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Increase in photosynthetic carbon assimilation and gas exchange through foliar application of melatonin in green bean plants

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Abstract

Crop productivity depends largely on photosynthetic efficiency, which is key to converting light energy into assimilates for biomass accumulation. The use of biostimulants such as melatonin (MEL) has emerged as a sustainable alternative to improve internal processes in plants and increase production. However, its effect on beans has not yet been clearly described. This study evaluated the foliar application of MEL on physiological and productive variables of Strike beans (*Phaseolus vulgaris* L.). The plants were grown in vermiculite/perlite substrate (2:1) for 60 d, applying MEL [0, 1, 10, and 100 µM] weekly from 15 d after sowing. All three doses increased biomass and yield; treatment with 100 µM increased biomass by 64.9%, and 1 µM increased yield by 223.7%. Photosynthetic rate and transpiration also improved, with 10 µM being the most effective dose. Finally, sucrose concentration increased by up to 81%. Therefore, the results show MEL as a potential biostimulant for Strike bean production.

Keywords: biomass; biostimulant; carboxylation; melatonin; *Phaseolus vulgaris*; photosynthetic rate.

Introduction

Photosynthesis is the central process in biomass production and can determine up to 90% of crop yield (Yamori 2020). Through the diffusion of carbon dioxide (CO_2) in the stomata and its subsequent fixation in the chloroplasts, plants synthesize carbohydrates which, in the form of sucrose, are transported by the phloem to the growing organs (Xu *et al.* 2015). Due to this central function, any limitation in photosynthetic efficiency directly impacts agricultural productivity (Wu *et al.* 2019).

In this context, the application of biostimulants has been proposed as a sustainable strategy to optimize key physiological processes in plants. Among them, melatonin (N-acetyl-5-methoxytryptamine) has shown positive effects on growth and photosynthesis regulation, both under optimal conditions and under stress (Calvo *et al.* 2014). Previous studies have demonstrated the effect of melatonin (MEL) on photosynthetic capacity in different species (Kuppusamy *et al.* 2023). In legumes, application of MEL has been reported to improve photosynthetic rate, stomatal conductance, transpiration, and the accumulation

Highlights

- Foliar application of melatonin increased yield by 218% in bean plants
- A melatonin dose of 10 µM improved photosynthetic gas-exchange parameters
- Total chlorophyll was not affected by the application of melatonin in beans

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Abbreviations: ABA – abscisic acid; *ANOVA* – analysis of variance; Chl – chlorophyll; DAS – days after sowing; DM – dry mass; FM – fresh mass; LSD – Least significant difference; MEL – melatonin; P_N – net photosynthetic rate; ROS – reactive oxygen species.
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of photosynthetic pigments. For example, in common beans, increases in growth and chlorophyll (Chl) content were observed (Azizi *et al.* 2022); in soybeans under water stress, MEL mitigated the negative effects on gas exchange and photosynthetic efficiency (Zhang *et al.* 2019); and in lentil, foliar application increased biomass, pigment concentration, and photosynthetic parameters (Yasmeen *et al.* 2022).

Although MEL has shown positive effects on key points in the photosynthetic process in various plant species, the physiological and biochemical mechanisms mediated by MEL in beans are not yet fully understood, which limits our understanding of its potential as a biostimulant in this species. Therefore, the objective of this study was to evaluate the effect of foliar application of MEL on biomass, yield, photosynthetic rate, stomatal conductance, transpiration, chlorophyll concentration, and total carbon and soluble sugar contents in ejotero bean (*Phaseolus vulgaris* L.) cv. Strike plants.

Materials and methods

Crop management: The experiment was conducted at the Food and Development Research Center in Delicias, Chihuahua, Mexico (28°11'N, 105°28'W), during September and October 2022, under a 40% shade net. The environmental conditions corresponded to the typical semi-arid climate of the region, characterized by mean daytime temperatures ranging from 27 to 32°C and nighttime minima from 14 to 20°C, according to regional meteorological data obtained from the *WeatherSpark* climate database, corresponding to the 2022 seasonal records for Delicias, Chihuahua (WeatherSpark 2002). The natural photoperiod during this period was approximately 12 ± 1 h of daylight, with mean solar radiation values equivalent to PPFD between 750 and 900 µmol m^{-2} s^{-1} under the shade net at midday. These light intensity estimates align with radiation data reported for northern Chihuahua (Rodríguez Mejia *et al.* 2022).

