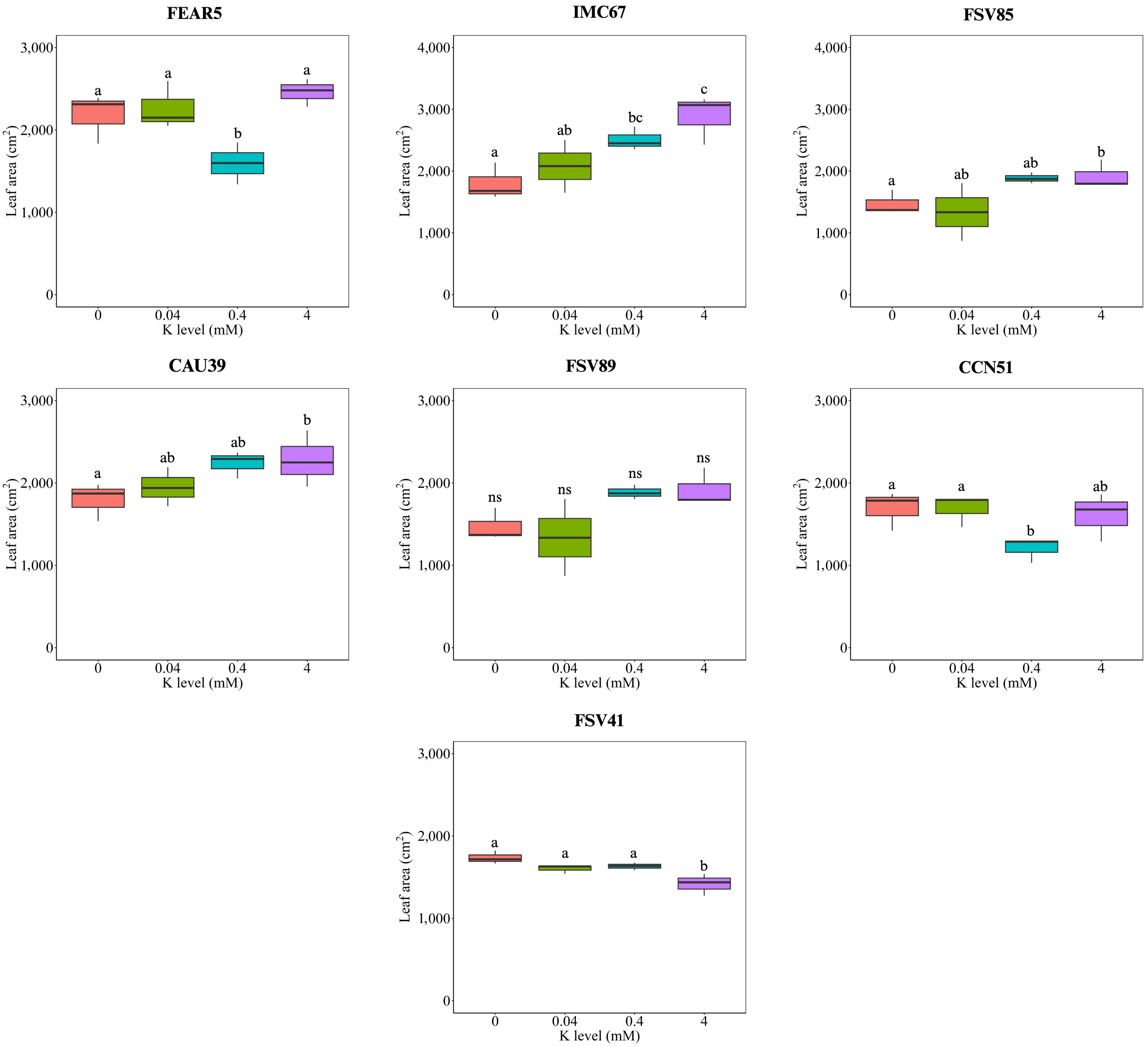

Fig. 3 Leaf area of seven *T. cacao* cultivars (FEAR5, IMC67, FSV85, CAU39, FSV89, CCN51, and FSV41) grown under different K levels (0, 0.04, 0.4, and 4 mM). Values represent means ± SD of three biological replicates. One-way ANOVA was performed separately for each cultivar. Different lowercase letters indicate significant differences among K treatments. 'ns' indicates non-significant differences, based on Fisher's LSD test at $p < 0.05$.

suggesting that FEAR5 could be more tolerant to K deficiency, while IMC67 and FSV85 are more sensitive to K deficiency.

We did not find evidence of a significant effect of K nutrition on the root or shoot content of K, N, Mg, or Ca across the various *T. cacao* cultivars (Supplementary Table S3). Overall, based on these analyses, we obtained the following order of nutrient content for roots: N ≥ K ≥ Mg > Ca, and for leaves: N ≥ K ≥ Ca > Mg. The content of each nutrient in the foliar tissue of the cacao plants under K sufficiency is summarized in Table 1. In addition, the transfer efficiency of nutrients to roots and leaves did not significantly differ between deficiency and sufficiency conditions for any of the cultivars or K treatments (Supplementary Table S4).

