

Light quality and zinc concentrations interfere with the *in-vitro* cultivation of *Selenicereus undatus*

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ABSTRACT: The cultivation of pitahaya (*Selenicereus undatus*) has attracted increasing interest due to its hardiness, early fruiting, economic value, and medicinal potential. However, low propagation rates remain a limitation for commercial-scale production. This study aimed to evaluate the effects of different spectral light qualities (white, blue, purple and red LEDs) and zinc (Zn) concentrations (8.60 and 17.20 mg·L⁻¹) on the growth, pigment content, anatomy, and Zn deposition in *S. undatus* cladodes *in vitro*. Biometric parameters, photosynthetic pigments, anatomical features, and energy-dispersive X-ray spectroscopy analysis were assessed. White and purple lights, combined with 8.60 mg·L⁻¹ Zn, led to greater shoot length and higher fresh and dry mass of roots and shoots. White light also increased total chlorophyll content at both Zn concentrations. The number of vascular bundles increased with 17.20 mg·L⁻¹ Zn, especially under purple light. The largest cladode cross-sectional area was observed under red light with high Zn concentration. Zn accumulation was low, with slightly higher atomic percentages in central ribs (0.30%) and at the margins (0.77%) under white light and high Zn concentration treatment, suggesting limited translocation and possible compartmentalization in vacuoles or apoplastic spaces. Stomatal density appeared to be modulated by both factors, increasing under red light and decreasing under blue light, depending on Zn concentration. Overall, white and purple LED lights with 8.60 mg·L⁻¹ Zn optimized *S. undatus* growth and pigmentation *in vitro*. These findings enable improved micropropagation protocols for commercial production and potential biofortification strategies.

Key words: antioxidant activity, micropropagation, photomorphogenesis, photosynthetic pigments, pitahaya.

INTRODUCTION

Pitahaya is an exotic fruit that belongs to the Cactaceae family. Its cultivation has aroused the interest of many producers and researchers due to its hardiness, early production, high economic yield and medicinal properties, as it can reduce the incidence of certain diseases such as diabetes, cancer, inflammation, and heart problems (Trivellini et al. 2020, Jiang et al. 2021). Pitahaya cultivation has gained increasing economic importance globally, particularly in tropical and subtropical regions of Asia, Latin America, and the Middle East, driven by growing consumer demand for exotic functional foods (Le Bellec et al. 2006, Mizrahi 2014).

Among the best-known pitahaya species is *Selenicereus undatus*, which produces red-skinned fruit with white flesh (Oo et al. 2023). While betalains are most abundant in red or pink-fleshed species, the peel of *S. undatus* also contains these natural pigments, though at lower concentrations than in the pulp of red-fleshed varieties. Moreover, it has greater economic importance compared to other species of *Selenicereus* genus.

While *S. undatus* propagates readily from stem cuttings, the growing commercial demand for pitahaya requires more efficient propagation methods than conventional techniques can provide. However, production expansion remains constrained by the limited availability of high-quality planting material, as conventional propagation methods yield only 2–3 viable cuttings per mother plant annually (Mizrahi 2014). *In-vitro* micropropagation has emerged as a biotechnological approach to overcome these limitations by enabling year-round, large-scale multiplication, achieving 10–12 shoots per explant (Cristina et al. 2023), in contrast to the seasonal dependence of conventional cuttings.

Moreover, the production of disease-free plantlets under aseptic conditions effectively eliminates pathogen transmission commonly associated with field-derived cuttings, while the reduced spatial requirements and simplified transport logistics make this technique economically feasible for commercial cultivation (Zakaria 2022, Al-Qthanin et al. 2024). Despite these advantages, the *in-vitro* environment may induce genetic variation (Chu and Chang 2022). Consequently, recent research has focused on assessing biometric and anatomical parameters under controlled conditions to refine micropropagation protocols that enhance propagation efficiency while ensuring genetic fidelity (Kulus and Woźny 2020, Torres-Silva et al. 2020, Lee and Chang 2022).

The *in-vitro* tissue culture technique has been used for the vegetative propagation of the pitahaya, with micropropagation being the main biotechnological tool used, which makes it possible to multiply plants on a large scale in a nutritionally and environmentally controlled environment (Cristina et al. 2023, Clairvil et al. 2025). Light quality is one of the environmental factors that most influences tissue culture, directly interfering in the production of pitahaya seedlings *in vitro* (Huang et al. 2022).

Despite advances in *in-vitro* propagation, suboptimal lighting remains a critical constraint in commercial facilities. Traditional fluorescent lamp systems, still widely used due to lower costs, provide inefficient spectral output with excessive heat generation, resulting in etiolated shoots and poor acclimatization rates (Lazzarini et al. 2018). While LED technology offers precise spectral control, high capital costs and lack of standardized protocols limit its widespread adoption in *in-vitro* propagation systems, particularly in developing regions where pitahaya cultivation is economically significant (Dutta Gupta and Jatothu 2013).

One previous study indicated that pitahaya grown *in vitro* under red light had lower biomass production, stem and cross-sectional diameter, as well as disturbances in photosynthetic activities (Winson et al. 2021).

The negative effects caused by some qualities of light can be mitigated by the use of adequate concentrations of minerals such as zinc (Zn) (Da Cruz et al. 2019). Zn is one of the essential components for the production of enzymes that act in photosynthesis, cell division, and root growth. It also enhances the tolerance of the plant's photosynthetic apparatus to different light qualities (Rai-Kalal and Jajoo 2021, Karmous et al. 2023).

Moreover, pitahaya cultivation increasingly occurs in Zn-deficient tropical soils (affecting 30–50% of agricultural lands globally), in which plants with standard *in-vitro* Zn nutrition may exhibit poor field establishment (Alloway 2009, Çakmak and Kutman 2018). Zn serves essential roles as a carbonic anhydrase cofactor and structural component of stress-regulatory transcription factors (Broadley et al. 2007). Therefore, investigating Zn supplementation during micropropagation enables pre-conditioning plantlets through biofortification for establishment in Zn-limited soils and exploring synergistic Zn-light interactions that may enhance explant quality beyond individual factor effects.

The aim of this study was to evaluate the biometric characteristics, photosynthetic pigments, cladode anatomy, and energy-dispersive X-ray spectroscopy of pitahaya (*S. undatus*) plants grown *in vitro* under different light qualities and Zn concentrations in the growing medium.

MATERIAL AND METHODS

The experiment was conducted at the Plant Tissue Culture Laboratory of the Department of Agriculture at the Universidade Federal de Lavras, in Lavras, Minas Gerais, Brazil.

