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Neodymium and zinc stimulate growth, biomass accumulation and nutrient uptake of lettuce plants in hydroponics

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ABSTRACT

We evaluated the effects of neodymium (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}) and zinc (0.1, 0.2 and 0.3 mg · L^{-1}), as well as their interaction on lettuce plants in hydroponics. Applications of 2.885 mg Nd · L^{-1} and 5.770 mg Nd · L^{-1} increased plant height, number of leaves and leaf area, as well as fresh and dry stem, root and total biomasses. Root volume was greater in plants treated with 2.885 mg Nd · L^{-1}. With 0.1 mg Zn · L^{-1}, plant height, leaf area and fresh stem, root and total biomass were greater, while applying 0.3 mg Zn · L^{-1} increased the ratio of dry biomass of stems and roots. Plants exposed to 5.770 mg Nd · L^{-1} + 0.3 mg Zn · L^{-1} exhibited greater leaf length. The ratios of fresh and dry biomass of stems and roots increased in plants treated with 8.655 mg · L^{-1} Nd + 0.3 mg Zn · L^{-1}. Dry biomass weights of stems, roots and total were the highest in plants treated with 20 mg Nd · L^{-1} + 0.1 mg Zn · L^{-1}. Nd significantly increased foliar concentration of N, P and K. Hence, Nd and Zn improve growth and nutrition.

Keywords: inorganic biostimulants, *Lactuca sativa*, lanthanides, micronutrients, rare earth elements

INTRODUCTION

Lettuce (*Lactuca sativa* L.) is a vegetable of great economic importance, due to its high consumption and demand (Wardany and Anjawati, 2020). It is considered a nutritious food, as it is a source of minerals, vitamins, carotenoids, flavonoids and phenolic acids, and its fresh consumption fosters human health (Shi et al., 2022; Yang et al., 2022). Lettuce and other leafy green vegetables need considerable volumes of irrigation water to produce quality products (Souri and Hatamian, 2019; Amiri Forotaghe et al., 2021). Therefore, finding methods or procedures to improve water use efficiency as well as their production and quality are quite important. Some of the rare earth elements (REE) can be classified as inorganic biostimulants, due to their beneficial effects on plant metabolism, improving the physiological characteristics when supplied in appropriate concentrations (Ayub et al., 2023). It has been documented that they stimulate seed germination (Sun et al., 2018), improve photosynthetic capacity (García-Jiménez et al., 2017), promote tolerance mechanisms against abiotic stress (Elbasan et al., 2020) and increase the quality and production of crops (Xia et al., 2022).

Neodymium (Nd) is a REE that has important effects on the growth and physiological processes of several species (Zhang et al., 2013; Abou El-Nour and Attia, 2022). Low concentrations of this element mitigate the negative effects of cadmium (Cd) toxicity by optimising the activities of the antioxidant enzymes superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) in Jerusalem artichoke (*Helianthus tuberosus*) (Tang et al., 2017). Likewise, it prolongs the vase life of white lily (*Lilium candidum*) by improving the water retention capacity of the petals (Zheng and Guo, 2019). Neodymium has also been shown to stimulate the germination

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of seeds of astragalus (*Astragalus gallinaceus*) (Sun et al., 2008), sicklepod (*Cassia obtusifolia*) (Yao et al., 2008), dong quai (*Angelica sinensis*) (Chen et al., 2010) and wheat (*Triticum aestivum*) (Basu et al., 2016). This beneficial element also promotes root length of dendrobium (*Dendrobium densiflorum*) cuttings (Luo et al., 2008), rice (*Oryza sativa*) seedlings (Shi et al., 2021) and onion (*Allium cepa*) bulbs (Kotelnikova et al., 2022). Furthermore, it increases the yield of pepper (*Capsicum annuum*) (Abou El-Nour and Attia, 2022) and the content of macronutrients in sugarcane (*Saccharum* spp.) (Ramírez-Antonio et al., 2023).

Zinc (Zn) is the second essential element for the human body (Hara et al., 2022); it is required to maintain the catalytic activity of approximately 10% of human proteins and prevents lipid peroxidation (López-Morales et al., 2020). In higher plants, Zn plays a vital role as a metal component and a cofactor of many enzymes (Cabot et al., 2019), participating in membrane function, photosynthesis, gene expression, and defence against drought and pathogens, as well as in the synthesis of hormones involved in the growth and development of plants (Hefferon, 2019). In corn (*Zea mays*) seeds, Zn increased the germination percentage and the vigour index of the seedlings; during the reproductive stage of this crop, it favoured its growth and yield (Subbaiah et al., 2016). In chickpea (*Cicer arietinum*) plants, the addition of Zn promoted growth parameters and increased grain yield (Pal et al., 2020). Likewise, Zn enrichment has positive effects on the development and morphology of wheat (Sher et al., 2022). Additionally, micronutrients deficiency, especially that of Fe and Zn, is a widespread phenomenon in cropping systems in many parts of the world where calcareous soils are dominant (Souri et al., 2009; Souri and Hatamian, 2019). An integrative study addressing the impact of a micronutrient and a beneficial element in leafy green vegetables is lacking. Therefore, the objective of this research was to evaluate the main and interaction effects of Nd and Zn on the growth variables of lettuce plants cv. 'Ruby Sky' grown in a hydroponic system.

MATERIALS AND METHODS

Experiment management

The experiment was carried out under greenhouse conditions in the autumn–winter cycle in Montecillo, state of Mexico, Mexico (19.96° north latitude and 98.9° west longitude, altitude 2244 m). During the experiment there was an average day-length of 9 hr, at 27.9/11.6°C day/night temperature, photosynthetically active radiation of 490 μmol · m^{-2} · s^{-1}, and relative humidity of 31% during the day and 72% at night. Lettuce seedlings cv. 'Ruby Sky' (Lot 1w01019728X8, USA), 40-day-old (average height of 7 cm and between 5 and 6 true leaves), were placed in a floating root hydroponic system, in plastic containers (Cubasa, 1566 TSS, Mexico) of 900 mL capacity, with Steiner nutrient solution (Steiner, 1984) at 50% of its original strength, during the first 10 days; subsequently and until harvest it was supplied at 100%. The composition of the Steiner solution at 100% and the chemical sources used are presented in Table 1. To provide oxygen to the root, pumps (Elite, HA800, China) and polyethylene hose with a diameter of 4 mm were installed and connected to a digital timer (Steren, TEMP-08E, Mexico) with eight events, programmed every 3 hr with oxygenation times of 15 min.

Experimental design and application of treatments

A 4 × 3 factorial experiment was set up. The first study factor was Nd with four levels (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}), while the second study factor was Zn with three levels (0.1, 0.2 and 0.3 mg · L^{-1}). Since it was a two-factor analysis, the results discussed for Zn and Nd are the averages from the two-factor analysis, as well as their interactions. The sources of Nd and Zn were $NdCl_3 \cdot 6H_2O$ (Sigma-Aldrich, USA) and $ZnSO_4 \cdot 7H_2O$ (Fermont, Mexico), respectively. Each treatment had three replicates, which were distributed completely at random. The experimental unit was a single plant established in the floating root system in the container described above. The treatments were added via Steiner

Table 1. Composition of the Steiner nutrient solution and chemical sources used in this experiment.