Impact of K on photosynthesis

The daily integral of the net photosynthesis (AUDPC(*A*)) dataset from our study provided valuable insights into the cumulative impact of K deficiency on overall photosynthetic performance (Fig. 7). Under K deficiency IMC67 and FSV89 had significantly lower AUDPC(*A*) values (Fig. 7). In contrast, K deficiency did not have a significant impact on FEAR5 (Fig. 7). An examination of *A* values during the day (Supplementary Table S5) reveals that the lower values were recorded in the afternoon (at 4:00 pm), under K deficiency showing a significant reduction in photosynthetic activity due to the lack of K for most of the cultivars (except for FSV85 and CAU39).

For *E*, less variation was obtained in comparison to *A* (Supplementary Table S6). The maximum values under K sufficiency conditions were generally observed in the morning, with FEAR5 and IMC67 exhibiting the highest transpiration rates. Particularly in the afternoon (at 4:00 pm), a significant decrease in *E* under K deficiency was observed for IMC67. AUDPC(*E*) did not significantly change across

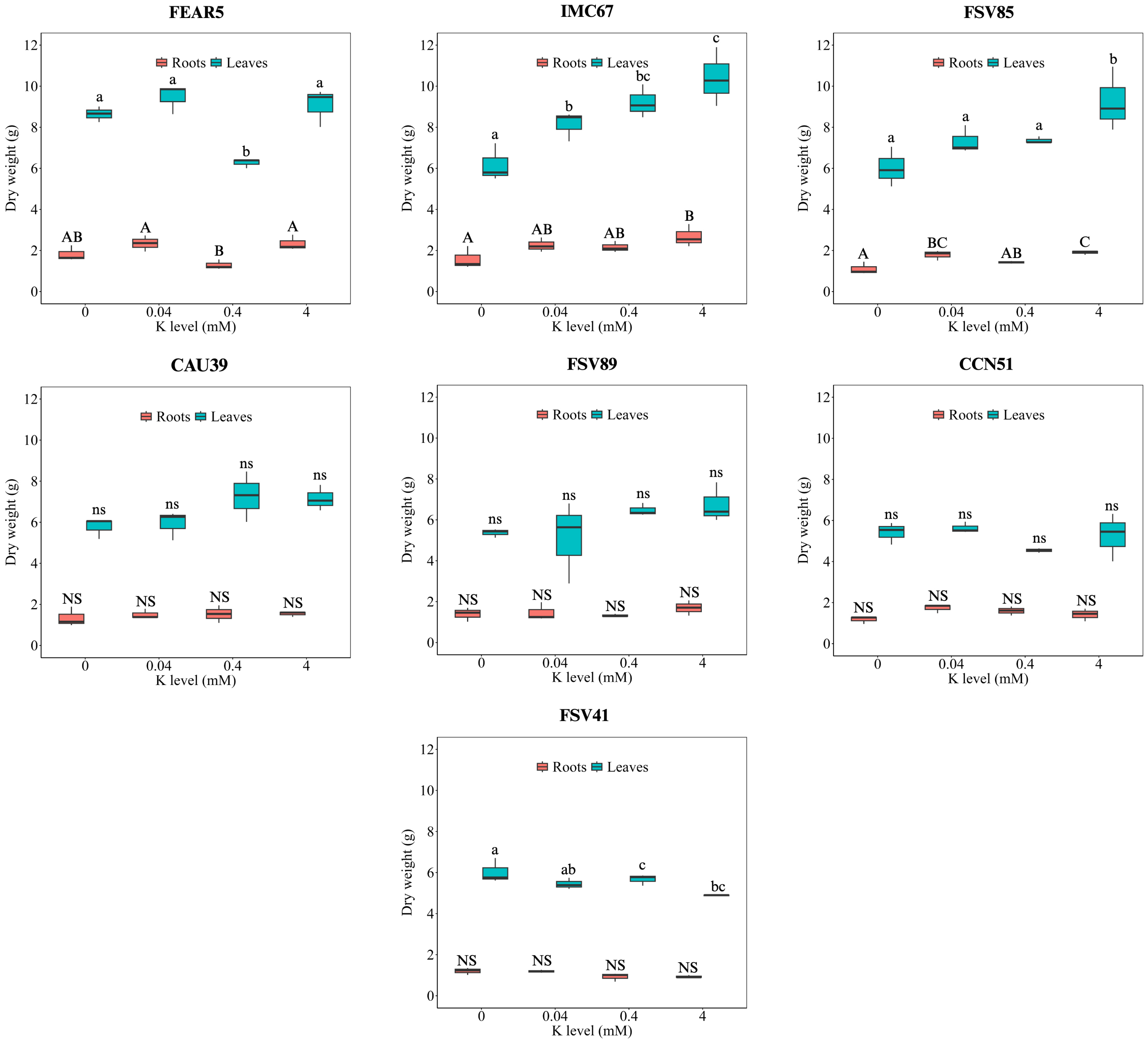

Fig. 4 Dry weight of leaves and roots of seven *T. cacao cultivars* (FEAR5, IMC67, FSV85, CAU39, FSV89, CCN51, and FSV41) grown under different K levels (0, 0.04, 0.4, and 4 mM). Values represent means ± SD of three biological replicates. One-way ANOVA was performed separately for each cultivar and tissue (leaves and roots). Different lowercase letters indicate significant differences among K treatments for leaves, and uppercase letters for roots. 'ns' indicates non-significant differences in leaf tissues and 'NS' indicates non-significant differences in root tissues, based on Fisher's LSD test at $p < 0.05$.