Strike variety ejotero bean seeds provided by *Hydro Environment*® were used. Four seeds were sown in each pot. The seeds were sown directly in 13-L plastic pots filled with vermiculite and perlite in a 2:1 (v/v) ratio. After emergence, thinning was carried out, leaving two vigorous seedlings per pot to ensure uniform development. During the experiment, the plants were watered with a standard Hoagland nutrient solution adapted to the physiological needs of beans, with a pH of 6 ± 0.1. At 32 d after sowing (DAS), 500 mL of nutrient solution was applied to each pot every 48 h until the flowering stage, and at 53 DAS, 1 L was applied every 48 h until harvest. Melatonin (MEL) was applied foliarly using a hand-held sprayer, ensuring uniform coverage of all leaves on both sides (upper and lower leaf surfaces) until the point of runoff. To prevent direct sunlight exposure, minimize photodegradation, and enhance absorption efficiency under mild temperature and humidity conditions, the applications were performed early in the morning (08:00–09:00 h).

Experimental design: A completely randomized design was used with a single-factor arrangement and four concentrations, corresponding to foliar spray doses of MEL: Control (no MEL application), MEL 1 [1 µM], MEL 10 [10 µM], and MEL 100 [100 µM]. Each treatment had six replicates. The treatments were applied at 15 DAS and then weekly, for a total of five applications.

Yield: At 53 DAS, when plants reached physiological maturity, they were harvested for sampling. One plant per pot was randomly selected and its fresh mass was recorded using a compact balance (*EK-120*, *A&D Co.*, *Ltd.*, Tokyo, Japan). The plant was then separated into leaves, stem, pods, and roots, and the fresh mass of each organ was determined. Yield was expressed as the fresh pod mass per plant [g(FM) per plant].

Biomass: The separated material was rinsed three times with distilled water and dried on filter paper at room temperature for 24 h. It was then oven-dried in a laboratory chamber (*Shel-Lab 1380FX*, Oregon, USA) at 70°C for 24 h. Once the samples had reached constant mass, they were weighed using an electronic analytical balance (*EK-120*, *A&D Co*., *Ltd.*, Tokyo, Japan). Total biomass was expressed as the sum of the dry mass of the four plant organs [g(DM) per plant].

Photosynthetic pigments: Fresh leaf samples were taken to quantify the photosynthetic pigments in the leaves. Ten discs were taken from the leaf blade of different leaves (avoiding veins) using a 7-mm diameter metal punch. Their mass was measured using an electronic analytical balance (*EK-120*, *A&D Co*., *Ltd.*, Tokyo, Japan), and they were placed in a test tube with 10 mL of pure methanol (CH_3OH). The tubes were double-sealed with *Parafilm*® thermoplastic olefin self-sealing film. The samples were then shaken with a standard heavy-duty vortex mixer (*945300, VWR*, New Jersey, United States) and left to stand for 24 h in complete darkness. After this period, the samples were shaken again for 1 min, and their absorbance was measured with a UV-visible spectrophotometer (*GENESYS™ 10S*, *Thermo Fisher Scientific*, Wisconsin, United States). A wavelength of 666 nm was used for the quantification of Chl *a*, 653 nm for Chl *b*, and the sum of Chl *a* plus Chl *b* is total Chl. Pigment concentrations were calculated according to the solvent used (methanol) with the following formulas and expressed in micrograms of pigment per square centimeter [µg cm^{-2}]:

$$\text{Chl } a = (15.65 \times ABS_{666}) - (7.34 \times ABS_{653})$$

$$\text{Chl } a^* = (\text{Chl } a \times V_1 \times P_1)[P_2 \times (\pi \times r^2) \times n]$$

$$\text{Chl } b = (27.05 \times ABS_{653}) - (11.21 \times ABS_{666})$$

$$\text{Chl } b^* = (\text{Chl } b \times V_1 \times P_1)[P_2 \times (\pi \times r^2) \times n]$$

$$\text{Total chlorophyll} = \text{Chl } a^* + \text{Chl } b^*$$

where ABS_{666} is equal to the absorbance obtained in the spectrophotometer at 666 nm; ABS_{653} is equal to

the absorbance obtained in the spectrophotometer at 653 nm; ABS_{470} is equal to the absorbance obtained in the spectrophotometer at 470 nm; V_1 is equal to the extraction volume; P_1 is equal to the mass in grams per leaf disc; P_2 is equal to the total mass of the leaf discs; r is equal to the radius of the punch, and *n* is equal to the number of leaf discs weighed.

