



# Soil Application of Zinc for Potato Biofortification in the Central Andes of Peru

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## Abstract

Zinc is essential for human health, yet dietary deficiencies persist in many regions. This study evaluated the effectiveness of soil-applied zinc to enhance zinc content in potato tubers grown in Peru's central Andes, as an agronomic biofortification strategy. Field trials were conducted over two seasons in four Andean sites using five Zn rates (0–32 kg ha<sup>-1</sup>). One variety was tested in 2016–2017, and four in 2017–2018. Yield, Zn content, accumulation, partial balance, and dietary contribution were assessed. In both seasons, Zn fertilization did not significantly affect tuber yield. In 2016–2017, Zn content in tubers increased by up to 86% and accumulation by 74% at 16 kg Zn ha<sup>-1</sup>. The estimated dietary contribution rose by 79%, with Achoscuyo showing the highest response and Lucma the lowest. Site differences were more evident at intermediate and high doses. In 2017–2018, Zn accumulation in shoots exceeded that in tubers by up to 2.8-fold, and Zn content in the peel was twice that of the flesh. Maximum Zn content and accumulation varied among varieties and doses. Canchán and Perricholi showed high Zn content and accumulation at 16 kg Zn ha<sup>-1</sup>. Principal component analysis revealed that Zn dose was positively associated with Zn content and negatively with tuber yield. The response to Zn fertilization depended on site, dose, and genotype. Soil-applied Zn increased Zn content in potatoes without compromising yield. Selecting varieties with high tuber Zn accumulation improved nutritional outcomes and fertilizer use efficiency.

**Keywords** Agronomic biofortification · Zinc content · Zinc accumulation · Potato · Andes

## 1 Introduction

Malnutrition is a global concern resulting from insufficient dietary intake and the consumption of low-quality foods that fail to meet energy and nutrient requirements (FAO et al. 2022). One major factor driving malnutrition is the lack of essential micronutrients such as zinc, iron, and vitamin A—a condition termed “hidden hunger,” which affects more than half of preschool-aged children and two-thirds of women of reproductive age worldwide (Stevens et al. 2022). Zinc is vital for human growth and development from fetal stages

through old age (Savarino et al. 2021; Thompson 2022), and its deficiency can cause impaired cognitive development, weakened immune function, increased oxidative stress, and delayed sexual maturation (Chasapis et al. 2012; Hussain et al. 2022; Salgueiro et al. 2004). Globally, 17% of the population has inadequate zinc intake. This proportion is higher in Africa (25%) and Latin America and the Caribbean (28%), moderate in Asia (18%), and lower in Europe (8%) and Oceania (11%) (Cediél et al. 2015; Wessells and Brown 2012). In Peru, the rate reaches 34.5%, with low-income rural households being the most affected (Curi et al. 2020; Gupta et al. 2020; Trujillo et al. 2022).

Biofortification involves increasing the nutritional value of food so that it contains higher levels of readily absorbable micronutrients compared with conventional counterparts (Lowe 2021), using three main approaches: transgenesis, conventional breeding, and agronomic biofortification (Garg et al. 2018). The latter relies on nutrient enrichment through fertilization (Szerement et al. 2022). This strategy is more adaptable to diverse crops and can be deployed

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more rapidly than either conventional or transgenic biofortification (Bhardwaj et al. 2022). Agronomic biofortification has proven effective in enhancing zinc content in the edible portions of several crops by optimizing fertilization rates, sources, and timing (Montalvo et al. 2016). Research on cabbage and canola (Mao et al. 2014); rice (Coffin and Slaton 2020); wheat (Zulfiqar et al. 2020); maize (Liu et al. 2017); green beans (de Almeida et al. 2020); and potatoes (Banerjee et al. 2016; Khan et al. 2019; Kromann et al. 2017) confirms biofortification as an effective strategy for increasing zinc concentrations in food.

However, the effectiveness of agronomic biofortification depends not only on the amount of micronutrient applied but also on how efficiently the crop absorbs it and redistributes it to edible organs. A study in rice demonstrated that a substantial portion of absorbed Zn accumulates in vegetative tissues, with limited remobilization to the grain, thereby diminishing the nutritional impact of biofortification (Wu et al. 2010). Furthermore, the response to zinc fertilization can vary markedly among varieties and locations, reflecting genetic differences in uptake and translocation efficiency, as well as distinct soil and climate characteristics. For example, a study on maize in Malawi by Botoman et al. (2022) reported that zinc concentration in maize grain displayed substantial spatial variation across regions, mainly linked to soil properties such as pH and available Zn content. In contrast, Rasheed et al. (2023), working with lentils, found that different genotypes exhibited marked variation in Zn partitioning and accumulation across tissues, directly influencing micronutrient use efficiency and its bioavailability in grain. This variability presents an ongoing challenge for standardizing biofortification strategies.

Potato is the fourth most important food crop globally, after maize, rice and wheat (FAO 2023a), and it plays a central role in the diet of developing countries (Wijesinha-Bettoni and Mouillé 2019). In Peru, its cultivation sustains more than 710 000 families, 24% of whom are located in the central highlands, a region that accounts for approximately 28% of national production (Ministry of Agrarian Development and Irrigation 2024). Potato remains a staple food for the Peruvian population (Devaux et al. 2019), with per capita consumption reaching 92 kg annually (FAO 2023b). It supplies energy along with substantial amounts of iron, potassium, phosphorus, magnesium, and vitamins B and C (Beals 2019; Burlingame et al. 2009). Its high caloric yield in a short growing period and on relatively small land areas, compared with other food crops (Lutaladio and Castaldi 2009), makes it appealing to both smallholders and larger producers.

Despite advances worldwide in agronomic biofortification, no studies in Peru have assessed how soil-applied zinc fertilization influences the concentration and accumulation

of this micronutrient in tubers of commercial potato varieties cultivated in acidic Andean soils. This study addresses that knowledge gap by conducting a detailed evaluation of agronomic attributes (tuber yield and aerial biomass), nutritional metrics (zinc content and accumulation in shoots, tubers, peel, and pulp), physiological indicators (zinc use efficiency), and human nutrition outcomes (contributions to the estimated daily requirement).

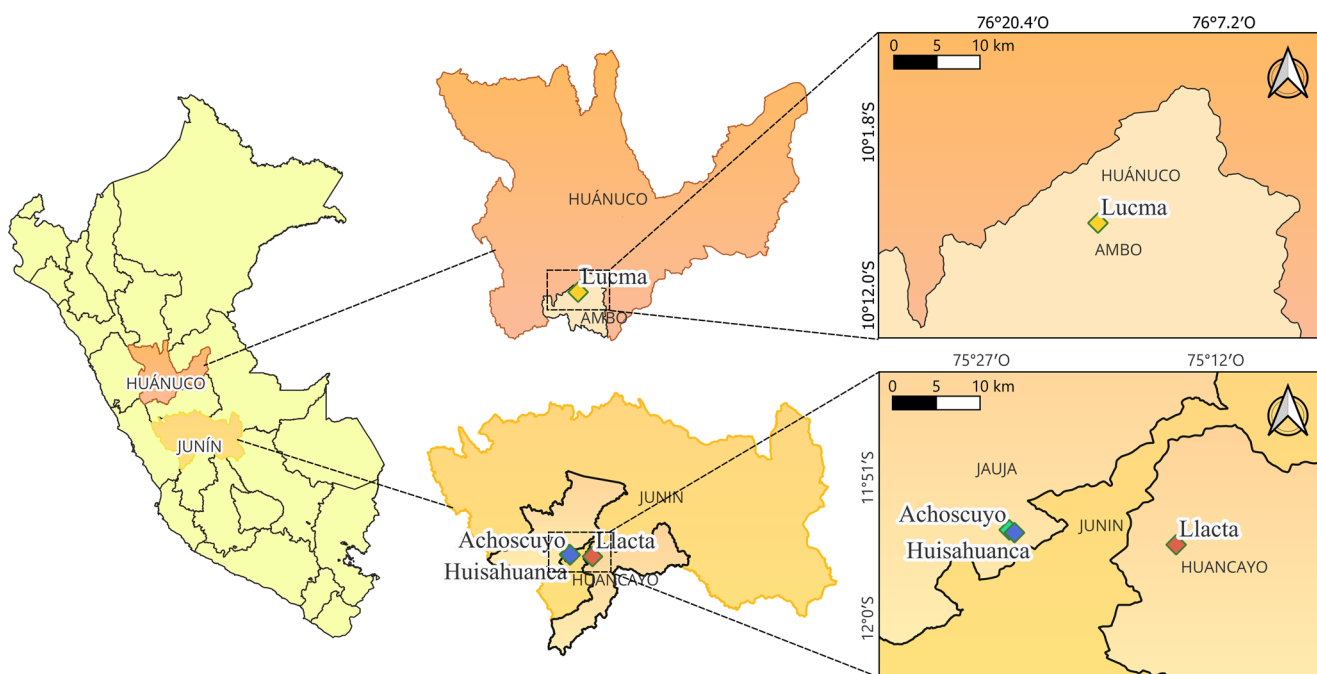
The objective of this study was to determine the effect of varying soil-applied zinc rates on the content, accumulation, and distribution of the micronutrient in potato tubers, while accounting for crop variety and location. The following hypotheses guided the research: (i) soil-applied zinc increases the content and accumulation of the micronutrient in tubers without adversely affecting yield; (ii) the response to zinc depends on the applied rate, potato variety, and production environment; (iii) zinc application results in limited absorption efficiency by the crop and low redistribution to edible organs; and (iv) this practice can meaningfully support the population's nutritional requirements. Given the high prevalence of zinc deficiency in Peru and the dietary relevance of potatoes in Andean rural communities, this research provides field-based evidence that can support fertilization strategies and guide interventions aimed at improving nutritional outcomes through sustainable agriculture.