cultivar or K treatment (Supplementary Fig. S6). Similarly, g_s was not significantly affected by K treatment in most *T. cacao* cultivars (Supplementary Table S7). Nevertheless, a significant decrease in g_s was observed for IMC67 under K deficiency, particularly in the afternoon (4:00 pm). However, AUDPC(g_s) was not significantly impacted by K treatment for all the cultivars (Supplementary Fig. S7).

In addition, *Ci* did not significantly change among the K treatments across all seven cacao cultivars (Supplementary Table S8). Nevertheless, for *A/Ci*, significant differences were found across most cultivars, with a reduction up to 50% (Supplementary Table S9). For example, under K deficiency at the end of the day (4:00 pm), a significant decrease in *A/Ci* was observed for IMC67 and FEAR5. WUE values remained relatively stable across K treatments, although a tendency toward lower values was generally observed under K-deficient conditions (Supplementary Table S10). This reduction was only significant in the early afternoon for IMC67 and FSV85. Similarly, WUE*i* exhibited a similar trend, with lower values generally observed under K deficiency. Some significant differences were detected in the afternoon for IMC67 and FSV85 (Supplementary Table S11).

Finally, for F_v/F_m, no significant differences were found among the different K treatments or across cultivars (Supplementary Table S12). The values ranged from 0.74 to 0.81 and are typically considered normal for unstressed plants[36]. Similarly, we did not observe significant differences in quenching parameters (Supplementary Table S13), suggesting that thermal dissipation was not associated with an adaptation mechanism to K stress in the present study.

