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ARTICLE

In vitro regeneration of *Gerbera jamesonii* under mannitol-induced osmotic stress using plant growth regulators

Regeneração in vitro de Gerbera jamesonii sob estresse osmótico induzido por manitol utilizando reguladores de crescimento vegetal

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Abstract
Gerbera is a commercially important ornamental species that is highly susceptible to drought stress, which can significantly limit growth and productivity under adverse environmental conditions. This study aimed to evaluate the effects of osmotic stress on *in vitro* regeneration and to optimize plant growth regulator combinations for improving regeneration under drought-simulated conditions. Osmotic stress was induced by supplementing Murashige and Skoog medium with mannitol at concentrations of 10-50 g L^{-1}, and plant growth responses were evaluated. The results indicated that increasing mannitol levels progressively inhibited growth, with 40 g L^{-1} causing marked reductions in plant height, leaf number, leaf area, and fresh weight. To alleviate these effects, different cytokinins and auxins were applied. Among cytokinin treatments, 0.5 mg L^{-1} benzyladenine significantly enhanced shoot proliferation, producing more than 13 shoots per explant. In addition, all auxin treatments resulted in 100% rooting efficiency and significantly improved root number and length. These findings demonstrate that appropriate combinations of plant growth regulators can effectively mitigate drought-induced inhibition and promote regeneration under osmotic stress. The optimized regeneration protocol provides a foundation for future in vitro selection and the subsequent development of drought-tolerant gerbera genotypes.
Keywords: Abiotic stress, micropropagation, ornamental plant, root induction, shoot organogenesis, tissue culture.

Resumo
A gerbera é uma espécie ornamental de grande importância comercial, altamente sensível ao estresse hídrico, o que pode limitar significativamente o crescimento e a produtividade em condições ambientais adversas. Este estudo teve como objetivo avaliar os efeitos do estresse osmótico na regeneração *in vitro* e otimizar combinações de reguladores de crescimento vegetal para melhorar a regeneração sob condições simuladas de seca. O estresse hídrico foi induzido pela suplementação do meio de Murashige e Skoog com manitol em concentrações de 10-50 g L^{-1}, e as respostas de crescimento das plantas foram avaliadas. Os resultados indicaram que o aumento das concentrações de manitol inibiu progressivamente o crescimento, sendo que 40 g L^{-1} causaram reduções marcantes na altura das plantas, número de folhas, área foliar e massa fresca. Para mitigar esses efeitos, diferentes citocininas e auxinas foram aplicadas. Entre os tratamentos com citocininas, 0,5 mg L^{-1} de benziladenina promoveu significativamente a proliferação de brotos, produzindo mais de 13 brotos por explante. Além disso, todos os tratamentos com auxinas resultaram em 100% de enraizamento e melhoraram significativamente o número e o comprimento das raízes. Esses resultados demonstram que combinações adequadas de reguladores de crescimento vegetal podem mitigar efetivamente a inibição induzida pela seca e promover a regeneração sob estresse osmótico. O protocolo de regeneração otimizado fornece uma base para futura seleção in vitro e o subsequente desenvolvimento de genótipos de gérbera tolerantes à seca.
Palavras-chave: Estresse abiótico, micropropagação, indução de raízes, organogênese de brotos, planta ornamental, cultura de tecidos.

Introduction

Climate change is increasingly reshaping agricultural systems, with drought stress emerging as a major constraint to crop productivity and quality. This challenge is particularly critical in ornamental horticulture, where visual quality directly determines market value (Paiva, 2023). *Gerbera jamesonii*, one of the most widely cultivated ornamental species worldwide, plays a key role in the global cut flower industry due to its high commercial demand (Milani et al., 2022; Priya et al., 2023). However, its sensitivity to water deficit conditions makes production vulnerable, as drought stress severely restricts plant growth, reduces yield, and diminishes flower quality (Kharrazi et al., 2020; Ahsan et al., 2023). Ensuring stable and high-quality gerbera production under such conditions has therefore become an urgent priority for sustainable floriculture.

Among the available strategies, plant tissue culture has gained attention as a powerful tool for improving stress tolerance and propagation efficiency (Paiva et al., 2025). *In vitro* regeneration systems not only enable rapid multiplication but also create opportunities for selecting plants with enhanced adaptive traits (Wijerathna-Yapa et al., 2024). This potential is closely linked to somaclonal variation, which generates genetic diversity among regenerated plants and provides a valuable resource for identifying drought-tolerant somaclones (Asadi et al., 2020; Şimşek et al., 2024).