## 2 Materials and Methods

### 2.1 Study Area and Crop Management

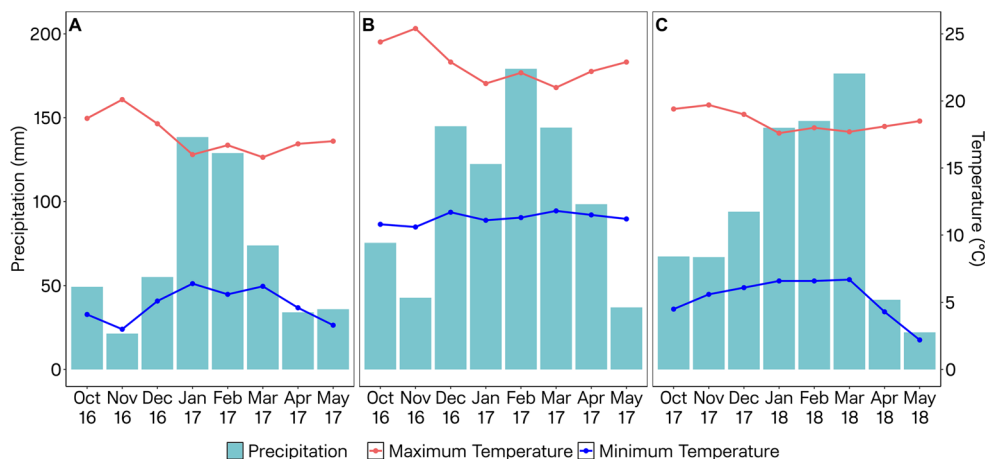
Field trials were implemented in Achoscuyo, Huisahuanca, and Lucma during the 2016–2017 season (Experiment 1) and in Llacta during the 2017–2018 season (Experiment 2) (Fig. 1). These populated centers lie within the Junín and Huánuco regions, which together represent nearly 20% of the national potato cultivation area (MIDAGRI 2024). Meteorological information was obtained from the National Service of Meteorology and Hydrology of Peru (SENAMHI) (SENAMHI 2023) and supplemented with precipitation records drawn from Peruvian Interpolated data of SENAMHI's Climatological and Hydrological Observation (Aybar et al. 2020) and temperature records obtained from ERA5 (Copernicus Climate Change Service and Climate Data Store 2023) (Fig. 2).

The characteristics of the sites where the trials were carried out, the crop management practices, and the base fertilization scheme are presented in Table 1. Fertilization in the experimental fields was designed to satisfy the crop's nutritional requirements, following local rate guidelines, and applied as follows: At planting, 1/3 of the nitrogen dose, 2/3



**Fig. 1** Map showing the locations where the trials were conducted

**Fig. 2** Monthly precipitation and minimum/maximum temperature patterns in Achoscuyo and Huisahuanca (2016–2017, **A**), Lucma (2016–2017, **B**), and Llacta (2017–2018, **C**)



**Table 1** Site characteristics and crop management for four field trials with Zn fertilizer

Experiment	2016–2017 season		2017–2018 season	
Site characteristics				
District, Province	Achoscuyo, Jauja	Huisahuanca, Jauja	Lucma, Huánuco	Llacta, Huancayo
Altitude (m.a.s.l.)	3764	3702	2948	3590
Accumulated precipitation (mm)	537	537	844	760
Crop management				
Planting time	October 25, 2016	October 25, 2016	November 19, 2016	November 26, 2017
Harvest time	May 23, 2017	May 23, 2017	May 15, 2017	May 12, 2018
Number of plots or subplots per trial	25	30	20	80
Plot area (m <sup>2</sup> )	40	25	24	16
Fertilizer rate (kg ha <sup>-1</sup> )	240 N, 69.8 P, 265 K, 24.1 Mg, 49 S	240 N, 69.8 P, 265 K, 24.1 Mg, 49 S	200 N, 87.2 P, 166 K, 12.1 Mg, 24 S	240 N, 70.6 P, 199.2 K, 12.1 Mg, 24 S

of the P dose, 1/10 of the K dose, and full doses of Mg and S were incorporated; during hilling (45 days after planting), 1/3 of the N dose, 1/3 of the P dose, and 4.5/10 of the K dose were applied; and at 75 days after planting, the final 1/3 of the N dose and 4.5/10 of the K dose were applied. Ammonium nitrate, diammonium phosphate, potassium chloride, and Sulpomag were the fertilizers used.

Applications of 0.5 L ha<sup>-1</sup> of Afungil® (250 g L<sup>-1</sup> Difenoconazole) and 0.4 L ha<sup>-1</sup> of Orondis Ultra® (250 g L<sup>-1</sup> Mandipropamid + 30 g L<sup>-1</sup> Oxathiapiprolin) were used to manage early and late blight, respectively. To control the Andean weevil, 0.5 L ha<sup>-1</sup> of Regent SC® (Fipronil 200 g L<sup>-1</sup>) was applied. The trials were conducted under rainfed conditions, and all field operations were performed manually.

## 2.2 Characteristics of Soils

Composite samples (20 subsamples) were collected from the soil of each plot for chemical analysis. The analyses followed the methodologies endorsed by the Ministry of Agriculture and Irrigation (MINAGRI) of Peru (Bazán 2017). pH and electrical conductivity were measured in a 1:1 soil-to-water suspension. Texture was assessed using the Bouyoucos method, and organic matter content using the Walkley and Black procedure. Available phosphorus was quantified by the Olsen method, and available potassium through ammonium acetate extraction followed by atomic absorption spectrophotometry. Soil cation exchange capacity was determined via the Kjeldahl distillation approach, and exchangeable cations by atomic absorption spectrophotometry. Available zinc content in the soil was measured using a solution of 0.25 N NaHCO<sub>3</sub>–0.01 M EDTA–0.01 N NH<sub>4</sub>F (ASI method, Agro Service International Inc.) and ranged between 2.30 and 7.40 mg kg<sup>-1</sup>, values that exceed the critical threshold (Zn > 1.5 mg kg<sup>-1</sup>) (Benton Jones Jr 2001). The soil analysis results are summarized in Table 2.

## 2.3 Treatments and Experimental Design

### 2.3.1 2016–2017 Season

During the 2016–2017 season, an experiment was carried out using a randomized complete block factorial design with two factors: the Zn dose applied to the soil (five levels: 0, 4, 8, 16, and 32 kg Zn ha<sup>-1</sup>) and location (three sites: Achoscuyo, Huisahuanca, and Lucma). The trial included 6, 5, and 4 replications at Achoscuyo, Huisahuanca, and Lucma, respectively. The potato variety used was Yungay, planted at a density of 0.8 m between rows and 0.4 m between plants.