Nutrient	Concentration (mg · L^{-1})	Chemical sources	Brand
N	168.00	$Ca(NO_3)_2 \cdot 4H_2O$ and KNO_3	Meyer and Meyer
P	31.00	KH_2PO_4	J.T. Baker
K	273.00	KNO_3, K_2SO_4 and KH_2PO_4	Meyer, J.T. Baker, and Meyer
Ca	180.00	$Ca(NO_3)_2 \cdot 4H_2O$	Meyer
Mg	48.00	$MgSO_4 \cdot 7H_2O$	Meyer
S	112.00	K_2SO_4 and $MgSO_4 \cdot 7H_2O$	J.T. Baker and Meyer
Fe	5.00	Fe-EDTA[1]	Sigma-Adrich, J.T. Baker and Meyer
Cu	0.02	$CuSO_4 \cdot 5H_2O$	Fermont
Zn	0.11	$ZnSO_4 \cdot 7H_2O$	Fermont
Mn	0.62	$MnSO_4 \cdot H_2O$	Fermont
B	0.44	H_3BO_3	J.T. Baker
Mo	0.10	$H_2MoO_4 \cdot H_2O$	J.T. Baker

Source: According to the methodology described by Steiner and van Winden (1970).

Universal Nutrient Solution when nutrition was provided at 100%. The nutrient solution was prepared using tap water (pH = 7.1; electrical conductivity = 0.342 dS · m^{-1}; total dissolved solids 135 mg · L^{-1}; ions in mg · L^{-1}: NO_3^- 18.130, PO_4^{3-} 0.015, SO_4^{2-} 0.024, Cl^- 22.41, HCO_3^- 132.490, K^+ 8.432, Ca^{2+} 29.441, Mg^{2+} 24.531, Na^+ 27.975). The macro and micronutrient sources used are presented in Table 1. A closed hydroponic system was used, where the nutrient solution with different levels of Nd and Zn was completely renewed after every 10 days. After every 48 hr, the water lost within the system was replenished. The pH of the solution was adjusted to 5.5 using 1N H_2SO_4 (Meyer, Mexico).

Growth variables evaluated

When the plants were 98-day-old, they were removed from the floating root hydroponic system. At the end of the harvest, the following determinations were made. Plant height was measured in each plant from the base of the stem to the highest leaf, using a measuring tape (Truper®, FIN-55M, Mexico). The number of leaves was counted manually for each plant. Leaf length was measured in each plant with the help of a measuring tape (Truper®). Root volume was determined using the displacement method, using a 500 mL graduated cylinder. Leaf area was measured with a leaf area integrator (LI-COR-3000A, USA).

Determination of the weights of fresh and dry biomass

Fresh biomass was determined by separately weighing the stem and root of each plant on an analytical scale (Adventurer Ohaus Pro, AV213C, USA). Subsequently, the samples were dried in a forced air oven (Riossa, HCF-125, Mexico) at 70°C for 72 hr and weighed on an analytical scale (Adventurer Ohaus Pro) to obtain the dry biomass of each organ. The total fresh biomass was obtained by adding the fresh biomass of stem and root. Total dry biomass was calculated by adding the dry biomass of stem and root. The difference between fresh stem and root biomass was expressed as the ratio of the weight of fresh shoot and root biomass. The difference between dry biomass of shoot and root was expressed as the ratio of the weight of dry biomass of shoot and root.

Foliar concentrations of N, P and K

For the determination of N concentration, 0.25 g of each sample was weighed and subjected to wet digestion with a biacid mixture of H_2SO_4:$HClO_4$ (2:1, v:v) and 1 mL of H_2O_2 at 30%, in a digestion plate at 350°C. At the end of digestion, the obtained extracts were filtered and made up to 25 mL with deionised water. N was evaluated with the micro-Kjeldahl method. A volume of 10 mL of the resulting extract was distilled adding 50% NaOH. The distillate was received in 4% H_3BO_3 with a mixture of indicators (methyl red and bromocresol green), and titration was carried out with H_2SO_4 0.05 N.

For the determination of P and K, 0.5 g of each plant sample was weighted, a mixture of HNO_3:$HClO_4$ (2:1, v:v) was added and they were placed in a digestion plate at 160°C. The samples were then filtered and made up to 25 mL with deionised water. The concentrations of the elements were read in an inductively coupled plasma optic emission spectroscopy system (Agilent, ICP-Optical Emission Spectrometer, 725-ES, USA).

Statistical analysis

A two-way analysis of variance (ANOVA) and Tukey's mean comparison test ($p \leq 0.05$) were performed, for which the statistical software Statistical Analysis System (SAS Institute, 2009) version 9.4 was used.

The study was carried out as a factorial experiment. Therefore, in the statistical analysis, the main effects of the two study factors (Nd and Zn) and the interaction between factors (Nd × Zn) were evaluated. The main factor effects are the overall impact of each factor considered independently. The secondary or interaction effects are defined by the relationship between the independent factors or variables, that is, the cross effects.

EXPERIMENTAL DESIGN

The study was carried out as a 4 × 3 factorial experiment, with four levels (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}) for Nd as the first factor, and three levels (0.1, 0.2 and 0.3 mg · L^{-1}) for Zn as the second factor. The interactions among both factors were also evaluated, resulting in a total of 12 treatments to evaluate. Herewith, we present the effects of the individual factors (Nd and Zn) and their interactions (Nd × Zn).

Growth variables

The Nd factor had a significant effect on plant height, number of leaves, leaf length, root volume and leaf area. The Zn factor and the Nd × Zn interaction only caused significant effects on leaf length and leaf area (Table 2).

The 2.885 mg Nd · L^{-1} and 5.770 mg Nd · L^{-1} doses increased the plant height by 9% and 9.3% (Figure 1A),

Table 2. Significance of the study factors and their interaction in growth variables of lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants.

Study factors	Plant height	Number of leaves	Leaf length	Root volume	Leaf area
Nd	0.0012*	0.0001*	0.0196*	0.0250*	<0.0001*
Zn	0.9442ns	0.7758ns	0.0008*	0.6681ns	0.0001*
Nd × Zn	0.1283ns	0.3965ns	0.0152*	0.5860ns	0.0198*

*, significant ($p \leq 0.05$); ns, not significant ($p > 0.05$).

