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Physiological and Ultrastructural Responses of Sweet Potato cv. Campina to Sodium Selenite During in Vitro Micropropagation

Respostas Fisiológicas e Ultraestruturais de Batata-Doce cv. Campina ao Selenito de Sódio Durante a Micropropagação in Vitro

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Abstract

Selenium (Se) is an essential micronutrient involved in antioxidant protection, immune regulation, and human metabolic health. However, Se deficiency affects nearly 15% of the global population, reinforcing the need for effective biofortification strategies. This study evaluated the physiological and ultrastructural responses of *Ipomoea batatas* L. cv. Campina plantlets cultured in vitro under increasing sodium selenite concentrations. Nodal segments were grown on Murashige and Skoog (MS) medium supplemented with 0, 5, 10, 15, 20, or 25 µM Se in a completely randomized design with seven replicates. After 30 days, shoot length, leaf number, senescence, biomass, and Se accumulation were quantified. Shoot elongation remained highest in the control and at 5–15 µM Se, while green leaf number and fresh biomass peaked at 5 µM. Senescent leaves increased markedly at 25 µM, and dry biomass was greatest in the control and 5 µM treatments. Selenium accumulation increased proportionally with external concentrations. Moderate supplementation (5 µM) enhanced growth and maintained epidermal integrity, whereas higher doses induced reduced biomass, leaf senescence, and stomatal deformation. These findings demonstrate that controlled Se supplementation during micropropagation is an effective strategy for producing Se-enriched sweet potato plantlets with predictable mineral content, supporting their use in nutritional and functional food applications.

Keywords: Selenium Biofortification. *Ipomoea batatas*. Plant Tissue Culture. Ultrastructure. In vitro Propagation.

Resumo

O selênio (Se) é um micronutriente essencial envolvido na proteção antioxidante, na regulação do sistema imunológico e na manutenção da saúde metabólica humana. Entretanto, a deficiência de Se afeta cerca de 15% da população mundial, reforçando a necessidade de estratégias eficazes de biofortificação. Este estudo avaliou as respostas fisiológicas e ultraestruturais de brotações de *Ipomoea batatas* L. cv. Campina cultivadas in vitro sob concentrações crescentes de selenito de sódio. Segmentos nodais foram cultivados em meio Murashige e Skoog (MS) suplementado com 0, 5, 10, 15, 20 ou 25 µM de Se, em delineamento inteiramente casualizado com sete repetições. Após 30 dias, foram quantificados o comprimento da parte aérea, o número de folhas verdes e senescentes, a biomassa fresca e seca e o acúmulo de Se. O alongamento dos brotos permaneceu maior no controle e entre 5 e 15 µM de Se, enquanto o número de folhas verdes e a biomassa fresca atingiram seus maiores valores em 5 µM. As folhas senescentes aumentaram significativamente em 25 µM, e a biomassa seca foi maior no controle e em 5 µM. O acúmulo de selênio aumentou proporcionalmente às concentrações externas. A suplementação moderada (5 µM) promoveu o crescimento e manteve a integridade epidérmica, enquanto doses superiores reduziram a biomassa, intensificaram a senescência foliar e causaram deformações estomáticas. Esses resultados demonstram que a suplementação controlada de Se durante a micropropagação é uma estratégia eficaz para produzir mudas de batata-doce biofortificadas com conteúdo mineral previsível, apoiando seu uso em aplicações nutricionais e alimentos funcionais.

Palavras-chave: Biofortificação com Selênio. *Ipomoea batatas*. Cultura de Tecidos Vegetais. Ultraestrutura. Propagação i*n Vitro*.

1 Introduction

Micronutrient deficiencies remain a major global public health concern, particularly in developing countries (WHO, 2018). The World Health Organization refers to the insufficient intake of essential nutrients as "hidden hunger," a condition that affects nearly one-third of the global population (Naeem *et al*., 2022). Among the essential micronutrients, selenium (Se) plays key roles in antioxidant defense, immune regulation, and metabolic homeostasis (Gupta; Gupta, 2017; Wong *et al*., 2010). Approximately 15% of the world's population does not meet the minimum dietary requirement for Se (Naeem *et al*., 2022), reinforcing the need for strategies that increase its concentration in staple foods (Lidon *et al*., 2018; Manojlović *et al*., 2019; Thakur *et al*., 2022).