**Table 2** Soil physicochemical properties at the four field trial sites

Site	Achoscuyo	Huisahuanca	Lucma	Llacta
Soil properties				
Sand (%)	42	24	41	39
Lime (%)	40	44	29	29
Clay (%)	18	32	30	32
Soil texture class	Loam	Clay loam	Clay loam	Clay loam
pH (H <sub>2</sub> O)	4.38	6.16	5.86	4.55
Electrical conductivity (dS m <sup>-1</sup> )	0.16	0.32	0.15	0.16
Organic matter (%)	2.97	4.14	3.45	0.95
P-Olsen (mg kg <sup>-1</sup> )	21.8	11.1	4.9	10.5
K-ammonium acetate (mg kg <sup>-1</sup> )	103	96	245	236
Cation exchange capacity (cmol <sub>c</sub> kg <sup>-1</sup> )	11.20	17.60	12.80	12.80
Ca <sup>2+</sup> exchangeable (cmol <sub>c</sub> kg <sup>-1</sup> )	1.82	12.60	3.41	1.18
Mg <sup>2+</sup> exchangeable (cmol <sub>c</sub> kg <sup>-1</sup> )	0.45	1.58	2.20	0.78
K <sup>+</sup> exchangeable (cmol <sub>c</sub> kg <sup>-1</sup> )	0.18	0.21	0.56	0.55
Na <sup>+</sup> exchangeable (cmol <sub>c</sub> kg <sup>-1</sup> )	0.09	0.10	0.14	0.11
Al+H–exchangeable (cmol <sub>c</sub> kg <sup>-1</sup> )	1.60	0.00	0.10	0.85
Non-acid cations saturation (%)	61.35	100	98.44	77.51
Available zinc (mg kg <sup>-1</sup> )	3.90	7.40	4.10	2.30

### 2.3.2 2017–2018 Season

In the 2017–2018 season, an experimental field was established to assess the application of different Zn doses across four commercial potato varieties. The experiment employed a split-plot design with two factors (potato variety and zinc dose), randomly distributed across four blocks. Three modern potato varieties (Canchán, Perricholi, and Yungay) and one native variety (Peruanita), all widely cultivated in Peru, were allocated to the main plots and planted at a density of 0.8 m between rows and 0.4 m between plants. Five Zn doses (0, 4, 8, 16, and 32 kg Zn ha<sup>-1</sup>) were assigned to the subplots. Zinc sulfate (ZnSO<sub>4</sub>·7 H<sub>2</sub>O) served as the zinc source in all trials and was applied at planting with the base fertilization, positioned at the bottom of the furrow.

## 2.4 Shoot and Tuber Yield

### 2.4.1 2016–2017 Season

In this season, only tuber yield (kg ha<sup>-1</sup>) was initially evaluated. It was measured at harvest by weighing the tubers from the two central rows of each experimental unit. A sample of

approximately 2 kg of tubers was collected for Zn content determination.

#### 2.4.2 2017–2018 Season

During this same period, both shoot biomass and tuber yield were assessed. Shoot biomass was estimated by randomly extracting two plants per experimental unit, 27 days before harvest (the onset of senescence), by cutting the aerial portion (stems and leaves) at the plant collar. The samples (leaves and stems combined) were rinsed with distilled water to remove surface particles and oven-dried at 65 °C for 24 h, then weighed to determine shoot biomass yield.

Tuber yield was measured at harvest using the same procedure applied in the 2016–2017 season. The dried biomass samples of shoots and tubers were subsequently used for analysis of Zn content.

#### 2.5 Determination of Zn Content and Accumulation

Foliage and tuber samples were oven-dried at 65 °C for 24 h (Kalra 1998) to determine dry matter percentage. In the 2016–2017 experiment, tubers were dried with their peels intact, whereas in the 2017–2018 experiment, the tuber peels and pulp were dried separately. After drying, all samples were finely ground using an electric grinder. Sub-samples of 1.0 g from each ground material were digested with a 5:1 mixture of nitric and perchloric acids (Zasoski and Burau 1977). Zn concentrations were then quantified by atomic absorption spectrophotometry using a ContrAA 300<sup>®</sup> Analytik Jena spectrophotometer.

Zn accumulation was calculated based on the dry weight of shoots and tubers, using the Zn content determined for the respective plant tissues. Shoot biomass values, tuber yield, and dry matter percentage were subsequently employed to compute Zn accumulation in shoots and tubers. The following formula was used:

$$Zn\ acum. = Zn\ cont. \times Fresh\ wt. \times Dry\ matter\ (\%)$$

where *Zn acum.* is zinc accumulation ( $g\ ha^{-1}$ ), *Zn cont.* is zinc content ( $mg\ kg^{-1}$ ), and *Fresh wt.* is the fresh weight of shoots or tubers ( $Mg\ ha^{-1}$ ).

#### 2.6 Partial Zinc Balance

In the 2017–2018 season, Zn accumulation in shoots and tubers was considered in the partial Zn balance analysis, which was calculated using the formula described by Fixen et al. (2015).

$$PNB\ (\%) = \frac{Zn\ accumulation\ shoot + tuber\ (g\ ha^{-1})}{amount\ of\ Zn\ applied\ (kg\ ha^{-1}) \times 1000} \times 100$$

The partial nutrient balance functions as a simplified indicator of nutrient recovery efficiency, expressed as the ratio between the nutrient removed by the crop and the nutrient supplied through fertilizers.

#### 2.7 Contribution of Biofortified Potato Consumption to Zn Nutritional Requirements

Daily Zn intake from potato consumption in Peru was estimated using the Zn content determined in tubers from the 2016–2017 and 2017–2018 seasons, assuming an average daily intake of 250 g of fresh potato per person (FAO 2023b) and a daily zinc requirement of 11 mg (National Institute of Health 2022). This estimation was derived using the following formula:

$$Daily\ intake\ Zn\ (\%) = \frac{Zn\ tuber\ content\ (mg\ kg^{-1})}{Tuber\ dry\ matter\ (\%)} \times \frac{250}{11 \times 1000}$$

#### 2.8 Statistical Analysis

Results obtained for the variables evaluated across the trials were subjected to analysis of variance (ANOVA) after verifying the assumptions of error normality and variance homogeneity. When ANOVA indicated significant differences, means were compared using Tukey's HSD test at a 0.05 significance level. A principal component analysis (PCA) and a correlation analysis were also conducted for the factors evaluated in the 2017–2018 season. The analyses were performed in the R statistical environment, version 4.2.2 (R Core Team 2023) using the agricolae package for ANOVA and mean comparison, the factoextra package for PCA visualization and interpretation, the corrplot package to generate the correlation matrix plots, and the ggplot2 package for data visualization.

### 3 Results

#### 3.1 Shoot and Tuber Yield

##### 3.1.1 2016–2017 Season

Application of increasing Zn doses did not influence tuber yield at any location (Supplementary Material 1). However, significant yield differences occurred among the locations where the trials were implemented. Tuber yield in Lucma ( $35.41\ Mg\ ha^{-1}$ ) was significantly higher than yields

recorded in Achoscuyo and Huisahuanca (25.78 and 27.17 Mg ha<sup>-1</sup>, respectively).

### 3.1.2 2017–2018 Season

In the 2017–2018 season, tuber yield and shoot dry biomass did not exhibit differences in response to increasing soil-applied Zn (Supplementary Material 2); however, significant variation occurred among varieties for both variables (Table 3), with the Peruanita variety presenting the lowest yield.

## 3.2 Zn Content in Shoots and Tubers

### 3.2.1 2016–2017 Season

Zn application significantly increased Zn content in tubers. In Achoscuyo, clear differences among doses were detected, with the highest content recorded at 16 kg Zn ha<sup>-1</sup>, representing an 86% increase relative to the treatment without Zn (Table 4). At 32 kg Zn ha<sup>-1</sup>, the content declined slightly but remained significantly greater than the control, corresponding to a 60% increase. In Lucma, significant differences among doses were likewise observed, with the maximum content at 16 kg Zn ha<sup>-1</sup>, yielding a 26% increase over the control. In Huisahuanca, no statistical differences emerged, although a positive trend with increasing doses was evident, reaching a 36% increase relative to the control at 32 kg Zn ha<sup>-1</sup>. When locations were compared at the same dose, at 16 kg Zn ha<sup>-1</sup>, Achoscuyo exhibited significantly higher Zn content than Huisahuanca and Lucma. At 32 kg Zn ha<sup>-1</sup>, Huisahuanca showed the highest value, though not significantly different from Achoscuyo.