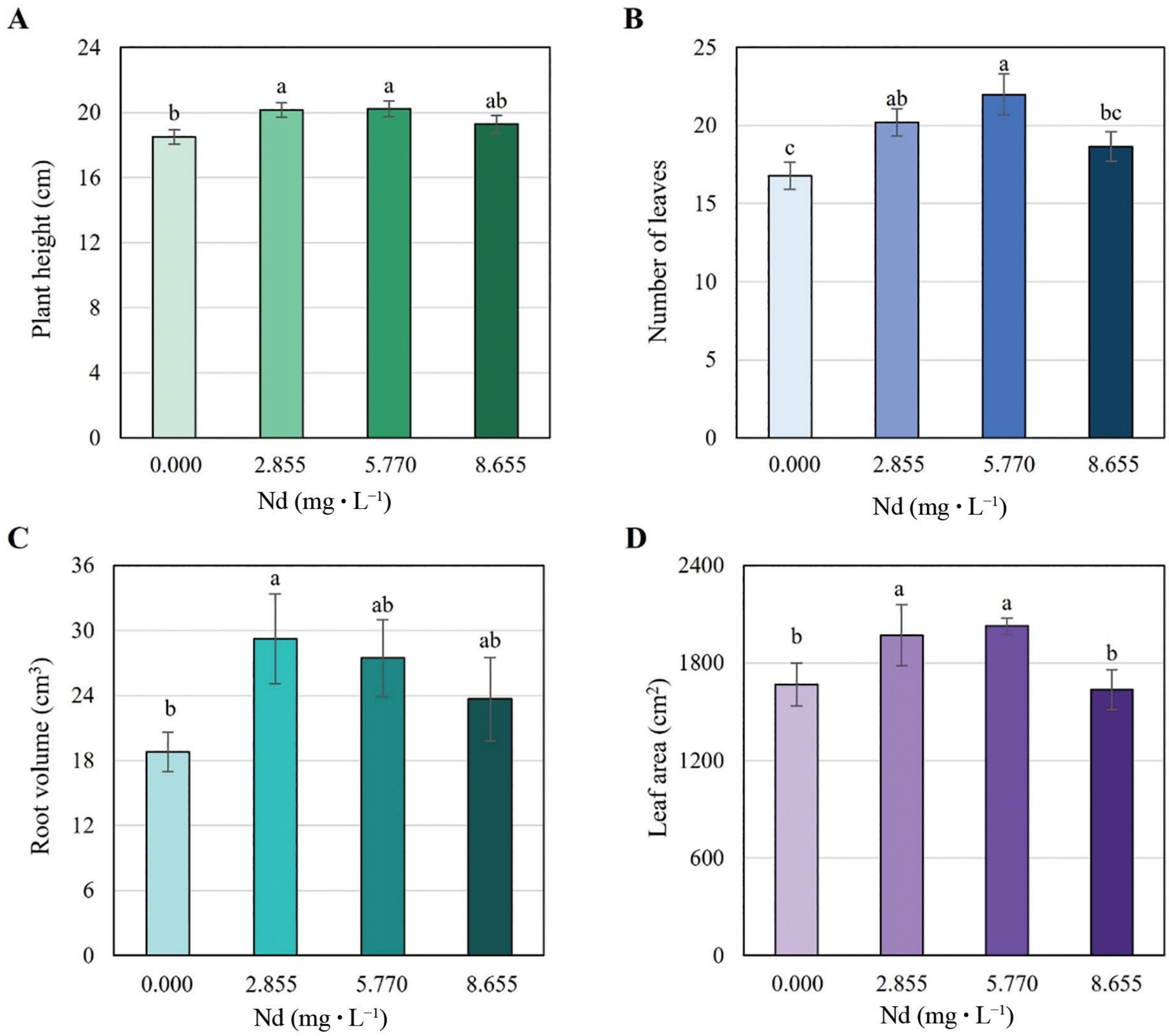

Figure 1. Plant height (A), number of leaves (B), root volume (C) and leaf area (D) of lettuce (*Lactuca sativa*) cv. 'Ruby Sky' treated for 48 days with different concentrations of Nd (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}). Bars ± SD (standard deviation) with different letters in each subfigure indicate significant statistical differences (Tukey, $p \leq 0.05$).

and the number of leaves by 20.5% and 31.1% (Figure 1B), respectively, as compared with the control. Root volume increased by 55.6% with the supply of 2.885 mg Nd · L^{-1}, compared with the treatment without Nd. The results obtained in the 5.770 mg Nd · L^{-1} and 8.655 mg Nd · L^{-1} treatments were not statistically different from that of the 2.885 mg Nd · L^{-1} dose (Figure 1C). The application of 2.885 mg Nd · L^{-1} and 5.770 mg Nd · L^{-1} increased leaf area by 18.3% and 21.6%, compared with the control (Figure 1D).

As the Zn dose increased, leaf length was also augmented. In the treatment with 0.3 mg Zn · L^{-1}, leaves reached 18.2 cm in length, which is a mean value of 7.7% greater than those observed in plants exposed to 0.2 mg Zn · L^{-1} and 0.1 mg Zn · L^{-1}. On the contrary, a negative relationship was observed between the concentration of Zn in the nutrient solution and leaf area; the highest average value was recorded with the dose 0.1 mg Zn · L^{-1} (2,043.8 cm^2), exceeding the leaf areas recorded in plants treated with 0.2 mg Zn · L^{-1} and 0.3 mg Zn · L^{-1} by 14.7% and 17.4%, respectively.

The 5.770 mg Nd · L^{-1} + 0.3 mg Zn · L^{-1} treatment increased leaf length by 22.4%, compared with the 0.1 mg Zn · L^{-1} treatment without Nd. There were no significant differences at the 0.1 mg Zn · L^{-1} and 0.2 mg Zn · L^{-1} levels, regardless of the Nd dose offered (Figure 2A). Interestingly, the negative effects of the concentrations of 0.2 mg Zn · L^{-1} and 0.3 mg Zn · L^{-1} on leaf area stand out when they were supplied in the absence of Nd and with the highest dose of this element (8.655 mg Nd · L^{-1}), as observed in Figure 2B.

Lettuce plants showed differential growth in response to the levels of Nd and Zn supplied through the nutrient solution. The 5.770 mg Nd · L^{-1} dose stimulated plant growth, while plants treated with 0.1 mg Zn · L^{-1} showed better development (Figure 3).

