Boosting the nutritional value of edible dahlia flowers with nano-zinc oxide (ZnO)

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Abstract

Edible flowers of dahlia represent a novel source of functional foods, and their nutritional enhancement through agronomic zinc biofortification is scarcely explored. This study establishes, for the first time, the efficacy of foliar-applied zinc oxide nanoparticles (ZnO NPs) as a novel biofortification strategy for this crop. The study compared foliar applications of ZnO NPs with those of zinc sulphate ($ZnSO_4$) at 50 mg L^{-1} or 100 mg L^{-1} in dahlia flowers cv. 'Yaretzi'. Plants were grown in open-field pots. Levels of bioactive compounds, antioxidant activity, and mineral composition were measured. Results show that ZnO NPs treatment significantly increased chroma by 20% (14.63 ± 0.87), anthocyanins by 40% (0.21 ± 0.02 mg C3G 100 g^{-1}) and Zn content by 37% (49.7 ± 0.57 mg kg^{-1}), compared to the treatment with $ZnSO_4$. Antioxidant capacity (152.61 ± 2.54 µmol Fe^{2+}/g) and protein (5.6 ± 0.03%) and fibre (30.3 ± 0.4%) were also increased. Findings indicate that foliar applications of ZnO NPs exhibit enhanced effectiveness, compared to $ZnSO_4$, for increasing the nutrient-richness of dahlia flowers. Consequently, foliar application of ZnO NPs emerges as a promising agronomic strategy to cultivate dahlia flowers as a functional food for combating zinc deficiencies, subject to future comprehensive assessment of nanoparticle toxicology in food chain.

Keywords: bioactive compounds; biofortification; functional food; mineral composition; ZnO nanoparticles (ZnO NPs)

Introduction

The *Dahlia* genus (Asteraceae, Coreopsideae) is endemic to Mexico, where 36 of the world's 42 species are discovered. The genus comprises perennial herbs and shrubs primarily adapted to terrestrial environments (American Dahlia Society [ADS], 2025; Carrasco-Ortiz *et al.*, 2019; Sánchez-Chávez *et al.*, 2026). Its remarkable floral diversity has established its primary value as an ornamental resource; yet, as an endemic genetic resource, it also holds

significant cultural, economic, and largely untapped culinary potential (Mejía-Muñoz *et al.*, 2020; Nsabimana and Jiang, 2011; Reyes-Santiago *et al.*, 2024). Paradoxically, while extensive hybridization has yielded approximately 61,000 cultivars, these are derived from just four species (*D. coccinea*, *D. pinnata*, *D. merckii*, and *D. imperialis*) and represent only ~10% of the genus's genetic diversity (Mera-Ovando and Bye-Boettler, 2006; Wang *et al.*, 2024). This limited genetic base exists besides severe threats of extinction because of climate change, habitat alteration, and wildfire (Mejía-Muñoz *et al.*, 2015). Scientific research now validates much of the ancestral knowledge of dahlia's health benefits, and positions these flowers as a promising functional food. Beyond their traditional use as garnishes and their value in modern gastronomy, dahlia flowers contain a rich profile of bioactive compounds—including phenols, flavonoids and anthocyanins (Kumari *et al.*, 2017). All these have antioxidant activity that underpins their health-promoting properties (Hernández-Epigmenio *et al.*, 2022; Mulík *et al.*, 2024; Mulík and Ozuna, 2024; Najar *et al.*, 2024).

The rising global demand for functional foods is fuelled by shifting consumer preferences towards novel and health-promoting ingredients. This has led to a significant increase in interest in edible flowers (EFs). Among EFs, dahlia flowers have attracted particular attention because of their historical culinary use and rich phytochemical profile. This has positioned them as a strong candidate for dietary diversification and targeted nutritional enhancement (Costa *et al.*, 2022; Granados-Balbuena *et al.*, 2023; Whitley, 1985). The high antioxidant and therapeutic value of consuming either wild or cultivated dahlia flowers is receiving growing interest (Chetia *et al.*, 2025). Recent studies have characterised their phytochemical profiles and mineral contents, and this has further validated their dietary potential (Granados-Balbuena *et al.*, 2024a; Marcos-Gómez *et al.*, 2025; Rivera-Espejel *et al.*, 2019). However, critical knowledge gaps persist, particularly in: (a) biofortification strategies for EFs (an underexplored area in dahlias); (b) optimisation of agronomic management, and (c) post-harvest processing and food safety protocols. This presents a critical opportunity to expand our utilisation of the remaining 90% of dahlia species for both ornamental purposes and as innovative candidates for commercial production of EFs.

The pursuit of sustainable development and food security has emerged as a global priority, particularly in addressing persistent hunger—a challenge for many human populations globally (Cakmak and Kutman, 2017; White and Broadley, 2009). A critical aspect of this challenge is micronutrient malnutrition—the so-called 'hidden hunger'. Micronutrient malnutrition often stems from diets dominated by energy-dense but nutrient-poor foods as well as from physiological stressors, such as pregnancy or underlying health conditions (Rizvi *et al.*, 2023). One of these malnutrition conditions is due to zinc (Zn) deficiency. This impairs physical development and increases susceptibility to diarrheal diseases, respiratory infections, and childhood mortality (Sharma *et al.*, 2025). These conditions disproportionately impact marginalised communities, especially those inhabiting regions with nutrient-depleted soils. These are often characterised by high salinity or carbonate dominance, or poor physical structure (Minnocci *et al.*, 2018). Among the strategies to minimise this deficiency is biofortification, which is the process by which the nutrient density of food crops is increased through conventional plant breeding, improved agronomic practices, and/or modern biotechnology without sacrificing any characteristics that are preferred by consumers or most importantly by farmers (Azeem *et al.*, 2025; Sharma *et al.*, 2025). Biofortification to create functional super-foods is gaining prominence as a scalable solution in these areas by enhancing the mineral concentrations of various edible crops by employing novel phytogenetic, genetic, or agronomic approaches (Cakmak and Kutman, 2017). Of these, agronomic biofortification offers the most immediate, expedient, and cost-effective implementation pathway. This can be achieved by working with both conventional and underutilised crops, such as dahlia (Du *et al.*, 2019).

The effectiveness of soil applications of these mineral nutrients is influenced by multiple factors, such as soil water content, irrigation practices, soil physicochemical properties (pH, texture, structure, etc.), nutrient solubility, chemical source, and dose (Hatamian *et al.*, 2018). Given these limitations, foliar sprays emerge as a viable alternative to soil applications, as they increase the precision of application and also offer advantages in terms of efficiency, speed, adaptability, and immediate correction of deficiencies (Davarpanah *et al.*, 2017). Furthermore, by requiring smaller amounts of fertiliser, foliar sprays reduce the ecological impact on agroecosystems compared to soil application (Niu *et al.*, 2021). The use of Zn oxide nanoparticles (ZnO NPs) has gained relevance as an inorganic source of Zn with a stable chemical structure, high specific surface area, and redox capacity (Bala *et al.*, 2019; Karimian and Samiei, 2023). These characteristics provide ZnO NPs greater penetration into leaf tissues and mobility within the plant while also minimising losses because of leaching or immobilisation in soil—these two factors being typical drawbacks with conventional fertilisers, such as zinc sulphate ($ZnSO_4$), zinc nitrate ($Zn(NO_3)_2$) or Zn chelates (ethylenediamine-N,N'-bis(2-hydroxyphenylacetic acid [EDDHA], ethylenediaminetetraacetic acid [EDTA], and diethylenetriaminepentaacetic acid [DTPA]) (Bautista-Diaz *et al.*, 2021; Mahdavi *et al.*, 2022). After foliar application, ZnO NPs appear to enter the plant mainly through the stomata, they accumulate initially in the apoplast and then dissolve progressively,

releasing Zn^{2+} absorbed by the mesophyll cells, while part of a nanoparticulate fraction may also be internalised. This may account for their distinct distribution within leaf tissues, compared to $ZnSO_4$ (Zhu *et al.*, 2020). A gradual release of Zn may improve Zn accumulation and translocation and support Zn-dependent metabolic processes, including Cu/Zn-superoxide dismutase activity, thereby contributing to improved growth and stress tolerance (Rameshraddy *et al.*, 2017).

Despite the promising agronomic benefits of ZnO NPs, their application in edible crops necessitates careful toxicological assessment (Hou et al., 2018). Recent studies have highlighted that nanoparticle size critically determines respiratory deposition, with a 67.5% reduction in deposition fraction as particle size increases from 10 nm to 100 nm (Khadanga and Mishra, 2024). The multiple-path particle dosimetry modelling confirms significant nanoparticle retention in the pulmonary lobes, while *in vivo* studies demonstrate that inhaled nanoparticles can translocate to the bloodstream and brain, potentially triggering oxidative stress, inflammation, and tissue damage. Additional concerns include dermal absorption, environmental persistence, and limited knowledge about long-term health consequences (Kah *et al.*, 2021). Consequently, while this study focuses on establishing biofortification efficacy, comprehensive risk evaluations, including respiratory exposure assessment, translocation studies and dietary safety analysis, remain essential before commercial implementation in the food chain.

Building upon these advantages, this study pioneers the Zn biofortification of edible dahlia flowers using foliar-applied nanoparticles. This innovative approach significantly enhances Zn accumulation and bioactive compound content, establishing a new paradigm for nutritional improvement in ornamental-edible species. Furthermore, ZnO NPs are compatible with sustainable management systems, as their use reduces both dose and application frequency needed to fulfil the crop's nutritional demands (Almendros *et al.*, 2022). This study, therefore, evaluates the effects of foliar applications of ZnO NPs versus $ZnSO_4$ on Zn enrichment, bioactive compounds, and mineral composition of dahlia cv. 'Yaretzi.' It is anticipated that the findings will provide a technical foundation for leveraging this underutilised genetic resource, supporting the plant's culinary diversification while maximising its nutritional potential.