Plant material and *in-vitro* culture

Cladodes of pitahaya (*S. undatus*), 1.5-cm long, were grown in 250-mL flasks with 50 mL of MS medium (Murashige and Skoog 1962), 30 g·L⁻¹ of sucrose and two concentrations of zinc: 8.60 mg·L⁻¹ (standard MS concentration, used as control)

or $17.20 \text{ mg}\cdot\text{L}^{-1}$ ($2\times$ MS concentration), supplied as $\text{ZnSO}_4\cdot 7\text{H}_2\text{O}$. The pH of the media was adjusted to 6.0 ± 0.2 , and they were autoclaved at 121°C and 1.2 atm for 20 min.

Five cladodes per flask were inoculated in a laminar flow chamber, with a total of 20 flasks per treatment (100 explants per treatment). The flasks were kept in a growth room at $25 \pm 2^\circ\text{C}$ for eight weeks under a 16-hour photoperiod using LED lamps (Empalux FT8 HO, 36W/6400K) of different light qualities (white: WL, blue: BL, purple: PL, and red: RL), with a light intensity of $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of photosynthetically active radiation.

The estimation of photosynthetic photon flux density (PPFD) was obtained through illuminance (lux) measurements performed with a digital lux meter (Politem, model POL-10B). Measurements were taken at three different positions on the cultivation surface (left, center, and right), approximately 3 cm above the culture flasks. The values obtained were averaged using the arithmetic mean and then converted into PPFD based on specific conversion factors for each light spectrum, according to the spectral characteristics of the LED light sources used.

The estimated PPFD values for each light quality were as follows: white light (WL): $2.41 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; blue light (BL): $3.07 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; purple light (PL), composed of a combination of blue (450 nm) and red (650 nm) wavelengths: $2.16 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; and red light (RL): $1.99 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Biometric characteristics

The biometric characteristics, aerial part length, and fresh and dry masses of the aerial part and root were evaluated after eight weeks of *in-vitro* cultivation in five plants collected at random from each treatment.

The length of the aerial part was measured with a millimeter ruler. The dry masses of the root and aerial part were obtained after drying the fresh material at 65°C for 72 hours in an oven with forced air circulation. The fresh and dry masses were quantified on a precision scale with four decimal places (OHAUS model PR224BR), and the dry masses were quantified after the temperature of the materials had stabilized in a Styrofoam box.

Photosynthetic pigments

Photosynthetic pigments were analyzed using cladodes ($\pm 0.050 \text{ g}$) from five *S. undatus* plants randomly collected from each treatment after eight weeks of *in-vitro* cultivation. The cladodes were transferred to test tubes with 5 mL of 80% acetone for the extraction of chlorophylls and carotenoids. The tubes were wrapped in aluminum foil to prevent chlorophyll degradation.

Samples were stored in a refrigerator at $4 \pm 2^\circ\text{C}$ for 24 hours prior to analysis. Absorbance was then measured at room temperature using an Elisa Multiskan GO spectrophotometer (Thermo Fisher Scientific) calibrated before analysis at wavelengths of 470 (Abs_{470}), 647 (Abs_{647}), and 663 nm (Abs_{663}) (Scopel et al. 2011). The contents of chlorophyll *a*, chlorophyll *b*, total chlorophyll, and carotenoids were determined using equations (Lichtenthaler and Wellburn 1983, Lichtenthaler and Babani 2021).

The wavelength measurements were made in two replicates per treatment, with each one evaluated in triplicate. The triplicate used corresponds to technical repetitions. The analysis was carried out using Skanit Software 5.0 for Microplate Readers, version 5.0.0.42.

Anatomical analysis

The anatomical analysis was carried out on cladodes collected at random from five plants per treatment and eight weeks after *in-vitro* cultivation. The cladodes were fixed in FAA solution (formaldehyde, acetic acid, and 50% ethanol in a ratio of 0.05:0.05:0.90) for 72 hours and bleached with 70, 80, 90, and 100% alcohol at 2-hour intervals (Johansen 1940, Clairvil et al. 2025). The cladodes were immersed in a solution of 50% alcohol and 50% pure resin for 72 hours, fixed with pure resin and hardened in a solution of 15% pure resin plus 1% hardener to facilitate cutting.

Atomic analysis was carried out on five cross-sections per plant, with 9- μm -thick sections made using a semi-automatic rotary microtome (MRS 3500), stained with Toluidine blue solution (0.05%) and mounted on glycerin gelatine as permanent slides.

The anatomical analyses carried out were counting the number of vascular bundles and the cross-sectional area (mm^2). The sections were observed under a light microscope (Nikon, Eclipse E100) coupled to a digital camera (Infinity) to capture the images. Photomicrographs were used to measure the anatomical characteristics (using the 4x objective to observe the cross-sectional area of the cladodes and 10x for the number of vascular bundles) with the aid of software (UTHSCSA-Imagetool) and calibrated with a microscope. Due to the size of the images compared to the microscope camera, each cross-section of the cladodes was photographed in two parts (top and bottom) to make it easier to measure the area.

Energy-dispersive X-ray spectroscopy

Fresh cladode samples from *S. undatus* plants cultivated *in vitro* with 8.60 or 17.20 $\text{mg}\cdot\text{L}^{-1}$ of Zn were collected and mounted on aluminum stubs using double-sided carbon tape, then dried in an oven at 70°C for 12 hours. After this procedure, the samples were transferred to a desiccator containing silica gel, in which they remained for 24 hours. Energy-dispersive X-ray mapping was performed using a TESCAN-CLARA (Czech Republic), equipped with an energy-dispersive X-ray spectroscopy detector (Bruker, Quantax EDX, model XFlash Detector 6|60), based on spectroscopic emissions under an applied voltage of 20 kV, at magnifications of 200 $\times$ and 400 $\times$.

Due to cost and logistical limitations associated with sample collection and handling, it was not possible to perform multiple replicates for all treatments. Therefore, representative cladodes from each treatment were selected for analysis. The microanalyses by X-ray spectroscopy included the determination of the percentage of chemical elements (atomic percentage) contained in the *S. undatus* cladodes, focusing on the central ribs and rib margins. Additionally, stomatal density (mm^2) was evaluated using three distinct samples.

Statistical analysis

The experimental design was completely randomized in a 2×4 factorial scheme, with two Zn concentrations (8.60 or 17.20 $\text{mg}\cdot\text{L}^{-1}$) and four LED light qualities (WL, BL, PL, and RL), totaling eight treatments. Each treatment consisted of 20 independent replicates (flasks), with each flask containing five cladodes and representing one experimental unit. Measurements were taken from individual cladodes within each flask, and the mean value per flask was used for statistical analysis. Data were subjected to analysis of variance (ANOVA), and means were compared using the Scott-Knott's test ($p < 0.05$) using SISVAR software, version 5.6 (Ferreira 2011).