Weights of fresh and dry biomass

The Nd factor had a significant effect on the weights of fresh and dry biomass of stem and root. This is not the case in the ratio of fresh and dry biomass of stem and root. The Zn factor caused significance in most of the

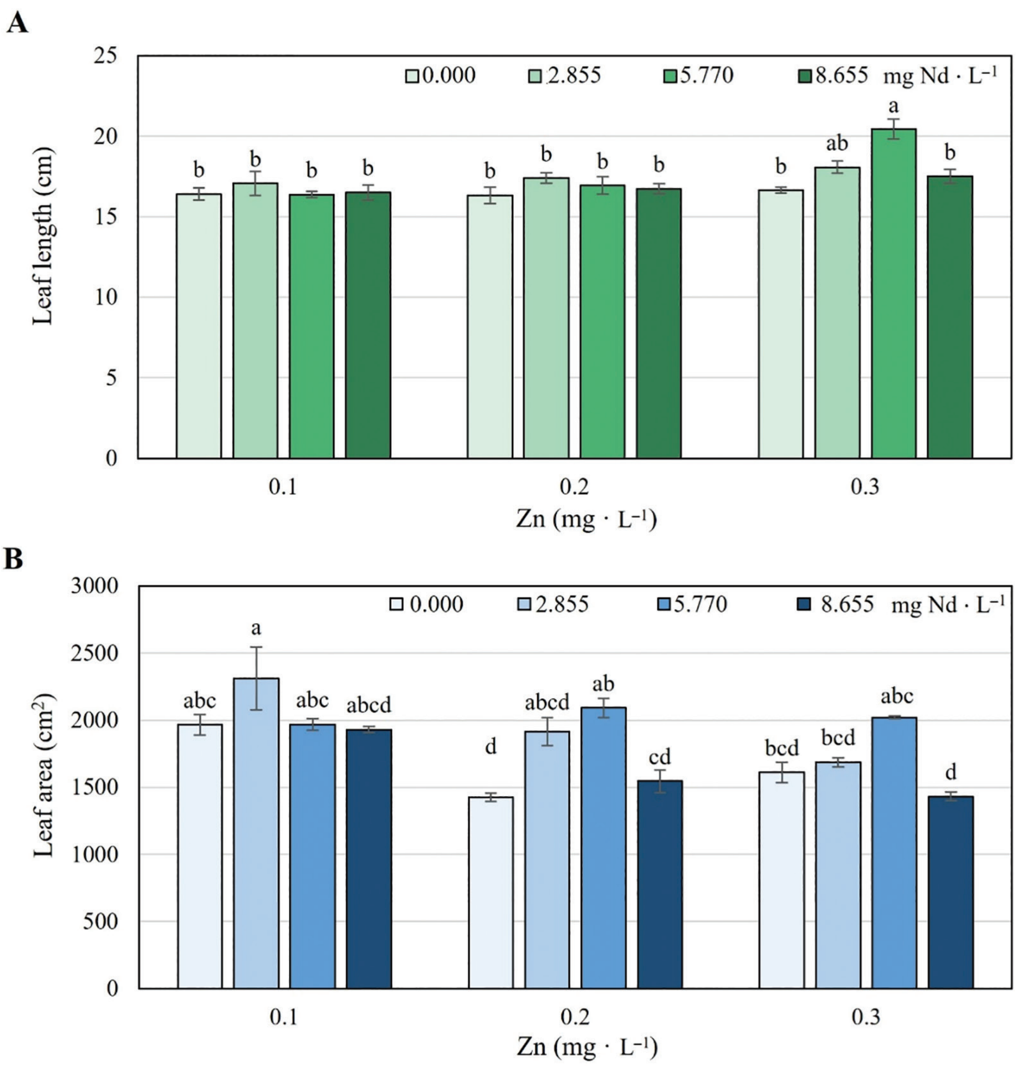

Figure 2. Leaf length (A) and leaf area (B) of lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants treated for 48 days with different concentrations of Nd (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}) and Zn (0.1, 0.2 and 0.3 mg · L^{-1}). Bars ± SD (standard deviation) with different letters in each subfigure indicate significant statistical differences (Tukey, $p \leq 0.05$).

variables evaluated, with the ratio of fresh stem and root biomass. The Nd × Zn interaction had significance in the ratios of fresh and dry biomass of stem and root, as well as in the dry biomass of stems, roots and total (Table 3).

Concentrations of 2.885 mg Nd · L^{-1} and 5.770 mg Nd · L^{-1} significantly increased the fresh biomass of stems, 24.6% and 27.2%, respectively, as compared with the treatment without Nd. A similar response was also observed in the dry biomass of shoots (Figure 4A). Likewise, doses of 2.885 mg Nd · L^{-1} and 5.770 mg Nd · L^{-1} increased on average 22.2% and 33.4% of the fresh and dry root biomasses, respectively, compared with the results recorded in plants that did not receive Nd (Figure 4B). Total fresh and total dry biomass in these treatments were higher by 25.3% and 31.6%, compared with the control without Nd (Figure 4C).

The highest values of fresh and dry biomass weights were recorded in plants treated with 0.1 mg Zn · L^{-1}. In stems, this treatment surpassed the rest by 19.7% and 27.6% in the weight of fresh and dry biomass, respectively (Figure 4D). Likewise, in roots the fresh and dry weights were higher by 20% and 23.9% (Figure 4E). Consequently, the total fresh and dry biomass exceeded the highest Zn levels evaluated by 19.8% and 27.1% with this dose of Zn (Figure 4F).

The Zn factor also had significant effects on the stem:root dry biomass ratio (Table 3). There were significant differences between the levels of 0.2 mg Zn · L^{-1} (5.56) and 0.3 mg Zn · L^{-1} (6.74), while the dose of 0.1 mg Zn · L^{-1} (6.26) was not different from the other two.

The dry biomasses of stems, roots and total were higher by 53.9, 59.7 and 54.7% in the 2.885 mg Nd · L^{-1} + 0.1 mg Zn · L^{-1} treatment, compared with the 0.3 mg Zn L^{-1} level without Nd (Figures 5A–5C). The dry stem biomass decreased notably with the treatments of 0.2 mg Zn · L^{-1} plus the application of 2.885 and 8.655 mg Nd · L^{-1}, and 0.3 mg Zn · L^{-1} without Nd (Figure 5A). Plants grown with 8.655 mg

Figure 3. Growth of lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants treated for 48 days with different concentrations of Nd (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}) and Zn (0.1, 0.2 and 0.3 mg · L^{-1}).

Table 3. Significance of the study factors and their interaction in the weights of fresh and dry biomasses, and their relationships, in lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants.

Study factors	FM			Stem:root FM ratio	DM			Stem:root DM ratio
	Shoot	Root	Total		Shoot	Root	Total	
Nd	0.0006*	<0.0001*	0.0004*	0.3680ns	<0.0001*	0.0001*	<0.0001*	0.5537ns
Zn	0.0009*	<0.0001*	0.0005*	0.1334ns	<0.0001*	0.0004*	<0.0001*	0.0023*
Nd × Zn	0.2578ns	0.1038ns	0.2535ns	0.0186*	0.0049*	0.0311*	0.0054*	0.0433*

*, significant ($p \leq 0.05$); ns, not significant ($p > 0.05$).
DM, dry matter; FM, fresh matter.

