Physiological Responses of Purple Passion Fruit (*Passiflora Edulis* Sims F. *Edulis*) Plants to Deficiencies of the Macronutrients, Fe, Mn, and Zn during Vegetative Growth

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**ABSTRACT**

The purple passion fruit (*Passiflora edulis* Sims f. *edulis*) is a promising crop in Colombia because of its high potential for international markets and high profitability. However, without adequate fertilization, the metabolic processes of plant growth can be affected. The objective of this research was to evaluate the effect of macro- and micronutrient deficiencies on growth, photosynthesis, and transpiration in purple passion fruit plants during vegetative development. Seedlings with four to six leaves (three-months-old) were transplanted to a sand culture and subjected to mineral deficiencies using the missing element technique under greenhouse conditions. The plants subjected to Fe deficiency had the lowest maximum photosynthetic rate at saturation by light (1.72 µmol CO₂ m⁻² s⁻¹) at 72 days after treatment, while the lowest apparent quantum efficiency (0.008 µmol CO₂ µmol photons⁻¹) was observed in the plants with Mg deficiency. The lowest values of maximum photochemical efficiency of photosystem II, Fv/Fm (0.69) and transpiration rate (2.39 µg H₂O cm⁻² s⁻¹) were found in the plants with P deficiency. The mineral nutrient deficiencies negatively affected metabolic processes in the purple passion fruit plants, with the highest impact on photosynthesis observed with the Fe or Mg deficiencies. The plants subjected to P deficiencies were the most affected plants in terms of transpiration rate.

**KEYWORDS**

Leaf area; chlorophyll a fluorescence; leaf number; photosynthesis; transpiration

**Introduction**

The purple passion fruit (*Passiflora edulis* Sims f. *edulis*) is native to southern Brazil, Paraguay, and northern Argentina (Ocampo and Wyckhuys, 2012; Pinzón et al., 2007; Rendón et al., 2013); its fruit has a high alimentary value because of its organoleptic and nutritional characteristics (Jiménez et al., 2011), such as high contents of organic acids, provitamin A, niacin, riboflavin, and ascorbic acid (Ángel-Coca et al., 2011; Fischer et al., 2018; Wenkam, 1990). Colombia produced around 24,700 t of purple passion fruit in 2018 (Agronet, 2018), gaining an economic benefit in the country’s export fruit market, along with banana (*Musa × paradisiaca* L.) and cape gooseberry (*Physalis peruviana* L.), in recent years (Conde et al., 2013; Suárez, 2017), with an 11% increment in the exportation volume between 2018 and 2019 (Analde, 2019). However, harvest losses in the field generally exceed 40% of the total production costs as a result of poor harvest and post-harvest management (Diaz et al., 2012) and a lack of fertilizer practices that would guarantee high yields with high-quality fruits.
In order to maintain a high level of crop production, it is necessary to supply mineral nutrients in adequate amounts, and thus ensure the expression of the crop’s genetic potential (Fageria, 2012). Otherwise, deficiencies of mineral nutrients in plants result in metabolic disorders, which can interrupt crop development (Taiz et al., 2017), decrease yield, and affect parameters of fruit quality, such as fruit appearance, size, color, or skin texture (Da Costa et al., 2006). In the cape gooseberry, deficiencies of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), or boron (B) reduce the number of fruits per plant; yield is more affected by the absence of B, N or K (yield reduction of 90%) and P (yield reduction of 50%) (Martínez et al., 2008). In banana passion fruit (Passiflora tripartita var. mollissima), deficiencies of either N, K, or Mg significantly diminish the number of leaves and dry matter production (Lizarazo et al., 2013a), similar to deficiencies in manganese (Mn), zinc (Zn), and B (Lizarazo et al., 2013b). In Passiflora sp., N deficiency reduces yield by 44% and lowers the total titratable acidity in fruits, as compared with plants that receive a higher dose of N (350 g plant⁻¹ year⁻¹) (Picanço et al., 2016). Each essential mineral nutrient fulfills a specific function in plant metabolism (Taiz et al., 2017), and its deficiency produces metabolic alterations that can threaten plant survival (Vatansever et al., 2017).

In the purple passion fruit, studies of plant physiological responses to growth conditions are scarce. Pérez-Martínez and Melgarejo (2015) characterized the physiological performance of purple passion fruits in the reproductive stage based on photosynthetic parameters, and Rodriguez et al. (2019b) studied the variability for photosynthetic and physiological adaptations in contrasting environments. Quiroga et al. (2018) evaluated the effect of foliar applications of boron on the phenological development and fruit set of purple passion fruits. However, to our knowledge, there are no studies on physiological responses of this crop under conditions of nutrient deficiencies; additionally, the effects of mineral deficiencies on its growth, photosynthetic, and biochemical responses are unknown. Therefore, the objective of this research was to analyze some aspects of photosynthesis and growth in purple passion fruit plants in the vegetative stage of growth under deficiencies of N, P, K, Mg, Ca, Fe, Zn, or Mn. We hypothesized that a nutrient deficiency would negatively affect physiological variables in the purple passion fruit plants and result in detrimental growth, as compared to plants provided with a complete nutrient solution.