In this process, plant growth regulators play a decisive role in controlling morphogenesis and determining regeneration outcomes (Winarto et al., 2025). Cytokinins such as benzyladenine (BA), zeatin, and kinetin primarily stimulate cell division and shoot induction, thereby enhancing shoot proliferation. In contrast, auxins such as indole-3-acetic acid (IAA) and naphthaleneacetic acid (NAA) regulate root initiation and elongation, contributing to the development of a complete plantlet (Ibrahim and Yassin, 2020; Rodrigues et al., 2020). Under drought stress conditions, the balance between cytokinins and auxins becomes particularly critical, as it influences not only organ formation but also the plant's physiological adaptation to stress (Safana et al., 2022; Tran et al., 2025). Optimizing the type and concentration of these regulators can therefore improve regeneration efficiency, maintain growth under drought stress, and increase the likelihood of selecting drought-tolerant regenerants (Ilyas et al., 2021).

Therefore, this study aims to evaluate the effects of various plant growth regulators on shoot regeneration in gerbera under drought stress and to identify optimal treatment strategies to enhance regeneration efficiency and support the development of drought-tolerant plants for ornamental production.

Materials and Methods

Plant material

Four-week-old *in vitro* gerbera shoot cluster (*Gerbera jamesonii* L.) cultivar 'Jent'.

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Effects of drought stress on the growth of gerbera shoots

Gerbera shoots (approximately 1 cm in height) were cultured on Murashige and Skoog (MS) basal medium supplemented with 30 g L^{-1} sucrose and mannitol at concentrations of 10, 20, 30, 40, and 50 g L^{-1}. The medium was solidified with 7.5 g L^{-1} agar, and the pH was adjusted to 5.7-5.8 before autoclaving. Cultures were maintained at 24-26 °C under a 12-h photoperiod with a light intensity of 3,000 ± 200 lux and a relative humidity of 75%-80%. After six weeks of culture, plant height, number of leaves, leaf area, and fresh weight were recorded to determine the mannitol concentration that induces drought stress.

Effects of cytokinin on shoot formation in gerbera under drought stress

Gerbera shoots were cultured on MS basal medium supplemented with 30 g L^{-1} sucrose, 40 g L^{-1} mannitol, 0.1 mg L^{-1} IAA, and cytokinins in the form of BA, zeatin, or kinetin at concentrations of 0.5, 1.0, and 1.5 mg L^{-1}. All media were adjusted to pH 5.7-5.8 before autoclaving and solidified with 7.5 g L^{-1} agar. Cultures were maintained under the same environmental conditions described for the previous experiment. After six weeks of culture, shoot number per explant, shoot cluster height, shoot cluster diameter, leaf number, and fresh weight were recorded for analysis.

Effects of auxin on root formation in gerbera under drought stress

Regenerated shoots obtained from the optimal shoot induction medium were transferred to MS basal medium supplemented with 30 g L^{-1} sucrose, 40 g L^{-1} mannitol, and either IAA or NAA at concentrations of 0.1, 0.2, and 0.3 mg L^{-1}. The culture medium was prepared as described above. All cultures were maintained under the same environmental conditions. After six weeks of culture, key parameters were assessed, including plant height, leaf number, rooting rate, root number, and root length.

Experimental design and statistical analysis

Each experiment was conducted using a completely randomized design. Each treatment consisted of 30 explants, randomly allocated into three independent biological replicates, with 10 explants per replicate. The experimental unit was defined as one culture vessel containing 10 explants. Data are presented as the mean ± standard deviation of three biological replicates. Statistical analyses were performed using Jamovi version 2.7. Differences among treatments were evaluated by one-way analysis of variance, followed by Tukey's honestly significant difference test for multiple comparisons at a significance level of $p < 0.05$ (Mohammed et al., 2022).