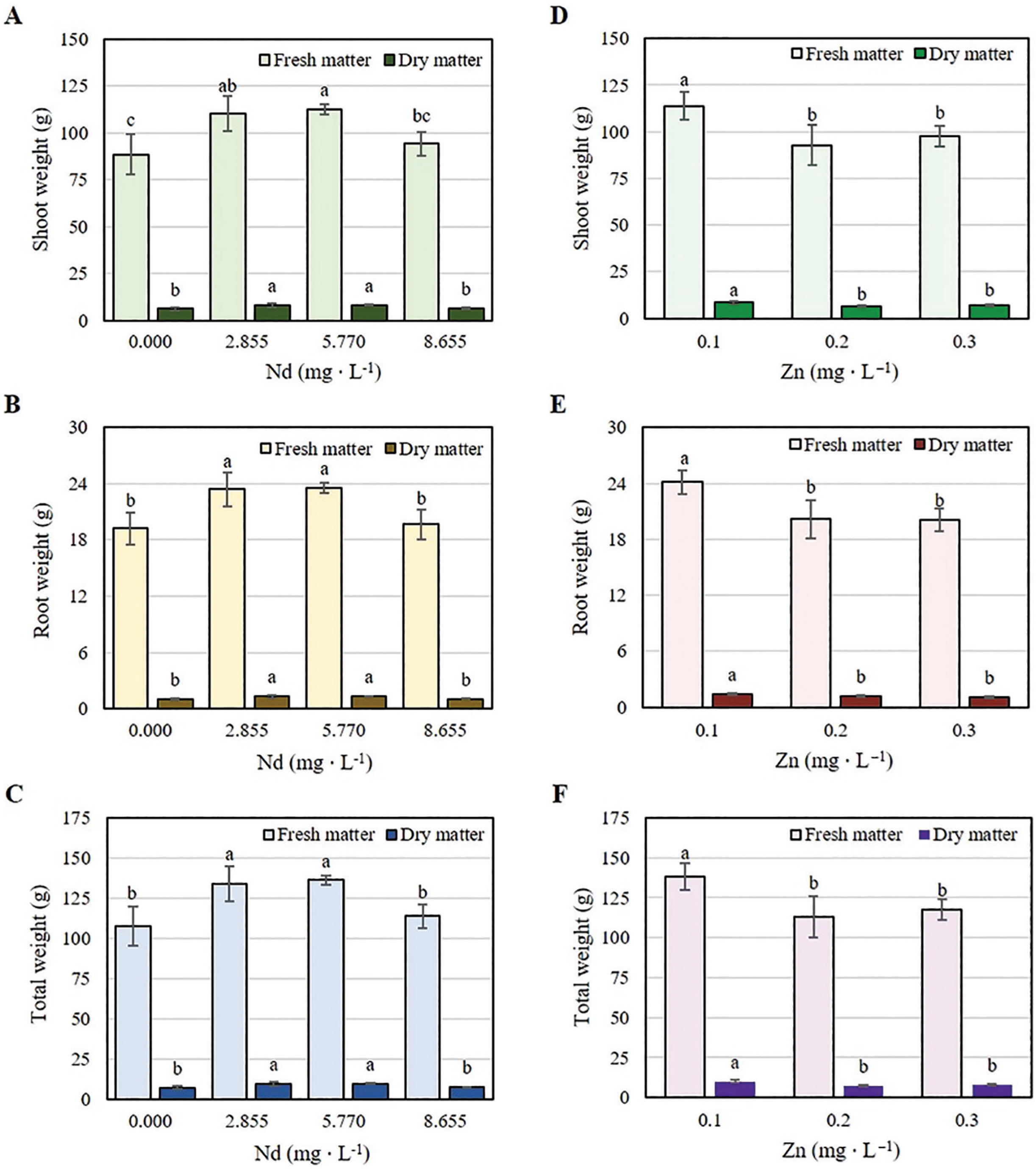

Figure 4. Fresh and dry biomass of stem (A and D), root (B and E), and total (C and F) of lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants treated for 48 days with different concentrations of Nd (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}) and Zn (0.1, 0.2 and 0.3 mg · L^{-1}). Bars ± SD (standard deviation) with different letters in each subfigure indicate significant statistical differences (Tukey, $p \leq 0.05$).