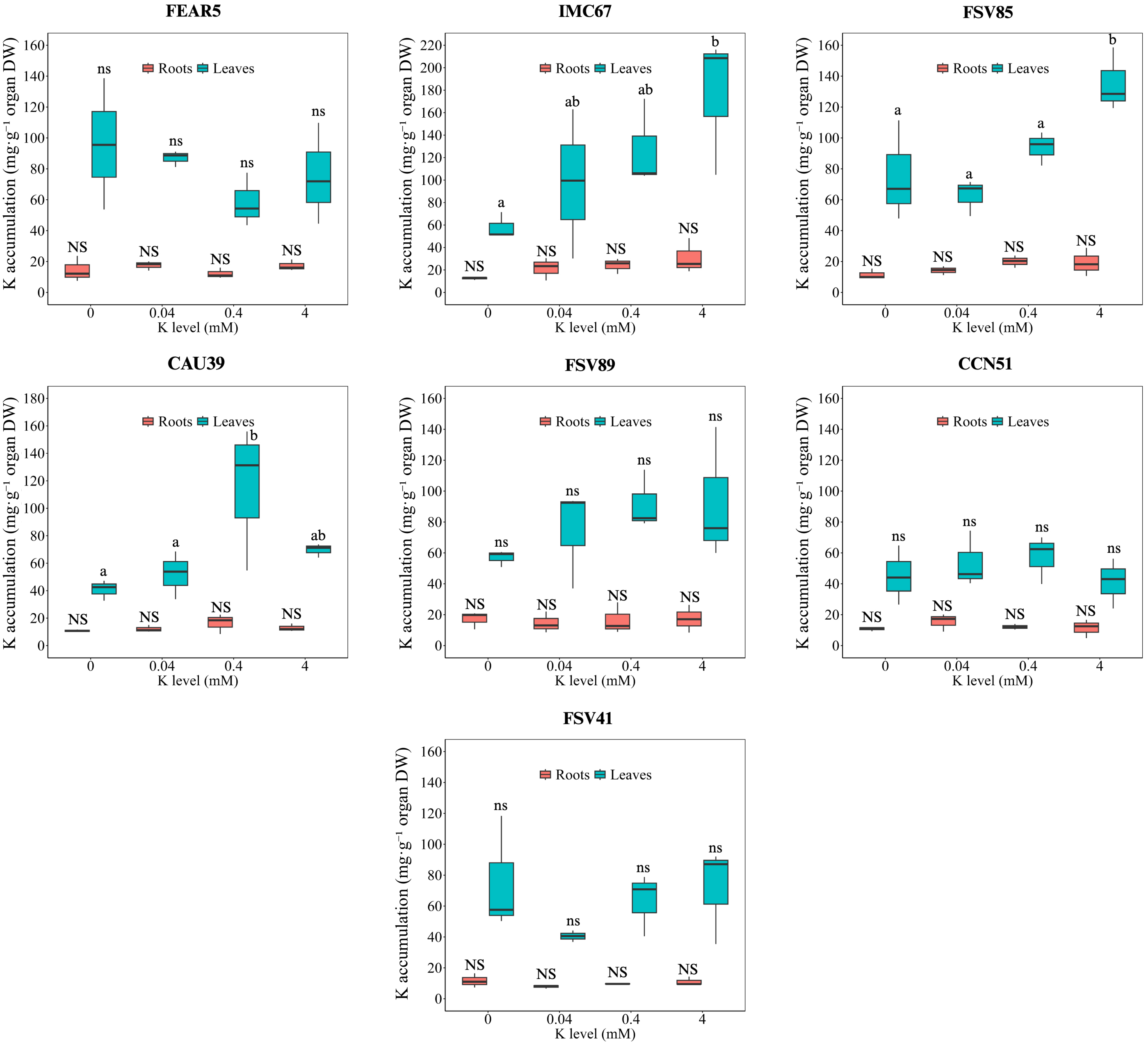

Fig. 5 K accumulation in leaves and roots of seven *T. cacao* cultivars (FEAR5, IMC67, FSV85, CAU39, FSV89, CCN51, and FSV41) grown under different K levels (0, 0.04, 0.4, and 4 mM). Values represent means ± SD of three biological replicates. One-way ANOVA was performed separately for each cultivar and tissue (leaves and roots). Different lowercase letters indicate significant differences among K treatments for leaves, and uppercase letters for roots. 'ns' indicates non-significant differences in leaf tissues and 'NS' indicates non-significant differences in root tissues, based on Fisher's LSD test at $p < 0.05$.

Discussion

In this study, we tested the hypothesis that *T. cacao* cultivars might exhibit diverse morphophysiological responses under different K nutritional regimens. By comparing these cultivars, we aimed to provide quantitative data on key parameters of growth and morphophysiology that could be used as a basis for future efforts to improve K nutrition in cacao. Indeed, genetic factors play a pivotal role in determining the nutritional requirements and growth characteristics of cultivars[1,2]. Notably, compared with other cacao cultivars tested in this study, FEAR5 and IMC67 exhibited greater nutrient uptake during the early growth of the plant, leading to greater plant height, leaf area, and biomass accumulation (Figs 3, 4; Supplementary Table S2). Additionally, these findings highlight the fact that the variation in growth and biomass production among cacao cultivars may result from inherent genetic variability. In connection with this, Ruseani et al.[37] showed that different cacao cultivars exhibit specific nutritional demands and varying abilities to absorb available nutrients, leading to significant differences in growth patterns. Furthermore, these results emphasize the importance of setting a nutritional formulation according to the needs of each cultivar, thereby optimizing the growth response and avoiding potential issues such as overfertilization or deficiencies[38].

One of the main physiological functions of K is to act as an osmolyte controlling cell expansion, which, together with cell division processes, is a crucial process for plant growth[4]. Therefore, a lack of K can disturb the development of vegetative organs[7]. Our study revealed a range of responses among the seven cacao