RESULTS AND DISCUSSION

After eight weeks of *in-vitro* exposure of *S. undatus* plants to different LED light qualities (WL, BL, PL, and RL), significant interactions between factors (Zn $\times$ light) were observed for multiple growth, biochemical, and anatomical parameters. Growth-related variables included shoot length, shoot fresh mass and dry mass, and root fresh mass and dry mass. Biochemical parameters encompassed chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), total chlorophyll (Chl *T*), and carotenoid (Car) contents. Anatomical characteristics included the number of vascular bundles, cladode cross-sectional area, atomic percentage of chemical elements (Elem., %), and stomatal density (SD, in mm^2) (Tables 1, 2, 3, 4, and 5; Figs. 1, 2, 3, and 4).

The length of the aerial part of the *S. undatus* plants was greater under WL, regardless of the concentration of Zn, and in PL, with 8.60 $\text{mg}\cdot\text{L}^{-1}$ of Zn in the medium (Table 1).

The higher length of the aerial part of *S. undatus* plants under WL is related to its biological effects on plants, being considered a trigger signal that regulates the growth and development of plant tissues or organs (Li et al. 2013, Zhao et al. 2020, Araújo

et al. 2021). The highest length of the aerial part observed under PL, with 8.60 mg·L⁻¹ of Zn, may be related to the activation of genetic and metabolic processes, which influence the signaling of light receptor phytochromes, responsible for regulating plant growth and development (Weremczuk-Jeżyna et al. 2021). On the other hand, the lower length of the aerial part of the plants under BL, PL and RL, in a medium with 17.20 mg·L⁻¹ of Zn, may have occurred due to a combination of stresses caused both by the wavelengths of each quality of light and by the higher concentration of Zn, which may have made the growth medium more saline at the higher concentration, impairing the absorption of water and nutrients (Akin 2021, Sarropoulou et al. 2023).

Table 1. Length (LAP), fresh mass (FMAP) and dry mass (DMAP) of the aerial part, fresh mass (FMR) and dry mass (DMR) of the roots, in g·plant⁻¹, of *Selenicereus undatus* at eight weeks of *in-vitro* cultivation, as a function of zinc (Zn) concentrations (8.60 and 17.20 mg·L⁻¹) and light quality (white, blue, purple and red)*.

	Zn	Light quality				C.V.
		White	Blue	Purple	Red	
LAP	8.60	3.620 ^{0.3797} Aa	2.060 ^{0.0991} Ba	3.140 ^{0.3842} Aa	2.075 ^{0.1831} Ba	31.3
	17.20	3.730 ^{0.2667} Aa	2.550 ^{0.2320} Ba	3.120 ^{0.3112} Ba	2.670 ^{0.2971} Ba	
FMAP	8.60	1.584 ^{0.0051} Ba	0.926 ^{0.1099} Da	2.070 ^{0.0375} Aa	1.352 ^{0.1440} Ca	14.0
	17.20	1.616 ^{0.0093} Aa	1.096 ^{0.1028} Ba	1.424 ^{0.1005} Ab	1.126 ^{0.0843} Ba	
DMAP	8.60	0.058 ^{0.0074} Ba	0.034 ^{0.0039} Ca	0.078 ^{0.0028} Aa	0.052 ^{0.0041} Ba	20.9
	17.20	0.056 ^{0.0024} Aa	0.042 ^{0.0060} Ba	0.036 ^{0.0030} Bb	0.048 ^{0.0035} Ba	
FMR	8.60	0.184 ^{0.0042} Aa	0.070 ^{0.0180} Ca	0.196 ^{0.0173} Aa	0.132 ^{0.0238} Ba	24.5
	17.20	0.164 ^{0.0057} Aa	0.090 ^{0.0111} Ba	0.220 ^{0.0188} Aa	0.135 ^{0.0230} Aa	
DMR	8.60	0.016 ^{0.0011} Aa	0.004 ^{0.0011} Ba	0.016 ^{0.0031} Aa	0.008 ^{0.0022} Ba	42.7
	17.20	0.018 ^{0.0013} Aa	0.010 ^{0.0007} Aa	0.014 ^{0.0012} Aa	0.010 ^{0.0006} Aa	

*Averages (± standard error) followed by the same uppercase letter in the row (light quality) and lowercase letter in the column (Zn concentration) do not differ by the Scott-Knott's grouping test ($p < 0.05$); C.V.: coefficient of variation (%).

The fresh mass and dry mass of the aerial part of *S. undatus* plants differed between Zn concentrations only for the PL quality, with the highest value at 8.60 mg·L⁻¹ of Zn. Among the light qualities, PL, regardless of Zn concentration, and WL with 17.20 mg·L⁻¹ of Zn, gave the highest averages (Table 1).

The higher fresh mass of *S. undatus* plants under PL and Zn may be due to the combination of the length of the light and the concentrations of this mineral, which together influence the regulation of plant metabolism, photosynthesis and cell growth (Hacisalihoglu 2020). In addition, the concentration of 8.60 mg·L⁻¹ of Zn may increase the efficiency of purple light in the accumulation of fresh biomass, which corroborates the results of other studies in which an increase in biomass was observed in plants of *Oryza sativa*, *Lactuca sativa*, and *Cucumis sativus* under the same quality of light (Lim et al. 2023). A similar result was also observed for the fresh mass of potato seedlings grown *in vitro* under WL (Khalil et al. 2023).

The PL combined with the lower Zn concentration boosted growth, promoting greater dry mass, with biomass accumulation and higher carbohydrate content (Lee and Nam 2023). Together, these two factors may have led to greater photosynthetic and photochemical efficiency, contributing to an increase in the mass of *S. undatus* plants (Yu et al. 2017, Xu et al. 2020). The combination of 17.20 mg·L⁻¹ of Zn with WL can also optimize mass accumulation in plants, possibly due to variations in photosynthetic activity and metabolic demands (Wei et al. 2022).

This effect can be explained by the fact that Zn is a structural and catalytic cofactor of key enzymes involved in protein synthesis, carbohydrate metabolism, and ribosome stability processes essential for plant growth. Additionally, Zn activates carbonic anhydrase, a key enzyme in CO₂ fixation during photosynthesis, thereby increasing photosynthetic efficiency and biomass accumulation (Singh et al. 2019).

The fresh root mass of *S. undatus* plants did not differ between Zn concentrations for each quality of light, but was higher under PL and WL, regardless of Zn concentration, and in RL for the highest concentration of that mineral (Table 1).

The higher fresh root mass observed under WL suggests that a greater amount of energy was directed towards root development (Zheng et al. 2019), while PL enabled plant growth by reducing the accumulation of reactive oxygen species

(Saleem et al. 2019). In addition, the increase in root fresh mass under these conditions may be related to the improvement in enzymatic function and metabolism provided by Zn ($8.60 \text{ mg}\cdot\text{L}^{-1}$), and the combination of PL or WL with this mineral may also influence the synthesis and distribution of auxins and other phytohormones that regulate root growth (Suganya et al. 2020, Hamzah Saleem et al. 2022).