Total carbon: An organic elemental analyzer (*FLASH 2000*, *Thermo Fisher Scientific*, Massachusetts, United States) was used to quantify total carbon, following the methodology described by Krotz and Giazzi (2014) and adapted for plant material. 0.3 mg of ground plant material (leaf tissue) was weighed into a soft tin microcontainer using an ultra-microbalance (*XP6 Excellence Plus XP*, *Mettler Toledo*, Ohio, USA), after which 9 mg of vanadium pentoxide (V_2O_5) was added before sealing. The sealed capsules were then loaded into the automatic sampler carousel for analysis. The results were expressed as a percentage of total carbon [%].

Photosynthetic rate, stomatal conductance, and transpiration: Photosynthetic activity and gas exchange were measured in the leaves when the plant reached physiological maturity, between 10:00 and 11:00 h. A portable *LI-COR 6400* meter (Lincoln, Nebraska, USA) was used, and a healthy leaf with uniform color and free of damage was selected from each plant. A concentration of 400 µmol mol^{-1} of CO_2 was used in the reference cell, while the sample cell was maintained at approximately 380 µmol mol^{-1} of CO_2. The air vapor pressure deficit in the sampling chamber was less than 1.5 kPa, and the temperature of the block housing the leaf was 25°C. Photosynthetic activity was expressed as µmol(CO_2) m^{-2} s^{-1}, and stomatal conductance was reported as mol(H_2O) m^{-2} s^{-1}. Transpiration was reported as mmol(H_2O) m^{-2} s^{-1}.

Sucrose: Leaf samples for sucrose quantification were collected between 8:00 and 9:00 h from fully developed leaves and immediately stored at –20°C until analysis, to minimize light variation in soluble sugar concentrations.

Extraction to determine sucrose concentration was performed following the methodology proposed by Irigoyen *et al.* (1992). An amount between 0.25–0.5 g of fresh plant material (leaf tissue) was homogenized with 5 mL of 96% ethanol, and then rinsed twice with 5 mL of 70% ethanol. The resulting homogenate was centrifuged at 5,500 rpm for 10 min, and the resulting supernatant was used to determine concentrations of proline and soluble sugars. The concentration of soluble sucrose was expressed as mg g^{-1}(FM).

Statistical analysis: Once the data were obtained, they were subjected to a *Shapiro–Wilk*'s test to check for normal distribution. In addition, they were subjected to a *Bartlett*'s test to check for homogeneity of variances. Once the assumptions were verified, the data were subjected to a one-way analysis of variance (*ANOVA*) and a test of separation of means using *Fisher*'s LSD test. The *SAS 9.0* statistical package was used for the statistical analyses. Different letters indicate statistically significant differences according to *Fisher*'s LSD test ($p \leq 0.05$). Significance level:*: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

Results and discussion

Biomass: A key variable for determining the effectiveness of the treatments is the quantification of accumulated dry biomass (Sánchez Chávez *et al.* 2006). In the present study, significant differences were found in total biomass accumulation due to the application of MEL (Fig. 1*A*). The most favorable treatment was MEL 100, with a significant increase of 64.9% compared to the control, followed by the MEL 1 treatment, with a significant increase of 57.7% compared to the control (Fig. 1*A*). However, although the increase in biomass accumulation was slightly greater when the MEL dose was increased from 1 to 100 µM, there was no significant difference between these treatments (7.2%), so the most efficient option was treatment MEL 1. The data obtained in this study are consistent with those obtained by Ahmad *et al.* (2022), who reported a 71.1% increase in total dry biomass of corn seedlings when a dose of 100 µM melatonin was