Materials and Methods

Experimental site and plant material

The study was conducted from March 2024 to November 2024 under open-field conditions in the horticulture area adjacent to the floriculture unit at the Autonomous University Chapingo (UACh) located in Texcoco de Mora, State of Mexico, Mexico (19°29'23" N, 98°52'24" W). The site lies at an elevation of 2,268 m above sea level, with an average annual temperature of 15.6°C. Dahlia plants (*Dahlia* × *hortorum*) cv. 'Yaretzi' were propagated from tuberous roots collected from the 'San Martín' experimental field (19°29'58" N, 98°52'44" W) managed by the Department of Plant Science (UACh). Plant propagation began in late March 2024 using five 210-L high-density polyethylene containers (≈40 tuberous roots/container) filled with a 2:1 (v/v) peat–perlite substrate. Sprout emergence occurred 15 days after planting (DAP), with subsequent transplantation at 40 DAP into individual 6-L black polystyrene bags containing the same substrate mixture (Figure**s** 1A and 1B). Drip irrigation was administered at 0.5–3.0 L/plant per session (1–2 times weekly), with volume and frequency adjusted according to the prevailing weather conditions (temperature and relative humidity) and crop phenological stage. Nutrient management followed a 120–0–200 ($N–P_2O_5–K_2O$) fertilisation regimen, split into two applications: first at transplantation, and the second just pre-flowering (BBCH stage 51). Throughout the trial, integrated pest management and weed control followed established commercial protocols for ornamental dahlia production.

Experimental design and sampling

The study employed a completely randomised design with five treatments and four biological replicates per treatment (n = 4). Each biological replicate constituted an experimental unit of three plants (60 plants in total). Five treatments were evaluated: (T1) absolute control (no Zn application); (T2 and T3) two concentrations of ZnO nanoparticles (50 mg L^{-1} and 100 mg L^{-1}; Investigación y Desarrollo de Nanomateriales S.A. de C.V., Mexico); and (T4 and T5) two concentrations of $ZnSO_4$ (50 mg L^{-1} and 100 mg L^{-1}; Merck®, Germany). All Zn treatments included 100 µL L^{-1} of Silwet® L-77 adjuvant (trisiloxane-based; Arista-Lifescience, Mexico). Foliar applications were made at three phenological stages: 3 and 5 weeks post-transplanting (vegetative phase) and at flower bud stage (pre-anthesis). Applications were made between 08:00 and 09:00 h using a 0.5-L fine sprayer to ensure complete leaf coverage (both surfaces), with the substrate protected by a plastic film to prevent soil contamination. Inflorescences were asynchronously harvested beginning 25 August 2024 using sterilised pruning shears. Samples were collected at the precise phenological stage when the stamens became visible in the first row of tubular florets. To minimise post-harvest stress, harvesting was conducted during optimal morning hours

Figure 1. Plant material of dahlia cv. 'Yaretzi'. (A) General view of the crop under open-field conditions at the experimental site; (B) a representative in florescence exhibiting characteristic morphology of the cultivar.

(between 07:00 and 09:00 h). Flower heads were immediately transported for processing in dry ice-cooled containers to the Plant Physiology Laboratory (Department of Plant Science, UACh).

At the laboratory, the capitula were separated manually into individual florets and subjected to lyophilisation using a BK-F10PT freeze dryer (BIOBASE®, USA). For each replicate (n = 4 per treatment), 50-g samples of ray florets (ligules) were evenly distributed in standard trays (180 × 20 mm) and processed at -56°C and 0.1 mbar for 72 h until constant weight was achieved. The freeze dryer was pre-stabilised to target parameters before each run to ensure consistent processing conditions. The resulting lyophilised material was then crunched into a fine powder using a mortar and pestle ready for subsequent analysis of bioactive compounds (total phenols [TP], total flavonoids [TFl], and total anthocyanins [TAn]) and antioxidant capacity (AC).

Reagents

All chemicals used in this study, including those for the determination of photosynthetic pigments, sucrose, bioactive compounds, antioxidant capacity, and mineral composition, were of analytical grade and purchased from Sigma-Aldrich, USA.

Characterisation of nanoparticles

Zinc oxide powder was applied as a nanofertiliser. For characterisation, the sample was dispersed by

ultrasonication and deposited onto a 300-mesh copper grid coated with a Lacey Formvar/carbon support film (Ted Pella, USA). The analysis was carried out using a JEOL JEM-2200FS-CS transmission electron microscope (JEOL, Japan) operated at 200 kV. Morphology was examined by scanning transmission electron microscopy (STEM), crystallinity by selected-area electron diffraction (SAED), and chemical composition and elemental mapping by energy-dispersive X-ray spectroscopy (EDS) using an Oxford UltimR-Max detector (Oxford Instruments, UK). The material exhibited nanometric dimensions, with particle sizes ranging from 29.52 nm to 116.80 nm, with an average size of 64.66 nm (Figures 2C and 2D). The particles were predominantly elongated, with well-defined faces resembling small prisms or rods, and some agglomeration was observed (Figures 2A and 2b). Diffraction patterns indicated a highly ordered crystalline material (Figure 3B). EDS spectra obtained at different points showed only Zn and O signals, with no evident impurities detected within the limits of the technique, suggesting a relatively homogeneous composition (Figure 3A).

Colour, total soluble solids (TSS), and titratable acidity (TA)

Flower colour parameters were quantified using a portable SP62 sphere colorimeter (X-Rite®, USA), measuring CIELAB coordinates: L* (lightness), C* (chroma), and h° (hue angle). For physicochemical analyses, TA was determined following the method described by Tomasik (2003): briefly, a 0.5-g sample was homogenised with 10-mL distilled water using an Ultra-Turrax T25 homogeniser (IKA®, USA) for 2 min, filtered, then titrated against 0.1-N NaOH with 2% phenolphthalein as indicator (results expressed as %citric acid). TSS were measured by placing filtrate droplets on a PAL-1 digital refractometer prism (ATAGO®, Japan), with results reported in °Brix.

Photosynthetic pigment and leaf area

The extraction and quantification of chlorophylls a and b (Chl a and Chl b) and total carotenoids (TC) was carried out by the method described by Wellburn (1994).

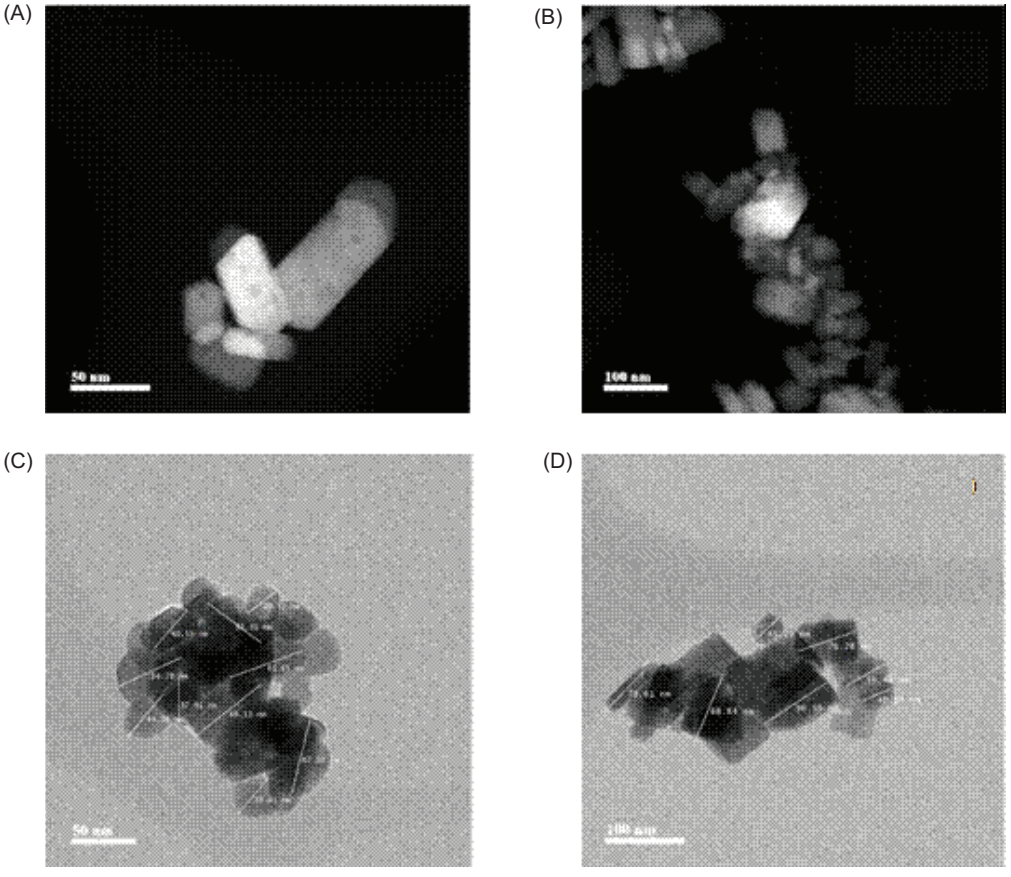

Figure 2. Morphological and dimensional characterisation of ZnO nanomaterial applied as a nanofertilizer. (A and B): nanoparticle morphology obtained by STEM; (C and D): particle size measurements obtained by transmission electron microscopy (TEM).

