



Impact of fruit development, methyl jasmonate treatment, and soil physicochemical factors on targeted functional metabolites in *Physalis peruviana* L.

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Abstract

Physalis peruviana L. is a tropical fruit that is nutritionally valuable due to its rich content of health-promoting compounds, including flavonoids, tocopherols, and carotenoids. This study aimed to examine the variation in the concentration of five functional metabolites: epicatechin, α -tocopherol, δ -tocopherol, γ -tocopherol, and β -carotene, throughout immature and mature fruit developmental stages; and to evaluate the incidence of soil physicochemical factors (SPF), and the exogenous methyl jasmonate (MeJA) application on the accumulation of these metabolites in mature fruits. Targeted metabolite quantification was performed using high-performance liquid chromatography coupled with diode-array and fluorescence detection (HPLC-DAD/FLD). The results showed stage-dependent fluctuations in metabolite levels, with a marked increase in tocopherols and β -carotene during the ripening stage. Spearman's correlation was observed among metabolites and some SPF analyzed in sampling 0, for immature and mature fruits. No statistically significant differences were observed with MeJA treatments, except for α -tocopherol. These findings provide novel insights into the developmental stage, SPF correlations, and elicitor-mediated regulation of bioactive metabolites in *P. peruviana* fruits, supporting their use in functional food development.

Keywords Cape gooseberries · Fruit development · Functional metabolites · Goldenberry · Bioactive compounds · Soil physicochemical variables · Uchuva

Introduction

Physalis peruviana L., commonly known as goldenberry, or uchuva, is a perennial shrub native to the Andean region and a member of the Solanaceae family [1–5]. The fruit is increasingly appreciated worldwide for its unique flavor and rich nutritional and phytochemical profile, including high

levels of carbohydrates, dietary fiber, ascorbic acid, tocopherols, carotenoids (notably β -carotene), and phenolic compounds [6].

During fruit development and ripening, *P. peruviana* undergoes significant biochemical and physiological changes. In unripe stages, lutein predominates, while at full ripeness, β -carotene and its esters become the major carotenoids, constituting up to 55% of total carotenoids, a process that is accompanied by chromoplast structural changes for pigment deposition [3]. Total carotenoid content can decline in overripe fruits due to degradation and breakdown processes [1–5, 7].

Phenolic compounds, including flavonoids such as epicatechin, and tocopherols (i.e., α -, δ -, γ -tocopherol), contribute markedly to the fruit's antioxidant and nutraceutical properties [6, 8–11]. Genotypic variation and harvest timing significantly influence the levels of phenolics, β -carotene, and antioxidant activity, with mature fruits typically

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showing elevated β -carotene and ascorbic acid but reduced total phenolics in some cultivars [1, 6, 12–13].

The application of exogenous elicitors such as methyl jasmonate (MeJA) has emerged as a promising strategy not just for developmental regulation but to enhance bioactive compound accumulation in fruits. MeJA is a lipid-derived plant hormone involved in defense signaling, stress responses, and regulation of metabolism, including secondary metabolite pathways [14]. In various crops such as apple, papaya, raspberry, grape, and strawberry, MeJA treatments have been shown to increase phenolic compounds, carotenoids, flavonoids and antioxidant enzyme activity, and to improve postharvest quality [14–17]. Specifically, in apples, MeJA enhanced β -carotene biosynthesis and flavanol accumulation, while in raspberry and plums, it stimulated PAL activity and phenolic content [15].

Despite the documented benefits of MeJA in enhancing fruit quality in other species, its influence on metabolite composition in *P. peruviana*, especially concerning flavonoids and tocopherol content, remains underexplored. To date, studies on goldenberry have primarily focused on carotenoid changes during ripening and cultivar effects, while little is known about the developmental variation of epicatechin or vitamin E isoforms, or their modulation by elicitor treatments [1–2, 7].

For *P. peruviana*, few studies have independently evaluated specific functional metabolites; most reports focus on compound families, which highlights the need for more targeted approaches. Therefore, this study was designed to (i) evaluate the variation in concentrations of epicatechin, α -, δ -, and γ -tocopherol, and β -carotene across different fruit developmental stages, as well as exploring the relationships between soil physicochemical factors and the concentration of targeted metabolites in *P. peruviana* fruits; and (ii) assess the effect of preharvest foliar spray application of MeJA on the accumulation of these functional metabolites in mature fruits.

Materials and methods

Plant material

Healthy *Physalis peruviana* L. fruits at both immature (unripe green fruit at sampling times) and mature (ripe, ready-to-eat fruits at sampling time) stages were collected. Four samplings (days 0, 14, 34, and 55) were carried out between July 31st and September 25th, 2023 at two commercial plantations (referred to as 1 and 2) located in the municipality of La Unión, department of Antioquia (Colombia), at altitudes of 2366.1 and 2414.5 m.a.s.l. Five samplings (days 0, 14, 36, 65, 93, and 120) were carried out between

November 7th, 2023 and March 7th, 2024 at two commercial plantations (referred to as 3 and 4), again located in the municipality of La Unión, department of Antioquia (Colombia), at altitudes of 2507.8 and 2505.8 m.a.s.l. respectively. It should be noted that the results of the farms were separated into two groups based on the sampling dates. Therefore, the results of farms 1 and 2 were analyzed jointly in one group, and the results of farms 3 and 4 were analyzed jointly in another. The sampling was done with permission obtained under the Marco de Acceso a los Recursos Genéticos y sus Productos Derivados of the Ministerio de Ambiente y Desarrollo Sostenible (Ministry of Environment and Sustainable Development), contract No. 126, May 13th, 2016. Samples were processed and analyzed in the laboratory of the Grupo Diagnóstico y Control de la Contaminación - GDCON (Environmental Pollution Diagnosis and Control Research Group, by its acronym in Spanish) at the Universidad de Antioquia.