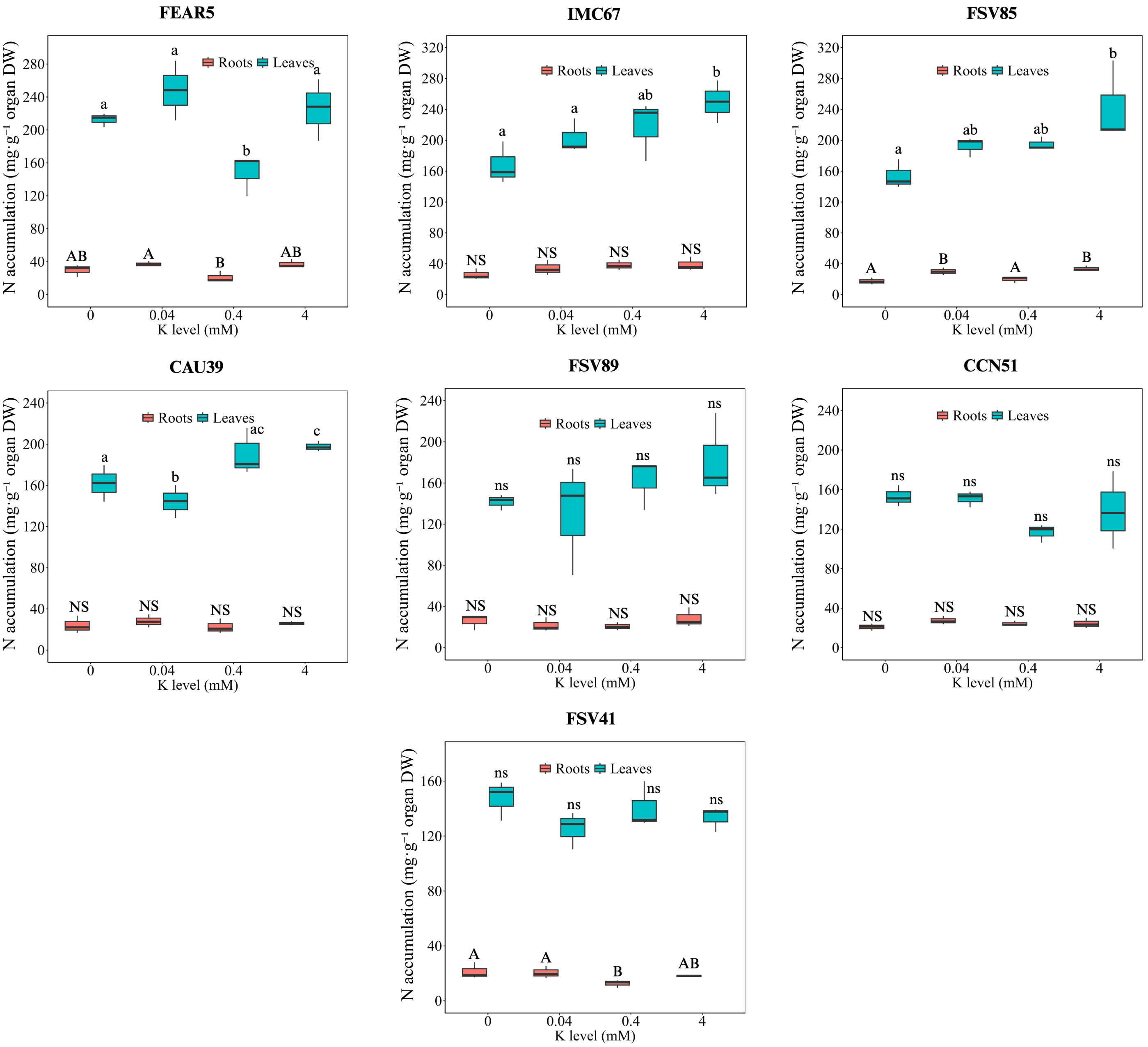

Fig. 6 N accumulation in leaves and roots of seven *T. cacao* cultivars (FEAR5, IMC67, FSV85, CAU39, FSV89, CCN51, and FSV41) grown under different K levels (0, 0.04, 0.4, and 4 mM). Values represent means ± SD of three biological replicates. One-way ANOVA was performed separately for each cultivar and tissue (leaves and roots). Different lowercase letters indicate significant differences among K treatments for leaves, and uppercase letters for roots. 'ns' indicates non-significant differences in leaf tissues and 'NS' indicates non-significant differences in root tissues, based on Fisher's LSD test at $p < 0.05$.

Table 1. Summary of macronutrient content (K, N, Mg, and Ca) in dried foliar tissue of 130-day-old plants from seven *T. cacao* cultivars, grown under sufficient nutrient conditions (4 mM K). These data are extracted from Supplementary Table S3, where the detailed statistical analysis is presented.

Cultivar	K	N	Mg	Ca
	mg·g^{-1} DW			
FEAR5	8.60 ± 4.62	24.77 ± 1.89	5.80 ± 0.10	14.63 ± 3.92
IMC67	17.67 ± 7.89	26.27 ± 1.45	4.20 ± 0.26	9.83 ± 2.03
FSV85	15.00 ± 3.63	26.20 ± 1.95	5.13 ± 1.70	11.70 ± 1.35
CAU39	9.83 ± 1.52	27.77 ± 1.98	6.60 ± 0.20	14.43 ± 3.78
FSV89	13.93 ± 7.07	26.60 ± 2.21	4.83 ± 1.36	9.87 ± 2.54
CCN51	7.60 ± 1.47	26.10 ± 1.91	5.70 ± 0.89	14.73 ± 1.17
FSV41	14.60 ± 6.35	27.27 ± 1.88	5.10 ± 0.96	11.20 ± 1.92

cultivars examined. While several morphological parameters, such as stem diameter, leaf number, and primary root elongation, were generally unaffected by K deficiency (Supplementary Table S2), the leaf area was significantly impacted in three cultivars (IMC67, FSV85, and CAU39), with a decrease of up to 38% comparing sufficiency and deficiency K conditions (Fig. 3). Taken together, these findings suggest that leaf expansion in these cacao cultivars is more sensitive to K deficiency than other vegetative growth processes. Similarly, in cotton, a reduction of up to 62% in leaf area was observed under K deficiency, while a lesser impact was obtained for leaf number (17%)[7]. Thus, these findings are consistent with the key role of K in cell expansion for the formation of leaves.