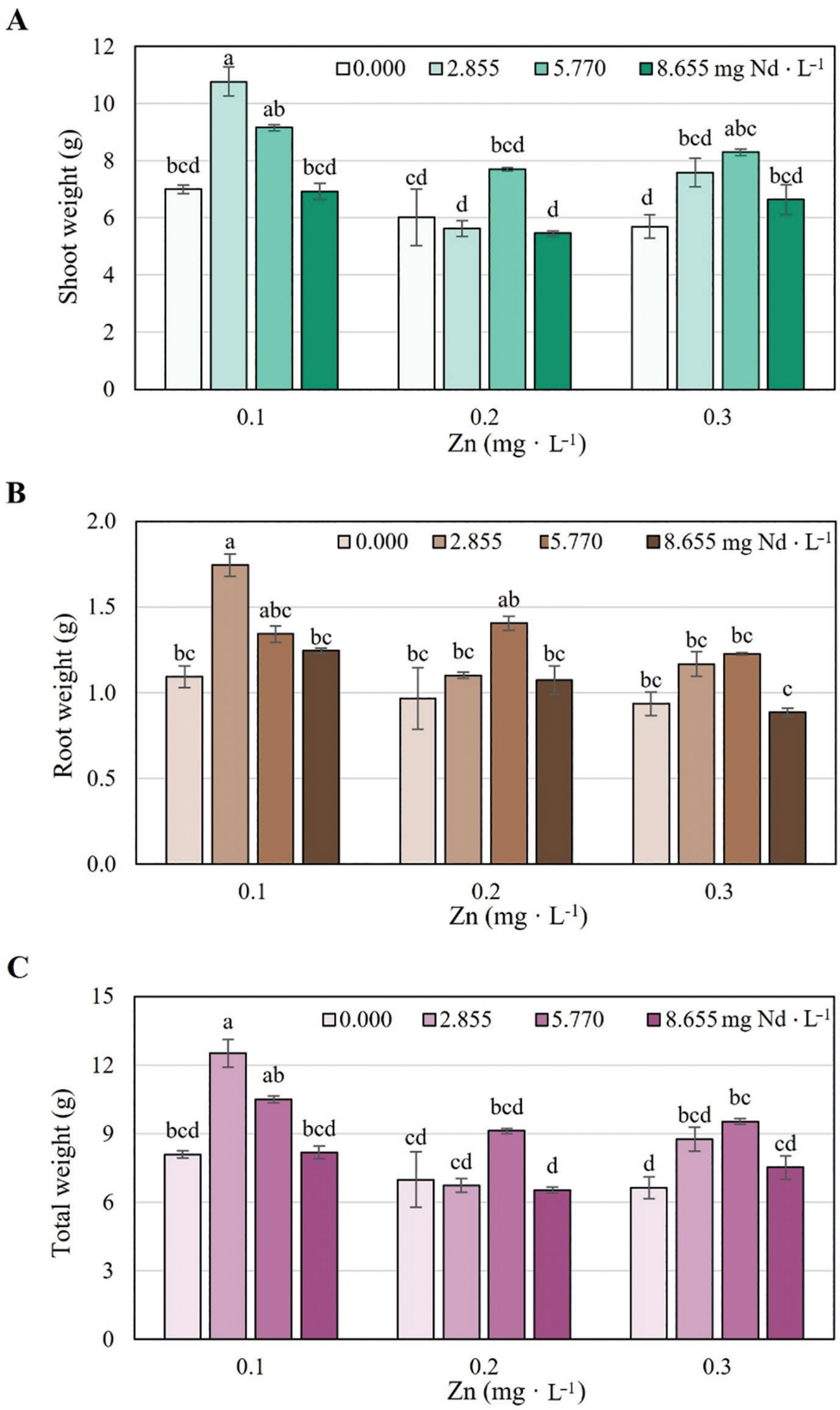

Figure 5. Dry biomass of stem (A), root (B) and total (C) of lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants treated for 48 days with different concentrations of Nd (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}) and Zn (0.1, 0.2 and 0.3 mg · L^{-1}). Bars ± SD (standard deviation) with different letters in each subfigure indicate significant statistical differences (Tukey, $p \leq 0.05$).

Nd · L^{-1} + 0.3 mg Zn · L^{-1} decreased dry root biomass (Figure 5B). Furthermore, the lowest total dry biomass was recorded in the 8.655 mg Nd · L^{-1} + 0.2 mg Zn · L^{-1} and 0.3 mg Zn · L^{-1} without Nd treatments (Figure 5C).

The stem:root fresh biomass ratio was higher in plants grown in the 8.655 mg Nd · L^{-1} + 0.3 mg Zn · L^{-1} treatment, compared with the 8.655 mg Nd · L^{-1} + 0.1 mg Zn · L^{-1} and 0 mg Nd · L^{-1} + 0.2 mg Zn · L^{-1} treatments (Table 3). Regarding stem:root dry biomass ratio, a significant increase was observed with the 8.655 mg Nd · L^{-1} + 0.3 mg Zn · L^{-1} treatment, compared with the 0.2 mg Zn · L^{-1} dose in combination with 2.885 mg Nd · L^{-1} and 8.655 mg Nd · L^{-1} (Table 4).

Foliar concentrations of N, P and K

The Nd factor and the Nd × Zn interaction caused significant effects on the foliar concentrations of N, P and K. This same result was observed for the Zn factor, except for the absence of a significant effect on the foliar P concentration (Table 5).

The N concentration was higher with the treatment 8.655 mg Nd · L^{-1} + 0.1 mg Zn · L^{-1}, at 24.4, 40.4 and 34.8% with respect to treatments without Nd in combination with 0.1, 0.2 and 0.3 mg Zn · L^{-1}, respectively (Figure 6A). The concentration of P was reduced by 28.6% and 28.3% in leaves treated with 0.2 mg Zn L^{-1} without Nd, in comparison with the treatments at 5.770 mg Nd · L^{-1} + 0.3 mg Zn · L^{-1} and 2.885 mg Nd · L^{-1} + 0.2 mg Zn · L^{-1}, respectively (Figure 6B). In turn, the treatment at 5.770 mg Nd · L^{-1} + 0.3 mg Zn L^{-1} increased the foliar concentration of K on average by 58%, with respect to all the other treatments (Figure 6C).

RESULTS AND DISCUSSION

Herein, we demonstrated that Nd had stimulatory effects on plant growth (i.e., plant height, number of leaves, root volume leaf area as well as fresh biomasses of stems, roots and total. Previous studies have confirmed that Nd promotes growth in various crops. In spinach (*Spinacia oleracea*), Nd improved the rate of photosynthesis, the carboxylation activity of the ribulose bisphosphate carboxylase oxygenase enzyme (RuBisCo), while increasing biomass and plant growth (Liu et al., 2006). In wheat cv. 'Bainong 207', the application of 30 µM $NdCl_3$ (4.33 mg · Nd L^{-1}) increased plant height, root length and total fresh biomass (Lu et al., 2020). In pepper cv. 'California Wonder', the foliar application of 3.4 µM $Nd(NO_3)_3$ (0.50 mg · Nd L^{-1}) significantly improved growth, yield and quality of the crop (Abou El-Nour and Attia, 2022). In sugarcane cv. 'Mex 69-290', the 100 µM Nd and 150 µM Nd treatments (14.4 mg · Nd L^{-1} and 21.6 mg · Nd L^{-1}) stimulated plant height, root length, root volume, and fresh and dry biomass of stems, leaves and roots (Ramírez-Antonio et al., 2023).

The stimulatory effects of Nd on the growth of lettuce plants were concentration dependent. We observed that the growth variables decreased with the 8.655 mg Nd · L^{-1} concentration, compared with the 2.885 mg Nd · L^{-1} and 5.770 mg Nd · L^{-1} levels (Figure 1). Therefore, it is inferred that higher doses could reduce plant growth. This phenomenon is known as hormesis and is defined as a biphasic response, in which low concentrations of a factor stimulate positive effects in crops, while higher doses can be harmful, even causing toxicity and cell death (Calabrese and Agathokleous, 2021; Erofeeva, 2022). Several studies have pointed out that REEs have hormetic effects on plant growth and development (Tommasi et al., 2023). In rice and wheat seedlings, stimulant effects were recorded at a dose of 15 µM Nd (2.16 mg · Nd L^{-1}); however, with increasing concentrations (30 µM Nd and 74 µM Nd corresponding to 4.33 mg · Nd L^{-1} and 10.7 mg · Nd L^{-1}, respectively) there was a gradual decrease in the growth of both species (Basu et al., 2016). The growth of pak choi (*Brassica chinensis*) seedlings was favoured by applying 297 µM Nd (42.8 mg · Nd L^{-1}), although, by raising the level to 891 µM Nd (128 mg · Nd L^{-1}), growth was inhibited (Rezaee et al., 2018). The effects of REE depend on the dose, application frequency, exposure time, agronomic management, development stage and the genotype tested (Gómez-Merino et al., 2023). It is also important to highlight that Nd had no significant effect on the ratios of fresh and dry biomass of stems and roots, which indicates generalised growth stimulation.

Under our experimental conditions, the supply of 0.1 mg Zn · L^{-1} triggered significant increases of fresh and dry biomasses of stems, roots and total, as well as foliar area. On the contrary, greater leaf length was recorded as Zn doses increased. Effects on the growth and morphology of some crops in response to Zn have been reported. In lettuce var. *crispa*, there was a significant effect on the fresh and dry biomass of the plant with the application of 3.3 mg Zn · L^{-1} (Sago et al., 2018) and 0.65 mg Zn · L^{-1} in the cv. 'Filó' (Meneghelli et al., 2021). In basil (*Ocimum basilicum*), vegetative growth was positively influenced with the addition of 0.09 mg

Table 4. Ratios of fresh and dry stem:root biomasses in lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants treated with Nd and Zn.