Results

Effects of drought stress on the growth of gerbera shoots

Table 1 presents the effects of mannitol on the growth of gerbera shoots after six weeks of culture, indicating a clear inverse relationship between mannitol concentration and various growth parameters, suggesting significant osmotic stress. The control group exhibited a height of 5.63 cm; however, the 40 g L^{-1} mannitol treatment resulted in a height of only 1.53 cm, representing a reduction of approximately 73% compared to the control. Similarly, the number of leaves decreased from an average of 18.56 in the control group to 7.64 at 40 g L^{-1}, reflecting a reduction of about 59%. The leaf area also demonstrated a significant decline, from 13.13 cm² in the control group to 2.15 cm² at 40 g L^{-1}, indicating an 84% reduction. Fresh weight measurements decreased from 0.73 g in the control group to 0.29 g at 40 g L^{-1}, equivalent to a reduction of approximately 60%. These findings suggest that the 40 g L^{-1} mannitol treatment effectively induces osmotic stress in gerbera plants, making it a suitable concentration for further studies on the effects of drought stress on plant growth and development (Fig. 1).

Table 1. Effects of mannitol on the growth of gerbera shoot after six weeks of culture

Mannitol (g L^{-1})	Plant height (cm)	Leaf number	Leaf area (cm²)	Fresh weight (g)
Control	5.63 ^{a}	18.56 ^{a}	13.13 ^{a}	0.73 ^{a}
10	4.32 ^{b}	15.42 ^{b}	8.96 ^{b}	0.65 ^{b}
20	2.74 ^{c}	12.31 ^{c}	5.47 ^{c}	0.53 ^{c}
30	2.68 ^{c}	9.87 ^{d}	5.53 ^{c}	0.43 ^{c}
40	1.53 ^{d}	7.64 ^{e}	2.15 ^{d}	0.29 ^{d}
50	0.93 ^{e}	4.08 ^{f}	0.75 ^{e}	0.09 ^{e}

Means followed by the same letter within a column are not significantly different at the 5% level according to Tukey's test.

Fig. 1. Effects of mannitol on the growth of gerbera shoot after six weeks of culture.

Effects of cytokinin on shoot formation in gerbera under drought stress

Table 2 summarizes the effects of different cytokinin treatments on shoot formation in gerbera under drought stress after six weeks. The control group exhibited the lowest metrics, with a shoot number of 1.53, cluster height of 1.03 cm, and cluster diameter of 1.12 cm. Among the treatments, BA at 0.5 mg L^{-1} proved to be the most effective, resulting in 13.32 shoots, a cluster height of 2.13 cm, and a cluster diameter of 3.25 cm, along with 30.50 leaves, 7.23 cm² leaf area, and a fresh weight of 1.12 g. The 1.0 mg L^{-1} BA treatment showed slightly lower results with 10.25 shoots, while the 1.5 mg L^{-1} concentration further decreased growth metrics. Kinetin at 1.0 mg L^{-1} yielded 11.70 shoots and demonstrated notable growth, whereas zeatin treatments, particularly at 1.0 mg L^{-1} reached 11.24 shoots but did not surpass the effectiveness of BA. Overall, BA at 0.5 mg L^{-1} emerged as the most effective treatment for enhancing shoot formation under drought conditions (Fig. 2).

Table 2. Effects of cytokinin on shoot formation in gerbera under drought stress after 6 weeks

Cytokinin (mg L^{-1})			Shoot number	Cluster height (cm)	Cluster diameter (cm)	Leaf number	Leaf area (cm^2)	Fresh weight (g)
BA	Kinetin	Zeatin						
Control			1.53 ^{e}	1.03 ^{f}	1.12 ^{f}	12.37 ^{d}	0.82 ^{h}	0.31 ^{f}
0.5			13.32 ^{a}	2.13 ^{c}	3.25 ^{a}	30.50 ^{a}	7.23 ^{b}	1.12 ^{a}
1.0			10.25 ^{b}	2.19 ^{c}	3.11 ^{b}	24.25 ^{b}	7.54 ^{a}	1.16 ^{a}
1.5			6.97 ^{c}	3.04 ^{a}	2.74 ^{d}	14.70 ^{d}	6.48 ^{c}	1.02 ^{b}
	0.5		4.15 ^{d}	1.42 ^{d}	1.36 ^{e}	13.37 ^{d}	1.22 ^{g}	0.42 ^{e}
	1.0		11.70 ^{b}	2.08 ^{c}	2.89 ^{cd}	24.15 ^{b}	6.41 ^{c}	0.91 ^{bc}
	1.5		10.56 ^{b}	2.59 ^{b}	2.61 ^{d}	26.38 ^{b}	6.26 ^{d}	0.87 ^{c}
		0.5	5.13 ^{cd}	1.16 ^{e}	1.44 ^{e}	18.07 ^{c}	1.18 ^{g}	0.39 ^{e}
		1.0	11.24 ^{b}	1.53 ^{d}	3.02 ^{c}	25.43 ^{b}	2.37 ^{f}	0.63 ^{d}
		1.5	10.31 ^{b}	1.61 ^{d}	2.73 ^{d}	26.68 ^{b}	5.03 ^{e}	0.58 ^{d}