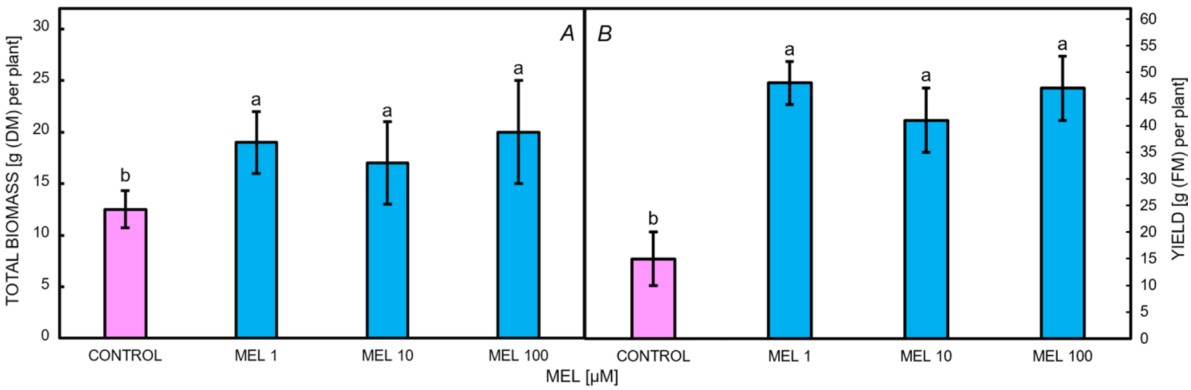

Fig. 1. Effect of foliar application of melatonin on biomass (*A*) and yield (*B*) of green bean plants. Columns are the means of three replicates ± standard error ($n = 3$), and *different letters* above the error bars indicate a significant difference according to *Fisher*'s LSD test ($p \leq 0.05$).

applied to corn seedlings fertilized with an optimal nitrogen dose. Other authors, such as Qiao *et al.* (2019), indicated that corn seedlings treated with 1 µM MEL increased their dry biomass by 50.6% at 28 DAS under sufficient nitrogen conditions compared with untreated plants.

Yield: Yield is closely related to biomass production and the physiological status of plants, making it a reliable indicator of the effectiveness of applied treatments (Salcido-Martínez *et al.* 2020). The data obtained in this research study showed significant differences in yield as a result of MEL application (Fig. 1*B*). The treatment that obtained the highest pod production was MEL 1, which increased by 223.7% compared to the control, with no significant differences when the dose was increased 10 times and 100 times. MEL has been related to the regulation of endogenous growth promoters such as auxin. This regulation has been described as accelerated growth in the root zone. When root architecture is modified by the action of MEL, nutrient and water absorption are promoted (Sukumar *et al.* 2013). Adequate mineral supply and proper water absorption ultimately increase the plant's ability to produce biomass and yield. As shown in Fig. 1*B*, plants with higher biomass accumulation were also able to produce the highest fruit biomass. In addition, the application at the lowest doses (1 µM) was the most effective, achieving a 2.2-fold increase in yield compared to the control.

Total Chl: The quantification of total Chl in bean plants is essential as a physiological indicator because it provides direct information on the functional status of the photosynthetic apparatus, the overall health of the plant, and its ability to perform photosynthesis efficiently (Mathobo *et al.* 2017). In the present study, no significant differences in total Chl concentration were found as a result of MEL application (Fig. 2*A*). Although a slight decrease in Chl content was observed with increasing MEL doses, no statistically significant differences (p>0.05) were found between treatments. These results suggest that MEL, within the concentration range tested, did not significantly alter chlorophyll biosynthesis or degradation in this study. This is consistent with previous studies indicating that low to moderate concentrations of MEL often do not affect Chl contents under non-stressful conditions (Arnao and Hernández-Ruiz 2014, Zhang *et al.* 2014).

Photosynthetic rate: Another complementary variable is the photosynthetic rate (P_N). This variable directly evaluates the plant's ability to capture atmospheric carbon and convert it into biomass, a key process for crop growth, development, and yield (Xu *et al.* 2015). In the present study, significant differences in P_N were found as a result of MEL application (Fig. 2*B*). The treatment with the highest rate was MEL 10, which recorded an 86% increase compared to the control. The MEL 1 and MEL 100 treatments also resulted in significant increases compared to the control, although they were lower than those of MEL 10. These results suggest that MEL, especially at intermediate concentrations, can improve photosynthetic performance, possibly by improving stomatal conductance, antioxidant activity, or photosystem efficiency. This result is consistent with previous studies (Arnao and Hernández-Ruiz 2014, Zhang *et al.* 2014). The decrease observed at 100 µM may indicate a threshold beyond which MEL loses its stimulating effect or begins to exert negative feedback, a trend consistent with other dose-response studies in plants (Ahmad *et al.* 2021).

Stomatal conductance and transpiration rate: Evaluating stomatal conductance and transpiration rate in bean plants is crucial because these physiological parameters are closely related to gas exchange, water balance, and photosynthetic efficiency in plants (Muhammad *et al.* 2024). In the present study, statistically significant differences were found in both variables due to the application of MEL (Table 1). In general, the results were consistent with the obtained P_N data (Fig. 2*B*). The treatment with the highest values was MEL 10, which recorded a 6- and 4.6-fold increase compared to the control in stomatal conductance and transpiration rate.