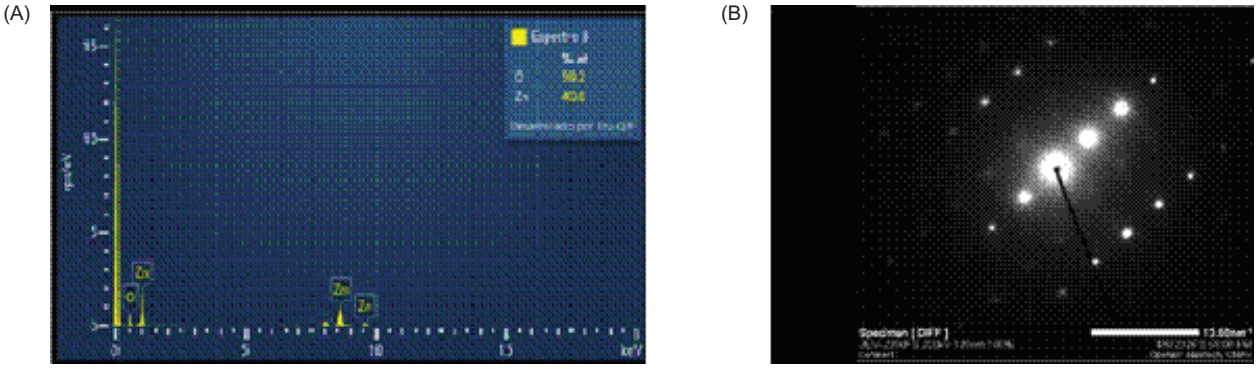

Figure 3. ZnO nanoparticles: (A) elemental analysis (chemical composition) by energy-dispersive X-ray spectroscopy (EDS), and (B) crystalline structure by selected-area electron diffraction (SAED).

Briefly, a sample of fresh leaf tissue (5 g) was placed in a 100-mL flask with 80 mL of 80% acetone. Absorbance was recorded at 665 nm, 653 nm, and 470 nm using an ultraviolet (UV)/visible spectrophotometer Lambda 25® (PerkinElmer, USA) with 1-cm pathlength quartz cuvettes. Pigment concentrations were calculated using the following equations:

$$\text{Chl a} = 12.72A_{665} - 2.59A_{653},$$

$$\text{Chl b} = 20.36A_{653} - 5.19A_{665},$$

$$\text{TC} = (1{,}000A_{470} - 1.63\ \text{Chl a} - 104.96\ \text{Chl b}) \div 221.$$

To quantify foliar development, leaf area (LA) was determined according to a procedure described by Liu *et al.* (2022) with slight modifications. Briefly, prior to flower harvest, all leaves were measured using a CI-202 Laser Leaf Area Meter (CID Bio-Science, USA). The results are expressed in cm^2.

Sucrose

The sucrose was quantified according to the method described by Irigoyen *et al.* (1992) with slight modifications: Briefly, 0.5-g fresh dahlia ligulate florets was homogenised three times, the first time with 5 mL of 96% ethanol and then twice with 5 mL of 70% ethanol. The homogenate was centrifuged at 3,740×g for 10 min at 4°C. For colorimetric analysis, 0.1 mL of supernatant was reacted with 3 mL of freshly prepared anthrone reagent (1% w/v anthrone in concentrated H_2SO_4). The mixture was incubated in a boiling water bath (100°C) for exactly 10 min, then immediately cooled on ice. Absorbance was measured at 650 nm against a reagent blank using a Lambda X® spectrophotometer (PerkinElmer) with 1-cm pathlength quartz cuvettes. Concentration of sucrose was determined from a standard curve (0–100 µg mL sucrose) and expressed as mg g^{-1} fresh weight (FW).

Bioactive compounds

Extraction

The extraction of bioactive compounds was conducted by the method described by Aguiñiga-Sánchez *et al.* (2017) with modifications. Four biological replicates (n = 4) were analysed per treatment. Lyophilised floral tissue (0.50 ± 0.02 g per replicate) was homogenised in 5 mL of 80% methanol (v/v, high performance liquid chromatography [HPLC] grade) using a IKA T25 Ultra-Turrax at 10,000 rpm for 2 min. The homogenate was centrifuged at 6,000×g for 10 min at 4°C. The supernatant was used to quantify phenols, flavonoids, anthocyanins, and antioxidant capacity as described below. For variables quantified from lyophilised tissue, results were converted on an FW basis using the moisture content determined for each treatment according to the following equation:

Value on FW basis = value on DW basis × (100 – moisture, %) ÷ 100.

The corresponding moisture values used for conversion were obtained from the proximate analysis of the same treatment.

Phenols, flavonoids, total anthocyanins, and ascorbic acid (AA)

Total phenols (TP) were quantified according to the Folin–Ciocalteu method described by Silveira *et al.* (2020). Two 0.250-mL samples of the above supernatant were chosen, to which were added 0.750 mL of 2% (v:v) Na_2CO_3 and 0.250 mL of 50% Folin–Ciocalteau.

The mixture was incubated for 1 h and the absorbance was measured at 725 nm on a Lambda 25® UV-visible spectrophotometer (PerkinElmer). Quantification was performed using a gallic acid standard curve (0–500 mg L^{-1}, $R^2 > 0.99$), with results expressed as mg gallic acid equivalent (GAE) per 100 g FW (mg GAE 100 g^{-1} FW).

Total flavonoids were determined according to the method described by Chang *et al.* (2002). Briefly, 0.250 mL of the above supernatant was mixed with 0.075 mL of 5% (w/v) sodium nitrite ($NaNO_2$) and vortexed for 5 min. Subsequently, 0.150 mL of 10% (w/v) aluminium chloride ($AlCl_3$) was added, followed by 0.500 mL of 1-M sodium hydroxide (NaOH) and 2.025 mL of deionised water. The reaction mixture was incubated for 40 min at ambient temperature (25 ± 2°C) in the dark. Absorbance was measured at 510 nm using a Lambda 25® UV-Vis spectrophotometer (PerkinElmer). Quantification was performed against a quercetin standard curve (0–200 mg L^{-1}, $R^2 > 0.98$), with results expressed as mg quercetin equivalent (QE) per 100 g FW (mg QE 100 g^{-1} FW).

Total anthocyanin content was quantified using the pH differential method (Giusti and Wrolstad, 2001), with modifications. Two 0.5-mL aliquots of the above supernatant were separately mixed with either 2.0 mL of 0.025-M potassium chloride buffer (pH 1.0) or 2.0 mL of 0.4-M sodium acetate buffer (pH 4.5), followed by vortexing for 1 min. Absorbance measurements were accomplished at two wavelengths: 520 nm to quantify anthocyanins at their peak absorption, and 700 nm to correct for potential light scattering from sample turbidity, using a Lambda 25® UV-Vis spectrophotometer (PerkinElmer). Anthocyanin concentration was calculated by comparing the difference in absorbance between two pH conditions, with results expressed as milligram of cyanidin-3-glucoside (C3G) equivalent per 100 g of FW (mg C3G100 g^{-1} FW). This calculation incorporated molar absorptivity (26,900 $L \cdot cm^{-1} \cdot mol^{-1}$) and molecular weight (449.2 g/mol) of C3G as reference standards.

Antioxidant capacity

The antioxidant capacity of flower extracts was comprehensively evaluated using three validated assays, each performed with four biological replicates (n = 4) and three technical replicates per sample. The methods were: ABTS 2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid) radical scavenging (ABTS), ferric reducing antioxidant power (FRAP), and 2,2-diphenyl-1-picrylhydrazyl (DPPH). The ABTS assay was carried out as described by Re *et al.* (1999), for which ABTS solution was prepared by mixing equal volumes of 7 mM of ABTS reagent ((2,2'-azino-bis(3-ethylbenzothiazoline)-6-sulfonic acid)) and potassium persulfate ($K_2S_2O_8$) at 2.45 mM (w:v), which was left to stand for 116 h at room temperature. Subsequently, 20% ethanol was diluted to obtain an absorbance value of between 0.24 and 0.67 at 734 nm; then, 10 µL of the sample diluted in ethanol + 90 µL of distilled water + 3 mL of ABTS applied every 30 s were added and left to react for 15 min. The absorbance was obtained at 734 nm and the results are expressed as µmol TE (Trolox equivalent) g^{-1}.

The FRAP assay was used to determine antioxidant capacity as described by Benzie and Strain (1996). Briefly, 2.3 mL of FRAP reagent was mixed with 0.7 mL of aqueous extracts. The mixture was then incubated at 37°C for 30 min in the dark. This mixture was then filtered with Whatman® 40 qualitative filter paper (Sigma-Aldrich) and centrifuged at 11,500 rpm for 20 min. The absorbance value was obtained at 593 nm and the results were expressed as µmol Fe^{2+} g^{-1}. The DPPH assay was carried out as described by Brand-Williams *et al.* (1995) with modifications. Briefly, 1 mL of 0.1-mM solution of DPPH reagent in methanol was mixed with 2 mL of extract (v/v) and the mixture allowed to stand for 15 min at room temperature before obtaining the absorbance value at 517 nm, where 20% (v:v) methanol was used as a blank. Antioxidant capacity was expressed on a dry weight (DW) basis, without conversion to FW, and DPPH values are presented as %inhibition.