The root dry mass of the *S. undatus* plants did not differ between Zn concentrations for each quality of light, but it was higher under PL and WL for the concentration of $8.60 \text{ mg}\cdot\text{L}^{-1}$ of Zn, and did not differ between qualities of light for the highest concentration of this mineral (Table 1).

The absence of a difference in root dry mass between Zn concentrations, for each light quality, suggests that the plants may have reached a saturation point in the use of Zn, in which additional concentrations do not result in more benefits for root growth (Balafrej et al. 2020). The higher root dry mass values observed under PL and WL with $8.60 \text{ mg}\cdot\text{L}^{-1}$ of Zn suggest that these qualities of light, associated with this concentration of Zn, contributed more effectively to root growth (Hacisalihoglu 2020). The lack of variation between light qualities with $17.20 \text{ mg}\cdot\text{L}^{-1}$ of Zn suggests that, at higher concentrations, Zn may be saturating the plants' demand, leading to a more uniform response, regardless of light quality (Lassoued and Essaid 2022).

The Chl *a* content was higher in plants grown under WL and PL with $8.60 \text{ mg}\cdot\text{L}^{-1}$ of Zn and under the former with $17.20 \text{ mg}\cdot\text{L}^{-1}$ of Zn (Table 2).

Table 2. Chlorophyll *a*, chlorophyll *b*, total chlorophylls, and carotenoids content, in $\mu\text{g}\cdot\text{g}^{-1}$ of fresh mass, of *Selenicereus undatus* plants after eight weeks of *in-vitro* cultivation, as a function of zinc (Zn) concentrations (8.60 and $17.20 \text{ mg}\cdot\text{L}^{-1}$) and light quality (white, blue, purple and red)*.

	Zn	Light quality				C.V.
		White	Blue	Purple	Red	
Chlorophyll <i>a</i>	8.60	0.21 ^{0.01} Ab	0.16 ^{0.01} Bb	0.21 ^{0.02} Aa	0.05 ^{0.01} Ca	13.69
	17.20	0.27 ^{0.01} Aa	0.23 ^{0.01} Ba	0.19 ^{0.01} Cb	0.04 ^{0.01} Da	
Chlorophyll <i>b</i>	8.60	0.19 ^{0.01} Aa	0.16 ^{0.01} Aa	0.14 ^{0.01} Aa	0.03 ^{0.01} Ba	23.40
	17.20	0.22 ^{0.02} Aa	0.19 ^{0.02} Ba	0.10 ^{0.02} Bb	0.04 ^{0.01} Ca	
Chlorophyll <i>T</i>	8.60	0.40 ^{0.01} Ab	0.32 ^{0.01} Bb	0.36 ^{0.03} Ba	0.09 ^{0.01} Ca	16.64
	17.20	0.49 ^{0.03} Aa	0.43 ^{0.03} Ba	0.29 ^{0.03} Cb	0.07 ^{0.01} Da	
Carotenoids	8.60	0.08 ^{0.01} Ab	0.05 ^{0.01} Bb	0.07 ^{0.01} Ba	0.02 ^{0.01} Da	13.11
	17.20	0.09 ^{0.01} Aa	0.07 ^{0.01} Ba	0.05 ^{0.01} Cb	0.02 ^{0.01} Da	

*Averages ($\pm$ standard error) followed by the same uppercase letter in the row (light quality) and lowercase letter in the column (Zn concentration) do not differ by the Scott-Knott's grouping test ($p < 0.05$); C.V.: coefficient of variation (%).

The increase in Chl *a* content in plants under WL and PL, with $8.60 \text{ mg}\cdot\text{L}^{-1}$ of Zn, and WL, with $17.20 \text{ mg}\cdot\text{L}^{-1}$ of Zn, shows that the combination of light quality and Zn concentration can be synergistic in plant metabolism (Hashim et al. 2021, Hamzah Saleem et al. 2022). WL makes all wavelengths of light available to plants, while PL only makes blue and red wavelengths available, intensifying photosynthetic activity and pigment metabolism (Blidar et al. 2021). Zn acts as a precursor in the biosynthesis of chlorophylls in some plant species, such as tobacco plants (Zhang et al. 2020).

Selenicereus undatus plants had a higher Chl *b* content when grown under WL, regardless of the concentration of Zn in the medium, and under BL and PL, at the lowest concentration of the mineral (Table 2).

The increase in Chl *b* content in plants under WL, regardless of Zn concentration, may be associated with its contribution to optimizing photosynthetic efficiency (Liu et al. 2021). Chl *b* complements light capture by absorbing wavelengths that Chl *a* does not use efficiently, transferring energy to photosystem II (Shevela et al. 2021, Janeeshma et al. 2022). Studies have shown that WL promotes a balanced development of photosynthetic pigments, increasing the stability of the photosynthetic apparatus in species such as *Camellia oleifera* Huajin (He et al. 2020).

Chl *T* and car content were higher in *S. undatus* plants under WL, regardless of Zn concentration, while the lowest values occurred under RL, with no statistical difference (Table 2).

The higher Chl *T* levels under WL, regardless of Zn concentration, suggest that this light provides more adequate energy for maximum pigment synthesis and photosystem efficiency (Hotos and Antoniadis 2022). In contrast, the lower levels

under RL may reflect its lower effectiveness in stimulating Chl *b* synthesis, reducing total pigment accumulation (Zou et al. 2021, Xu et al. 2022). Although RL favors processes such as elongation and photomorphogenesis, it has been observed that it can limit photosynthetic development in species such as *Solanum melongena* L. (Di et al. 2021).