Likewise, the lowest conductance was observed in untreated plants, indicating restricted stomatal opening. These results suggest that moderate MEL concentrations

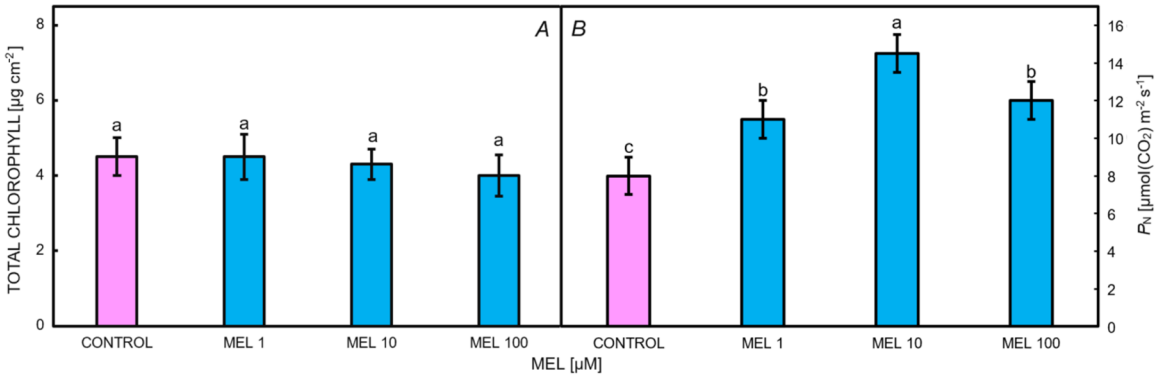

Fig. 2. Effect of foliar application of melatonin on total chlorophyll concentration (*A*) and photosynthetic rate, P_N (*B*) in green bean plants. Columns are the means of three replicates ± standard error (n = 3), and *different letters* above the error bars indicate a significant difference according to *Fisher*'s LSD test (p≤0.05).

can promote stomatal opening, thus facilitating CO_2 absorption and improving photosynthetic performance. This result is consistent with previous findings indicating that MEL can modulate stomatal behavior, possibly through interactions with abscisic acid (ABA) and reactive oxygen species (ROS) signaling pathways (Sharma *et al.* 2020). The significant increase in stomatal conductance at 10 µM is consistent with the peak observed in P_N under the same treatment, reinforcing the functional link between stomatal regulation and photosynthetic efficiency.

In the case of transpiration rate, the lowest values were observed in untreated plants (Table 1). These data suggest that MEL increases water vapor loss through stomata, which is consistent with its observed effect on stomatal conductance and supports the idea that MEL modulates stomatal dynamics. Increased transpiration may contribute to improved leaf cooling and nutrient transport under non-stressful conditions or may reflect greater stomatal opening that also facilitates CO_2 uptake for photosynthesis (Zhang *et al.* 2019). However, the decrease in transpiration at 100 µM relative to MEL 10 indicates a potential concentration threshold above which the stimulating effects of MEL on stomatal behavior are reduced.

When compared to the control, both stomatal conductance and transpiration rate exhibited a parallel response pattern, showing notable increases at moderate MEL concentrations (10 µM), suggesting improved stomatal opening and CO_2 exchange. Under non-stressful conditions, this coordinated stimulation implies that MEL efficiently regulates stomatal dynamics, enhancing gas exchange and photosynthetic efficiency. As is consistent with its dose-dependent physiological function, the decrease in both parameters at higher concentrations (100 µM) suggests a threshold beyond which MEL's regulatory effect on stomatal behavior diminishes.

Table 1. Effect of foliar application of melatonin (MEL) at doses of 0, 1, 10, and 100 µM on stomatal conductance [mol(H_2O) m^{-2} s^{-1}] and transpiration rate [mmol(H_2O) m^{-2} s^{-1}] in green bean plants. Results are the means of three replicates ± standard error (n = 3), and *different upperscript letters* indicate a significant difference according to *Fisher*'s LSD test (p≤0.05).