In Brazil, low Se availability in most soils limits its uptake and accumulation in edible plant tissues (Lopes *et al*., 2017). Agricultural biofortification—defined as the enhancement of the nutritional composition of crops through agronomic, biotechnological, or genetic approaches—has emerged as a promising strategy to mitigate Se deficiencies and improve the nutritional quality of food crops (Schiavon *et al*., 2020).

Sweet potato (Ipomoea batatas L.) is one of the world's most important tuber crops, cultivated across tropical, subtropical, and temperate regions of Africa, the Americas, and Asia (Faostat, 2020). In Brazil, the crop has high economic and social relevance, particularly in the Northeast and South, where production exceeds 317 and 252 thousand tons annually, respectively (IBGE, 2021). However, conventional vegetative propagation facilitates the accumulation and dissemination of fungal, bacterial, and viral pathogens, thereby reducing vigor and productivity across successive planting cycles.

Micropropagation provides an efficient platform for large-scale production of pathogen-free, genetically uniform planting material (Yokoya; Yoneshigue-Valentin, 2011). Recent advances in sweet potato micropropagation have improved plantlet quality through optimized culture media, growth regulators, and sanitation protocols (Behera *et al*., 2022; Beyene *et al*., 2020; Kumar *et al*., 2019). Moreover, the integration of mineral supplementation into *in vitro* systems enables precise manipulation of nutrient uptake, facilitating the biofortification of plant tissues under controlled environmental conditions (Puccinelli *et al*., 2020; Silva *et al*., 2021a; Sivanesan; Park, 2014).

Although several studies have explored Se biofortification in field-grown and hydroponic crops, the use of selenium supplementation during in vitro micropropagation of sweet potato remains limited. This represents a critical gap, as in vitro systems offer a highly controlled environment for studying Se dose–response relationships and for producing nutritionally enriched, disease-free planting material.

Therefore, this study investigates biometric performance and selenium accumulation in *Ipomoea batatas* L. cv. Campina plantlets cultured in vitro under increasing sodium selenite concentrations. The aim is to establish a reliable protocol for producing Se-biofortified sweet potato plantlets suitable for agricultural or functional food applications.

2 Material and Methods

2.1 Plant material

Nodal segments of *Ipomoea batatas* L. cv. Campina were excised from in vitro stock plants maintained on semi-solid Murashige and Skoog (MS) medium (Murashige; Skoog, 1962). Each explant contained two nodes and one fully expanded leaf. The basal medium consisted of MS salts supplemented with 30 g L^{-1} sucrose and solidified with 5.6 g L^{-1} agar (AGARGEL®). The pH was adjusted to 5.8 ± 0.02 prior to autoclaving at 121 °C for 15 min under 1.2 atm pressure.

2.2 Experimental treatments and culture conditions

Selenium was supplied as sodium selenite (Na_2SeO_3) at concentrations of 0, 5, 10, 15, 20, and 25 µM. The experiment was arranged in a completely randomized design with six treatments and seven replicates, each composed of three culture tubes containing one explant. In total, 21 explants were established per treatment, yielding 126 experimental units. Cultures were maintained in a growth chamber at 25 ± 2 °C under a 16-h photoperiod and a photosynthetic photon flux density of 52.5 µmol m^{-2} s^{-1}, measured with a digital light meter (Equitherm 813-A).

2.3 Growth measurements

After 30 days of in vitro culture, shoot length was measured with a graduated ruler, and the

number of green and senescent leaves was recorded. Fresh mass was determined immediately after harvesting. Dry mass was obtained by drying shoots in a forced-air oven at 65 °C until constant weight.

2.4 Selenium quantification

Selenium concentration in shoot tissues was determined by inductively coupled plasma mass spectrometry (ICP-MS), following the analytical procedures described by Featherstone *et al*. (2004). Samples were digested and analyzed under standardized analytical conditions to ensure accuracy and reproducibility.

2.5 Anatomical and ultrastructural analyses (SEM)

Leaf fragments (5 × 5 mm) were collected from the abaxial surface of fully expanded leaves after 30 days of in vitro culture. For each Se concentration, leaves from three independent plantlets were sampled.