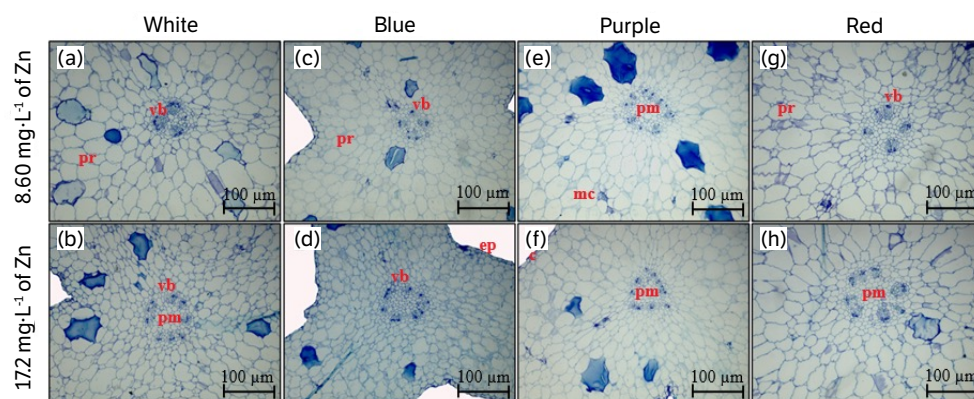
The higher levels of car under WL, regardless of Zn concentrations, may indicate that their combination stimulated car production, possibly enhancing protection against oxidative stress and supporting secondary antennae in photosynthesis (Zulfiqar et al. 2021). Evidence suggests that both light quality and Zn influence the expression of genes related to car synthesis (Regni et al. 2022, Cruz-Cruz et al. 2024). In addition to their role in car metabolism, Zn acts as a precursor in chlorophyll biosynthesis in some species and is an essential component of proteins involved in the metabolism of photosynthetic pigments. Moreover, adequate Zn availability protects the photosystems against photooxidative damage, reducing chlorophyll degradation under light stress conditions (Shoji et al. 2019).

The number of vascular bundles differed between Zn concentrations for the light qualities, except for PL. The highest averages were observed in plants in medium containing 17.2 mg·L⁻¹ of Zn. Among the light qualities evaluated, the highest number of vascular bundles was observed for plants under PL with 8.60 mg·L⁻¹ of Zn and did not differ between light qualities for the highest concentration of this mineral (Table 3 and Fig. 1).

Table 3. Number of vascular bundles (NVB) and cross-sectional area of the cladodes (CSAC) of *Selenicereus undatus* plants after eight weeks of *in-vitro* cultivation, as a function of zinc (Zn) concentrations (8.60 and 17.20 mg·L⁻¹) and light quality (white, blue, purple and red)*.

	Zn	Light quality				C.V.
		White	Blue	Purple	Red	
NVB	8.60	3.00 ^{0.32} Cb	5.80 ^{0.20} Bb	9.80 ^{0.20} Aa	5.80 ^{0.49} Bb	10.43
	17.20	8.60 ^{0.40} Aa	7.80 ^{0.37} Aa	9.40 ^{0.24} Aa	8.60 ^{0.40} Aa	
CSAC	8.60	1.07 ^{0.025} Bb	0.81 ^{0.015} Da	0.96 ^{0.008} Ca	1.36 ^{0.034} Ab	23.40
	17.20	1.17 ^{0.072} Ba	0.62 ^{0.005} Db	0.81 ^{0.004} Cb	1.64 ^{0.021} Aa	

*Averages (± standard error) followed by the same uppercase letter in the row (light quality) and lowercase letter in the column (Zn concentration) do not differ by the Scott-Knott's grouping test ($p < 0.05$); C.V.: coefficient of variation (%).



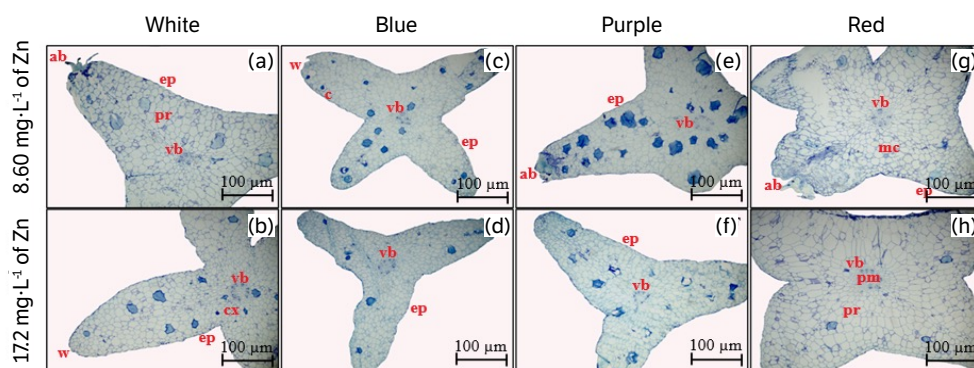
vb: vascular bundle; pr: reserve parenchyma; pm: medullary parenchyma; ep: epidermis; mc: mucilaginous cavity; c: cuticle.

Figure 1. Number of vascular bundles of *Selenicereus undatus* plants after eight weeks of *in-vitro* cultivation, as a function of zinc (Zn) concentrations (8.60 and 17.20 mg·L⁻¹) and light quality: (a and b) white, (c and d) blue, (e and f) purple, and (g and h) red. Scale bar = 100 μm.

The higher number of vascular bundles in *S. undatus* plants at the higher Zn concentration may be associated with its role in regulating physiological processes, such as the activation of essential enzymes for protein synthesis and growth hormones (Hasan et al. 2024). The concentration of 17.20 mg·L⁻¹ of Zn made it possible to maximize the number of vascular bundles, as well as the area of cladodes, and was important in improving the vascular architecture and structural development of the plant (Stangoulis and Knez 2022). On the other hand, the higher number of vascular bundles observed in plants

grown under PL may be due to greater efficiency in the transportation of water and nutrients in *S. undatus* plants under this condition (Cioć and Pawłowska 2020). In addition, the effects of the different qualities of WL, BL, PL, and RL on the number of vascular bundles make it possible to infer that there is a direct influence of light quality on photomorphogenic processes, such as the differentiation of vascular tissues and cell expansion (Li et al. 2021).

The cross-sectional area of the cladodes differed between Zn concentrations for the light qualities and between them at each Zn concentration. The highest average value was observed for *S. undatus* plants under RL and with $17.20 \text{ mg}\cdot\text{L}^{-1}$ of Zn (Table 3 and Fig. 2).



ab: axillary bud (areole); ep: epidermis; pr: reserve parenchyma; vb: vascular bundle; w: wing; cx: cortex; c: cuticle; mc: mucilaginous cavity; pm: medullary parenchyma.

Figure 2. Cross-sectional areas of the cladodes of *Selenicereus undatus* plants after eight weeks of *in-vitro* cultivation, as a function of zinc (Zn) concentrations (8.60 and $17.20 \text{ mg}\cdot\text{L}^{-1}$) and light quality: (a and b) white, (c and d) blue, (e and f) purple, and (g and h) red. Scale bar = $100 \mu\text{m}$.

The higher cross-sectional area of the cladodes observed in plants grown under RL may be due to the ability of this light to stimulate elongation and cell division in specific tissues (Huang et al. 2022), and the combination of light and the supply of higher concentrations of Zn may have triggered a synergistic interaction in plant development (Toscano et al. 2021).