Materials and Methods

Plant Material and Experiment Conditions

This study was carried out in a greenhouse of the Departamento de Biología, Universidad Nacional de Colombia, Bogotá (Colombia), with an average of 62.6 ± 3.0% relative air humidity, 18 ± 3.0°C air temperature, 12 h light–12 h dark photoperiod, and 100 µmol m⁻²s⁻¹ photosynthetic photon flux density (PFD), located at 4°38’08” N latitude and 74°04’58” W longitude at 2,640 m.a.s.l. The purple passion fruit (Passiflora edulis Sims f. edulis) plants were propagated using seeds from a certified nursery under greenhouse conditions. When the plants completed 10 weeks after seedling emergence (four to six fully expanded true leaves and 16 ± 2.7 cm height, 3 months in age), they were transplanted, one plant per black plastic bag (30 x 15 cm), which contained a mixture (1:1 w/w) of quartz sand with two particle sizes: 0.7 and 1.5 mm. The plants were watered daily with 100 ml of distilled water per plant. Starting at transplant, a “complete” nutrient solution (Table 1) was applied to the plants once a week in order to obtain homogeneous plants free of symptoms of nutrient deficiencies. Sixty days later, the nutrient deficiencies were induced using the missing element technique (Cabezas and Sánchez, 2008). The treatments consisted of the control (“complete” nutrient solution) and the ones lacking one of the following mineral elements (Table 1): nitrogen (-N), phosphorus (-P), potassium (-K), magnesium (-Mg), calcium (-Ca), iron (-Fe), zinc (-Zn), and manganese (-Mn). The composition of the complete nutrient solution was based on the accounts of
Passiflora crops (Angulo, 2009; García, 2002; Jiménez et al., 2009; Mendonça-Freitas et al., 2008; Rivera et al., 2002). During the treatments, 100 ml of “complete” or “deficient” nutrient solution, according to the treatment, were applied to each plant three times per week for 72 days.

Variables of Growth, Mineral Deficiency Symptoms, Photosynthesis, and Transpiration

Seventy-two days after starting the treatment applications (dat), leaf area, number of leaves, total dry mass, and symptoms of mineral deficiencies were assessed in the final experiment. The leaf area was determined using Imagel® software. Afterward, the plants were dried in an oven at 70°C for 72 h, and the total dry mass (aerial plus root parts) was quantified. A visual description of the deficiency symptoms was done for each of the studied elements.

Light response curves of photosynthetic net carbon assimilation (A/PFD) were obtained with an infrared gas analyzer (IRGA, LCPro+, ADC BioScientific, Hoddesdon, UK). At 71 dat, the photosynthetic rate (μmol m⁻²s⁻¹) was recorded under different light intensities (μmol mol⁻¹) between 8:30 and 11:00 am in two leaves of the middle stratum (fourth and fifth leaves from the shoot apical bud) from 4 plants per treatment. All plants received the same conditions in terms of light incidence during the growth; no shading was applied.

The curves were generated reducing PFD in 10 steps from 2,000 to 0 μmol photons m⁻²s⁻¹ at a CO₂ concentration of 400 ppm, temperature of 18°C, and relative air humidity of 62%; within each step of changing light intensity, the data were registered when stable values were reached (ADC BioScientific, UK). The curves were adjusted to the rectangular hyperbolic model of Michaelis-Menten (Givnish et al., 2004; Pérez-Martínez and Melgarejo, 2015; Rodríguez et al., 2019b; Solarte et al., 2010) using the equation: \( A = \frac{\{A_{\text{max}} \cdot PFD/K+ \cdot PFD\}}{-Rd}, \) where \( A \) is the photosynthetic rate; \( A_{\text{max}} \) is the rate of photosynthesis at full light saturation; \( K \) is the constant for light saturation below half of the natural photon flux (PFD), and \( Rd \) is the respiration rate in the dark. The light compensation point (Ic) was calculated with the equation \( (K \cdot Rd)/(A_{\text{max}} \cdot Rd) \). Apparent quantum efficiency (φPFD) was based on the slope of the linear regression corresponding to the number of photons absorbed by the leaves in