Fragments were fixed in FAA solution (formalin: acetic acid: 70% ethanol, 5:5:90, v/v/v), dehydrated in a graded ethanol series, and dried using a K850 Critical Point Dryer® (Quorum Technologies) with liquid CO_2. Dried samples were mounted on aluminum stubs, sputter-coated with gold using a Quorum Q150R ES® metallizer, and examined in a Quanta 450-FEG scanning electron microscope (FEI®) operating in high vacuum at 10 kV.

Micrographs were captured from standardized, non-overlapping regions midway between the midrib and the leaf margin. For each selenium concentration, five micrographs were obtained at 1500× magnification, totaling 30 images. Stomatal density, aperture width, and aperture area were quantified from calibrated images using ImageJ®. Epidermal integrity was evaluated by grayscale histogram analysis and threshold-based segmentation to detect ultrastructural alterations associated with selenium exposure.

2.6 Statistical analysis

All biometric, anatomical, and selenium concentration data were subjected to analysis of variance (ANOVA). When significant differences were detected, means were grouped using the Scott–Knott test at $p \leq 0.05$.

Additionally, regression models were fitted to describe the quantitative relationship between external selenium concentration and selenium accumulation in shoot tissues. Linear and quadratic models were tested, and the model with the highest adjusted R^2 and significant coefficients ($p \leq 0.05$) was selected. Statistical analyses were performed in R, version 4.0.3 (R Core Team, 2021).

3 Results and Discussion

Growth and biomass parameters of *Ipomoea batatas* L. cv. Campina were significantly influenced by selenium supplementation (Table 1). The analysis of variance revealed treatment effects for shoot length (SL), number of green leaves (NGL), number of senescent leaves (NSL), fresh mass (FM), and dry mass (DM), demonstrating that selenium availability modulated the physiological performance of the plantlets.

Table 1 - Summary of the analysis of variance for shoot length (SL), number of green leaves (NGL), number of senescent leaves (NSL), fresh mass (FM), and dry mass (DM) of *Ipomoea batatas* cv. Campina grown in vitro under six selenium concentrations

FV	DF	Medium Square				
		SL	NGL	NSL	FM	DM
Treatment	5	0.255*	0.804*	0.201*	0.179*	8.87×10^{-4}*
Residue	36	0.005	0.109	0.020	0.015	1.18×10^{-4}
CV (%)	-	12.23	35.92	30.01	22.22	19.52

Significant at $p < 0.05$ by the F-test. CV (%): coefficient of variation.
Source: research data.

Seedlings grown in the control medium and under 5–15 µM Se showed the highest SL, while 20–25 µM significantly reduced shoot elongation. Leaf production was stimulated at 5 µM Se, and senescence increased progressively with rising Se concentration (Table 2), demonstrating a transition from beneficial to toxic selenium effects.

Table 2 – Shoot length (SL), number of green leaves (NGL), number of senescent leaves (NSL), fresh mass (FM), and dry mass (DM) of *Ipomoea batatas* cv. Campina cultured in vitro under six selenium concentrations. Values represent mean ± standard error

Conc. (µM)	SL (cm)	NGL	NSL	FM (g)	DM (g)
0	1.85 ± 0.09 a	1.00 ± 0.07 b	0.14 ± 0.07 c	0.58 ± 0.03 b	0.07 ± 0.01 a
5	1.91 ± 0.09 a	1.38 ± 0.18 a	0.38 ± 0.05 b	0.87 ± 0.08 a	0.08 ± 0.01 a
10	1.93 ± 0.09 a	0.86 ± 0.10 b	0.33 ± 0.01 b	0.50 ± 0.05 b	0.06 ± 0.01 b
15	1.81 ± 0.09 a	1.00 ± 0.14 b	0.33 ± 0.10 b	0.52 ± 0.03 b	0.06 ± 0.01 b
20	1.63 ± 0.07 b	0.95 ± 0.15 b	0.33 ± 0.01 b	0.44 ± 0.03 b	0.05 ± 0.01 b
25	1.44 ± 0.05 b	0.33 ± 0.01 c	0.67 ± 0.04 a	0.43 ± 0.04 b	0.05 ± 0.01 b
CV (%)	12.23	35.92	39.01	22.22	19.52

Means followed by the same lowercase letter within a column do not differ significantly according to the Scott–Knott test at 5% probability.
Source: research data.