Means followed by the same letter within a column are not significantly different at the 5% level according to Tukey's test.

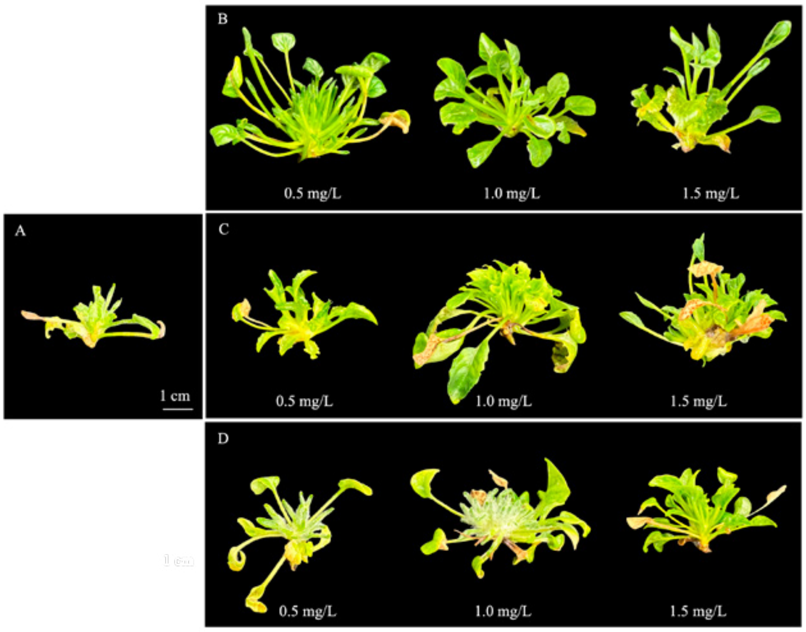

Fig. 2. Effects of cytokinins on shoot regeneration of gerbera cultured on MS medium containing 40 g L^{-} mannitol after six weeks of culture, supplemented with (A) Control – without cytokinin. (B) BA at 0.5, 1.0, and 1.5 mg L^{-1}. (C) Kinetin at 0.5, 1.0, and 1.5 mg L^{-1}. (D) Zeatin at 0.5, 1.0, and 1.5 mg L^{-1}.

Effects of auxin on root formation in gerbera under drought stress

The effects of auxin on root production in gerbera under drought stress during six weeks are shown in Table 3. According to the findings, the application of auxin has a considerable impact on several growth indices (Fig. 3). The control group exhibited the lowest plant height at 2.09 cm, whereas auxin treatments resulted in increased heights, with the highest measurement of 2.63 cm observed in the 0.2 mg L^{-1} NAA treatment, significantly surpassing the control. In terms of leaf number, the control group had 7.64 leaves, while auxin treatments enhanced leaf counts, peaking at 15.05 leaves for the 0.3 mg L^{-1} IAA treatment and 14.82 leaves at 0.2 mg L^{-1} IAA, both significantly higher than the control. Remarkably, all auxin treatments achieved a rooting rate of 100%, demonstrating the effectiveness of auxin in promoting root formation under drought stress. The control group showed no root development, while auxin treatments significantly increased the root number, with the highest count of 15.13 roots recorded at 0.2 mg L^{-1} IAA. Root length measurements also varied, with the 0.1 mg L^{-1} IAA treatment achieving a length of 4.30 cm, and the maximum length of 5.41 cm observed in the 0.1 mg L^{-1} NAA treatment.