| Treatments (ml L⁻¹) | Stock Solution | Control - N - P - K - Mg - Ca - Fe - Zn - Mn |
|---------------------|----------------|-----------------------------------------------|
| Ca(NO₃)₂·4H₂O (2 mol L⁻¹) | 1.5 0.0 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 |  |
| KNO₃ (2 mol L⁻¹) | 2.0 0.0 2.0 0.0 2.0 2.0 2.0 2.0 2.0 2.0 |  |
| NH₄H₂PO₄ (1 mol L⁻¹) | 0.5 0.0 0.5 0.5 0.5 0.5 0.5 0.5 0.5 0.5 |  |
| MgSO₄ (1 mol L⁻¹) | 2.0 2.0 2.0 2.0 0.0 2.0 0.0 2.0 2.0 2.0 |  |
| H₂BO₃ (25 mol L⁻¹) | 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 |  |
| (NH₄)₂SO₄ (1 mol L⁻¹) | 0.5 0.0 0.5 0.5 0.5 0.5 0.5 0.5 0.5 0.5 |  |
| NH₄Cl (1 mol L⁻¹) | 0.0 0.0 0.5 0.0 0.0 0.0 1.0 0.0 0.0 0.0 |  |
| NaNO₃ (2 mol L⁻¹) | 0.0 0.0 0.0 0.0 2.0 0.0 0.0 0.0 0.0 0.0 |  |
| Na₂SO₄ (1 mol L⁻¹) | 0.0 0.0 0.0 0.0 0.0 0.0 2.0 0.0 0.0 0.0 |  |
| MgCl₂ (1 mol L⁻¹) | 0.0 0.0 0.0 0.0 0.0 0.0 2.0 0.0 0.0 0.0 |  |
| CaCl₂ (2 mol L⁻¹) | 0.0 1.5 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 |  |
| KCl (1 mol L⁻¹) | 0.0 2.5 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 |  |
| KH₂PO₄ (1 mol L⁻¹) | 0.0 0.5 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 |  |
| K₂SO₄ (0.5 mol L⁻¹) | 0.0 1.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 |  |
| Fe·EDTA (25 g L⁻¹) | 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 |  |
| ZnSO₄·7H₂O (578 mg L⁻¹) | 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 |  |
| MnSO₄·H₂O (845 mg L⁻¹) | 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 |  |
| (NH₄)₂MoO₄·2H₂O·H₂O (88 mgL⁻¹) | 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 |  |
| CuSO₄·5H₂O (125 mg L⁻¹) | 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 |  |
order to fix 1 mol of CO₂ (Pérez-Martínez and Melgarejo, 2015; Rodríguez et al., 2019b; Solarte et al., 2010).

The transpiration (μg H₂O cm⁻² s⁻¹) and stomatal resistance of the leaves (s cm⁻¹) were determined with a steady-state porometer (LI-1200, LiCor Inc., Lincoln, USA) (Del Pozo et al., 2017) between 8:30 am and 11:00 am at 72 dat. Two leaves of the middle stratum from four plants were used per treatment for this measurement.

The maximum photochemical efficiency of photosystem II (Fv/Fm) was quantified using a chlorophyll fluorometer (Handy PEA, Hansatech Instruments Ltd., Norfolk, UK). The plants were placed in darkness overnight; before the measurement, the clip was fixed on the leaf for 30 min. The Fv/Fm measurement was performed by exposure to a saturating light pulse of 6,000 μmol m⁻² s⁻¹ for 1 s at pre-dawn (4:00–5:00 a.m.) (Baker, 2008; Brooks and Nigoyii, 2011; Kalaji et al., 2014; Maxwell and Johnson, 2000; Murchie and Lawson, 2013). The measurements were conducted in four plants per treatment using two leaves of the middle stratum from each plant at 72 dat.

**Experiment Design and Statistical Analysis**

A completely randomized design was established, with nine treatments corresponding to a “complete” nutrient solution (control) and treatments lacking one of the following mineral elements: nitrogen (-N), phosphorus (-P), potassium (-K), magnesium (-Mg), calcium (-Ca), iron (-Fe), zinc (-Zn), or manganese (-Mn). Four plants were monitored per treatment at 71 and 72 dat. The data were analyzed with SAS* 9.4 Statistical Analysis Software using analysis of variance (ANOVA); however, the assumptions of variance homogeneity and normality of the data were not adjusted to the parametric model; therefore, an analysis was performed with the Kruskal Wallis and Scott-Knott’s multiple comparison test (p < .05) to determine differences between the treatments.

**Results**

**Leaf Area, Number of Leaves, Total Dry Mass, and Symptoms of Mineral Deficiencies**

The control plants had (average ± standard deviation) the highest leaf area (348.24 ± 14.86 cm²), a maximum number of leaves (13.78 ± 2.84), and total dry mass (4.97 ± 1.04 g), as compared to other treatments; these variables significantly differed between the control plants and the plants deficient in Mg, Fe, Ca, Mn, or Zn. The plants with P deficiency possessed the lowest leaf area and the lowest number of leaves, which were reduced by 40.1 and 61.7%, respectively, as compared to the control (Table 2).

Although no statistically significant differences were obtained between the treatments for total dry mass, the control plants had the highest dry mass (4.97 g), whereas the plants with P or N deficiency presented the lowest weights of 2.60 or 2.76 g, respectively (Table 2). The control plants developed

| Treatment          | Leaf area (cm²) | Number of leaves | Total dry weight (g) |
|--------------------|-----------------|------------------|----------------------|
| Control (complete solution) | 348.24 ± 14.86 a | 13.78 ± 2.84 a | 4.97 ± 1.04 a |
| -N                 | 190.42 ± 43.95 b | 11.0 ± 1.58 a  | 2.76 ± 0.57 b      |
| -P                 | 139.65 ± 34.35 b| 8.5 ± 1.11 a   | 2.60 ± 0.63 b      |
| -K                 | 181.13 ± 20.59 b| 11.67 ± 1.47 a | 4.34 ± 0.36 a      |
| -Ca                | 332.66 ± 25.64 a| 11.33 ± 2.68 a | 4.76 ± 0.64 a      |
| -Mg                | 221.55 ± 84.22 b| 12.25 ± 1.48 a | 4.06 ± 1.65 a      |
| -Fe                | 272.15 ± 59.53 a| 12.32 ± 1.08 a | 4.44 ± 0.49 a      |
| -Zn                | 284.63 ± 39.22 a| 10.75 ± 1.48 a | 3.82 ± 0.85 a      |
| -Mn                | 241.46 ± 40.61 b| 10.39 ± 1.40 a | 3.35 ± 0.95 b      |