	Stomatal conductance [mol(H_2O) m^{-2} s^{-1}]	Transpiration rate [mmol(H_2O) m^{-2} s^{-1}]
CONTROL	0.0066 ± 0.001^{d}	0.2565 ± 0.049^{c}
MEL 1 µM	0.0197 ± 0.006^{c}	0.7035 ± 0.183^{b}
MEL 10 µM	0.0425 ± 0.012^{a}	1.4777 ± 0.368^{a}
MEL 100 µM	0.0312 ± 0.011^{b}	1.0788 ± 0.355^{ab}

Total carbon and sucrose concentration: In addition, leaf carbon and sucrose concentrations were evaluated as products of the photosynthesis process. For carbon concentration, no statistically significant differences were found (Fig. 3*A*), whereas the sucrose concentration did show statistically significant differences (p<0.05) due to the effect of MEL application on bean plants (Fig. 3*B*). Nevertheless, the plants supplied with the MEL 10 treatment obtained the highest foliar carbon concentration, being 1.4% higher than the control. These results suggest that MEL, regardless of its concentration, did not significantly alter the accumulation of structural or metabolic carbon in leaves under controlled conditions for bean cultivation. Carbon content is generally stable in plant tissues and reflects the balance between carbon fixation and allocation (Xing *et al.* 2021). The lack of variation may imply that, although MEL modified stomatal conductance, photosynthetic rate, and transpiration (as shown in Fig. 2*B* and Table 1), it did not result in a measurable change in total leaf carbon, possibly due to the short duration of the treatment or compensatory mechanisms that regulate carbon use and storage (Lobo *et al.* 2013). This result is consistent with previous findings in which MEL influenced physiological processes without significantly affecting elemental composition (Ahmad *et al.* 2021).

For sucrose, the three MEL treatments increased the concentration in bean plants. However, plants receiving the MEL 100 treatment exhibited the highest sucrose concentration, showing an 81% increase compared to the control. Thus, the results reported for sucrose concentration are consistent with previous findings indicating that MEL can increase sugar accumulation by stimulating photosynthetic activity and improving the translocation of photoassimilates (Arnao and Hernández-Ruiz 2014, Zhang

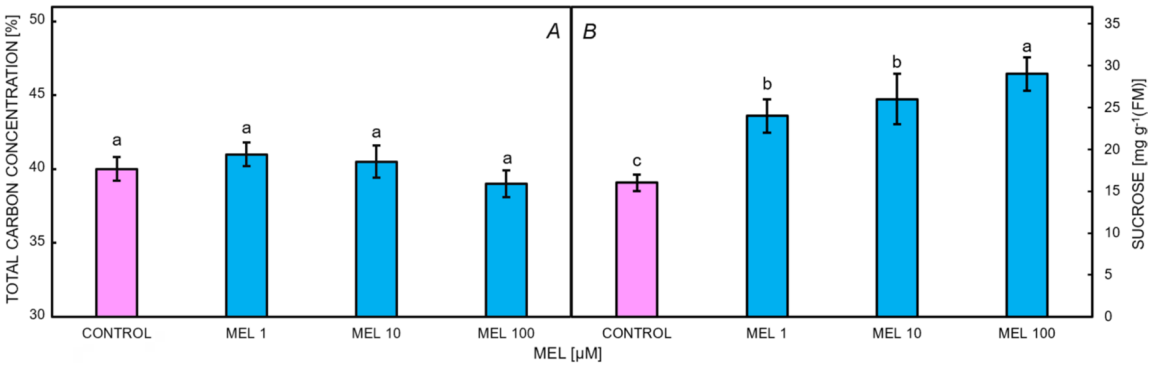

Fig. 3. Effect of foliar application of melatonin on leaf tissue carbon concentration (*A*) and leaf tissue sucrose concentration (*B*) in green bean plants. Columns are the means of three replicates ± standard error (n = 3), and *different letters* above the error bars indicate a significant difference according to *Fisher*'s LSD test (p≤0.05).

et al. 2014). The increase in foliar sucrose observed in the present study is consistent with the increase in P_N (Fig. 2*B*) and stomatal conductance (Table 1), reinforcing the hypothesis that MEL promotes source activity in leaves. The increase in sucrose content may play a key role in supporting plant energy demands, osmoregulation, and stress resistance (Zhong *et al.* 2020).

Conclusion: Foliar application of melatonin positively affected growth and yield, enhancing photosynthetic carbon assimilation and gas exchange through increases in photosynthetic rate, stomatal conductance, and transpiration rate in Strike bean plants. Overall, the 10 μM dose produced the most outstanding effects, acting as a biostimulant, and promoting favorable increases in the aforementioned variables at low doses, especially in photosynthetic rate and stomatal conductance, compared to the lowest (1 μM) and highest (100 μM) doses. Despite these findings, further studies are needed to clarify the role of melatonin as a biostimulant and its effect on photosynthetic parameters in legumes under field conditions.

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