The atomic percentage in the cladodes of *S. undatus* showed variations in chemical composition, influenced by the different Zn concentrations evaluated and the light quality to which the plants were exposed. Potassium (K) was the predominant element in all samples. Under low Zn concentration ($8.60 \text{ mg}\cdot\text{L}^{-1}$) and WL, the highest K levels were observed at the rib margins (81.17%). When Zn concentration increased ($17.20 \text{ mg}\cdot\text{L}^{-1}$), K content decreased under all light conditions, with the lowest values recorded in the central ribs under RL (31.22%) and at the margins under WL (39.76%) (Table 4 and Figs. 3a–3h).

The distribution of chemical elements in plant cladodes varies independently in response to Zn concentrations and light quality, suggesting distinct and separate physiological responses to each factor. Potassium remained predominant across all treatments, especially under low Zn concentration ($8.60 \text{ mg}\cdot\text{L}^{-1}$), with the highest concentrations in the central ribs under WL (39.22%) and at the rib margins under PL (35.64%). This aligns with K's essential role in osmotic regulation and enzymatic activation under metal stress (Johnson et al. 2022).

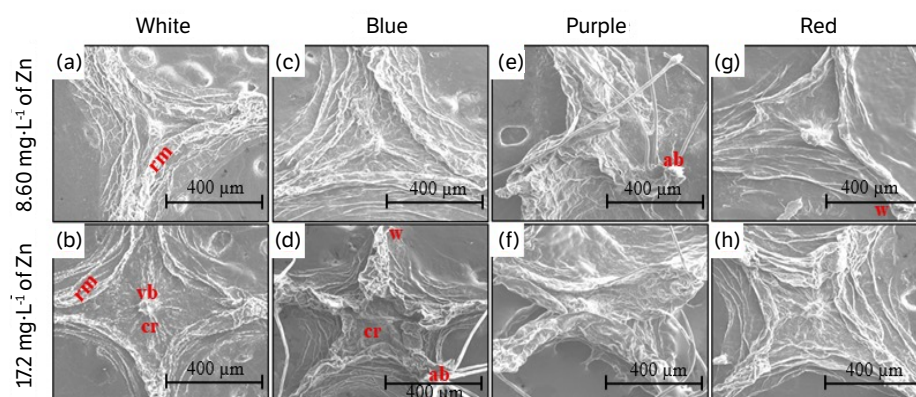
Calcium (Ca) showed an opposite pattern to potassium. In general, higher Ca levels were observed under high Zn concentration, especially at the rib margins under PL (38.83%). In the central ribs under BL and high Zn concentration, Ca content was also elevated (20.03%). Under low Zn conditions, Ca levels were moderate, particularly in the central ribs under PL (24.17%) (Table 4 and Figs. 3d–3f).

The high Ca content under high Zn concentration at the rib margins under PL suggests the dual role of Ca as a structural component and secondary messenger in stress signaling pathways, particularly during Zn-induced cellular disturbances (Shabbir et al. 2022). The accumulation patterns under different light qualities may be related to active Ca^{2+} transport mechanisms via plasmalemma ATPase-dependent processes (Miao et al. 2022, Pivato et al. 2023).

Table 4. Atomic percentage of chemical elements in *Selenicereus undatus* cladodes after eight weeks of *in-vitro* cultivation, as a function of zinc concentrations (8.60 and 17.20 mg·L⁻¹) and light quality (white, blue, purple and red)*.

	Zn	Light quality							
		White		Blue		Purple		Red	
		CR	RM	CR	RM	CR	RM	CR	RM
K	8.60	43.99 ^{1.55}	81.17 ^{2.82}	45.82 ^{1.54}	55.29 ^{1.82}	59.77 ^{1.94}	63.31 ^{2.08}	44.04 ^{1.52}	63.24 ^{2.20}
	17.20	32.13 ^{1.25}	39.76 ^{1.50}	33.32 ^{1.39}	50.76 ^{1.82}	38.37 ^{1.39}	48.26 ^{2.32}	31.22 ^{1.14}	32.27 ^{1.26}
Ca	8.60	15.65 ^{0.72}	10.52 ^{0.83}	15.59 ^{0.65}	9.51 ^{0.28}	24.17 ^{0.88}	12.41 ^{0.58}	11.96 ^{0.58}	13.49 ^{0.78}
	17.20	16.98 ^{0.81}	13.17 ^{0.75}	20.03 ^{1.02}	17.25 ^{0.86}	22.68 ^{0.93}	38.83 ^{2.15}	17.77 ^{0.75}	20.31 ^{0.94}
S	8.60	12.58 ^{0.70}	4.24 ^{0.63}	8.75 ^{0.50}	7.81 ^{0.46}	7.07 ^{0.42}	3.90 ^{0.35}	7.96 ^{0.51}	5.34 ^{0.54}
	17.20	14.67 ^{0.85}	13.92 ^{0.84}	11.41 ^{0.88}	11.19 ^{0.75}	13.49 ^{0.76}	4.93 ^{1.34}	19.36 ^{0.92}	17.70 ^{0.95}
Mg	8.60	13.78 ^{1.14}	0.00 ^{0.00}	11.22 ^{0.90}	7.54 ^{0.16}	1.22 ^{0.37}	3.08 ^{0.51}	14.15 ^{1.10}	2.71 ^{0.74}
	17.20	13.89 ^{1.24}	10.78 ^{1.13}	21.86 ^{1.86}	6.94 ^{0.96}	11.94 ^{1.08}	0.00 ^{0.00}	18.16 ^{1.33}	14.18 ^{1.27}
P	8.60	6.44 ^{0.52}	0.00 ^{0.00}	3.77 ^{0.35}	2.82 ^{0.32}	1.32 ^{0.25}	2.12 ^{0.31}	4.65 ^{0.43}	0.39 ^{0.21}
	17.20	8.56 ^{0.68}	7.47 ^{0.67}	8.47 ^{0.83}	4.55 ^{0.12}	3.66 ^{0.46}	0.00 ^{0.00}	8.05 ^{0.56}	6.64 ^{0.61}
Cl	8.60	5.77 ^{0.44}	2.78 ^{0.55}	13.30 ^{0.62}	16.28 ^{0.71}	4.68 ^{0.32}	10.74 ^{0.54}	9.04 ^{0.51}	11.09 ^{0.68}
	17.20	9.41 ^{0.63}	12.22 ^{0.74}	2.14 ^{0.56}	6.08 ^{0.25}	8.10 ^{0.54}	0.00 ^{0.00}	4.34 ^{0.38}	6.97 ^{0.55}
Fe	8.60	0.38 ^{0.25}	0.90 ^{0.42}	0.53 ^{0.20}	0.42 ^{0.02}	1.50 ^{0.20}	1.10 ^{0.22}	0.84 ^{0.23}	2.88 ^{0.42}
	17.20	1.25 ^{0.33}	0.92 ^{0.07}	2.24 ^{0.48}	2.51 ^{0.17}	1.19 ^{0.29}	4.51 ^{1.06}	0.67 ^{0.23}	1.23 ^{0.34}
Mn	8.60	0.18 ^{0.14}	0.26 ^{0.02}	0.14 ^{0.11}	0.34 ^{0.02}	0.28 ^{0.16}	0.42 ^{0.19}	0.11 ^{0.01}	0.00 ^{0.00}
	17.20	0.26 ^{0.17}	0.04 ^{0.01}	0.53 ^{0.40}	0.59 ^{0.33}	0.57 ^{0.26}	3.46 ^{1.01}	0.23 ^{0.02}	0.21 ^{0.02}
Na	8.60	1.11 ^{0.74}	0.00 ^{0.00}	0.50 ^{0.10}	0.00 ^{0.00}	0.00 ^{0.00}	2.37 ^{0.58}	7.19 ^{0.88}	0.73 ^{0.08}
	17.20	5.56 ^{1.05}	0.95 ^{0.08}	0.00 ^{0.00}	0.00 ^{0.00}	0.00 ^{0.00}	0.00 ^{0.00}	0.19 ^{0.04}	0.00 ^{0.00}
Zn	8.60	0.12 ^{0.09}	0.13 ^{0.03}	0.39 ^{0.22}	0.00 ^{0.00}	0.00 ^{0.00}	0.56 ^{0.21}	0.06 ^{0.01}	0.13 ^{0.03}
	17.20	0.30 ^{0.03}	0.77 ^{0.04}	0.00 ^{0.00}	0.12 ^{0.03}	0.00 ^{0.00}	0.00 ^{0.00}	0.00 ^{0.00}	0.49 ^{0.04}