### 3.2.2 2017–2018 Season

Zinc content in shoots and tubers was positively correlated with the applied Zn dose in all the potato varieties evaluated in this season (Fig. 3). All varieties exhibited the highest Zn content in shoots following application of 32 kg Zn ha<sup>-1</sup> (Fig. 3A–D). In tubers, the Perricholi and Yungay

**Table 3** Dry shoot biomass and tuber yield in the Llaeta 2017–2018 trial

Potato varieties	Shoot dry matter Mg ha <sup>-1</sup>	Fresh tuber yield
Canchan	1.64±0.12 a	18.02±1.06 a
Perricholi	1.40±0.11 ab	15.48±0.60 a
Peruanita	1.51±0.15 ab	12.46±1.04 b
Yungay	1.33±0.09 b	17.89±1.29 a

Values represent means±standard error (*n*=4). Means within a column followed by different lowercase letters differ significantly according to Tukey's HSD test (*p*<0.05)

**Table 4** Zn transport dynamics and estimated contribution to the daily Zn requirement (%) in tubers of the Yungay variety across three field trials in Junín (2016–2017)

Zn dose (kg ha <sup>-1</sup> )	Achoscuyo Zn content	Huisahuanca	Lucma
0	17.67±0.33 Ad	19.0±1.64 Aa	17.25±0.63 Ab
4	22.33±1.09 Acd	21.0±2.08 Aa	20.25±0.75 Aab
8	24.33±1.14 Abc	20.6±1.08 Aa	20.50±0.50 Aab
16	32.83±1.35 Aa	21.2±1.83 Ba	21.75±1.03 Ba
32	28.20±1.69 Aab	25.8±0.86 Aa	20.25±1.25 Bab
	Zn accumulation		
0	86.36±13.93 Ab	100.37±10.04 Aa	100.98±5.23 Ab
4	106.25±9.31 Aab	108.41±8.57 Aa	134.02±5.09 Aa
8	119.22±15.49 Aab	97.01±6.45 Aa	124.70±3.98 Aab
16	150.34±13.19 Aa	121.38±14.63 Aa	128.68±7.45 Aa
32	134.94±6.70 Aab	138.70±14.52 Aa	121.38±7.48 Aab
	Zn contribution		
0	7.56±0.13 Ad	8.32±0.81 Ab	6.83±0.26 Aa
4	9.50±0.33 Ac	9.24±0.87 Ab	7.86±0.28 Aa
8	10.20±0.56 Ab	8.97±0.46 ABb	8.16±0.24 Ba
16	13.5±0.57 Aa	9.58±0.63 Bab	8.49±0.14 Ba
32	11.8±0.71 Aa	11.60±0.76 Aa	7.80±0.57 Ba

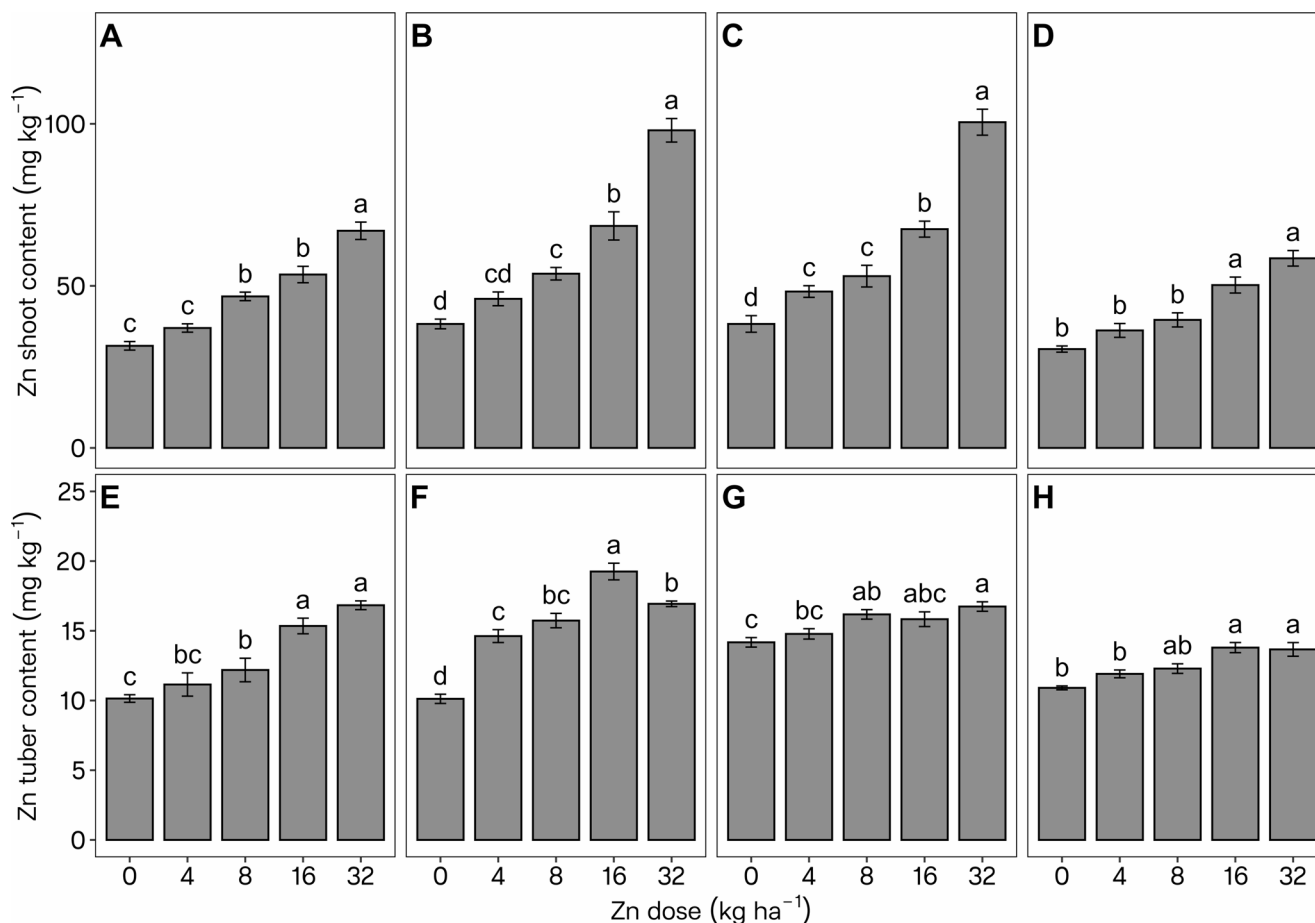
Values represent means±standard error. Different uppercase letters within rows (locations) and lowercase letters within columns (Zn doses) indicate significant differences according to Tukey's HSD post hoc test (*p*<0.05)

varieties attained their highest Zn content with the application of 16 kg Zn ha<sup>-1</sup>, exceeding the control by 90% and 27%, respectively (Fig. 3F and H). In contrast, the Canchán and Peruanita varieties reached their maximum Zn concentrations at 32 kg Zn ha<sup>-1</sup>, corresponding to increases of approximately 65% and 18% compared with the control, respectively (Fig. 3E and G).

## 3.3 Zn Accumulation in Shoots and Tubers

### 3.3.1 2016–2017 Season

Zn accumulation in tubers at Achoscuyo and Lucma increased significantly with higher Zn application rates (Table 4). In Achoscuyo, the 16 kg Zn ha<sup>-1</sup> dose produced a 74% increase in Zn accumulation relative to the control, although higher doses did not result in additional gains. In Lucma, the highest Zn accumulation occurred at 4 kg Zn ha<sup>-1</sup>, representing a 33% increase over the control; beyond this dose, no further significant differences were identified. In Huisahuanca, Zn application did not generate significant differences in Zn accumulation in tubers, though a trend toward greater accumulation with increasing doses was evident. Zn accumulation did not differ significantly among locations at the same dose. At lower doses, Huisahuanca and Lucma exhibited higher values than Achoscuyo, whereas at intermediate doses, Lucma showed the highest



**Fig. 3** Zinc content (dry weight basis) in shoots (A–D) and tubers (E–H) of four potato varieties during the 2017–2018 trial. Subfigures A and E correspond to Canchan, B and F to Perricholi, C and G to Peruanita, and D and H to Yungay. Data represent means  $\pm$  standard

error ( $n=4$ ). Bars with different lowercase letters denote significant differences among treatments (Zn doses) according to Tukey's HSD post hoc test ( $p < 0.05$ )

accumulation. At higher doses, differences among locations were less pronounced.