Ascorbic acid

The ascorbic acid content was determined using the 2,6-dichlorophenol-indophenol (DCPI) titration method (Association of Official Analytical Chemists [AOAC] Official Method 967.21, Tillmans, 1990). Fresh plant tissue (3.0 ± 0.1 g) was homogenised in 50 mL of 2% (w/v) oxalic acid, which served as both extraction solvent and stabilising agent (preventing ascorbic acid oxidation at pH < 3.0). A 10-mL aliquot of filtered homogenate was titrated against standardised DCPI solution (Tillmans reagent) until a persistent pink endpoint was obtained (15–30 s). Acid ascorbic content was calculated from a freshly prepared ascorbic acid standard curve (0–100 mg L^{-1}, $R^2 \geq 0.995$) and expressed as milligram ascorbic acid per 100 g FW (mg AA 100 g^{-1} FW). All extractions and titrations were performed under dim light to minimise photo-oxidation.

Proximate composition

The proximate composition of flower samples was determined by following standardised methods (Tomasik, 2003) with four biological replicates (n = 4) per treatment.

The results were expressed as percentage values. Total energy of one serving (100 g FW) was calculated according to the following equation:

Total energy = (Energy content of 1 g protein × g protein of sample) + (Energy content of 1 g fat × g fat of sample) + (Energy content of 1 g carbohydrate × g carbohydrate of sample) (Chahdoura *et al.*, 2015).

Mineral nutrients in flowers

The flowers were harvested and transported for analysis to the Fruit Tree Physiology Laboratory at Universidad Autonoma Chapingo, Mexico, where extraction and quantification of mineral nutrients was carried out by using the method described by Ontiveros-Capurata *et al.* (2022). Briefly, flowers were triple washed (1) with tap water, then (2) with 4-N HCl, and lastly (3) with deionised water. Surface water was allowed to evaporate completely at room temperature and leaves were dried at 75°C for 24 h in a Heratherm VCA 230® oven (Thermo Scientific™, Waltham, USA). Each sample was homogenised in a Willey R-TE-650/1 mill with 1-mm mesh (Tecnal, Brazil). The extraction and quantification of total-N were determined by the Kjeldhal method (Novatech®, USA and Micro Kjeldahl Labconco®, USA). Total P was determined by using the ammonium metavanadate method (NH_4VO_3) (Thermo Scientific™). The extraction of K^+, Ca^{2+}, Mg^{2+}, Fe^{2+}, Mn^{2+}, Cu^{2+}, Zn^{2+}, and Na^+ was carried out by triacid digestion (HNO_3, $HClO_4$, and H_2SO_4) (25 mL of mixture in a 10:10:25 ratio) using 25 mL of acid mixture on a hot plate under a fume-hood. Analyte quantifications was carried out using an Analyst 100® atomic absorption spectrophotometer (PerkinElmer). Results are reported as g kg^{-1} for macronutrients and mg kg^{-1} for micronutrients. The B concentration was determined by a colorimetric method using azomethine H reagent for plant ash extract (Gaines and Mitchell, 1979).

Data analysis

To validate the analysis of variance (ANOVA), Bartlett's test (homogeneity of variance) and Kolmogorov–Smirnov test (normality) were applied ($P \leq 0.05$) (Sokal and Rohlf, 1995). Subsequently, a simple rank analysis of variance and a multiple comparison of means were performed using Tukey's test ($P \leq 0.05$). Results were presented as mean ± standard error of mean (SEM) for four biological replicates (n = 4). In addition, Pearson's correlation matrix was also constructed between mineral nutrients and petal quality variables. In all procedures, the SAS software, version 9.0 (SAS Institute, Cary, NC, 2002) was used.

Results

Colour, total solid soluble, and titratable acidity

As presented in Table 1, colour parameters (L*, C*, and h°), TSS, and TA were evaluated across treatments. The ZnO NPs treatment (50 mg L^{-1} and 100 mg L^{-1}) significantly increased chroma values (C* = 14.63 ± 0.87 for both concentrations; $P < 0.05$), compared to controls. This enhanced colour saturation represented a key quality attribute, potentially improving both pollinator attraction and consumer appeal for ornamental/culinary uses. However, lightness (L*) and hue angle (h°) values remained statistically unchanged ($P > 0.05$) across all treatments. Similar stability was observed in other quality markers, with no significant treatment effects on either TSS content or TA levels under experimental conditions.

Photosynthetic pigments and leaf area

In dahlia flowers, Zn treatments had selective effects on pigment profiles. Foliar application of 100 mg L^{-1} ZnO NPs and $ZnSO_4$, together with 50 mg L^{-1} $ZnSO_4$,

Table 1. Effects of ZnO nanoparticles and $ZnSO_4$ on colour parameters and quality of edible flowers of dahlia cv. 'Yaretzi'.

Treatment (mg L^{-1})	Colour			Total soluble solids (°Bx)	Titratable acidity (% citric acid)
	L	Chroma	h°		
Control	60.36 ± 1.78^a	12.49 ± 1.04^b	64.38 ± 0.72^a	0.86 ± 0.02^a	3.23 ± 0.04^a
^{50}ZnO NPs	61.83 ± 1.56^a	14.63 ± 0.87^a	65.13 ± 1.34^a	0.88 ± 0.01^a	3.13 ± 0.03^a
^{100}ZnO NPs	62.90 ± 1.86^a	14.51 ± 0.60^a	65.33 ± 0.98^a	0.89 ± 0.02^a	3.16 ± 0.04^a
$^{50}ZnSO_4$	59.90 ± 2.11^a	12.08 ± 0.76^b	66.10 ± 1.12^a	0.84 ± 0.02^a	3.18 ± 0.04^a
$^{100}ZnSO_4$	60.46 ± 1.97^a	12.65 ± 0.81^b	65.34 ± 1.23^a	0.87 ± 0.02^a	3.17 ± 0.04^a

Notes: Mean values ± standard deviation (n = 4); values with the same superscript alphabets within each column do not differ statistically ($P \leq 0.05$; Tukey's test).
L: lightness; h°: hue angle; ZnO NPs: zinc oxide nanoparticles; $ZnSO_4$: zinc sulphate.

significantly increased both Chl b and TC contents. Chl b reached 0.322 ± 0.10, 0.376 ± 0.08, and 0.298 ± 0.11 µg g^{-1} FW, whereas TC reached 8.34 ± 0.001, 8.90 ± 0.002, and 8.76 ± 0.001 µg β-carotene equivalent g^{-1} FW. In contrast, no significant changes were observed in leaf area (15.92–16.20 cm^2) or Chl a concentration (0.92–1.04 µg g^{-1} FW). These findings showed that Zn acts as a key micronutrient that preferentially modulates biosynthesis pathways of accessory pigments while maintaining structural components of photosynthetic apparatus.

Sucrose and bioactive compounds

Our results revealed a differential accumulation pattern of secondary metabolites in response to Zn treatments (Table 3). While neither ZnO NPs nor $ZnSO_4$ significantly affected sucrose concentration ($P > 0.05$), other metabolites showed distinct responses: TP increased significantly ($P \leq 0.05$) with both ZnO NP treatments (6.56 ± 1.19 and 8.25 ± 1.08 mg GAE 100 g^{-1} FW for 50 mg L^{-1} and 100 mg L^{-1}, respectively), whereas ascorbic acid content varied across all treatments (0.85 ± 0.04–1.01 ± 0.01 mg 100 g^{-1} FW). Total flavonoids reached their highest concentrations under 100 mg L^{-1} treatments (8.20 ± 1.44 and 8.21 ± 1.53 mg QE 100 g^{-1} FW for ZnO NPs and $ZnSO_4$, respectively). Notably, TAn showed the most selective response, with a significant increase (0.21 ± 0.02 mg C3G 100 g^{-1} FW) only under 100 mg L^{-1} ZnO NPs, suggesting a nanoparticle-specific activation of metabolic pathways.

Antioxidant capacity

Edible flowers, particularly those of dahlia cv. 'Yaretzi', represent a valuable dietary source of bioactive compounds with demonstrated antioxidant capacity (Granados-Balbuena *et al.*, 2023; Ojeda-Barrios *et al.*, 2026). Our results indicated that Zn biofortification significantly modulated antioxidant capacity, although the effects varied between analytical methods. The ABTS assay revealed increased antioxidant capacity with 100 mg L^{-1} ZnO NPs (73.94 ± 1.90 µmol TE/g) and both $ZnSO_4$ concentrations (73.90 ± 2.70 and 75.03 ± 1.75 µmol TE/g for 50 mg L^{-1} and 100 mg L^{-1},

Table 2. Effects of ZnO nanoparticles and $ZnSO_4$ on photosynthetic pigment content and leaf area in dahlia cv. 'Yaretzi'.

Treatment (mg L^{-1})	Chlorophyll (µg g^{-1})		Total carotenoids (µg ß-carotene g^{-1})	Leaf area (cm^2)
	a	b		
Control	1.04 ± 0.20[a]	0.173 ± 0.02[c]	15.96 ± 1.40[a]	8.09 ± 0.002[b]
^{50}ZnO NPs	0.96 ± 0.10[a]	0.254 ± 0.09[b]	15.92 ± 1.48[a]	8.01 ± 0.001[b]
^{100}ZnO NPs	0.92 ± 0.18[a]	0.322 ± 0.1[a]	16.01 ± 2.61[a]	8.34 ± 0.001[a,b]
$^{50}ZnS_O4$	1.02 ± 0.21[a]	0.376 ± 0.08[a]	16.20 ± 1.31[a]	8.90 ± 0.002[a]
$^{100}ZnSO_4$	1.1 ± 0.18[a]	0.298 ± 0.11[a,b]	16.19 ± 3.78[a]	8.76 ± 0.001[a]

Notes: Mean values ± standard deviation (n = 4); values with the same superscript alphabets within each column do not differ significantly ($P \leq 0.05$; Tukey's test). Data is expressed on a fresh weight (FW) basis. ZnO NPs - zinc oxide nanoparticles; $ZnSO_4$ - zinc sulphate.