Table 2. Leaf area (cm²), number of leaves, and total dry mass (g) of the purple passion fruit plants 72 d subjected to nutrient deficiencies. n = 4. Means with the same letter do not differ significantly (p < .05) according to Scott-Knott’s test. Values are means with standard deviation.
fully expanded leaves, typical of the species. In the -N treatment, thinner and shorter stems, generalized chlorosis on mature leaves, and early leaf abscission were observed. The plants subjected to P deficiency had apical leaves with a leathery surface and chlorosis; the basal leaves presented slight chlorotic mottling throughout the leaf blade. The apical leaves in the K-deficient plants had deformed edges, while the basal leaves were smaller, with deformation and mild chlorosis. The Ca-deficient plants had twisted apical leaves and basal leaves of a leathery appearance. In the absence of Mg, small basal leaves had an interveinal chlorosis and early abscission. With the absence of Fe in the nutrient solution, the apical leaves had mild chlorosis, while the basal ones had twisted and dark green color. In the -Zn treatment, the basal leaves showed light chlorotic mottling and the apical leaves were curled. The Mn-deficient plants presented chlorotic apical leaves. The photographic record of the symptoms could be found in Cárdenas et al. (2019).

**Light Response Curves of Photosynthetic Net Carbon Assimilation**

The Amax (7.54 µmol CO₂ m⁻² s⁻¹) and apparent quantum efficiency (0.043 µmol CO₂ µmol photons⁻¹) were recorded in the control, plants treated with a complete nutrient solution (Table 3). Because of the stress caused by the nutrient deficiencies, the plants in the other treatments had a reduction in these variables at 71 dat. The plants grown under deficiency of N, P, or Mg presented low photosynthetic rates at all points of the curve, a lower Amax (2.23, 4.48, and 6.73 µmol CO₂ m⁻² s⁻¹, respectively) and a lower estimated ϕPFD (0.013, 0.033, and 0.008 µmol CO₂ µmol photons⁻¹, respectively) (Table 3); the plants deficient in Mg did not conform to the executed model (R² = 0.48), and their apparent ϕPFD was the lowest.

In the K-deficient plants, the values of Amax (5.62 µmol CO₂ m⁻² s⁻¹) and ϕPFD (0.04 µmol CO₂ µmol photons⁻¹) were lower than in the control treatment (Table 3). In the plants with Zn deficiency, ϕPFD (0.032 µmol CO₂ µmol photons⁻¹), Ic (11.88 µmol photon m⁻² s⁻¹) and Amax (4.21 µmol CO₂ m⁻² s⁻¹) were lower than in the control (Table 3). Deficiencies of Ca, Mn, or Fe negatively affected photosynthesis, with low photosynthetic rates obtained along the curve, and diminished ϕPFD (32%,

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**Table 3.** Parameters derived from the A/PFD curves at 71 dat in the purple passion fruit plants subjected to nutrient deficiencies. The data were adjusted to a rectangular hyperbolic function. n = 4. Values are means with standard deviation.

| Treatment | Equation | R² | Amax (µmol CO₂ m⁻² s⁻¹) | Ic (µmol photon m⁻² s⁻¹) | Rdark (µmol CO₂ m⁻² s⁻¹) | ϕPFD (µmol CO₂ µmol photons⁻¹) |
|-----------|---------|----|------------------------|------------------------|------------------------|-------------------------------|
| Control   | A = -1.51 + 7.54·PFD/((164.28 + PFD) | 0.96 | 7.54 ± 0.33 a | 41.14 ± 2.91 c | 1.51 ± 0.19 ab | 0.043 ± 0.009 a |
| -N        | A = -0.39 + 2.23·PFD/((386.69 + PFD) | 0.48 | 2.23 ± 1.37 ab | 80.76 ± 38.48 b | 0.36 ± 0.11 b | 0.013 ± 0.007 cd |
| -P        | A = -0.71 + 4.48·PFD/((59.63 + PFD) | 0.76 | 4.48 ± 0.74 a | 36.53 ± 30.36 cd | 1.7 ± 0.30 ab | 0.033 ± 0.003 ab |
| -K        | A = -2.07 + 5.61·PFD/((34.52 + PFD) | 0.92 | 5.62 ± 2.05 a | 20.25 ± 2.75 d | 2.07 ± 1.26 a | 0.04 ± 0.013 ab |
| -Ca       | A = -1.66 + 4.32·PFD/((35.53 + PFD) | 0.89 | 4.23 ± 0.28 a | 22.96 ± 0.63 d | 1.66 ± 0.26 ab | 0.029 ± 0.005 bc |
| -Mg       | A = -0.34 + 6.73·PFD/((34866.4 + PFD) | 0.28 | 6.73 ± 0.61 a | 183.33 ± 19.91 a | 0.34 ± 0.09 b | 0.008 ± 0.002 c |
| -Fe       | A = -0.90 + 1.72·PFD/((33.88 + PFD) | 0.88 | 1.72 ± 0.22 b | 37.17 ± 5.08 cd | 0.90 ± 0.23 ab | 0.020 ± 0.003 cd |
| -Zn       | A = -1.62 + 6.77·PFD/((61.58 + PFD) | 0.97 | 6.77 ± 5.38 a | 11.88 ± 0.76 d | 0.60 ± 0.12 b | 0.032 ± 0.003 ab |
| -Mn       | A = -0.73 + 3.25·PFD/((75.17 + PFD) | 0.96 | 3.25 ± 0.15 ab | 21.84 ± 0.26 d | 0.73 ± 0.23 ab | 0.029 ± 0.003 abc |