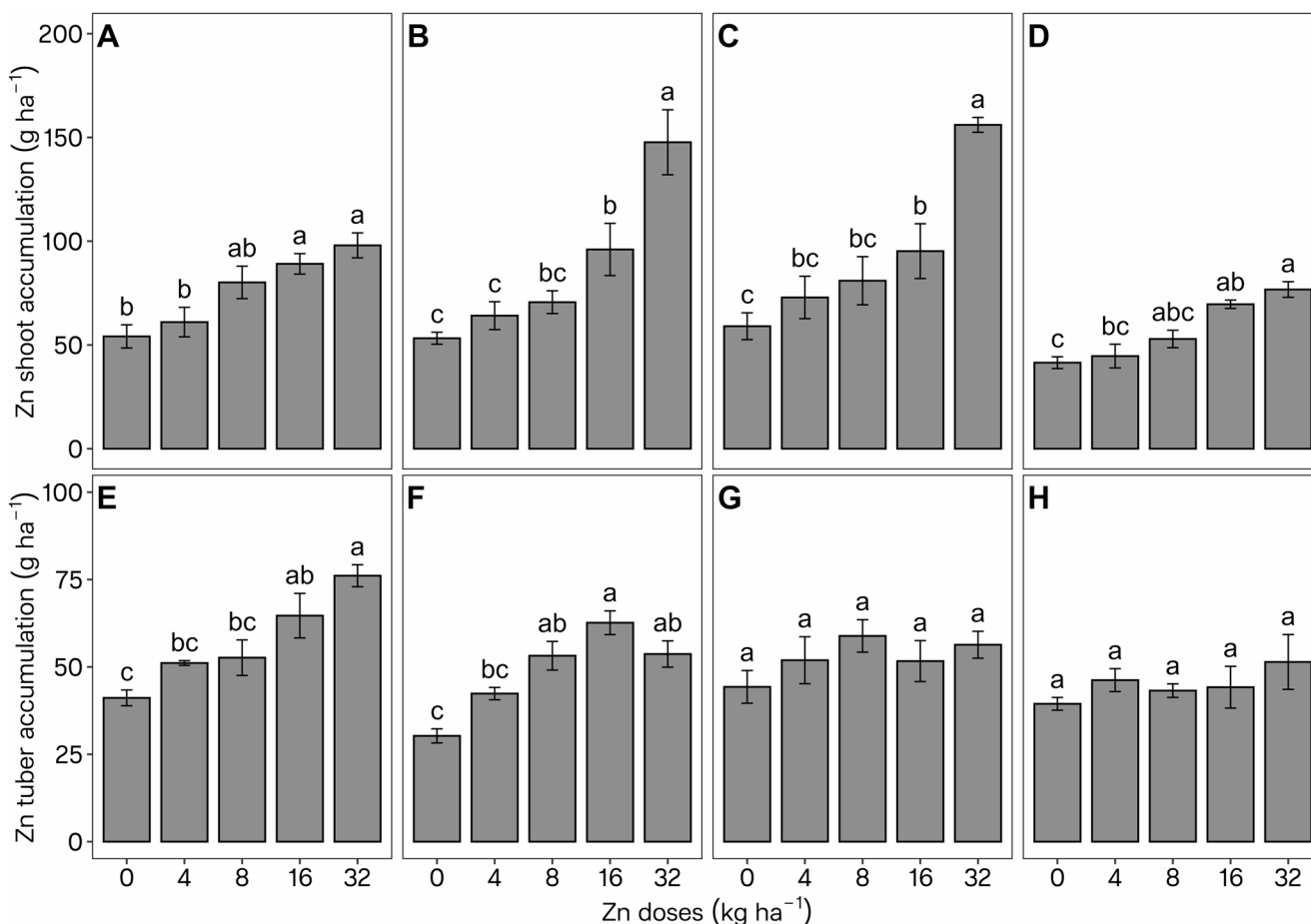
### 3.3.2 2017–2018 Season

Zn accumulation in shoots and tubers varied among the four potato varieties depending on the amount of Zn applied (Fig. 4). In all varieties, Zn accumulation in shoots increased in direct relation to the applied Zn dose. In the Canchán and Yungay varieties, the 8 kg Zn ha<sup>-1</sup> dose generated increases of 48.1% and 27.6% relative to the control, respectively (Fig. 4A and D); however, higher doses did not produce additional significant increases in shoot accumulation. Likewise, in the Perricholi and Peruanita varieties, application of 32 kg Zn ha<sup>-1</sup> resulted in substantial increases of 177.4% and 164.3%, respectively, compared with the control (Fig. 4B and C). In tubers of the Canchán and Perricholi varieties, Zn applications above 16 and 8 kg ha<sup>-1</sup>, respectively, did not yield significantly greater Zn accumulation (Fig. 4E and F). These doses produced increases of

57.2% and 75.7% compared with their controls and resulted in shoot-to-tuber accumulation ratios of 1.40 and 1.34 for Canchán and Perricholi, respectively (Supplementary Material 3). The Peruanita and Yungay varieties exhibited increases of up to approximately 30% in tuber Zn accumulation relative to their controls, with doses of 8 and 32 kg Zn ha<sup>-1</sup>, respectively (Fig. 4G and H). Shoot: tuber accumulation ratios ranged from 1.41 to 2.81 for Peruanita and from 1.07 to 1.61 for Yungay.

### 3.4 Zn Content in Potato Tuber Peel and Flesh

The tuber peel exhibited higher Zn content than the pulp in all varieties. The applied Zn doses significantly increased Zn content in the tuber peel across all four potato varieties (Fig. 5A–D). In the Canchan and Yungay varieties, the highest Zn content in the peel occurred with the 32 kg Zn ha<sup>-1</sup> application, representing increases of 106% and 59% relative to the control, respectively (Fig. 5A and D). In contrast, in the Perricholi and Peruanita varieties, the 16 kg Zn ha<sup>-1</sup>



**Fig. 4** Zinc accumulation in shoots (A–D) and tubers (E–H) in response to Zn application in four potato varieties during the 2017–2018 trial. Subfigures A and E correspond to Canchan, B and F to Pericholi, C and G to Peruanita, and D and H to Yungay. Data represent

means  $\pm$  standard error ( $n=4$ ). Bars with different lowercase letters denote significant differences among treatments (Zn doses) according to Tukey's HSD post hoc test ( $p < 0.05$ )

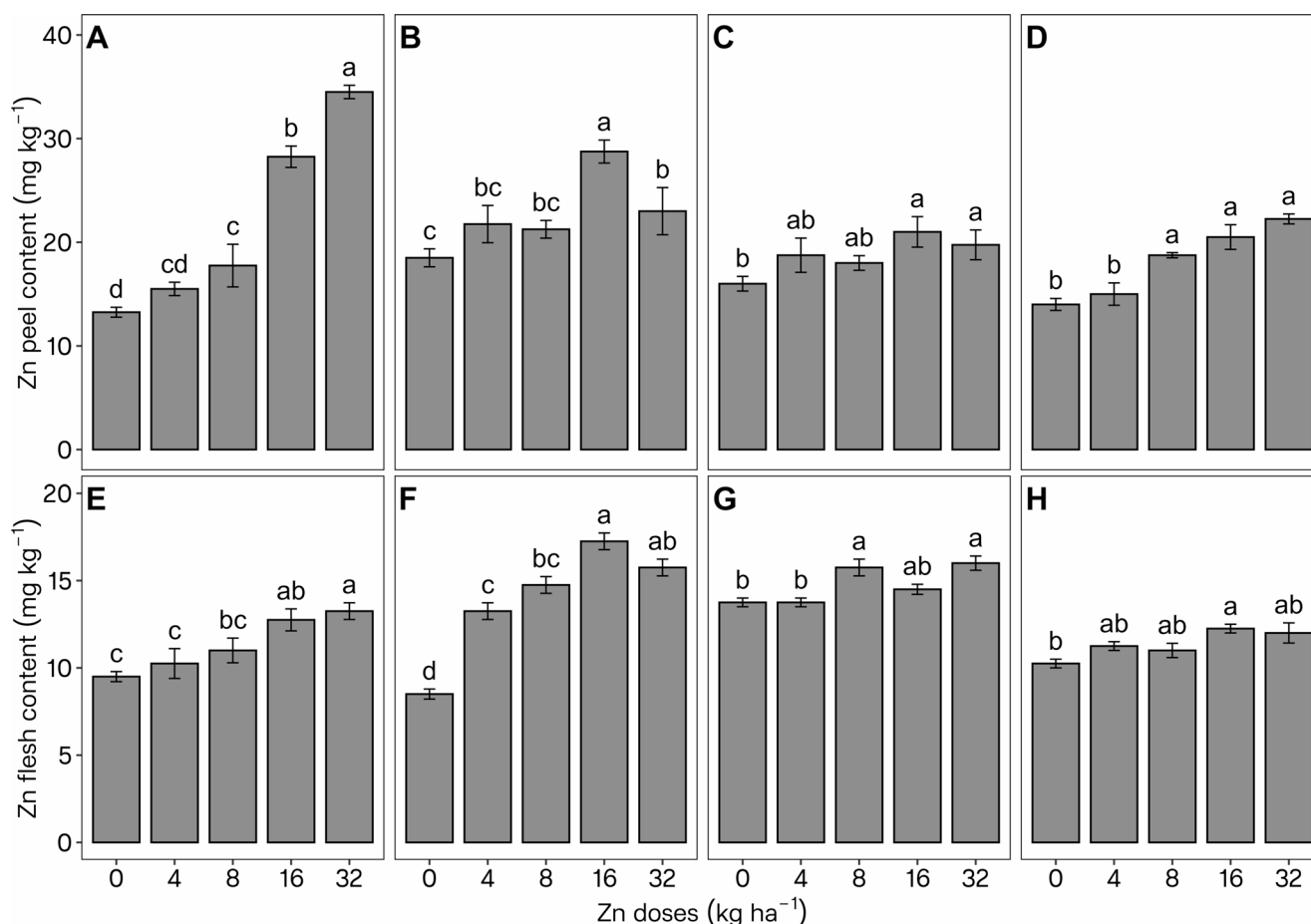
dose led to increases of 55% and 31%, respectively (Fig. 5B and C). In the tuber flesh, the 32 kg Zn ha<sup>-1</sup> dose yielded the highest Zn content in the Canchan and Peruanita varieties, corresponding to increases of 39.5% and 16.4% compared with their controls, respectively (Fig. 5E and G). For the Pericholi and Yungay varieties, Zn doses above 16 kg ha<sup>-1</sup> did not significantly enhance Zn content in the flesh (Fig. 5F and H). Nonetheless, this dose still produced increases of 103% and 20% relative to their respective controls.