A reduction in root growth is one of the primary consequences of K deficiency. This reduces the plant's ability to uptake nutrients and

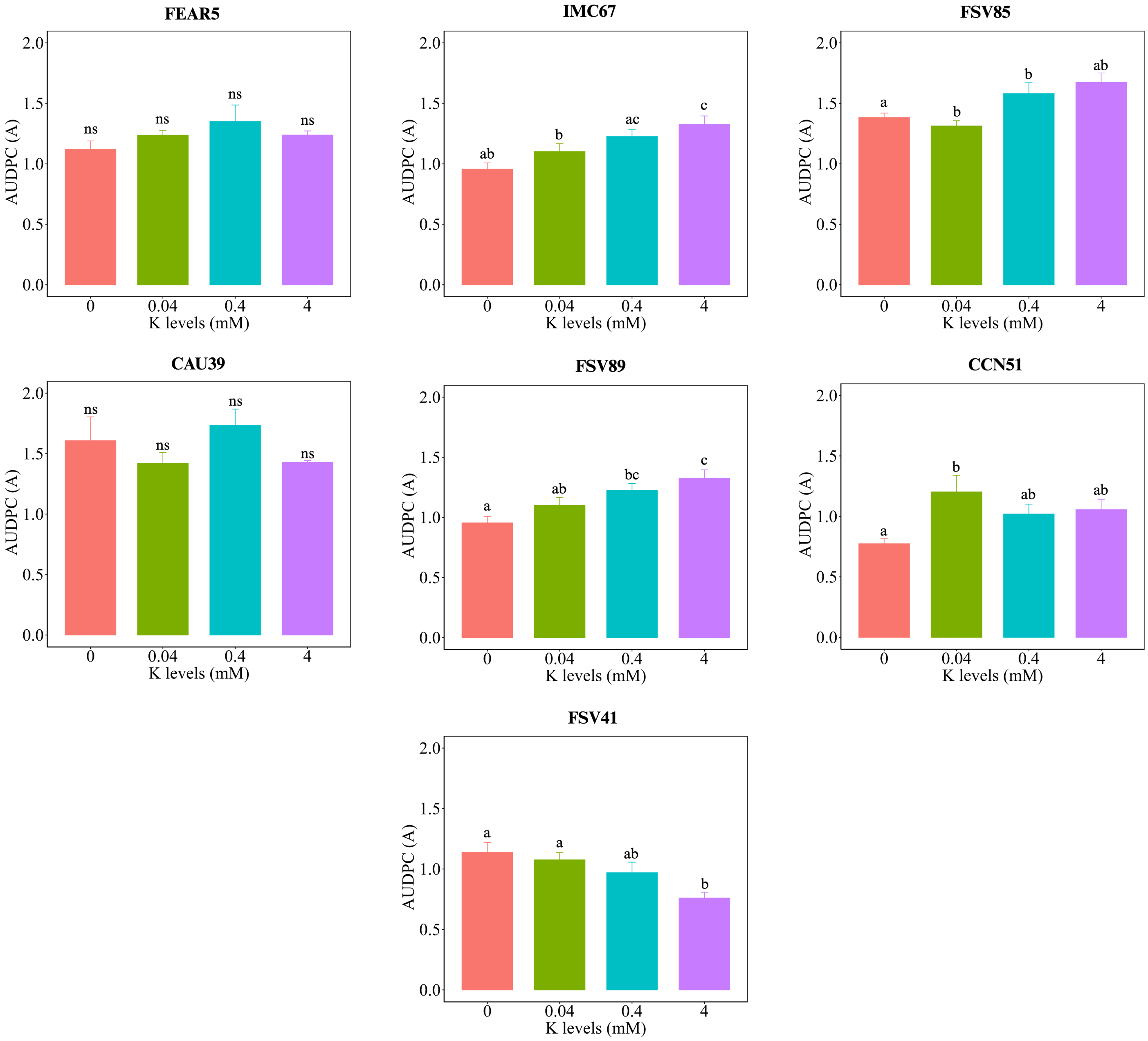

Fig. 7 Daily integral of net photosynthesis (AUDPC(A)) of seven *T. cacao* cultivars (FEAR5, IMC67, FSV85, CAU39, FSV89, CCN51, and FSV41) grown under different K levels (0, 0.04, 0.4, and 4 mM). Values represent means ± SD of three biological replicates. One-way ANOVA was performed separately for each cultivar. Different lowercase letters indicate significant differences among K treatments. 'ns' indicates non-significant differences, based on Fisher's LSD test at $p < 0.05$.

water from the soil and limits nutrient transport from roots to leaves, ultimately affecting overall plant growth[11,39]. In this study, we observed significant negative impacts of K deficiency on biomass accumulation in both the roots and leaves of IMC67 and FSV85, suggesting their sensitivity (Fig. 4). Conversely, no significant changes were observed for FEAR5, which is consistent with the interpretation that the latter exhibits a certain level of tolerance to K deficiency (Fig. 4). The differences observed in the root systems between tolerant and sensitive crop cultivars have been linked to the differential expression of morphological and physiological parameters. For instance, in K-deficient sweet potato, a sensitive cultivar exhibited a more drastic reduction in root biomass compared to the tolerant accession[39]. Similarly, in rice[40], and tobacco[41], changes in root architecture are directly linked to tolerance to K deficiency. In addition, several studies on other species, such as barley[42], and cotton[43], have demonstrated that K-efficient cultivars produce significantly more biomass than K-inefficient cultivars. These findings collectively suggest that greater biomass on roots and leaves under K deficiency may indicate greater K utilization efficiency in tolerant cultivars.