* Amax – maximum photosynthetic rate, Ic – light compensation point, Rdark – dark respiration, ϕPFD – apparent quantum efficiency, PFD – photosynthetic flux density.
32%, and 53%, respectively) or Amax (44%, 57%, and 77%, respectively), as compared to the control (Table 3). The plants with Fe deficiency presented the lowest photosynthetic rates among all treatments at 72 dat.

**Maximum Photochemical Efficiency of Photosystem II (Fv/fm)**

The control plants had the highest potential maximum photochemical efficiency of photosystem II (PSII) (Fv/Fm = 0.85) without presenting statistically significant differences with the other treatments, with exception of the plants subjected to P deficiency (Fv/Fm = 0.69) (Table 4).

**Transpiration and Stomatal Resistance**

The control plants had the highest transpiration (6.75 ± 1.14 µg H2O cm−2 s−1) and, thus, significantly differed from the plants grown under P deficiency. The P-deficient plants had the lowest transpiration rate (2.39 ± 0.74 µg H2O cm−2 s−1) and the highest stomatal resistance (9.44 ± 0.66 s cm−1) at 72 dat (Table 4).

**Discussion**

**Leaf Area, Number of Leaves, and Total Dry Mass**

The absence of N in the nutrient solution decreased the dry mass in the studied plants (Table 2), which was similar to that reported in banana passion fruit (P. mollissima) (Lizarazo et al., 2013a); additionally, the N deficiency reduced leaf area and affected leaf emission rate, similar to that observed in other Passiflora suberosa species, including P. tripartita Kunth var. mollissima (Rodríguez et al., 2019a). These results could be attributed to the high N requirement of Passiflora plants for constituting proteins, nucleic acids, secondary metabolites, coenzymes, chlorophyll, and phytohormones (Hawkesford et al., 2012; Vianna and Cordeiro, 2015). This leads to a low photosynthetic performance and, as a consequence, slow growth of organs and thin stems. Due to the high mobility of N in plants, the chlorosis observed in lower leaves spreads further throughout the plant (Taiz et al., 2017), similar to the symptoms observed in the present research.

At the same time, P is a component of nucleic acids and ATP (Marschner, 2012); therefore, when P is supplied at deficient quantities, the production of biomass decreased, as reported in P. mollissima (Cabezas and Sánchez, 2008). Also, leaf area was reduced in the P-deficient plants, as compared to the control treatment (Table 2) because of a restriction that could be imposed on cell division and expansion, as well as a low number of axillary buds and the consequent poor leaf emission, as shown in P. mollissima (Cabezas and Sánchez, 2008). This explained the reduced growth and poor leaf emission as well as chlorosis presented in leaf lamina of P-deficient plants, similar to that reported by Rodríguez et al. (2019a).

The plants with Ca deficiency had a lower production of dry matter and lower leaf area (Table 2) since, under this condition, cell elongation might be limited because Ca walls were weaker because Ca interchangeably joins R-COO− groups of polygalacturonic acids and is required to stimulate the synthesis of cell wall precursors (Marschner, 2012; Thor, 2019). The reduction of growth and leaf deformation are the symptoms typical of that deficiency, explained by the low mobility of Ca in plants and the alteration of properties of cell walls and membranes (Bhatia and Lal, 2018).

The Mg deficiency led to a lower dry mass, smaller leaf area, and a low number of leaves than in the control (Table 2), possibly because of a reduction in chlorophyll content and alteration of carbon fixation necessary for plant growth and development (Guo et al., 2016). The Mg deficiency might have also caused an alteration in enzyme activity, such as for RuBisCO involved in the reactions of
photosynthesis, in which Mg acts as a cofactor (Bhatla and Lal, 2018). The smaller contents of chlorophyll can be associated with the reduction in its synthesis and oxidative damage by reactive oxygen species that degrade chlorophyll molecule, decreasing photosynthesis rates and, thus, leaf growth and biomass production (Tanoï and Kobayashi, 2015). Due to its mobility in plants, Mg is transported to source leaves to avoid severe reductions in the photosynthesis rate (Bhatla and Lal, 2018), which might explain the symptoms of interveinal chlorosis observed in the basal leaves. The treatment -K also reduced growth in the studied plants; this mineral element participates in photosynthesis, enzymatic activation, and protein synthesis (Hafsi et al., 2014), and, under a K deficiency, a reduced activity of aquaporins could decrease hydraulic conductance and slow down the water supply necessary for cell growth (Wang et al., 2016). In addition, K regulates the stomatal opening and closing and affects leaf composition and development (Taiz et al., 2017). For this reason, the K-deficient plants tended to minimize leaf size more than leaf number (Table 2), thus reducing the resistance of the air boundary layer and gaining more efficient exchange of gases (Cabezasp and Sánchez, 2008). The symptoms presented in the lower leaves are associated with high mobility of this element in plants (Bhatla and Lal, 2018), similar to that reported by Rodríguez et al. (2019a).