### 3.5 Contribution of Biofortified Tubers to Daily Zn Requirement

#### 3.5.1 2016–2017 Season

The contribution of Zn to the estimated daily intake requirement exhibited a differential response depending on the applied dose at each location (Table 4). In Achosucyo, increasing Zn application significantly enhanced estimated

intake, reaching its maximum at the 16 kg Zn ha<sup>-1</sup> dose, corresponding to a 79% increase relative to the control. Higher doses did not yield further significant gains. In Huisahuanca, the estimated Zn intake showed a moderate response to fertilization; only the 32 kg Zn ha<sup>-1</sup> dose produced a significant increase over lower doses, equivalent to a 39% rise relative to the control, while the remaining doses did not differ statistically and demonstrated a less consistent upward trend. In Lucma, the response to fertilization was limited: although the control displayed the lowest value, the other doses produced only modest increases, with a maximum of 24% at 16 kg Zn ha<sup>-1</sup> and no consistent significant differences among treatments. When locations were compared at the same dose, significant differences were detected at intermediate and high rates. Achosucyo recorded the highest values beginning at 8 kg Zn ha<sup>-1</sup>, significantly exceeding Huisahuanca and Lucma at the 16 kg Zn ha<sup>-1</sup> dose. At the lowest doses (0 and 4 kg Zn ha<sup>-1</sup>), differences among locations were less evident.



**Fig. 5** Zinc content (dry weight basis) in the peel (A–D) and flesh (E–H) of tubers from four potato varieties during the 2017–2018 trial. Sub-figures A and E correspond to Canchan, B and F to Perricholi, C and G to Peruanita, and D and H to Yungay. Data represent means  $\pm$  standard

error ( $n=4$ ). Bars with different lowercase letters denote significant differences among treatments (Zn doses) according to Tukey's HSD post hoc test ( $p < 0.05$ )

### 3.5.2 2017–2018 Season

The estimated contribution of Zn to the daily diet varied significantly with the applied Zn dose in three of the four evaluated varieties (Table 5). In Canchan, the uptake increased progressively with higher Zn doses, with significant differences among most treatments; the highest value occurred at 32 kg Zn ha<sup>-1</sup>, representing a 63% increase relative to the control. In the Perricholi and Peruanita varieties, doses above 8 kg Zn ha<sup>-1</sup> did not generate significant increases in Zn intake. In contrast, the Yungay variety exhibited no significant differences among Zn doses.

### 3.6 Partial Zn Balance

The partial Zn balance decreased significantly with increasing Zn doses across all evaluated potato varieties (Table 6). In the Canchán, Perricholi, and Yungay varieties, a progressive decline in efficiency was observed as the Zn dose increased

from 4 to 8, 16, and 32 kg ha<sup>-1</sup>, with relative reductions of 41%, 66%, and 81% in Canchán; 42%, 63%, and 76% in Perricholi; and 47%, 69%, and 82% in Yungay, respectively.

In the Peruanita variety, a decline in efficiency with higher doses, was likewise evident, with relative decreases of 44% and 71% for 8 and 16 kg Zn ha<sup>-1</sup>; however, between

**Table 5** Estimated contribution to the daily zinc (Zn) requirement (%) from consumption of fresh potato in four varieties under different Zn fertilization rates (2017–2018 growing season)

Zn dose (kg ha <sup>-1</sup> )	Canchan	Perricholi	Peruanita	Yungay
0	5.66 $\pm$ 0.10 b	4.66 $\pm$ 0.31 c	8.84 $\pm$ 0.36 b	5.04 $\pm$ 0.20 a
4	6.00 $\pm$ 0.32 b	6.57 $\pm$ 0.23 b	8.79 $\pm$ 0.45 b	5.42 $\pm$ 0.12 a
8	6.66 $\pm$ 0.51 b	7.35 $\pm$ 0.29 ab	10.00 $\pm$ 0.24 a	5.60 $\pm$ 0.17 a
16	8.42 $\pm$ 0.36 a	8.67 $\pm$ 0.56 a	9.82 $\pm$ 0.31 a	6.19 $\pm$ 0.26 a
32	9.26 $\pm$ 0.18 a	8.06 $\pm$ 0.24 a	10.03 $\pm$ 0.26 a	6.19 $\pm$ 0.25 a

Values represent means  $\pm$  standard error ( $n=4$ ). Different lowercase letters indicate significant differences among treatments (Zn doses) according to Tukey's HSD post hoc test ( $p < 0.05$ )

**Table 6** Partial Zn balance (%) for four potato varieties during the 2017–2018 trial

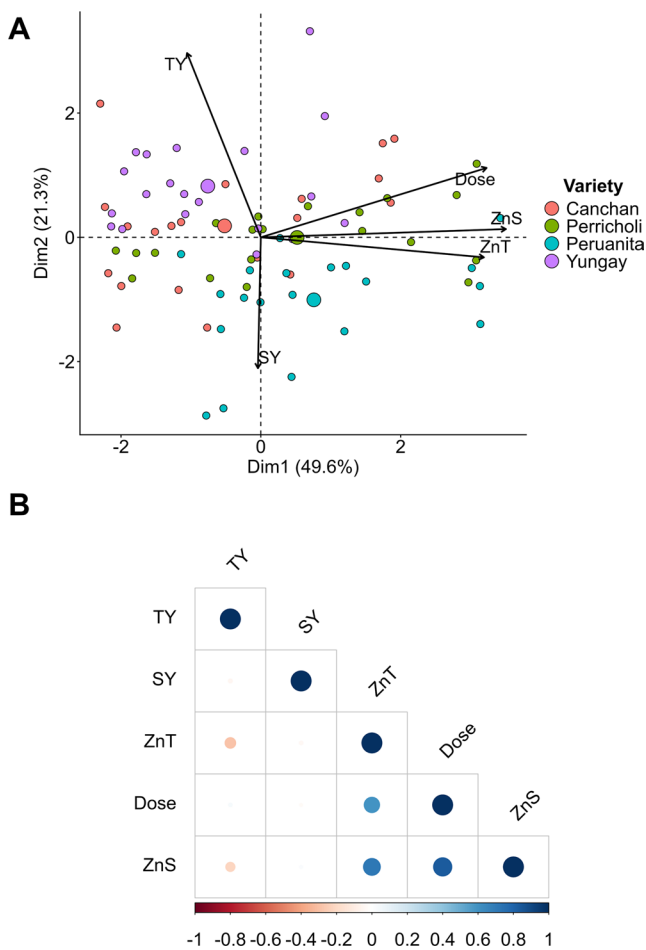
Zn dose (kg ha <sup>-1</sup> )	Canchan	Perricholi	Peruanita	Yungay
4	2.80±0.18 a	2.66±0.20 a	3.12±0.42 a	2.27±0.21 a
8	1.66±0.03 b	1.54±0.10 b	1.75±0.14 b	1.20±0.07 b
16	0.96±0.07 c	0.99±0.07 c	0.92±0.11 c	0.71±0.05 c
32	0.54±0.02 d	0.63±0.05 d	0.67±0.10 c	0.40±0.02 d

Values represent means±standard error. Different lowercase letters indicate significant differences among treatments (Zn doses) according to Tukey's HSD post hoc test ( $p < 0.05$ )

16 and 32 kg Zn ha<sup>-1</sup> (79%), no significant differences were detected.