Fresh mass reached its maximum at 5 µM Se, while dry mass remained highest in the control and 5 µM treatments. These findings suggest that low selenium doses enhance metabolic efficiency and promote biomass accumulation, whereas higher doses reduce water content and impair tissue formation due to Se toxicity (Gupta; Gupta, 2017; Ramos *et al*., 2010).

These results are consistent with previous studies demonstrating that moderate selenium supplementation can improve agronomic performance, nutritional quality, and yield in sweet potato

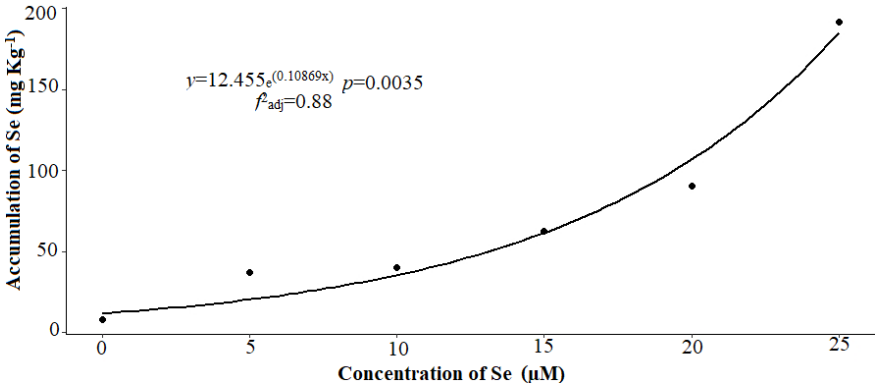
plants. In field-grown sweet potato, selenium fertilization promoted increases in branch number, vine length, tuber formation, and overall productivity, especially at moderate selenium supply levels (Zhang *et al*., 2024).

Additionally, selenium supplementation has been associated with improvements in carbohydrate metabolism, including increases in soluble sugars and starch content, indicating enhanced metabolic efficiency under optimal selenium availability (Zhang *et al*., 2024).

Similar trends have been reported in multi-genotype studies, in which selenium application increased tuber yield and improved nutritional attributes, although responses varied by genetic background and application method. These findings reinforce the beneficial role of selenium as a metabolic enhancer at low concentrations, particularly through its participation in antioxidant protection and redox balance (Liao *et al*., 2025).

Selenium accumulation increased consistently with external concentration (Figure 1). Regression analysis confirmed a strong dose–response relationship, indicating predictable selenium uptake under controlled in vitro conditions.

Figure 1 – Selenium (Se) concentration in shoots of *Ipomoea batatas* L. cv. Campina after 30 days of in vitro culture at different selenium concentrations (µM). Values are means ± standard error (n = 7)



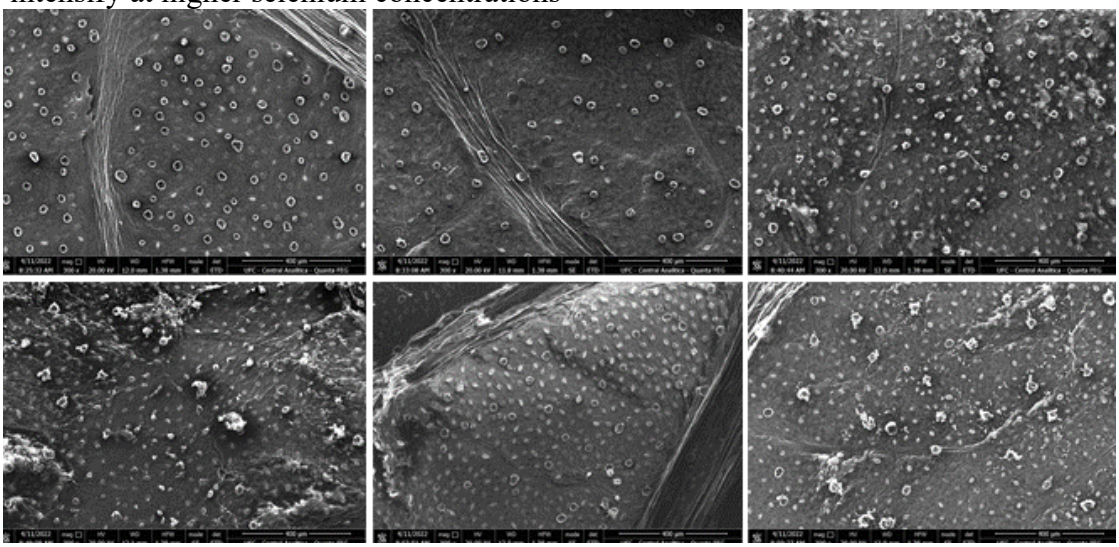
Source: research data.