Table 3. Effects of auxin on root formation in gerbera under drought stress after 6 weeks

Auxin (mg L⁻¹)		Plant height (cm)	Leaf number	Rooting rate (%)	Root number	Root length (cm)
IAA	NAA					
Control		2.09 d	7.64 b	0.00 b	0.00 d	0.00 d
0.1		2.18 c	14.38 b	100.00 a	3.33 c	4.30 c
0.2		2.22 c	14.82 a	100.00 a	15.13 a	5.12 ab
0.3		2.25 c	15.05 a	100.00 a	14.08 a	4.84 b
	0.1	2.43 b	7.61 b	100.00 a	10.03 b	5.41 a
	0.2	2.63 a	9.24 a	100.00 a	9.78 b	5.24 a
	0.3	2.58 a	11.08 a	100.00 a	12.51 ab	5.16 ab

Means followed by the same letter within a column are not significantly different at the 5% level according to Tukey's test

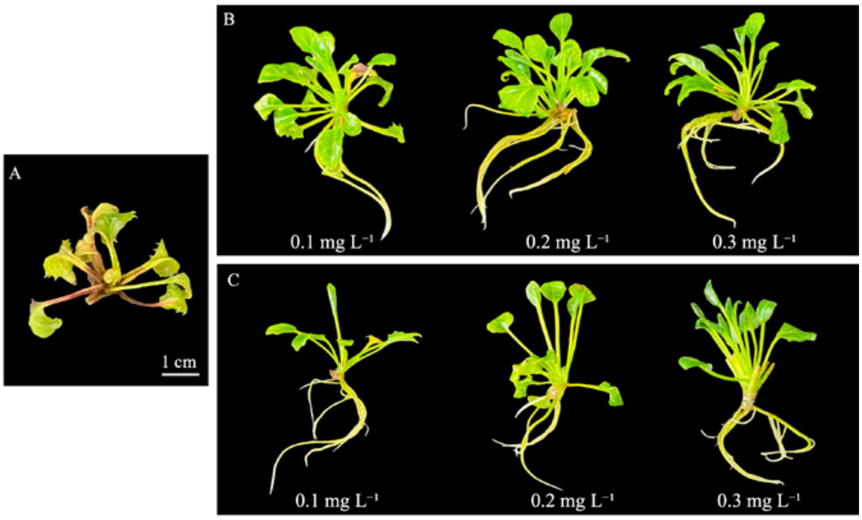

Fig. 3. Effecs of auxin treatments on root induction of gerbera cultured on MS medium containing 40 g L^{-1} mannitol after six weeks of culture, supplemented with (A) Control – without auxins. (B) IAA at 0.1, 0.2, and 0.3 mg L^{-1}. (C) NAA at 0.1, 0.2, and 0.3 mg L^{-1}.

Discussion

The marked reductions in plant height (73%), leaf number (59%), leaf area (84%), and fresh weight (60%) observed under 40 g L^{-1} mannitol confirm that this concentration imposed severe osmotic stress on gerbera plantlets (Table 1). Mannitol reduces the external water potential, thereby limiting water uptake and decreasing cell turgor, which restricts cell expansion and biomass accumulation (Havryliuk et al., 2024). The inhibition of vegetative growth is therefore a direct physiological consequence of impaired water status rather than merely a reduction in growth rate. Under osmotic stress, plants generally reallocate metabolic resources from growth to survival by activating stress-responsive pathways, including osmotic adjustment through the accumulation of compatible solutes such as proline and glycine betaine, antioxidant defense systems, and stress-related gene expression (Chen et al., 2024). However, when osmotic stress exceeds the plant's adaptive capacity, these protective mechanisms become insufficient to maintain normal cellular metabolism, leading to reduced cell division, impaired photosynthetic activity, and suppressed organ development (Thang et al., 2019; Cheheltanan et al., 2025). The substantial inhibition observed at 40 g L^{-1} therefore indicates that this concentration provides sufficient selection pressure while still permitting regeneration, making it appropriate for subsequent regeneration experiments.

Successful regeneration under osmotic stress is an important prerequisite for in vitro selection because regenerated tissues must retain sufficient developmental competence despite adverse conditions. Although regeneration under osmotic stress alone does not demonstrate drought tolerance, it allows the identification of genotypes or cell lines capable of maintaining morphogenic capacity under water-deficit conditions. Such materials may subsequently be evaluated using physiological, biochemical, molecular, and greenhouse-based drought assessments before being considered drought-tolerant genotypes. Therefore, the regeneration system established in this study should be regarded as a screening platform that facilitates the future selection of putative drought-tolerant germplasm rather than direct evidence of drought-tolerant plant development.