Nd (mg · L^{-1})	Zn (mg · L^{-1})	Stem:root FM ratio	Stem:root DM ratio
0.000	0.1	4.80 ± 0.21 ab	6.47 ± 0.42 ab
0.000	0.2	4.22 ± 0.19 b	6.47 ± 0.41 ab
0.000	0.3	4.49 ± 0.03 ab	6.09 ± 0.09 ab
2.885	0.1	4.65 ± 0.25 ab	6.17 ± 0.24 ab
2.885	0.2	4.82 ± 0.16 ab	5.11 ± 0.19 b
2.885	0.3	4.70 ± 0.06 ab	6.54 ± 0.48 ab
5.770	0.1	4.96 ± 0.09 ab	6.84 ± 0.18 ab
5.770	0.2	4.74 ± 0.09 ab	5.50 ± 0.12 ab
5.770	0.3	4.81 ± 0.11 ab	6.77 ± 0.09 ab
8.655	0.1	4.48 ± 0.13 b	5.57 ± 0.29 ab
8.655	0.2	4.53 ± 0.11 ab	5.17 ± 0.38 b
8.655	0.3	5.53 ± 0.35 a	7.56 ± 0.71 a

Means ± SD (standard deviation) with different letters in each column indicate significant statistical differences (Tukey, $p \leq 0.05$). DM, dry matter; FM, fresh matter.

Table 5. Significance of the study factors and their interaction in the foliar concentration of N, P and K, in lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants.

Study factors	Nitrogen (N)	Phosphorus (P)	Potassium (K)
Nd	<0.0001*	<0.0001*	<0.0001*
Zn	<0.0001*	0.4549ns	<0.0001*
Nd × Zn	<0.0001*	<0.0001*	<0.0001*

*, significant ($p \leq 0.05$); ns, not significant ($p > 0.05$).

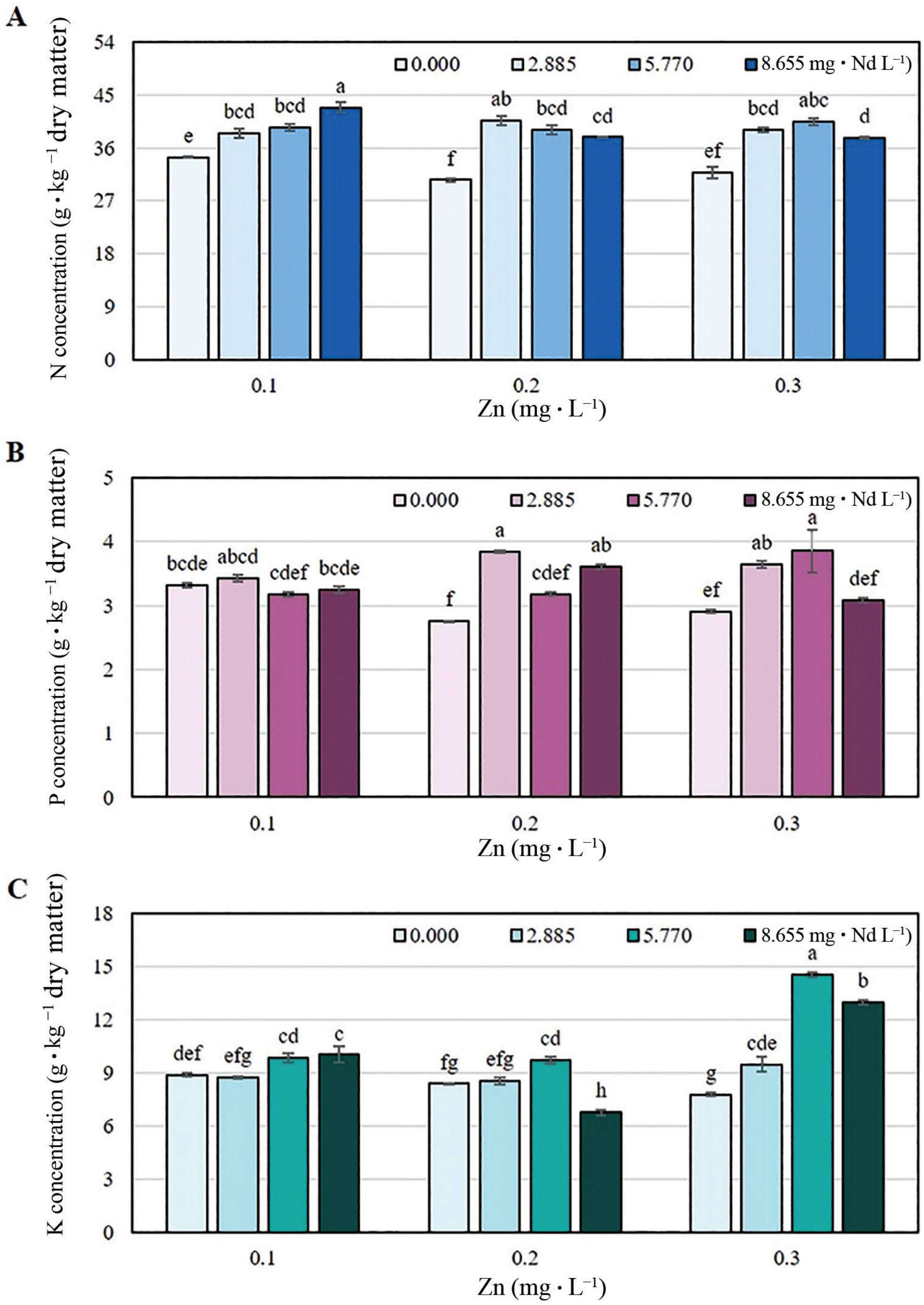

Figure 6. Foliar concentration of nitrogen (A), phosphorus (B) and potassium (C) in lettuce (*Lactuca sativa*) cv. 'Ruby Sky' plants treated for 48 days with different concentrations of Nd (0.000, 2.885, 5.770 and 8.655 mg · L^{-1}) and Zn (0.1, 0.2 and 0.3 mg · L^{-1}). Bars ± SD (standard deviation) with different letters in each subfigure indicate significant statistical differences (Tukey, $p \leq 0.05$).

Zn · L^{-1} to the nutrient solution (Hanif et al., 2017). On the other hand, in biofortification studies with Zn in arugula (*Eruca vesicaria*) (Rugeles-Reyes et al., 2019) and lettuce (Fortis-Hernández et al., 2022), the doses of Zn evaluated had no effect on the growth parameters. Zinc is a micronutrient that promotes plant growth in specific doses for each species. Additionally, the effect of Zn is highly influenced by the cultivar, the cultivation system, the application method and the chemical formula of the material used as evidenced in the following investigations. In lettuces cv. 'Phillipus' grown in hydroponics, the optimal Zn dose is 5.2 mg · L^{-1}; in cv. 'Melodion' and the var. *crispa*, it is 0.1 mg · L^{-1}; in the cv. 'Filó', 3.3 mg · L^{-1}; and in cvs. 'Saladela' and 'Vanda', it is 1.7 mg · L^{-1}. In these genotypes, negative effects on growth, development and performance have been reported with variable doses ranging from 0.15 mg · L^{-1} to 6.5 mg · L^{-1} (Barrameda-Medina et al., 2017; Konieczny and Kowalska, 2017; Sago et al., 2018; Meneghelli et al., 2021; De Lima et al., 2023).