Likewise, under the conditions of the Fe deficiency, a decline in dry mass accumulation at 72 da was observed, as compared to the control (Table 2); this effect could be due to a reduction in the metabolic activity of plants in the absence of Fe (Marschner, 2012). This element participates in photosynthesis, respiration, and DNA synthesis, among others (Vatansever et al., 2017) being involved in different metabolic pathways, such as redox homeostasis, N metabolism, chlorophyll synthesis, and the electron transport in chloroplasts and mitochondria; its deficiency alters the C fixation necessary for plant growth (López-Millán et al., 2013; Schmidt et al., 2020). A similar result was reported previously in Passiflora edulis f. flavicarpa (Scaramuzza et al., 2001), attributed to the importance of Fe for the activity of various enzymes (Barker and Pilbeam, 2015). Due to the low mobility of Fe in plants, the chlorosis was observed in the apical leaves, indicating the role of Fe in the synthesis of chlorophyll (Bhatla and Lal, 2018).

In the absence of Mn, meristematic tissues ceased growth, affecting the development of new organs and, in this way, altering the accumulation of biomass (Barker and Pilbeam, 2015), which led to a decrease in dry mass (Table 2), similar to that found for P. mollissima (Lizarazo et al., 2013b). The chlorosis presented in Mn-deficient plants could be attributed to the function of this element in the chloroplast development, so that, in the absence of Mn, the thylakoid membranes become disorganized and, thus, the leaf lamina acquires a color distortion (Bhatla and Lal, 2018). The detrimental effect of the Zn deficiency on plant growth could be explained by the importance of Zn for auxin synthesis; in this way, in the Zn-deficient plants, leaf area was reduced, internodes were shortened (Bhatla and Lal, 2018; Gil et al., 2012), and the synthesis of proteins and RNA was equally reduced

### Table 4. Maximum photochemical efficiency of PSII (Fv/Fm), transpiration (μg H₂O cm⁻² s⁻¹), and stomatal resistance (s cm⁻¹) at 72 da of the purple passion fruit plants subjected to nutrient deficiencies. n = 4. Means with the same letter do not differ significantly (p < .05) according to Scott-Knott’s test.

| Treatment | Fv/Fm | Transpiration (μg H₂O cm⁻² s⁻¹) | Stomatal resistance (s cm⁻¹) |
|-----------|-------|---------------------------------|-----------------------------|
| Control   | 0.85 ± 0.009 a | 6.75 ± 1.137 a | 3.58 ± 1.266 c |
| -N        | 0.80 ± 0.028 a | 4.46 ± 1.633 a | 5.88 ± 0.990 b |
| -P        | 0.69 ± 0.065 b | 2.39 ± 0.738 b | 9.44 ± 0.665 a |
| -K        | 0.82 ± 0.006 a | 4.13 ± 1.646 a | 5.29 ± 1.221 b |
| -Ca       | 0.80 ± 0.006 a | 4.98 ± 1.622 a | 4.38 ± 0.443 c |
| -Mg       | 0.81 ± 0.022 a | 4.45 ± 1.522 b | 3.93 ± 1.193 c |
| -Fe       | 0.81 ± 0.008 a | 3.04 ± 0.285 b | 5.49 ± 0.847 b |
| -Zn       | 0.82 ± 0.018 a | 5.64 ± 0.980 a | 3.66 ± 1.222 c |
| -Mn       | 0.80 ± 0.012 a | 3.59 ± 0.682 a | 5.72 ± 0.509 b |
(Broadley et al., 2012). On the other hand, chlorosis presented in the -Zn treatment, might be explained by the role of Zn in the chlorophyll synthesis (Marschner, 2012).

**Light Response Curves of Photosynthetic Net Carbon Assimilation**

The control plants, supplied with the complete nutrient solution, presented the highest photosynthetic capacity since an adequate supply of nutrients allowed for the highest photosynthetic rates at different densities of photonic flux (Table 3). However, the results for the control plants in our experiment were lower than the ones reported in the field by Rodriguez et al. (2019b) for *Passiflora edulis* Sims f. *edulis*, Pérez-Martínez and Melgarejo (2015) for *Passiflora ligularis* (Fernández et al., 2014) and *Passiflora morifolia* (Pires et al., 2011) because, in the field, the photosynthesis rates were higher due to higher rates of solar radiation as compared to those recorded in the greenhouse conditions of the present study.

Low photosynthesis rates were detected in the N-deprived plants in all points of the light saturation curve, which implied the importance of N for the synthesis of pigments and structural proteins in the photosynthetic apparatus, in which chlorophyll accounts for about 70–80% of the total N, and the formation of light-harvesting complexes, photosynthetic antenna proteins, stroma, thylakoids, and Calvin cycle enzymes (Ding et al., 2005). The low $R_{dark}$ presented in the -N plants (Table 3) could indicate that these plants diminished energy expenditure for growth and directed it toward maintenance of existing biomass (Boussadia et al., 2010), resulting in less mass than in the control; the control plants obtained approximately twice as much biomass than the N-deficient plants at day 72, according to Table 2.