*Atomic percentage of chemical elements in *S. undatus* cladodes ($\pm$ standard error); CR: central ribs; RM: rib margins.



rm: rib margins; vb: vascular bundle; cr: central ribs; ab: axillary bud (areole); w: wing.

Figure 3. Cross-sections of *Selenicereus undatus* cladodes after eight weeks of *in-vitro* cultivation, as a function of zinc (Zn) concentrations (8.60 and 17.20 mg·L⁻¹) and light quality: (a and b) white, (c and d) blue, (e and f) purple, and (g and h) red. Scale bar = 400 μ m.

Sulfur (S) levels were higher under BL and RL, with peak concentrations in the central ribs at high Zn concentration (21.86% under BL and 19.36% under RL). Under BL combined with 8.60 mg·L⁻¹ Zn, S also showed elevated values at the rib margins (7.81%) (Table 4; Figs. 3c, 3d, and 3h). Overall, S exhibited spectral sensitivity, with preferential accumulation in the central ribs under BL and at the margins under RL. These observations may be related to light-dependent regulation

of S assimilation pathways, in which specific photoreceptors modulate ATP sulfurylase activity (Yu et al. 2021, Bhadwal et al. 2024).

Magnesium (Mg) and phosphorus (P) varied among treatments. The highest Mg levels were observed in the central ribs under BL and high Zn concentration (21.86%), while P was highest in the central ribs under WL and high Zn concentration (8.56%). Mg was absent in some combinations, such as in the rib margins under WL and low Zn concentration, and under PL and high Zn concentration. Mg peaked in central ribs under BL and high Zn concentration (21.86%). P reached maximum values in the central ribs under WL and high Zn concentration (8.56%) (Table 4 and Figs. 3a, 3b, 3d, and 3f).

This variability may be associated with the roles of these minerals in chlorophyll synthesis (Mg) and energy metabolism (P), processes modulated by light quality and interactions with Zn (Santos et al. 2021, Gao et al. 2023, Gonzales-Alvarado and Cardoso 2024).

Chlorine (Cl), iron (Fe), manganese (Mn), sodium (Na), and, to a lesser extent, Zn presented lower atomic percentages in the cladodes. Cl was higher in the central ribs under BL and low Zn concentration (13.30%) and at the margins under the same conditions (16.28%). Fe content was highest in the central ribs under PL and high Zn concentration (4.51%). Mn was most abundant at the margins under PL and high Zn (3.46%). Na was higher in the central ribs under WL and high Zn concentration (5.56%), and at the margins under WL and low Zn (2.37%). Zn itself was detected at low levels, with slight increases under high Zn concentration in central ribs under WL (0.26 to 0.30%) and margins under white light (0.13 to 0.77%). It was also present in minimal amounts under several combinations, especially at the margins under BL and high Zn concentration (Table 4 and Figs. 3a–3f).

Zn showed limited translocation, with marginal increases in tissues exposed to WL (0.30% in central ribs, 0.77% at the margins) under high concentration. These tissue concentrations remained well below typical phytotoxicity thresholds reported for most crop species (100–300 mg·kg⁻¹ DW) and within or slightly above the range considered adequate for optimal plant metabolism (15–100 mg·kg⁻¹ DW) (Long et al. 2003, White and Brown 2010). The nutritional composition of *S. undatus* tissues typically contains 0.18–0.37 mg Zn/100 g fresh weight under normal conditions (Shah et al. 2023, Yasmin et al. 2024), suggesting that the observed accumulation represents a controlled response rather than unregulated uptake. The limited accumulation despite doubled Zn supplementation (from 8.60 to 17.20 mg·L⁻¹) indicates active compartmentalization strategies in vacuoles or apoplastic spaces, a well-documented tolerance mechanism in metal-accumulating plants that prevents cytoplasmic Zn concentrations from reaching toxic levels while maintaining sufficient bioavailability for essential metabolic functions (White and Broadley 2009, Abou Seeda et al. 2022).

The absence of toxicity symptoms, despite elevated Zn levels, may indicate the presence of exclusion mechanisms, potentially mediated by Ca²⁺-dependent membrane stabilization (Kaur and Garg 2021, Feng et al. 2023).