Table 3. Effects of zinc source (ZnO NPs vs. $ZnSO_4$) on accumulation of sucrose and bioactive compounds in edible flowers of dahlia cv. 'Yaretzi'.

Treatment (mg L^{-1})	Sucrose (mg g^{-1})	Total phenols (mg GAE 100 g^{-1})	Total flavonoids (mg QE 100 g^{-1})	Total anthocyanins (mg C3G 100 g^{-1})	Ascorbic acid (mg AA 100 g^{-1})
Control	11.87 ± 1.2[a]	6.56 ± 1.19[b]	5.86 ± 1.52[c]	0.15 ± 0.03[b]	0.85 ± 0.04[b]
^{50}ZnO NPs	11.89 ± 1.4[a]	8.22 ± 1.03[a]	8.20 ± 1.44[a]	0.16 ± 0.03[b]	1.01 ± 0.01[a]
^{100}ZnO NPs	13.24 ± 1.39[a]	8.25 ± 1.08[a]	8.21 ± 1.53[a]	0.21 ± 0.02[a]	0.95 ± 0.06[a]
$^{50}ZnSO_4$	12.98 ± 1.23[a]	7.51 ± 1.04[a,b]	6.15 ± 1.22[c]	0.16 ± 0.03[b]	0.99 ± 0.03[a]
$^{100}ZnSO_4$	13.55 ± 1.45[a]	7.72 ± 1.17[a]	7.24 ± 1.08[a]	0.14 ± 0.02[b]	0.98 ± 0.02[a]

Notes: Mean values ± standard deviation (n = 4); values with the same superscript alphabets within each column do not differ significantly ($P \leq 0.05$; Tukey's test). Data for total phenols, flavonoids, and anthocyanins is expressed on a fresh weight (FW) basis, converted using sample moisture content.
GAE: gallic acid equivalent; QE: quercetin equivalents; C3G: cyanidin-3-glucoside; AA: ascorbic acid; ZnO NPs: zinc oxide nanoparticles; $ZnSO_4$: zinc sulphate.

respectively). More strikingly, ZnO NPs at both concentrations (50 mg L^{-1} and 100 mg L^{-1}) showed maximum enhancement in ferric reducing capacity (FRAP), with values of 151.73 ± 1.79–152.61 ± 2.54 μmol Fe^{2+}/g. These findings not only confirmed the functional potential of dahlia flowers but also highlighted the superior efficacy of ZnO NPs in boosting antioxidant properties. Particularly strong response in the FRAP assay suggested that these treatments preferentially enhanced electron transfer-based antioxidant mechanisms, underscoring the importance of formulation (nanoparticles vs. conventional salts) in biofortification strategies.

Proximate composition

The values obtained from proximate analysis are shown in Table 5. Dahlia plants treated with ZnO NPs exhibited superior nutritional profiles compared to the control group, with significant increases in several key parameters. Flowers from treated plants showed higher moisture content (91.9 ± 0.02% and 91.2 ± 0.01%), protein levels (5.2 ± 0.01% and 5.6 ± 0.03%), crude fat content (4.6 ± 0.01% and 4.6 ± 0.03%), total carbohydrates (62.1 ± 0.5% and 62.5 ± 0.6%), and total energy value per 100 g FW (1,543.0 ± 3.6 kcal and 1,565.2 ± 2.9 kcal). Notably, the application of 100 mg L^{-1} ZnO NPs further enhanced fibre content (30.3 ± 0.4%) and ash percentage (13.3 ± 0.06%). In contrast, crude fat calories remained statistically unchanged across all treatments, with values ranging between 40.9 ± 0.8% and 41.2%. These results demonstrated that ZnO NP biofortification could effectively improve the nutritional quality of dahlia flowers without compromising their lipid-derived energy content.

Table 4. Antioxidant capacity modulation in edible flowers of dahlia cv. 'Yaretzi' following ZnO NP and $ZnSO_4$ treatments.

Treatment (mg L^{-1})	ABTS (μmol TE [Trolox equivalents/g])	FRAP (μmol Fe^{2+}/g)	DPPH (DPPH% inhibition)
Control	65.66 ± 1.1^{b}	145.23 ± 1.29^{b}	75 ± 0.3^{a}
^{50}ZnO NPs	65.56 ± 1.8^{b}	151.73 ± 1.79^{a}	74 ± 0.3^{a}
^{100}ZnO NPs	73.94 ± 1.9^{a}	152.61 ± 2.54^{a}	76 ± 0.3^{a}
$^{50}ZnSO_4$	73.90 ± 2.70^{a}	146.84 ± 1.72^{b}	73 ± 0.1^{a}
$^{100}ZnSO_4$	75.03 ± 1.75^{a}	125.02 ± 1.76^{b}	76 ± 0.2^{a}

Notes: Mean values ± standard deviation (n = 4); values with the same superscript alphabets within each column do not differ significantly ($P \leq 0.05$; Tukey's test). Data is expressed on a DW basis.
ABTS: 2,2'-azino-bis-3-ethylbenzthiazoline-6-sulfonic acid; FRAP: ferric reducing/antioxidant power; DPPH: 1,1-diphenyl-2-picrylhydrazyl; ZnO NPs: zinc oxide nanoparticles; $ZnSO_4$: zinc sulphate.

Table 5. Nutritional composition (proximate analysis) of edible dahlia flowers (cv. 'Yaretzi') biofortified with ZnO NPs or $ZnSO_4$.

Treatment (mg L^{-1})	Moisture (%)	Crude protein (%)	Crude fat (%)	Fibre (%)
Control	89.3 ± 0.03^{b}	4.6 ± 0.02^{c}	4.5 ± 0.02^{b}	28.3 ± 0.3^{c}
^{50}ZnO NPs	91.9 ± 0.02^{a}	5.2 ± 0.01^{a,b}	4.6 ± 0.01^{a}	29.3 ± 0.5^{b}
^{100}ZnO NPs	91.2 ± 0.01^{a}	5.6 ± 0.03^{a}	4.6 ± 0.03^{a}	30.3 ± 0.4^{a}
$^{50}ZnSO_4$	89.7 ± 0.01^{b}	4.8 ± 0.01^{b,c}	4.6 ± 0.03^{a}	28.5 ± 0.4^{b,c}
$^{100}ZnSO_4$	89.4 ± 0.02^{b}	4.9 ± 0.05^{b}	4.6 ± 0.05^{a}	28.9 ± 0.3^{b}
	Ash (%)	**Total carbohydrates (%)**	**kcal/100 g)**	**Calories of fat**
Control	12.9 ± 0.02^{c}	60.0 ± 0.4^{c}	1489.9 ± 2.9^{c}	40.9 ± 0.8^{a}
^{50}ZnO NPs	12.9 ± 0.03^{c}	62.1 ± 0.5^{a}	1543.0 ± 3.6^{a}	41.2 ± 1.2^{a}
^{100}ZnO NPs	13.3 ± 0.06^{a}	62.5 ± 0.6^{a}	1565.2 ± 2.9^{a}	41.2 ± 1.2^{a}
$^{50}ZnSO_4$	12.8 ± 0.04^{d}	60.1 ± 0.6^{c}	1497.0 ± 3.8^{c}	41.2 ± 1.4^{a}
$^{100}ZnSO_4$	13.0 ± 0.02^{b}	61.0 ± 0.4^{b}	1517.1 ± 3.9^{b}	41.2 ± 1.3^{a}

Notes: Mean values ± standard deviation (n = 4); values with the same superscript alphabets within each column do not differ significantly ($P \leq 0.05$; Tukey's test). Data is expressed on a DW basis.
TEOS: total energy per 100 g of fresh weight (FW); ZnO NPs: zinc oxide nanoparticles; $ZnSO_4$: zinc sulphate.

Mineral nutrients in flowers

Table 6 presents the mineral profile of zinc-biofortified dahlia flowers cultivated under different Zn treatments. Among the macronutrients analysed and treatments applied, plants treated with a high dose of ZnO NPs showed increased concentrations of P (3.1 ± 0.06 g kg^{-1}), K^+ (12.9 ± 1.30 g kg^{-1}), Mg^{2+} (2.7 ± 0.06 g kg^{-1}), and Ca^{2+} (2.2 ± 0.05 g kg^{-1}), with the exception of total N (20.3 ± 0.58 g kg^{-1} and 21.3 ± 0.78 g kg^{-1} for low and high doses, respectively). Notably, the 50-mg L^{-1} ZnO NP treatment showed statistically similar results for Ca^{2+} accumulation (2.2 ± 0.05 g kg^{-1}). The ZnO NP treatments induced distinct patterns of mineral accumulation in dahlia flowers. The 50-mg L^{-1} ZnO NP dose significantly enhanced iron (63.2 ± 3.73 mg kg^{-1}) and copper (12.8 ± 0.61 mg kg^{-1}) contents, while the 100-mg L^{-1} concentration proved more effective for Zn (39.7 ± 0.57 mg kg^{-1}) and Na (15.8 ± 0.1 mg kg^{-1}) accumulations. Similarly, both ZnO NP concentrations improved boron uptake (23.3 ± 2.20 and 21.9 ± 3.11 mg kg^{-1} for 50 mg L^{-1} and 100 mg L^{-1}, respectively). Manganese levels peaked with 100 mg L^{-1} ZnO NPs (28.6 ± 0.33 mg kg^{-1}) and both $ZnSO_4$ treatments (24.4 ± 0.38 and 28.6 ± 0.37 mg kg^{-1} for 50 mg L^{-1} and 100 mg L^{-1}, respectively), demonstrating concentration-dependent mineral uptake dynamics.