Generally, during vegetative growth, photosynthetic tissues have higher K requirements than heterotrophic tissues, such as roots, because K is essential for many physiological functions that take place in leaves[44]. Our nutrient accumulation results revealed that K predominantly accumulated in the leaves (5 to 7 times greater levels than that in the roots, Fig. 5). Under K deficiency, while there were no significant differences in K accumulation in roots, there was a notable reduction in K accumulation in leaves for some cultivar such as IMC67 and FSV85, but not for FEAR5 (Fig. 5). Therefore, photosynthetic tissues displaying higher growth rates require greater amounts of K. This result is consistent with the biomass data, where the shoot/root ratio had an average value of 6.0 (Supplementary Table S2), indicating greater allocation of biomass to leaves and, consequently, greater K requirements.

Additionally, it seems that for *T. cacao,* the cultivars that maintain high K accumulation in leaves under low-K conditions may exhibit high KUtE. Here, FEAR5 had no significant effect on K-sufficient or K-deficient conditions, suggesting that this cultivar is more tolerant to nutritional K limitation and has high KUtE characteristics. Conversely, IMC67 and FSV85 were negatively affected, indicating sensitivity to K deficiency (Fig. 5). Similar trends have been observed in other plant species, where higher K accumulation in leaves under low K has been correlated with higher KUtE. In soybean[45] and barley[46], tolerant cultivars accumulated significantly more K per plant under low-K conditions than sensitive cultivars. Along with these reports, our findings support the view that tolerant cultivars with high K accumulation in leaves may exhibit a greater ability to distribute and utilize K efficiently in photosynthetic tissues.

In plants, K and NO_3 uptake rates are often positively correlated. This process is likely related to the maintenance of the charge balance between cations/anions[47]. Understanding the interaction between K and N is therefore crucial for improving plant nutrition in crops since these nutrients are often required in greater amounts than others[27]. In our study, we showed that, under K deficiency, the leaves of IMC67, FSV85 and CAU39 exhibited a significant reduction in N accumulation, while no significant changes were observed in other cultivars, including FEAR5 (Fig. 6). Similarly, a reduction in N accumulation has been correlated with a lack of K for several crops[47]. NO_3 is transported in the xylem from roots to shoots using K as a counterion[47]. In some species, such as apple[11] and cotton[48], a lack of K significantly decreases NO_3 absorption and xylem translocation to shoots, leading to decreased leaf N accumulation. Overall, our results show that in IMC67 and FSV85 there is a close relationship between N and K nutrition. This suggests that in these cultivars, K deficiency negatively impacts the uptake and utilization of N, aggravating their general nutritional status. In contrast, the other cultivars seemed less affected by this issue. Thus, a proper supply of K may positively impact the uptake and utilization of N, improving the plant's general nutritional status.

Directly or indirectly, K has diverse functions as an osmolyte and an ion in photosynthetic processes[44]. K deficiency can prompt differential responses in plants, and a variety of studies have consistently shown an inhibitory effect of K deficiency on CO_2 assimilation[5]. This reduction in net CO_2 assimilation could result from the disruption of several processes, including limitations in CO_2 diffusion through stomata and leaf mesophyll, impairment of biochemical CO_2 fixation, and a decreased photochemical energy conversion rate[44]. Our data demonstrated a cultivar-specific response to K deficiency for photosynthesis in *T. cacao*, where IMC67 and FSV85 exhibited greater sensitivity to K deficiency, whereas FEAR5 appeared to be more tolerant (Fig. 7). Similarly, in cotton, a sensitive cultivar showed negative effects of K deficiency on several parameters, such as *A*, chlorophyll ($a + b$) content and chlorophyll fluorescence. Moreover, a cotton cultivar tolerant of K deficiency exhibited little impact on *A* or *Ci*[48]. Comparable findings have been reported for soybean[49], and maize[10], where *A*, *E*, and g_s were significantly decreased in the sensitive cultivar under K deficiency, while the tolerant cultivar showed little variation.

Overall, the findings of these reports, along with ours, highlight the necessity of considering genetic factors in determining how crops tolerate and respond to nutrient deficiencies. Some cultivars exhibit greater resilience and maintain better photosynthetic performance under low-K conditions, while others are more sensitive to this nutrient stress. Photosynthetic parameters may constitute valuable indicators for identifying potentially sensitive and tolerant cultivars. However, it may be difficult to extract clear tendencies from the data. Several studies have indicated that under K deficiency, initial growth limitations may precede the impairment of photosynthesis[50]. These observations align with our data, where biomass parameters were more strongly affected by limitations in K supply than photosynthesis parameters. This may indicate the complexity of the response to nutrient deficiencies and highlight the importance of considering multiple physiological and growth parameters to comprehensively understand their effects on plant growth and performance, particularly in the context of future crop improvement efforts.