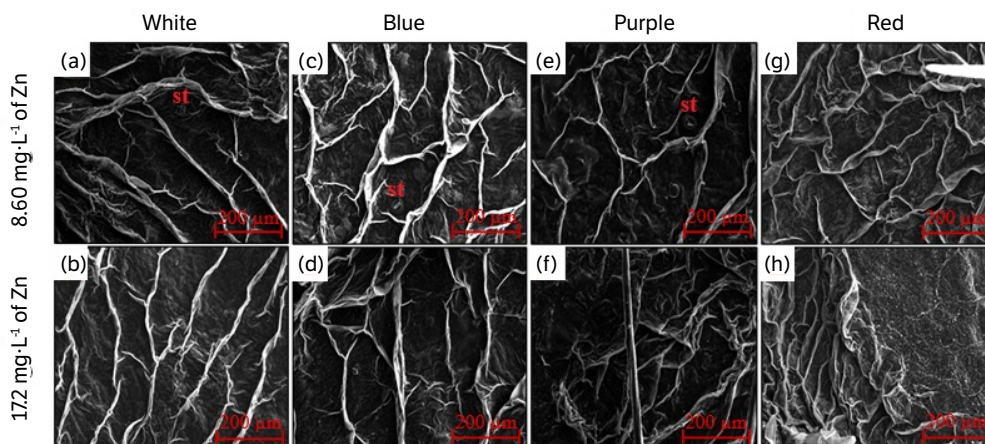
Stomatal density was independently affected by Zn concentration and light quality, indicating that each factor exerts a distinct influence. In plants cultivated with 8.60 mg·L⁻¹ of Zn, RL resulted in the highest stomatal density value, followed by BL, whereas WL and PL led to the lowest values, with no significant difference between them (Table 5 and Figs. 4A–4H). Under the higher Zn concentration (17.20 mg·L⁻¹), although RL still induced the highest stomatal density value, it was lower than that observed under the lower Zn concentration (Table 5 and Fig. 4h). In this condition, BL resulted in the lowest stomatal density, while WL and PL maintained intermediate and similar values (Table 5 and Figs. 4b, 4d, and 4f).

Table 5. Stomatal density (in mm²) of *Selenicereus undatus* plants after eight weeks of *in-vitro* cultivation, as a function of zinc (Zn) concentrations (8.60 and 17.20 mg·L⁻¹) and light quality (white, blue, purple, and red)*.

	Zn	Light quality				C.V.
		White	Blue	Purple	Red	
Stomatal density	8.60	75.00 ^{16.67} Ca	141.67 ^{14.43} Ba	75.00 ^{14.43} Ca	166.67 ^{8.33} Aa	27.77
	17.20	83.33 ^{8.33} Ca	66.67 ^{22.05} Bb	83.33 ^{22.05} Ca	100.00 ^{14.43} Ab	

*Means (± standard error) followed by the same uppercase letter in the row (light quality) and lowercase letter in the column (Zn concentration) do not differ significantly according to the Scott-Knott's clustering test ($p < 0.05$); C.V.: coefficient of variation (%).





st: stomata.

Figure 4. Paradermal sections of *Selenicereus undatus* cladodes after eight weeks of *in-vitro* cultivation, as a function of zinc (Zn) concentrations (8.60 and 17.20 $\text{mg}\cdot\text{L}^{-1}$) and light quality: (a and b) white, (c and d) blue, (e and f) purple, and (g and h) red. Scale bar = 200 μm .

The effects of Zn concentrations and light quality on stomatal density may be associated with distinct physiological regulatory mechanisms, as each factor operates independently (Shang et al. 2023, Zhao et al. 2025). Previous studies have shown that RL promotes higher stomatal density under low Zn concentrations, possibly via phytochrome-dependent signaling pathways that enhance stomatal cell division. In contrast, BL tends to reduce stomatal density under high Zn concentrations, which may reflect additive but independent effects of Zn-induced stress and cryptochrome-related photoreception (Paskhin et al. 2022, Bueno and Vendrame 2024).

The reduction in stomatal density under high Zn concentration and RL may be associated with dysfunction in reactive oxygen species homeostasis, since Zn-finger proteins such as drought and salt tolerance (DST) in rice negatively regulate stomatal closure and density through the modulation of antioxidant gene expression (Ding et al. 2023, Kang et al. 2024).

The maintenance of intermediate values under WL and PL across both Zn concentrations indicates that different light qualities, or even their combinations, may modulate compensatory responses in stomatal morphogenesis, possibly through adjustments in differential micronutrient uptake and hormonal signaling (Bueno and Vendrame 2024).

CONCLUSION

During the *in-vitro* cultivation of pitahaya (*S. undatus*), the manipulation of light quality and Zn concentrations enabled greater growth and accumulation of photosynthetic pigments, as well as variations in the number of vascular bundles and the cross-sectional area of cladodes. The best morphophysiological responses were observed under WL at both Zn concentrations, and under PL with 8.60 $\text{mg}\cdot\text{L}^{-1}$ of Zn. Zn accumulation remained low even at higher concentrations, suggesting efficient compartmentalization mechanisms that prevent phytotoxicity. Stomatal density was influenced by the combination of Zn levels and light quality, with WL and PL maintaining intermediate values at both concentrations, indicating that broader spectra can mitigate stress effects through compensatory physiological adjustments.

These findings provide practical guidelines for optimizing micropropagation protocols of *S. undatus*. For commercial production, white LED lighting combined with 8.60 $\text{mg}\cdot\text{L}^{-1}$ Zn is recommended to maximize shoot multiplication while maintaining healthy development. PL offers an alternative when enhanced pigmentation is desired for improved acclimatization. The tolerance to elevated Zn (17.20 $\text{mg}\cdot\text{L}^{-1}$) suggests potential for biofortification strategies during micropropagation, producing Zn-enriched plantlets for cultivation in deficient soils. Additionally, light quality manipulation can pre-condition explants for improved water use efficiency during *ex-vitro* acclimatization, potentially reducing transplant mortality in commercial nurseries.

CONFLICT OF INTEREST

Nothing to declare.

AUTHORS' CONTRIBUTION

Conceptualization: Clairvil, E. and Guimarães, M. A. **Methodology:** Clairvil, E., Guimarães, M. A. and Rodrigues, F. A. **Resources:** Clairvil, E., Guimarães, M. A., Rodrigues, F. A., Dória, J., Dias, G. M. G., Feitosa, B. H., Castro, E. M. and Pasqual, M. **Investigation:** Clairvil, E., Guimarães, M. A., Rodrigues, F. A., Dória, J., Dias, G. M. G., Feitosa, B. H., Castro, E. M. and Pasqual, M. **Data curation:** Clairvil, E., Guimarães, M. A., Rodrigues, F. A., Dias, G. M. G. and Feitosa, B. H. **Supervision:** Clairvil, E., Guimarães, M. A., Rodrigues, F. A., Dória, J., Dias, G. M. G., Feitosa, B. H., Castro, E. M. and Pasqual, M. **Original – draft writing:** Clairvil, E., Guimarães, M. A., Rodrigues, F. A., Dória, J., Dias, G. M. G., Feitosa, B. H., Castro, E. M. and Pasqual, M. **Writing – review and editing:** Clairvil, E. and Guimarães, M. A. **Final approval:** Clairvil, E.

DATA AVAILABILITY STATEMENT

All dataset were generated or analyzed in the current study.

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DECLARATION OF USE OF ARTIFICIAL INTELLIGENCE TOOLS

The authors declare that artificial intelligence tools were used during the preparation of this manuscript solely to support language editing, grammar correction, and improvement of clarity and readability.

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