Pearson's correlation analysis

Pearson's correlation analysis (Table 7) revealed significant relationships between mineral content and quality attributes in dahlia flowers. Strong negative correlations ($P < 0.05$) were observed between: total N and TFl, r = –0.396); P and TA (r = –0.441) or TFl (r = –0.794); K^+ and TFl (r = –0.560); Ca^{2+} and TA (r = –0.603), total phenols (r = –0.357), or TFl (r = –0.334); Mg^{2+} and TA (r = –0.582) or TAn (r = –0.405); Zn^{2+} and TA (r = –0.311) or TAn (r = –0.770); Fe^{2+} and TP (r = –0.612); and Cu^{2+} with TAn (r = –0.305), TFl (r = –0.392), or AA, r = –0.334). Conversely, significant positive correlations emerged between: total N and TA (r = 0.590); K^+ and TP (r = 0.379); Mg^{2+} and TSS (r = 0.327) or AA (r = 0.372); Fe^{2+} and TSS (r = 0.314) or TFl (r = 0.480); Cu^{2+} and TP (r = 0.569); Zn^{2+} and TSS (r = 0.486) or AA (r = 0.378); and Na^+ with TFl (r = 0.365) or AA (r = 0.453).

Discussion

Particularly in Mesoamerican cultures, EFs have held a prominent place in culinary traditions since ancient times. Here, species such as dahlia are prized for their cultural symbolisms, ornamental values, and culinary applications (Ghosh *et al.*, 2025; Granados-Balbuena *et al.*, 2023; Mejía-Muñoz *et al.*, 2020). In recent years, the cultural and culinary heritages associated with dahlia's EFs have gained renewed attention because of their (i) exceptional nutritional profile, being rich in bioactive phytochemicals (phenols, flavonoids, and anthocyanins), essential micronutrients and vitamins; (ii) low caloric density, making them ideal as components in health-conscious diets; and (iii) appealing sensory attributes

Table 6. Zinc biofortification effects on mineral composition in flowers of dahlia cv. 'Yaretzi'.

Treatment (mg L^{-1})	Macronutrients (g kg^{-1})				
	N-total	P	K^+	Ca^{2+}	Mg^{2+}
Control	20.3 ± 0.58^{a}	2.7 ± 0.05^{c}	8.1 ± 0.26^{c}	1.8 ± 0.03^{d}	2.2 ± 0.05^{c}
^{50}ZnO NPs	21.3 ± 0.78^{a}	2.8 ± 0.02^{b}	11.3 ± 0.36^{b}	2.2 ± 0.05^{a}	2.6 ± 0.02^{b}
^{100}ZnO NPs	21.1 ± 0.81^{a}	3.1 ± 0.06^{a}	12.9 ± 1.30^{a}	2.2 ± 0.05^{a}	2.7 ± 0.06^{a}
$^{50}ZnSO_4$	20.4 ± 0.44^{a}	2.8 ± 0.04^{b}	10.9 ± 0.42^{b}	1.8 ± 0.02^{c}	2.6 ± 0.03^{b}
$^{100}ZnSO_4$	20.7 ± 0.30^{a}	2.8 ± 0.02^{b}	11.8 ± 0.51^{a,b}	2.0 ± 0.04^{b}	2.3 ± 0.03^{c}
	Micronutrients (mg kg^{-1})					
	Fe^{2+}	Cu^{2+}	Mn^{2+}	Zn^{2+}	Na^+	B
Control	49.7 ± 1.80^{c}	9.2 ± 1.04^{b}	21.4 ± 0.33^{b}	36.2 ± 1.55^{c}	13.6 ± 0.04^{c}	17.2 ± 0.93^{c}
^{50}ZnO NPs	63.2 ± 3.73^{a}	12.8 ± 0.61^{a}	20.4 ± 0.28^{b}	43.5 ± 1.68^{b}	15.9 ± 0.07^{a}	23.3 ± 2.20^{a}
^{100}ZnO NPs	55.3 ± 3.20^{b}	9.8 ± 0.83^{b}	28.6 ± 0.33^{a}	49.7 ± 0.57^{a}	15.8 ± 0.1^{a}	21.9 ± 3.11^{a,b}
$^{50}ZnSO_4$	49.9 ± 1.39^{c}	13.0 ± 0.25^{a}	24.4 ± 0.38^{a}	42.4 ± 1.88^{b}	14.3 ± 0.08^{b,c}	19.9 ± 0.63^{b}
$^{100}ZnSO_4$	59.4 ± 1.41^{a,b}	12.1 ± 0.34^{a,b}	28.6 ± 0.37^{a}	41.3 ± 0.62^{b}	15.0 ± 0.1^{b}	20.1 ± 0.62^{b}

Notes: Mean values ± standard deviation (n = 4); values with the same superscript alphabets within each column do not differ statistically ($P \leq 0.05$; Tukey's test). Data is expressed on a DW basis.
ZnO NPs: zinc oxide nanoparticles; $ZnSO_4$: zinc sulphate.

Table 7. Mineral–bioactive compound relationships in Zn-treated dahlia cv. 'Yaretzi' edible flowers.

Mineral	TSS	TA	TAn	TP	TFl	AA
N-total	–0.233	0.590**	0.262	0.259	–0.396*	0.120
P	–0.296	–0.441*	–0.133	0.238	–0.794**	0.093
K^+	–0.058	0.154	–0.125	0.379	–0.560**	0.234
Ca^{2+}	0.084	–0.603**	–0.252	–0.357*	–0.334*	–0.034
Mg^{2+}	0.327*	–0.582**	–0.405*	–0.172	–0.582**	0.372*
Fe^{2+}	0.314	–0.063	0.065	–0.612**	0.480*	0.034
Mn^{2+}	–0.322	0.133	0.045	0.001	0.097	0.254
Cu^{2+}	0.274	0.114	–0.305*	0.569**	–0.392*	–0.334*
Zn^{2+}	0.486*	–0.311*	–0.770**	–0.121	–0.270	0.378*
Na^+	0.298	–0.223	–0.345*	0.234	0.365*	0.453*
B	0.113	–0.219	0.031	0.286	0.423*	0.019

Notes: TSS: total soluble solids (°Brix); TA: titratable acidity (% citric acid); TAn: total anthocyanins (mg C3G 100 g^{-1}); TP: total phenols (mg GAE g^{-1}); TFl: total flavonoids (mg QE 100 g^{-1}), AA: ascorbic acid (mg AA 100 g^{-1}); GAE: gallic acid equivalent; QE: quercetin equivalent; C3G: cyanidin-3-glucoside. *Significant at 5%, **significant at 1%. ns: not significant.

(vibrant colours, diverse textures, and distinctive aromas) (Marchioni *et al.*, 2024; Mulík *et al.*, 2024). All these align with modern gastronomic trends seeking novel food experiences (Calderón-Jurado *et al.*, 2023; Ojeda-Barrios *et al.*, 2026; Rivera-Espejel *et al.*, 2019). These characteristics make EFs particularly compatible with contemporary dietary patterns that emphasise plant-based nutrition and sustainable food production. Moreover, their high concentrations of antioxidant compounds and functional biomolecules enhance their nutritional value and are directly associated with health benefits, including metabolic regulation, prevention of chronic diseases, and body weight management (Abril-Carvajal *et al.*, 2022; Reyes-Santiago *et al.*, 2024).

This study provides the first scientific evidence that foliar applications of ZnO NPs significantly enhance chromaticity values ($P \leq 0.05$) of dahlia flowers, establishing a novel biofortification approach for this and other EF species. Our findings yield three key contributions: (1) biological—modulated pollinator attraction (bees/humming birds) through Zn-induced chromatic shifts, leveraging their well-documented spectral sensitivity (Chittka and Wells, 2004; Luizzi *et al.*, 2021); (2) agronomic—optimised nutrient delivery via ZnO NPs, offering superior efficiency over conventional methods; and (3) ecological—potential enhancement of pollination services through improved floral visibility. The increased chromaticity directly correlates with hedonic value (Yoshida *et al.*, 2009), a critical factor in premium EF markets, where colour drives ~70% of consumer preference. Comparative colour metrics contextualise our results: *D. variabilis* (L* = 50.17, C* = 34.59, and h° = 351.25; Costa *et al.*, 2022) and peach flowers (e.g. 'July Flame': L* = 62.36 ± 1.78, C* = 13.49 ± 1.04, h° = 65.38 ± 0.63; Calderón-Jurado *et al.*, 2023) demonstrate the competitive chromatic advantage of biofortified dahlias.