### 3.7 Interaction of Agronomic Factors

When varieties were compared, Peruanita exhibited the highest average efficiency in Zn utilization, followed by Canchan, Perricholi, and Yungay. Principal component analysis



**Fig. 6** Principal component analysis (**A**) and correlation matrix (**B**) for agronomic variables of potato in the 2017–2018 season. Variables include tuber yield (TY), shoot yield (SY), Zn content in shoots (ZnS), Zn content in tubers (ZnT), and Zn fertilization dose (Dose)

showed that the first two components explained 71% of the variation (Fig. 6A; Dim1=49.6%, Dim2=21.3%). PC1 represents a gradient in which Zn dose and zinc indicators (ZnS and ZnT) increase simultaneously, positioning treatments are from low dose/low Zn to high dose/high Zn. PC2 is primarily associated with tuber yield (TY) and is oriented nearly orthogonally—and somewhat inversely—to the Zn variables and dose, indicating that yield tends to decline as Zn content and applied dose increase. Shoot yield (SY) contributes minimally to these axes, appearing near the origin with a slight trend opposite to PC2. The dispersion by variety shows overlap in the first two dimensions, suggesting that the observed differences are driven mainly by changes in Zn dose and its influence on Zn levels, rather than by strong varietal contrasts.

The correlation matrix (Fig. 6B) reinforces these patterns. No notable correlation appears between TY and SY (value near zero). Zinc indicators are positively correlated with each other (particularly ZnS–ZnT) and are positively associated with Zn dose. In contrast, TY shows moderate to strong negative correlations with ZnT and ZnS and a weak association with dose. SY exhibits weak correlations with the other variables, without consistent trends. Overall, the findings demonstrate that increasing the Zn dose elevates Zn levels in shoots and tubers, while tuber yield is negatively affected under higher Zn concentrations.

## 4 Discussion

Local soil conditions largely determined the crop's response to Zn fertilization. In the experimental fields evaluated, soil Zn content was not limiting for shoot biomass production or tuber yield (Supplementary Materials 1 and 2), a result attributable to the acidic pH ranges (Table 3). These findings partially support the study's first hypothesis, as Zn fertilization did not negatively affect crop yield. Under acidic pH conditions, Zn availability typically increases due to reduced adsorption on soil minerals and greater solubilization; however, its uptake by the crop depends on the accessible fraction (Recena et al. 2021; Yu et al. 2023). Although in our results organic matter did not appear to exert a decisive effect on yield, previous studies indicate that it can influence Zn availability: in acidic soils, it retains the micronutrient in humic fractions (Drozdova et al. 2014), whereas low organic matter favors Zn fixation to clays (Chen et al. 2017). In this study, soils ranged from extremely acidic to slightly acidic, exhibited adequate levels of available Zn, and contained moderate to low organic matter—conditions that did not impose yield limitations. In contrast to our findings, Banerjee et al. (2017) and Sati et al. (2018) reported increases in shoot biomass with soil applications of 4.5 and

25 kg Zn ha<sup>-1</sup>, respectively, in soils with near-neutral pH. Regarding tuber yield, our results are consistent with those of Mao et al. (2014) and Alemu et al. (2024), who likewise found no significant yield response to Zn application in moderately alkaline or slightly acidic soils. Conversely, studies conducted in neutral soils have reported yield increases with Zn applications ranging from 4.5 to 25 kg ha<sup>-1</sup> (Banerjee et al. 2016; Dhar et al. 2024; Khan et al. 2019; Nagar et al. 2024). These contrasting findings underscore the importance of contextualizing Zn fertilization practices according to soil conditions and reinforce the relevance of our results in acidic soils—an environment still underrepresented in the current literature.

In addition to edaphic conditions, tuber yield reflected the influence of genetic and environmental factors, which became even more decisive in the absence of Zn limitations. In our study, significant differences were observed among varieties (2017–2018 season, Table 3) and among production zones (2016–2017 season, Supplementary Material 1), consistent with results reported by Kromann et al. (2017), Ramírez Maldonado et al. (2017), Islam et al. (2020), and Tessema et al. (2020). Despite lower N and K applications at the Lucma site, yields were higher there, likely due to more favorable climatic conditions, including higher mean temperatures and greater annual accumulated precipitation (Fig. 2). Overall, these findings indicate that yield variation was primarily driven by the interaction between genotype and environment, reinforcing that in acidic soils with adequate Zn availability, this micronutrient was not a limiting factor. This highlights the need for differentiated management strategies based on the edaphoclimatic context, rather than uniform micronutrient application. These results also support the study's second hypothesis, as the potato variety influenced the response to Zn fertilization.

During the 2017–2018 season, an increase in Zn content and accumulation in shoots was observed as applied doses increased (Figs. 3A–D and 4A–D). Although shoot biomass was lower than that of tubers, total Zn accumulation in shoots was higher, consistent with findings by Banerjee et al. (2016) and Kromann et al. (2017). In our study, Zn content in shoots remained below the toxicity threshold described by Noulas et al. (2018), established at 300 mg Zn kg<sup>-1</sup>. This pattern reflects the interaction of edaphic conditions, transport dynamics, and the physiological functions of Zn in aerial tissues. In acidic soils such as those evaluated here, low pH enhances Zn solubility and availability in the rhizosphere, thereby promoting root uptake (Barreto et al. 2024). Once absorbed, Zn is transported to aerial tissues mainly through the xylem, propelled by transpiration flow (Etienne et al. 2018), which is intensified by the high transpiration rates of leaves and stems and results in a sustained upward movement from root to shoot (Gupta et al.

2016; Reid et al. 2003). In these tissues, Zn performs essential physiological roles: it stabilizes photosystem II, protects cell membranes against oxidative damage through superoxide dismutase, and contributes to indoleacetic acid synthesis, thereby regulating plant growth (Hamzah Saleem et al. 2022; Natasha et al. 2022). Stems in particular, function as important storage sites, as Zn accumulates in cell walls and intercellular spaces, serving as a reservoir and a strategic point for redistribution via the phloem (Mengist et al. 2021). Although the tuber is the agronomically valuable organ in a potato, stems possess mineral contents comparable to forage crops, making them a complementary resource for animal feed and circular economy systems (Kaplan et al. 2018).

Soil Zn fertilization had a positive effect on both the content and accumulation of this micronutrient in tubers (Table 5; Figs. 3E–H and 4E–H), consistent with studies reporting similar improvements following Zn soil application (Banerjee et al. 2017; Hadi et al. 2015; Kromann et al. 2017). However, the response was not uniform across sites; for example, in Huisahuanca (2016–2017), no significant increases were detected. This aligns with findings by Mao et al. (2014), who observed limited effects in loam-textured soils with moderately alkaline pH. These results support the study's first and second hypotheses, demonstrating that soil-applied Zn can enhance Zn content and accumulation in tubers. The observed variability suggests that, beyond the applied dose, soil characteristics and agronomic management exert decisive influences on the effectiveness of Zn biofortification.

On top of soil properties, our findings also highlight the importance of interactions between Zn and other macronutrients. As described by Almendros et al. (2022), Zn uptake and mobility are influenced by nutrients such as magnesium (Mg) and sulfur (S), which exhibit synergistic relationships with Zn in the root system. In our study, locations such as Achoscuyo—with higher Mg and S fertilization (Table 1)—displayed a stronger Zn-accumulation response, whereas Lucma, with lower levels of these nutrients, exhibited a more limited effect (Table 5). Although antagonism between Zn and potassium (K) has been reported, this interaction was not evident in sites with elevated K fertilization, likely due to the overall nutritional balance. Furthermore, nitrogen (N) application can enhance Zn uptake and translocation by stimulating the synthesis of amino acids that act as ligands, facilitating Zn transport to storage organs. Montoya et al. (2020) reported this effect in wheat, attributing greater Zn accumulation to increased flow of transport compounds. In our trials, both Achoscuyo and Huisahuanca received the same N rate, yet only Achoscuyo exhibited a significant Zn response, suggesting that the positive N–Zn interaction depends on the broader nutrient balance. Collectively, these findings reinforce that agronomic Zn biofortification should

be evaluated within an integrated plant nutrition framework rather than in isolation.

In addition to soil conditions and mineral nutrition, genetic factors also appear to contribute to the differential Zn accumulation observed among varieties. In our trials, clear differences in Zn accumulation were detected among genotypes (Fig. 4), likely associated with traits that influence micronutrient translocation to storage organs (Leonel et al. 2017; Mengist et al. 2021). This finding supports our second hypothesis, showing that the response to Zn fertilization is modulated by genotype. It further suggests that genetic background influences not only yield but also the crop's nutritional profile, creating opportunities to select materials with superior micronutrient accumulation capacity. Taken together, these results indicate that both the edaphoclimatic environment and genotype exert significant effects on Zn accumulation (Amoros et al. 2020; Burgos et al. 2007; Kromann et al. 2017). Integrated strategies that combine fertilization management with varietal selection may therefore improve the nutritional value of potatoes within agricultural systems.