Among the cytokinin treatments, BA at 0.5 mg L^{-1} produced the highest shoot number, cluster size, leaf number, and fresh weight (Table 2), indicating that an appropriate cytokinin supply can partially overcome the inhibitory effects of osmotic stress on shoot morphogenesis. Rather than acting solely as a shoot-promoting hormone, cytokinin contributes to the maintenance of meristematic activity under stress by sustaining cell division, delaying senescence, maintaining chloroplast integrity, and promoting nutrient remobilization toward actively growing tissues (Hussain et al., 2025; Abd-Elsalam and Mohamed, 2024). Maintaining active shoot meristems under osmotic stress is physiologically important because it enables continued organogenesis despite restricted water availability, thereby preserving regeneration potential. The superior performance of BA compared with kinetin and zeatin may reflect its greater affinity for cytokinin receptors and its stronger activation of cytokinin-responsive signaling pathways involved in shoot meristem maintenance (Zubo et al., 2020; Schuffner et al., 2026). Nevertheless, the response remained concentration dependent, as increasing BA to 1.0 or 1.5 mg L^{-1} reduced regeneration efficiency. This observation suggests that excessive cytokinin disturbs endogenous hormonal homeostasis, resulting in abnormal shoot development and reduced regenerative competence (Petrášek et al., 2002). Similar responses have been reported in gerbera cv. Rosalin, where higher BA concentrations decreased shoot formation and shoot number per explant (Dutta and Gantait, 2016). Although zeatin and kinetin promoted regeneration to some extent, particularly at lower concentrations, their effects remained inferior to those of BA, consistent with previous observations in gerbera. In contrast, zeatin has been reported to be more effective in tomato under drought conditions (Tran et al., 2021), highlighting that cytokinin responses are highly genotype- and species-dependent.

Root development represents another critical component of plant adaptation to water-deficit conditions because a functional root system improves water acquisition and facilitates recovery following stress. All auxin treatments achieved 100% rooting (Fig. 3), demonstrating that root induction remained highly responsive despite osmotic stress. Auxins regulate adventitious root formation by stimulating root meristem initiation, cell division, and subsequent cell elongation (Verma et al., 2022). The superior root number obtained with 0.2 mg L^{-1} IAA and the greater root length observed with 0.1 mg L^{-1} NAA indicate that different auxins preferentially influence distinct phases of root development. A larger and longer root system may enhance the plant's capacity for water and nutrient uptake under stress conditions (Mohammadi et al., 2023), thereby supporting subsequent plant establishment after transfer to ex vitro conditions. Likewise, the increased plant height and leaf number observed in auxin-treated plantlets suggest that improved root formation indirectly supports shoot growth by enhancing resource acquisition and maintaining whole-plant physiological balance.

The optimized combinations of mannitol and plant growth regulators established in this study improve the efficiency of shoot regeneration and rooting under osmotic stress. These findings should not be interpreted as direct evidence of drought-tolerant plant development. Instead, they provide a reproducible regeneration system that can be integrated with future physiological, biochemical, molecular, and field evaluations to facilitate the identification and validation of drought-tolerant gerbera genotypes. Such an approach represents an important first step toward incorporating in vitro selection into breeding programs aimed at improving drought resilience.

Conclusion

MS medium supplemented with 40 g L^{-1} mannitol effectively simulated osmotic stress in gerbera. Under these conditions, MS medium containing 0.1 mg L^{-1} IAA and 0.5 mg L^{-1} BA enhanced shoot regeneration, while MS medium supplemented with 0.2 mg L^{-1} IAA promoted efficient rooting. These optimized culture conditions provide a practical protocol for developing drought-tolerant gerbera and support more sustainable ornamental plant production.

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Author Contribution

TTT: Conceptualization, Methodology, Data Curation, Formal Analysis Writing – Original Draft, Writing – Review & Editing. **MHLT:** Methodology, Supervision, Validation, Writing – Original Draft.

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability Statement

Data will be made available upon request to the authors.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that the use of AI and AI-assisted technologies was not applied in the writing process.

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