Photosynthetic pigments and leaf area serve as fundamental indicators of growth and development in plants, including dahlia (Martínez-Damián *et al.*, 2025). Chlorophyll levels drive photosynthetic efficiency and biomass production, while carotenoids provide photoprotection against oxidative stress (Kusumiyati *et al.*, 2025; Mallick *et al.*, 2024; Villegas-Olguín *et al.*, 2023). Together, they underpin plant vigour and are central to the visual appeal of many dahlia species cultivated for ornamental purposes (Bădulescu *et al.*, 2023). Foliar application of Zn (100 mg L^{-1} ZnO NPs, and 50 mg L^{-1} and 100 mg L^{-1} $ZnSO_4$) significantly enhanced Chl b and TC content in dahlia cv. 'Yaretzi' flowers, indicating improved Zn bioavailability in reproductive tissues (pistils, stamens, and petals). This micronutrient acts as a crucial cofactor for photosynthetic enzymes, including carbonic anhydrase and superoxide dismutase (Cakmak, 2000; Cakmak *et al.*, 2017) while simultaneously triggering carotenoid biosynthesis as a photoprotective response under prolonged exposure to light (Granados-Balbuena *et al.*, 2023). The accumulated carotenoids (lutein, β-carotene, and lycopene) not only mitigate oxidative stress but also generate characteristic yellow-to-red pigmentation in Asteraceae EFs, including dahlias, marigolds, and chrysanthemums (Kusumiyati *et al.*, 2025; Ohmiya, 2011). Comparative analyses reveal species-specific responses to Zn supplementation: while gladiolus 'White Prosperity' showed

increased chlorophyll (SPAD 54–64) with $ZnSO_4$ (Karimian and Samiei, 2023), Eustoma 'Mariachi Blue' achieved higher total chlorophyll (13.27 μg mg^{-1} FW) with ZnO NPs (Seydmohammadi *et al.*, 2019). Notably, dahlia carotenoid levels (8.01–8.90 μg β-carotene g^{-1} FW) were substantially lower than those in Tagetes spp. (2,843–3,998 μg 100 g^{-1} DW), highlighting important interspecific differences in these culturally significant Mesoamerican flowers (Mulik and Ozuna, 2020).

Petal colour of EFs is largely determined by the accumulation of fat- and water-soluble pigments, particularly carotenoids, flavonoids, and anthocyanins (Xu *et al.*, 2020). In the present study, foliar application of 100 mg L^{-1} ZnO NPs significantly enhanced total anthocyanin content in dahlia flowers, suggesting a response associated with pigmentation and antioxidant metabolism in floral tissues. This response may be particularly relevant in heliophilous species, such as dahlia, whose phenotypic plasticity enables them to thrive under intense light conditions (Granados-Balbuena *et al.*, 2024a; Villegas-Olguín *et al.*, 2023). Anthocyanins are the main flavonoid-derived pigments responsible for red, purple, and blue hues in petals, including those of dahlia cultivars (Granados-Balbuena *et al.*, 2024b). Recent studies on the dahlia cultivars 'La Baron' (dark pink to purple) and 'Colorado Classic' (light pink to bright lilac) have quantified their anthocyanin contents as 1.250 ± 0.002% DW and 1.138 ± 0.002% DW, respectively, with derivatives identified as delphinidin, cyanidin, petunidin, peonidin, and malvidin (Gontova *et al.*, 2024). In addition, our results were consistent with previous reports for cultivated dahlia flowers, where anthocyanin concentrations ranged from 4.01 to 25 mg C3G 100 g^{-1} FW (Costa *et al.*, 2022; Rivera-Espejel *et al.*, 2019).

Our study demonstrates that Zn biofortification significantly increased TP, TFl, and AA contents in dahlia flowers, with the exception of the 50 mg L^{-1} $ZnSO_4$ treatment, which showed no significant effect on TFl accumulation, compared to the control. This suggests a threshold effect in the regulation of this metabolic pathway. Beyond the overall increases in TP, TFl and AA, the pattern observed is consistent with a dose-dependent modulation of phenylpropanoid network, whereby Zn supply may enhance phenolic and flavonoid biosynthesis up to an optimum, but plateau or differentially affect specific branches once a threshold is reached (Mahdavi *et al.*, 2022). Such non-linear responses are biologically plausible, given Zn's tight coupling to redox homeostasis and enzyme regulation: moderate inputs can stimulate antioxidant-related metabolism, whereas higher levels may shift signalling and feedback control, thereby constraining further accumulation in particular subclasses (Ali *et al.*, 2025). Anthocyanins, a key flavonoid class in pigmented petals, are especially responsive to micronutrient-driven changes in redox balance and precursor availability; accordingly, shifts in AA likely reflect coordinated antioxidant protection and pigmentation in floral tissues (Ohno, 2025).

As a key micronutrient, Zn plays a crucial regulatory role in the shikimic acid and phenylpropanoid pathways, directly influencing the expression of genes responsible for the biosynthesis of secondary metabolites (Cakmak *et al.*, 2017; Palacio-Márquez *et al.*, 2023). This mechanism explains the observed accumulation of phenolic compounds, which serve dual functions: (1) as part of the plant's antioxidant defence system against oxidative stress in high metabolically active floral tissues (Martínez-Damián *et al.*, 2021; Singh *et al.*, 2021), and (2) as modulators of organoleptic properties (flavour and astringency) that influence both pollinator attraction and nutritional quality (Umar *et al.*, 2021). The effectiveness of Zn biofortification in enhancing secondary metabolites has been well-documented in economically important crops, such as wheat, beans, and tomatoes (Bautista-Diaz *et al.*, 2021; Du *et al.*, 2019), with similar patterns observed in our study. Specifically, we found results comparable to those reported by Fortis-Hernández *et al.* (2023) for TP (40.52 mg GAE 100 g^{-1} FW) and TFl (4.39 mg QE 100 g^{-1} FW), and consistent with the findings in *Stevia rebaudiana* by Velázquez-Gamboa *et al.* (2024), where ZnO NPs (75–100 mg L^{-1}) induced similar metabolic responses. Observed variations between studies can be attributed to several factors: (1) tissue-specific metabolic profiles (leaves as primary metabolic centres, versus flowers specialised in reproductive functions) (Xu *et al.*, 2020); (2) experimental parameters (application frequency, dosage, and analytical methods); and (3) inherent differences between species and cultivars (Mahdavi *et al.*, 2022). These findings underscore the importance of optimising Zn biofortification protocols according to target species and desired metabolic outcomes.

The findings of this study are particularly relevant because Zn biofortification research has focused mainly on conventional crops, such as cereals, fruit trees, vegetables, and medicinal plants (Preciado-Rangel *et al.*, 2021; Umar *et al.*, 2021). In contrast, ornamental species have remained largely unexplored, despite the long culinary use of dahlia. In this context, our results provide evidence that foliar Zn applications can modify the nutritional and phytochemical profile of edible dahlia flowers, consistent with reports of Zn-mediated responses in other plant systems (Azeem *et al.*, 2025; Fortis-Hernández *et al.*, 2024). These findings provide a useful basis for future studies aimed at evaluating Zn biofortification in dahlia and other edible flower species under different agronomic conditions.

Antioxidant capacity of EFs depends largely on bioactive compounds, such as polyphenols, carotenoids, and ascorbic acid (Marchioni *et al.*, 2024). Given the structural diversity of these phytochemicals, accurate antioxidant capacity assessment requires multiple analytical methods (Monroy-García *et al.*, 2025), prompting our use of ABTS, FRAP (125.02–152.61 μmol Fe^{2+}/g), and DPPH (73–76% inhibition) assays. Comparative analysis revealed that our FRAP values were substantially lower than those reported for pomegranate flowers (609.66–670.22 mmol Trolox/g FW; Zhang *et al.*, 2023), although similar to Zn-treated common beans (75% DPPH inhibition; Sida-Arreola *et al.*, 2017). Notably, lettuce biofortified with $ZnSO_4$ (75 μM) achieved higher antioxidant capacity (114 μM Trolox/100 g FW; Preciado-Rangel *et al.*, 2021) than our DPPH results, while ZnO NPs (20 mg L^{-1}) enhanced antioxidant capacity of basil (0.05 μM Trolox/100 g FW; Fortis-Hernández *et al.*, 2023). These interspecific variations highlight the need to explore wider ranges of Zn concentration (<50 mg L^{-1} and >100 mg L^{-1}) to optimise trade-off between antioxidant induction and potential phytotoxicity (Rizvi *et al.*, 2023). The methodological predominance of DPPH assays stems from the radical's stability, commercial availability, and procedural simplicity (Karimian and Samiei, 2023). However, our multi-method approach provided a more comprehensive antioxidant capacity assessment, reflecting Zn's dual role as an enzymatic cofactor (e.g., superoxide dismutase) and as a modulator of non-enzymatic antioxidant biosynthesis (Bala *et al.*, 2019; Nsabimana and Jiang, 2011). This is particularly relevant, given a delicate balance between the metabolic benefits of Zn and its capacity to induce oxidative stress at supraoptimal concentrations.

The incorporation of unconventional EFs, such as dahlia into modern diets, offers promising nutritional benefits for health-conscious consumers seeking low-calorie, nutrient-dense foods (Costa *et al.*, 2022). However, their high moisture content (≥88%) poses significant postharvest challenges, including rapid dehydration, microbial proliferation (fungal and bacterial pathogens), and consequently limited shelf-life (Monroy-García *et al.*, 2025). Our study revealed that ZnO NP treatments further elevated moisture levels beyond the reference value for dahlia cv. 'Yaretzi' (88.73%; Martínez-Damián *et al.*, 2025), potentially through Zn's regulation of aquaporin activity and subsequent effects on cellular turgor pressure. This physiological mechanism facilitates water and solute (e.g. sucrose, minerals) accumulation, ultimately influencing tissue expansion during floral development (López-Cervantes *et al.*, 2018; Saeed *et al.*, 2013). Comparative analyses showed species-specific moisture variations: rose (Rosa × grandiflora) exhibited lower values (84.56 ± 0.12%), while marigold (*Calendula officinalis*) maintained levels (89.34 ± 0.1%) comparable to dahlia (De Lima Franzen *et al.*, 2019). These differences reflect inherent physiological adaptations and highlight the need for tailored postharvest technologies to preserve the structural integrity and bioactive content of EFs.