This dose-dependent accumulation pattern is consistent with previous reports showing that increasing selenium fertilization progressively increases selenium concentrations in the roots, stems, leaves, and tubers of sweet potato plants (Zhang *et al*., 2024).

Furthermore, previous studies demonstrated substantial genetic variability in selenium accumulation capacity among sweet potato cultivars, highlighting the importance of genotype-specific strategies for biofortification (Liao *et al*., 2025). The predictable selenium uptake observed in the present study under controlled in vitro conditions underscores the potential of micropropagation systems to produce plant material with standardized selenium concentrations.

Ultrastructural analysis revealed clear dose-dependent modification of the abaxial leaf surface in response to selenium (Figure 2). Control plants (A) showed open stomata and a smooth epidermis. At 5 µM (B), stomata remained functional with slight aperture reduction. At 10 µM (C), some stomata exhibited partial closure, and the epidermis displayed initial irregularities.

Figure 2 - Scanning electron micrographs of abaxial leaf surfaces of *Ipomoea batatas* L. cv. Campina grown under six sodium selenite concentrations: A = 0 µM, B = 5 µM, C = 10 µM, D = 15 µM, E = 20 µM, F = 25 µM. Stomatal and epidermal alterations intensify at higher selenium concentrations



Source: research data.

At 15 µM (D), stomata were narrower, and localized wrinkling became evident. At 20 µM (E), guard cells exhibited deformation, and deposits suggestive of oxidized residues appeared. At 25 µM (F), stomata were nearly closed, and the epidermis displayed marked collapse and cuticular disruption. These results confirm that the cultivar experiences progressive oxidative and osmotic stress as Se concentration increases.

Integration of biometric, physiological, and ultrastructural responses indicates that 5 µM Se represents the optimal concentration for promoting growth while maintaining epidermal integrity. Concentrations above 15 µM trigger a clear transition to toxicity, marked by reduced shoot length, increased senescence, biomass reduction, and epidermal degradation. This dual response aligns with observations reported for basil, lettuce, and spinach, confirming that selenium acts as an essential micronutrient at low doses and as a stress-inducing agent at elevated levels (Hawrylak-Nowak, 2013; Puccinelli *et al*., 2020; Silva *et al*., 2021b).

The transition from beneficial to toxic selenium effects observed above 15 µM is also supported by previous studies demonstrating that selenium exerts a dual physiological role depending on concentration. Moderate selenium supply promotes plant growth and metabolic activity, whereas excessive selenium disrupts cellular homeostasis and may impair development and tissue integrity

(Liao *et al*., 2025; Zhang *et al*., 2024).

From a practical perspective, cv. Campina exhibits strong potential for controlled Se biofortification in vitro due to its predictable uptake behavior and well-defined toxicity threshold. These characteristics allow precise dose calibration to generate Se-enriched *Ipomoea batatas* plantlets with enhanced nutritional value and minimal physiological stress.

4 Conclusion

Low to moderate selenium supplementation improved the in vitro performance of *Ipomoea batatas* L. cv. Campina. The optimal concentration of Se was 5 µM, which promoted greater shoot development and the highest fresh biomass without inducing anatomical damage.

Dry mass remained highest in control and 5 µM treatments, indicating that these doses support balanced growth and metabolic stability. In contrast, 25 µM Se induced pronounced toxicity, including increased leaf senescence and epidermal structure deformation, indicating a clear shift from beneficial to harmful effects. Selenium accumulation in shoots increased proportionally with external concentration, confirming that in vitro supplementation is an effective strategy for producing selenium-enriched plantlets.

Overall, cv. Campina exhibits strong potential for controlled biofortification, provided that selenium concentrations remain within safe physiological thresholds.

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