P deficiency could reduce photosynthetic rates as indicated by Maathuis (2009) because P participates in the formation of triose phosphate during carbon fixation; therefore, chloroplasts demand high quantities of inorganic phosphate (Pi) for triose phosphate/phosphate translocators in thylakoids (Hawkesford et al., 2012; Maathuis, 2009). Consequently, the $qPFD$ in the P deficient plants was lower than in the control (Table 3). It has been reported that a P deficiency inhibits photosynthesis by decreasing the activity of the Calvin cycle, especially by affecting the activity of RuBisCO and regeneration of Ribulose-1,5-bisphosphate (Xu et al., 2007). On the other hand, K participates in photosynthesis, enzymatic activation, and regulation of hydric relations (Kazemi, 2014); its deficiency could slow down stomata opening and CO$_2$ absorption (Gonçalves et al., 2005) and, thus, negatively affecting photosynthesis (Table 3).

Magnesium deficiency affects photosynthetic capacity and increases the sensitivity of leaf tissues to light (Hawkesford et al., 2012); this mineral element is a structural component of chlorophyll and an enzymatic cofactor in phosphorylation processes (Marschner, 2012). In addition, during light harvesting and electron transport in thylakoids, the accumulation of H$^+$ occurs in the lumen of chloroplasts, while the separation of the resulting charge is counteracted by the flow of Mg$^{2+}$ from the lumen into the stroma (Maathuis, 2009). This could be the reason why the Mg deficiency affected the photosynthesis rates (Table 3). Sanz et al. (2001) indicated that Ca deficiency modifies the photosynthetic process by reducing the efficiency of carboxylation and, in turn, the general photosynthetic capacity. This is because Ca has several functions in photosynthesis since it modulates the activity of phosphatases in the carbon reduction cycle and regulates the kinase activity in chloroplasts through calmodulin (Marschner, 2012). Additionally, Ca in the stroma of chloroplasts regulates the activity of several enzymes, whereas thylakoid Ca is involved in the structure of PSII (Hochmal et al., 2015).

On the other hand, low values of $qPFD$, $I_c$, and $A_{max}$ in the Zn-deficient plants (Table 3), as compared with the control plants, indicated that the Zn-deficient plants could present a higher capacity of photosynthesis at lower intensities of solar radiation. Wang and Jin (2005) reported a decline in the net rate of photosynthesis and stomatal conductance in corn plants with a Zn deficiency.
The plants deficient in Fe presented low rates of photosynthesis (Table 3), which could be attributed to a deficiency stress that caused a significant reduction in net photosynthesis, altered the activity of the photosystems, and affected amounts of chlorophylls a and b and carotenoids (Bhatla and Lal, 2018). Abadía et al. (2004) reported that, although Fe is not part of the chlorophyll molecule, it is essential for chlorophyll synthesis and ferredoxin, which is an electron acceptor in photosystem I (Bhatla and Lal, 2018); additionally, its deficiency causes alterations in the structure of thylakoid membranes and disrupts the processes of conversion of photochemical energy (Roncel et al., 2016), which is why Fe deficiency severely affects the biosynthesis and maintenance of chlorophyll levels, reducing the photosynthetic capacity per unit area (Terry, 1980).

The low rates of photosynthesis in the Mn-deprived plants (Table 3) could be due to the importance of Mn in the photosynthetic process since this element is present in the PSII, where it catalyzes the reaction of water hydrolysis (Broadley et al., 2012). It also participates in the metabolic activation of different enzymes (Lizarazo et al., 2013b). Henriques (2003) indicated that Mn is involved in lipid metabolism; therefore, its deficiency could negatively affect photosynthesis by inhibiting the synthesis and assembly of thylakoids, which would further reduce the photosynthetic capacity of leaves (Bhatla and Lal, 2018).

**Maximum Photochemical Efficiency of PSII (Fv/fm)**

The purple passion fruit plants presented Fv/Fm values around 0.83, except for the plants subjected to P deficiency (Table 4). The Fv/Fm values 0.83 to 0.78 are typical for functional leaves in a large number of species (Osorio et al., 2014; Rodriguez et al., 2019b), presenting changes at the level of photosystem II and for the maximum photochemical efficiency when subjected to a severe stress; when the stress is not severe, plants have some protection and repair mechanisms, such as with the D1 protein, which protects the photosystems (Nixon et al., 2010).

However, the plants with P deficiency increased leaf fluorescence as a result of the nutrient stress (Baker, 2008; Table 4), which would indicate that this species is more sensitive to the deficiency of P in that phenological stage, significantly affecting the growth and emission of leaves (Table 2). In this regard, Lima et al. (1999) indicated that, under a P deficiency, the photochemical reactions of photosynthesis are affected, which is reflected in increased fluorescence (Table 4) and reduced photosynthetic rates (Table 3). This could be explained by the fact that, after adaptation in the dark, electron acceptors in thylakoids remain in the oxidized state; however, they might not be used in photochemical processes, so the energy dissipates as fluorescence (Conroy et al., 1986).