We aimed to discern whether the decrease in *A* under K deficiency was attributable to stomatal or nonstomatal limitations. We also measured g_s and estimated WUE*i*. In general, across the cultivars, we observed that there was a tendency for guard cell osmoregulation to be maintained, even under K deficiency (Supplementary Tables S7 & S11). An exception to this was found with IMC67, which displayed dynamic responses under K deficiency, with g_s showing both increases and decreases compared to those under sufficiency conditions (Supplementary Table S7). Thus, the overall data indicate that CO_2 diffusion through stomata might not be the primary cause of the reduction in *A*. This notion was further supported by the *Ci* and WUE*i* data, which revealed only minor differences for certain cultivars but did not reveal a clear effect of K supply on these parameters (Supplementary Tables S8 & S11). The pivotal role of K in regulating stomatal function and optimizing stomatal movement efficiency has been well established in the literature[5]. While it is common for g_s to decrease under K deficiency in various plant species, it is not the only limitation responsible for reduced *A*[5]. In particular, for several species, g_s accounts for only approximately 20%−24% of the total limitations[5]. Other factors, such as mesophyll conductance, may contribute significantly to this difference, representing more than 30%−50% of the total limitations on *A*. This response has been observed in *Brassica napus*[51], *Helianthus annuus*[52], *Carya cathayensis,* and *Hickory illinoensis*[53]. We thus suggest that in *T. cacao*, other limiting factors, such as mesophyll conductance or biochemical limitations, may play a more substantial role in photosynthetic performance. Additionally, the lack of g_s under K deficiency could be attributed to the possibility that the total leaf K content in cacao plants did not fall below critical levels, allowing for the maintenance of proper stomatal function. Nevertheless, further investigations will be necessary to fully characterize this response.

In cacao, grafting is the preferred asexual propagation method, where a plant is composed of a scion and rootstock[54]. Cacao breeding programs have primarily concentrated on selecting cultivars for use as scions[29,55]. However, comparatively fewer efforts have been dedicated to breeding programs aimed at enhancing root agronomical traits in cultivars destined for use as rootstocks. This is evidenced by the limited number of commercial clones that are currently used as rootstocks worldwide[29,30,56]. Several studies have shown significant progress in selecting rootstocks that are tolerant of soil diseases[57,58], tolerating soil acidity[59], optimizing the root-associated microbiome[60], maintaining drought tolerance[56], and selecting cultivars with low cadmium accumulation/translocation[61]. In contrast, less progress has been made in terms of other agronomic traits, such as the selection of nutrient-efficient cultivars.

To date, several studies have reported significant genetic variation in N use efficiency (NUE) among cacao cultivars, highlighting the need to tailor nitrogen application to the specific requirements of each clone[37,62]. Specifically, research on selecting cacao cultivars with higher KUE is more limited. For instance, Li et al.[63] investigated the effect of K concentration on nutrient uptake and use efficiency in three cacao cultivars and reported that an increase in K concentration in the soil had a positive impact on the accumulation of certain nutrients but decreased the accumulation of others with differential cultivar-specific responses. Nevertheless, this study did not identify rootstocks with higher KUE or determine the mechanisms governing this trait. Here, we demonstrated the potential of cacao genetic diversity in the development of K-efficient rootstocks. We propose FEAR5 as a potential rootstock with high KUE, offering new solutions for plant breeding programs aimed at developing cultivars with enhanced nutrient uptake and utilization. This approach could ultimately contribute to agricultural sustainability practices by reducing dependence on chemical fertilizers and improving resilience to environmental stresses.

Conclusions

The present study represents the first attempt to characterize KUE in commercially important cacao cultivars, focusing on evaluating nutrient efficiency as a desirable agronomic trait for rootstock selection. Our findings underscore the importance of considering cultivar-specific responses due to the complex interactions between genetic variability, nutrient requirements, environmental conditions, and plant growth dynamics. Overall, the results indicate that some *T. cacao* cultivars, such as IMC67 and FSV85, were more sensitive to K deficiency, while others, notably FEAR5, exhibited greater adaptability to low K. FEAR5 promoted superior growth, characterized by high root proliferation and leaf biomass accumulation, as well as sustained leaf K and N accumulation and efficient photosynthetic performance. Therefore, FEAR5 demonstrated greater morphophysiological tolerance to low K, resulting in greater KUE. To validate these conclusions, future research could include field trials during the reproductive phase to evaluate the practical applicability of these findings under natural growing conditions, considering multiple abiotic and biotic stresses. Additionally, further investigation into the molecular and biochemical mechanisms underlying these responses will be crucial for advancing our understanding of the contrasting responses of FEAR5 and IMC67. This approach will enable the identification of specific genes or pathways that may play pivotal roles in mediating these responses, offering insights into potential targets for breeding programs aimed at developing cacao cultivars with enhanced KUE.

Author contributions

The authors confirm their contributions to the paper as follows: study conception and design: Carmona-Rojas LM, Urrea-Trujillo AI, Rivoal J, Gutiérrez-Rodríguez EA, Córdoba-Gaona OJ; data collection: Carmona-Rojas LM, Sáenz-Gallego V, Loaiza-Ruiz RA; analysis and interpretation of results: Carmona-Rojas LM, Urrea-Trujillo AI, Rivoal J, Gutiérrez-Rodríguez EA, de Jesús Córdoba-Gaona O; draft manuscript preparation: Carmona-Rojas LM. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

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Conflict of interest

The authors declare that they have no conflict of interest.

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