Our study demonstrated that foliar application of ZnO NPs (50–100 mg L^{-1}) significantly improved key nutritional parameters in dahlia flowers, including protein, fibre, ash, carbohydrate content and caloric value—making them particularly valuable for gourmet cuisine and as functional foods. Comparative analysis revealed that conventional dahlia cultivation (without Zn biofortification) typically yields lower nutritional values: D. pinnata shows reduced ash (7.19 ± 0.08 g 100 g^{-1}), carbohydrates (47.03 ± 4.21 g 100 g^{-1}), and energy content (19.02 ± 3.07 kcal 100 g^{-1}) (Costa *et al.*, 2022), while maintaining higher crude protein (13.80 ± 0.54 g 100 g^{-1}) and comparable fibre levels (28.97 ± 3.58 g 100 g^{-1}). Similarly, dahlia × hortorum cultivars exhibited elevated carbohydrate percentages (64.3–67.0%) across various colour morphotypes (Rivera-Espejel *et al.*, 2019). Notably, our Zn-biofortified flowers surpassed the lipid content reported for wild and cultivated dahlia species (0.2–1.6%; Lara-Cortés *et al.*, 2014). These enhancements underscore Zn's crucial physiological roles as: (1) a structural component of carbonic anhydrase (regulating CO_2 fixation; Mahdavi *et al.*, 2022), (2) a chlorophyll biosynthesis cofactor, and (3) a mediator of carbohydrate translocation (Escudero-Almanza *et al.*, 2025). The observed nutritional variability also reflected genetic diversity within the Dahlia genus, resulting from both intentional breeding and natural hybridisation under a diversity of edaphoclimatic conditions (Carrasco-Ortiz *et al.*, 2019; Fujimoto and Onozaki, 2025; Gatt *et al.*, 1998; Şekerci and Gülşen, 2016). This genetic plasticity necessitates genotype-specific optimisation of biofortification protocols to maximise nutritional outcomes while maintaining ornamental and culinary quality.

Edible flowers represent a promising low-calorie source of essential minerals (P, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, and Na^+) to complement human nutrition (Araújo *et al.*, 2019; Calderón-Jurado *et al.*, 2023). This study demonstrated that agronomic biofortification with ZnO NPs under open-field conditions enhanced Zn accumulation in dahlia flowers (36.2–49.7 mg kg^{-1} DW), with ZnO NP treatments outperforming conventional $ZnSO_4$ treatments. The superior efficacy of ZnO NPs stems from their nanoscale properties, viz. increased foliar contact surface and controlled Zn^{2+} release (Cakmak *et al.*, 2017), enabling more efficient penetration without risk of phytotoxicity (Preciado-Rangel *et al.*, 2021). These findings

have particular relevance to ornamental edible species such as dahlia, where precise Zn dosing must preserve petal quality (Mejía-Muñoz *et al.*, 2020). Comparative analyses revealed that dahlia's mineral accumulation followed the patterns observed in other crops. Thus, amaranth shoots accumulated 98–115 mg kg^{-1} DW of Zn under similar treatments (Reshma and Meenal, 2022), while basil showed 19.9% increases (192 µg g^{-1} DW) with $ZnSO_4$ (Ciriello *et al.*, 2022). Notably, dahlia's K^+, Mg^{2+}, Ca^{2+}, and Na^+ levels remained below those reported for marigold (*Tagetes erecta*), calendula, lavender, and pansy (Araujo *et al.*, 2019), but levels exceeded those of iron, copper, and Zn in nasturtium and coriander. In this study, low doses of ZnO NP increased the Fe^{2+} concentration. The observed Fe^{2+} response was consistent with a dose-dependent competition for shared divalent cation transporters (e.g. IRT1) between Zn and Fe. At a low dose (50 mg L^{-1}), ZnO NPs may induce a non-specific upregulation of ZIP/YSL transporters, thereby enhancing concurrent Fe^{2+} uptake. However, higher doses (100 mg L^{-1}) probably saturate these transport systems, favouring Zn uptake and consequently reducing Fe transport because of direct competition (Escudero-Almanza *et al.*, 2025). Crucially, despite this competitive interaction at high Zn levels, dahlia flowers maintain a high basal Fe^{2+} content. This underscores the flower's intrinsic richness in iron and suggests the presence of robust homeostatic mechanisms. These potentially include efficient metal chelation, vacuolar compartmentalisation, and potential stabilisation by ferredoxins, which collectively preserve iron bioavailability (White and Broadley, 2009; Wu *et al.*, 2024). These variations reflect both genetic factors (differential expressions of ZIP, HMA, and MTP transporters in non-hyperaccumulators) and organ-specific allocation patterns in reproductive tissues (Sabzeali *et al.*, 2025).

Plant development depends on the maintenance of a precise equilibrium between the availability of mineral nutrient and their complex interactions as metabolic cofactors and inhibitors. This is particularly true for the biosynthesis of secondary metabolites that mediate environmental adaptations (Ghosh *et al.*, 2025). In EFs, these secondary compounds evolved primarily as pollinator attractants (Wink, 2010) and exhibit variable mineral bioavailability across floral structures (pistils, stamens, and petals) and developmental stages (Pinedo-Espinoza *et al.*, 2020). While vegetative organs (leaves and stems) typically serve as primary nutrient reservoirs, with minerals often remobilised post-anthesis (Chahdoura *et al.*, 2015), deficiencies during flowering can lead to severe reproductive impairment, including floral abortion or morphological deformity that compromise seed set (Brown *et al.*, 2002). In this context, the mineral profile of flowers holds particular significance for human nutrition, as micronutrients, such as Zn, Fe, and Cu, play crucial roles in our cellular processes ranging from neurotransmission to enzymatic catalysis (Hou, 2022). Notably, the consumption of Zn-biofortified dahlia flowers may help to address widespread dietary Zn deficiencies, given this element's involvement in more than 300 enzyme reactions in humans (Ahmed *et al.*, 2024). This dual function (supporting both plant reproduction and human health) positions mineral-enhanced EFs as strategic components in sustainable food systems. The ephemeral nature of EFs demands careful management of nutrient allocation to optimise both agronomic yield and nutritional quality.

The safety of EFs, a growing functional food niche, is challenged by an underdeveloped regulatory framework, particularly regarding maximum residue limits of pesticides and heavy metals (Ojeda-Barrios *et al.*, 2026; Sánchez-Chávez *et al.*, 2026). From a food-safety perspective, use of ZnO NPs in EFs should be approached with caution because these products are commonly consumed fresh, which increases the relevance of dietary exposure to residual contaminants or nanoparticulate fractions, while external hazards in EFs may include both microbial and chemical impurities (Matyjaszczyk and Śmiechowska, 2019). Moreover, the safety of edible flower consumption remains under discussion because information on maximum safe daily intake is still limited and official safety requirements or guidelines are scarce (Dos Santos and Reis, 2021; Purohit *et al.*, 2021). Thus, although ZnO NPs may improve Zn delivery, further studies are needed to determine Zn residues and nanoparticulate fractions in edible tissues and to assess dietary exposure, long-term consumption safety, and the possible transfer of nanoparticles through the food chain, which are not sufficiently interpreted (Sharma *et al.*, 2025). Nevertheless, when EFs are produced under controlled conditions and handled hygienically, they may be considered a safe and attractive complement to the diet, providing bioactive compounds (e.g. polyphenols) and micronutrients of nutritional interest (Nicolau and Gostin, 2016). Surveillance data indicates that the main safety concerns of EFs are associated with microbial pathogens (e.g. Salmonella) and chemical contaminants, including pesticide residues, environmental pollutants, and potentially elevated metal concentrations (Carpena *et al.*, 2024). For biofortified flowers, however, a proactive risk assessment remains essential, together with the standardisation of species-specific biofortification strategies, validated analytical protocols, and robust evidence on stability, bioaccessibility, and consumer-relevant exposure.

Conclusions

Foliar application of ZnO NPs improved the nutritional and bioactive profile of dahlia EFs (cv. 'Yaretzi') and was more effective than conventional $ZnSO_4$ under

controlled open-field conditions. Specifically, 100 mg L^{-1} ZnO NPs increased several key quality attributes, including chroma, anthocyanin content (0.21 mg C3G 100 g^{-1}), Zn concentration (49.7 mg kg^{-1}), antioxidant capacity (152.61 μmol Fe^{2+} g^{-1}), and proximate composition (e.g. 5.6% protein; and 30.3% fibre), without compromising floral appearance. Taken together, these findings support ZnO NPs as a promising nano-fertiliser approach to enhance the functional food potential of dahlia EFs. From a practical perspective, the results indicate that growers may use foliar ZnO NP programmes to increase micronutrient density and quality traits in EFs, provided that application rates are optimised and aligned with good agricultural practices to minimise off-target deposition. For food technologists, EFs should be managed as high-care fresh produce: rigorous hygiene, cold-chain control, and routine monitoring of microbiological hazards and chemical residues remain central to safeguarding safety and maintaining shelf quality. For nutritionists, EFs are best regarded as a complementary source of bioactive compounds and micronutrients rather than a principal vehicle for dietary Zn, given the small portions typically consumed as garnishes; nonetheless, they may add value within diversified diets. This work was limited to a single cultivar and a controlled production setting; therefore, further validation across cultivars, flower species, and commercial environments is warranted. Future research should address scalability, the long-term environmental fate of ZnO NPs (including potential soil accumulation and effects on non-target organisms), consumer acceptance of nano-biofortification, and additional safety evidence (e.g. *in vitro* toxicity and bioaccessibility assessments) to support responsible deployment.

Data Availability Statement

The data that supported the findings of this study is available from the corresponding author upon reasonable request.

Mandatory Disclosure on Use of Artificial Intelligence

The authors declare that no AI-assisted tools were used in the preparation of this manuscript. All references have been manually verified for accuracy and relevance.

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Conflict of Interest

The authors declared no conflict of interest.

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