**Transpiration and Stomatal Resistance**

The plants with K deficiency presented higher stomatal resistance at 72 dat than the control plants (Table 4), similar to that reported by Hawkesford et al. (2012). These results implied that, under the K deficiency, transpiration decreased and stomatal resistance increased because of the role of K+ in stomatal regulation associated with turgor changes in guard cells (Hasanuzzaman et al., 2018). This may explain the low rates of photosynthesis observed in these plants (Table 3), resulting from low rates of stomatal conductivity (Wang et al., 2013). On the other hand, the increase in stomatal resistance under P deficiency generated less transpiration (Table 4), similar to that reported by Veronica et al. (2017), which could be attributed to the conditions of stomatal limitation.

With the absence of N in the nutrient solution, the decrease in transpiration could be explained by the increase in stomatal resistance (Table 4). Zhu et al. (2014) indicated that N deficiency can influence stomatal opening and, therefore, transpiration. The alteration of photosynthesis rates, transpiration, and stomatal opening in the N-deprived plants suggest that the primary metabolism of plants was severely affected (Argyropoulou et al., 2015), thus, altering the accumulation of dry matter and leaf expansion (Table 2). In the Mg-deficient plants, stomatal closure resulted in an increased stomatal
resistance, which affected photosynthesis (Table 3) and transpiration (Table 4). Hariadi and Shabala (2004) indicated that an Mg deficiency reduced stomatal conductance or increased resistance of mesophyll to CO₂ inflow, which diminished the photosynthetic capacity (Table 3), while Kobayashi et al. (2013) indicated a reduction in transpiration rate.

Likewise, for Ca deficiencies, a decrease in the stomatal opening has been reported (Hawkesford et al., 2012), similar to that observed in the present experiment since this mineral element is essential for tonoplast channels (Hawkesford et al., 2012), regulates stomatic movement by oscillations in Ca concentration in the cytosol and is regulated by Ca-dependent protein kinases (Atif et al., 2019). Under a Zn deficiency, stomatal conductance and transpiration rate could be negatively affected (Khan et al., 2004), as found in the present study (Table 4), which can be attributed to Zn involvement in the regulation of stomatal opening since it is required for the maintenance of a high concentration of K in the guard cells (Sharma et al., 1995). When decreasing the stomatal opening, the gas exchange becomes limited, presenting less transpiration, similar to the data reported in Pistacia vera L. grown under a Zn deficiency (Tavallali et al., 2009).

The increase in stomatal resistance that led to the decrease in transpiration in the Fe-deficient plants (Table 4) can be attributed to the accumulation of H₂O₂ in the guard cells leading to stomatal closure mediated by abscisic acid (Bright et al., 2006) or involving a Ca-dependent protein kinase that induces stomatal closure (Zou et al., 2015); this increase in H₂O₂ contents in Fe-deficient plants could be due to the lesser synthesis of antioxidant enzymes, which generated the accumulation of reactive oxygen species (Sharma et al., 2016). The decrease in transpiration caused by the increment in stomatal resistance in the -Mn plants (Table 4) can be associated with the role of Mn in stomatal movement. According to Hayashi et al. (2010), the reversible phosphorylation of the H⁺-ATPase in the cytoplasmatic membrane of stomata is regulated by an Mg²⁺/Mn²⁺ protein located in the membrane and depending on the activity of the 2 C protein (PP2C) in the guard cells, so that the deficiency of Mn could alter the stomatal movement, increasing the stomatal resistance (Table 4).

In the present research, the alterations in the physiological variables and growth, caused by the mineral deficiencies, were evidenced, validating our hypothesis and indicating that an adequate amount of mineral nutrients should be supplied to avoid alterations in the metabolism of purple passion fruit plants. These alterations could negatively impact fruit yield, given that the poor management of mineral nutrition reduces plant growth by affecting metabolic processes and decreases productivity and fruit quality (Aular et al., 2014), such as that the deficiency of N and P reduced the number of fruits per plant in P. edulis f. flavicarpa (Freitas et al., 2006); also, the Ca deficiency impacted fruit quality in terms of fruit firmness, while the K deficiency affected pericarp wrinkling (Freitas et al., 2011). Few studies have evaluated the effect of fertilization on the quality and yield of purple passion fruit (Flechas et al., 2020). For this reason, in the future research, physiological responses of the purple passion fruit under field conditions should be evaluated, so that the reproductive stage of growth can be reached and the effect of mineral deficiencies on fruit production can be observed, which would allow for more efficient fertilizer applications.

**Conclusion**

The deficiencies of macronutrients and micronutrients affected metabolic processes, such as photosynthesis and growth, in the purple passion fruit plants at the vegetative stage of development. Although the responses to the nutrient stress varied between the treatments, the P deficiency had the greatest impact on plant growth since the P-deficient plants decreased the production of leaves and dry matter and reduced the maximum photochemical efficiency of PSII and the variables associated with photosynthesis. For the micronutrients, the greatest effect on plant growth was presented with -Fe, which resulted in the lowest maximum rate of photosynthesis and apparent quantum efficiency, as well as the lowest transpiration. These could indicate a high need for these
nutrients at this phenological stage of purple passion fruit plants, which should be considered in fertilization programs. For the deficiencies of the other mineral nutrients, reductions in dry weight, leaf production and transpiration rate were recorded along with changes in photosynthesis parameters.

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