The joint effect of Nd and Zn stimulated plant growth, as observed in the increase of leaf length with the 5.770 mg Nd · L^{-1} + 0.3 mg Zn · L^{-1} treatment. The ratios of fresh and dry stem and root biomasses were highest with the 8.655 mg Nd · L^{-1} + 0.3 mg Zn · L^{-1} treatment. These positive effects may be attributed to the fact that Zn accelerates the growth process and development of plants due to its role as a cofactor in the biosynthesis of the amino acid tryptophan, which acts as a precursor of auxins, hormones that play a role in the process of cell division and elongation (Nejad et al., 2014; García-López et al., 2018). In addition, Zn participates in photosynthesis, respiration, and nitrogen and carbon metabolism, physiological processes that mediate plant growth (Ramzan et al., 2020). Additionally, REEs, including Nd, increase plant biomass by stimulating photosynthetic processes, through an increase in electron transfer rates and efficiency in the photochemical activity of photosystem II (PSII) (Kovaříková et al., 2019). The REEs also modify the absorption of nutrients (Wu et al., 2014; De Olviera et al., 2015; Hu et al., 2016) and participate in the formation of adventitious roots, cell differentiation and morphogenesis of the root (Zhang et al., 2013), thus stimulating plant growth. In soybean, La increased the foliar concentration of P, K, Ca, Mg, S and Mn when 160 µM La was supplied (de Oliveira et al., 2015). Cerium, another REE, increased the foliar concentrations of K, Ca, Mg, Cu, Fe and Mn in horseradish (*Armoracia rusticana*) (Wang et al., 2008) and those of K, Mg, Ca, Zn and Mo in rice (Liu et al., 2012). Similar results were found in this research, where the foliar N concentration increased by 24.4% with the 8.655 mg Nd · L^{-1} + 0.1 mg Zn · L^{-1} treatment in comparison with the treatment without N and 0.1 mg Zn · L^{-1}. Indeed, REEs increase nitrate reduction and N assimilation by stimulating the activities of key enzymes in N metabolism such as nitrate reductase (NR), nitrite reductase (NiR), glutamate synthase (GOGAT), glutamine synthetase (GS), glutamate dehydrogenase (GDH), urease and glutamic-pyruvic transaminase (TGP) (Cao et al., 2007; Yin et al., 2009). Interestingly, with respect to the 0.1 mg Zn · L^{-1} treatment without Nd, the foliar concentrations of P and K, were higher by 15.6% and 63.3%, respectively, in the 5.770 mg Nd · L^{-1} + 0.3 mg Zn · L^{-1} treatment.

Both biostimulation and biofortification may not only enhance the growth and nutritional value of crops, but may also contribute to sustainable agriculture under limiting conditions aggravated by climate change (Mandal et al., 2023; Mandal et al., 2024). This is particularly important for Mexico, since climate change and heat waves are affecting temperatures in many parts of the country. Mexico is classified as one of the most vulnerable countries to the effects of climate change (Arce-Romero et al., 2020; Hernández-Rodríguez et al., 2023). These changes generate different environmental conditions to which crops develop different strategies of adaptation, as is the case of what is presented in this study. The lettuce cultivar tested here showed some changes in its development cycle, and finally managed to thrive in challenging environmental situations. Thus, these findings also demonstrate the importance of biostimulation and biofortification in addressing abiotic stressors exacerbated by global climate change.

Lettuce is severely affected by climate change (Pathak et al., 2023). Consequently, the relative low values of the growth data we recorded in our study could have been influenced by the environmental conditions of our experiment, including day-length (9 hr), day/night temperature (27.9/11.6°C, respectively), photosynthetically active radiation (490 µmol · m^{-2} · s^{-1}) and day/night relative humidity (31/72%), as well as the size on the plastic containers. Lettuce is a crop plant that grows best in cold and temperate climates. Its relative growth rate decreases with increasing temperature, which in turn can prolong the crop cycle with differences of ten days from transplant to harvest (Wheeler et al., 1993). For optimal growth, in general, lettuce requires temperatures between 15°C and 20°C during the day, and 5°C–10°C at night. With reduced luminosity (short days and weak light intensity), high daytime temperatures delay the formation of leaves to integrate the rosette, while low temperatures favour it (Yan et al., 2019). From planting, temperature impacts germination, root growth and nutrient uptake (Pregitzer and King, 2005), which in turn influences plant growth. Additionally, container capacity is likely to have been a limiting factor for growth. According to Zhou et al. (2022), light intensity of 350–500 µmol · m^{-2} · s^{-1} is recommended at low temperatures (15°C); light intensity of 350–600 µmol · m^{-2} · s^{-1} is recommended at medium temperatures (23°C); and the range of 500–600 µmol · m^{-2} · s^{-1} is a recommendable light intensity for lettuce grown at high temperatures (30°C).

CONCLUSIONS

All the Nd levels tested increased plant height, number of leaves, root volume, leaf area and fresh biomass of stems, roots and total of lettuce plants. Specifically, the 5.770 mg Nd · L^{-1} treatment caused the highest values in the growth parameters. The magnitude of the biostimulant effects of Nd on lettuce plants would depend on the dose supplied. The 0.1 mg Zn · L^{-1} treatment increased leaf area and fresh stem, root and total biomass. The stem:root ratio of dry biomass was higher with the 0.3 mg Zn · L^{-1} dose. Furthermore, Nd had a greater influence on the growth parameters than Zn. Likewise, the joint supply of both elements, in variable doses, increased leaf length, dry biomass of stems, roots and total, and the ratio of fresh and dry biomass of stems and roots. Importantly, Nd significantly increased foliar concentrations of N, P and K. These findings demonstrate that the interaction of Nd and Zn has positive effects on the growth and nutrition of lettuce plants.

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AUTHOR CONTRIBUTIONS

L.I.T.-T. developed the concept and designed the experiment. I.R.-L. performed the experiments and collected data. M.G.P.-S. provided help and advice on supervising the research study. F. C. G.-M. and L.I.T.-T. performed the formal analysis of data. I.R.-L. and L.I.T.-T. wrote the first draft of the manuscript. L.I.T.-T. prepared the figures. F.C.G.-M. participated in writing, review and editing of the manuscript. L.I.T.-T. and F.C.G.-M. provided the resources. M. G. P.-S. and S.M.R.-O. reviewed the manuscript. All authors read and approved the final version of this manuscript.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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