The highest ratios between Zn content in shoots and tubers were registered at the greatest applied Zn doses (Fig. 3, Supplementary Material 3). In potatoes, the tuber functions as a storage organ to which essential minerals such as Zn should be mobilized from vegetative tissues (Golovko and Tabalenkova 2019). However, in our study, most of the absorbed Zn accumulated in shoots (leaves and stems), with limited redistribution to tubers, as reflected by the absence of significant increases in shoot biomass or yield. This retention may be explained by Zn compartmentalization in vacuoles or cell walls, particularly within vascular tissues, where it becomes stabilized in the phloem under high-availability conditions, thereby restricting redistribution (Samardjieva et al. 2015). In contrast, greater remobilization from vegetative organs to tubers has been documented in Zn-deficient soils, whereas under sufficient conditions, the root-xylem-phloem flow predominates as the main transport pathway (Impa et al. 2013; Mengist et al. 2021). This low remobilization efficiency has also been noted by Kromann et al. (2017), who reported that shoots contained 7 to 11 times more Zn than peeled tubers following soil applications. Similarly, White et al. (2012) attributed the low Zn concentration in tubers to restricted Zn mobility in the phloem, even under foliar fertilization. Collectively, these earlier findings align with our results, demonstrating that potato exhibits limited capacity to redistribute Zn to the tubers even when soil Zn availability is adequate, representing a major physiological constraint for biofortification strategies targeting edible organs. These results confirm the hypothesis that soil-applied Zn shows limited efficiency in absorption and redistribution to tubers.

Zn distribution within the tuber was not uniform, with higher concentrations detected in the peel than in the pulp (Fig. 5). This differential accumulation can be partly attributed to the direct absorption of Zn through the living epidermis during early tuber development, before the periderm fully suberizes and forms an effective physical barrier (Subramanian et al. 2011). This mechanism was corroborated by Vergara Carmona et al. (2019), who observed greater Zn accumulation in the periderm and cortex following immersion of tubers in Zn solutions, compared with the central tissue region. Similarly, Kromann et al. (2017) reported that soil applications of up to 40 kg Zn ha<sup>-1</sup> increased Zn concentration more markedly in the peel than in the pulp. Beyond Zn, the peel contains elevated levels of protein, fiber, and other essential minerals (Vaitkevicienė 2019), underscoring its nutritional importance. Together, these findings highlight the need to revalue potato peel not as waste but as a strategic component in biofortification programs, with strong potential to enhance micronutrient intake through whole-tuber consumption.

In the Peruvian context, where potato is a staple food and consumption may reach up to 800 g per person per day in rural areas (Burgos et al. 2019), increasing Zn content in tubers has substantial nutritional implications. Our results show that soil-applied Zn can produce biofortified potatoes capable of supplying up to 12% of the daily Zn requirement for adults (Tables 5 and 6), positioning potatoes as a viable vehicle for micronutrient delivery in agronomic biofortification strategies. These findings support the hypothesis that this practice can meaningfully contribute to meeting human nutritional needs in rural settings, particularly given the low phytate content of tubers (Ravindran et al. 1994)—compounds known to inhibit Zn absorption in other foods but whose low levels in potatoes enhance Zn bioavailability (Raboy 2020). This advantage was recently confirmed by Liria-Domínguez et al. (2023), who reported that yellow-fleshed biofortified potatoes exhibit high Zn concentrations and a large fraction of potentially absorbable Zn, reinforcing their value as an effective nutritional source of this micronutrient. Unlike crops in which phytates restrict Zn absorption, in potatoes, the micronutrient is present in a more accessible form for human assimilation.

The low recovery of applied Zn observed in our study highlights the limited efficiency with which this micronutrient is utilized by potato crops under high Andean conditions (Table 7). This inefficiency may be attributed to the use of ZnSO<sub>4</sub>, a highly soluble source that, when combined with high humidity and frequent rainfall, promotes Zn leaching beyond the root zone. In acidic soils, Zn remains primarily as Zn<sup>2+</sup> ions, which are highly mobile and susceptible to leaching, with losses reported to reach up to 90% under comparable conditions (de Francisco et al. 2024). Additionally, the

presence of clays may enhance Zn fixation and restrict its availability through adsorption processes and interactions with organic matter (Zhang et al. 2017). This pattern of low recovery is consistent with findings by Baghla et al. (2025), who noted that Zn efficiency generally declines as application rates increase, reaching values below 1% in some cases (Kumar et al. 2022). However, part of the unabsorbed Zn may remain in the soil and be taken up by subsequent crops, suggesting that total agronomic efficiency may be underestimated when assessed only in the initial crop. Although our study did not evaluate this residual effect, previous research has demonstrated its relevance. For example, Shrestha et al. (2021) found that applying 2.5 and 5.0 kg Zn ha<sup>-1</sup> to wheat, cauliflower, or tomato significantly increased yield and Zn concentration in a subsequent maize crop without additional fertilization. Similar outcomes have been reported in maize–wheat rotations, where continuous or alternating applications of 5–7.5 kg Zn ha<sup>-1</sup> maintained high yields (Butail et al. 2022). In the Peruvian Andes, where potatoes are often included in rotations with cereals, legumes, or pastures (Arce et al. 2019), this residual effect could have important agronomic implications. Studies using isotopically labeled fertilizers have shown that successive crops may recover more Zn than the original crop (Matiello et al. 2021), reinforcing the need to evaluate the residual availability of Zn in highland acidic soils to develop more sustainable and effective fertilization strategies within biofortification programs.

Our results revealed an inverse relationship between tuber yield and zinc content in both storage and vegetative organs, posing a significant challenge for agronomic biofortification under climate change conditions (Fig. 6). This pattern may be partially explained by the mineral dilution effect, widely documented in horticultural crops, wherein increased yield—driven by elevated photosynthetic rates under higher atmospheric CO<sub>2</sub>—leads to a disproportionate accumulation of carbohydrates relative to absorbed micronutrients (Mayer et al. 2022; White and Broadley 2005). Compounding this effect are rising temperatures, which not only reduce the efficiency of storage organ filling but may also induce excessive vegetative growth, as recently reported for potato (Zhang et al. 2024). This interpretation is consistent with our findings, which showed a negative correlation between shoot biomass and yield. Such a relationship suggests that greater vegetative growth may impair the efficiency of nutrient allocation to storage organs, ultimately affecting productivity and nutritional quality. In addition, the increasing incidence of flash droughts has been shown to exacerbate vegetation loss and delay recovery (Chai et al. 2025), potentially disrupting nutrient uptake and further limiting the success of biofortification strategies. These insights present an agronomic dilemma: how to achieve high yields without compromising micronutrient density

in edible organs. In the context of climate change—where elevated CO<sub>2</sub> and higher temperatures alter crop physiology and nutrient composition—it will be essential to develop strategies that optimize both productivity and nutritional value. Recent evidence further shows that the increasing frequency of flash droughts leads to abrupt vegetation loss and delayed recovery (Chai et al. 2025), adding to the uncertainty surrounding the resilience of biofortification strategies in future climate scenarios.

Agronomic biofortification through soil Zn applications requires a gradual and targeted approach, as its effectiveness depends on micronutrient bioavailability along the entire pathway from soil to human consumption (de Valença et al. 2017). To enhance its impact, this strategy should be complemented with genetic biofortification (Zhao and Shewry 2011), particularly where nutrient availability limits Zn accumulation in edible plant tissues (White and Broadley 2009). In this regard, the use of biofortified potato clones or genotypes with greater intrinsic Zn accumulation capacity—developed through conventional breeding or biotechnological approaches—represents a viable option. Previous studies indicate that genetically improved potato clones can contribute to improved nutrition in populations with restricted access to micronutrient-rich foods (Burgos et al. 2007; Burlingame et al. 2009; Zevallos et al. 2024).

## 5 Conclusions

This study demonstrates that in the acidic soils of the central highlands of Peru, soil-applied zinc increases the accumulation of the micronutrient in potato plants, although its concentration in the edible pulp remains limited. This finding partially confirms the proposed hypotheses, indicating that zinc fertilization enhances Zn accumulation without affecting yield, while also revealing physiological constraints on micronutrient redistribution. Because most absorbed zinc is retained in nonedible tissues, zinc fertilization should be complemented with genetic improvement strategies that promote more efficient mobilization toward the tubers. In contexts of high food insecurity and climate change, integrating agronomic and genetic biofortification represents an effective and sustainable approach to improve the nutritional quality of Andean crops and help reduce malnutrition in rural communities.

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## Declarations

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**Consent to Participate** Not applicable.

**Consent for Publication** Not applicable.

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