Methyl jasmonate treatment

In each farm, twelve plants (three plants per treatment and the other three plants for control, triplicate samples) were randomly selected in different positions along the slope of each field and marked. Only fruits from healthy plants that were free from disease symptoms, pests, or physical damage were collected. The fruits were collected at two defined developmental stages: stage 1: immature green fruits and stage 2: mature, ready to eat fruits. For each developmental stage, at least 5 biological fruits were collected from the plant. After collection, a 20 mL foliar spray of methyl jasmonate (MeJA) treatment was applied at low [0.5 μ L/mL], medium [2.5 μ L/mL], and high [5.0 μ L/mL] concentration to each corresponding plant on days 0, 14, 34, and 55 to samplings 0, 1, 2 and 3, respectively, from farms 1 and 2; and days 0, 14, 36, 65, 93, and 120 to samplings 0, 1, 2, 3, 4 and 5, respectively, from farms 3 and 4. The sampling days were set based on the availability and conditions of the crops visited. Fruits were placed in clean, labeled plastic bags, indicating the fruit developmental stage, triplicate plants, farm, and collection date.

Plant extracts

Fruits were first stored at -80 ± 1 °C, then homogenized using a food processor. Homogenized material was also stored at -80 ± 1 °C until analysis. To obtain extracts, 1 g of sample was weighed in a 15 mL falcon tube, adding 5 mL of a mixture of acetone: ethanol (1:1) with 100 mg/L of butylhydroxytoluene (BHT) to conserve target functional metabolites. After vigorous shaking for 1 min, 0.6 g of magnesium sulfate (MgSO_4) was added. The mixture was shaken again

and centrifuged at 3000 rpm for 5 min at 25 °C. Finally, 1 mL of supernatant was transferred to an amber HPLC vial to inject 20 µL into the HPLC system.

Selection of functional metabolites

In order to choose the compounds analyzed in this study, a review of the literature on the most common bioactive metabolites reported in Hass avocado, goldenberry, and violet passion fruit was conducted for project 2,020,000,100,437, which is funded by the General Royalties System of Colombia. This led to the selection of epicatechin, α -tocopherol, δ -tocopherol, γ -tocopherol, and β -carotene for investigation in *P. peruviana* fruits.

Chemical reagents

(-)-Epicatechin, β -carotene, α -tocopherol, δ -tocopherol, (+)- γ -tocopherol, and methyl jasmonate were purchased from Sigma-Aldrich (St. Louis, MO, USA). Acetonitrile, ethyl acetate, and methanol (HPLC grade purity), acetone and ethanol (analytical grade), BHT (commercial grade), and formic acid (for analysis, ACS) were acquired from ITW Reagents Panreac. Water was prepared using a Milli-Q reagent water system.

Standard preparation

A standard solution of epicatechin was prepared in ethanol at 1009 mg/L. β -carotene was prepared in acetone at 749 mg/L. Additionally, α -tocopherol 987 mg/L, δ -tocopherol 1000 mg/L, and γ -tocopherol 540 mg/L were prepared in a mixture of acetone: ethanol (1:1). All stock solutions of analytical standards were stored in amber vials at -19 ± 1 °C for the preparation of calibration curves for each compound during the validation of the analytical

method on the HPLC-DAD/FLD system and subsequent sample analyses. Calibration curves were prepared with the following final metabolites concentrations at mg/L: 0.3; 1.0; 5.0; 10.0; 15.0; 20.0; 25.0; 50.0.

HPLC-DAD/FLD analysis

Chromatographic analysis was carried out using high performance liquid chromatography with diode array detection and fluorescence detection 11,000/1200 (HPLC-DAD/FLD). OpenLab Chemstation Edition C.01.07 was used to control the instruments and for data acquisition and processing. According to the acceptance criteria of EPA 8000D, the analytical method accomplishes the criteria for linearity given that, according to statistical analyses, there is a linear relationship between the variables. This was the case for pressure, as an $RSD \leq 20\%$ was obtained; trueness, as recovery was found to be between 70 and 130%; and robustness, as precision and trueness were found within the working range. As the matrix effect exceeded the 20% acceptance criterion, it is recommended to correct the quantification with a matrix curve or standard addition. Each analytical batch (up to 20 samples), included solvent blanks, controls (fortified samples to 30% or 70%), and calibration curves in solvent and matrix. Routine verification of instrumental performance, background monitoring, and carry-over checks with methanol blanks were performed to ensure analytical integrity throughout the analysis.

HPLC was performed using a CH0-5690 – Develosil® 5 µm RP-Aqueous C30 14 LC 250 × 4.6 mm Column from Nomura Chemical - Phenomenex®, and a gradient system with the mobile phase (Table 1) consisting of solvent A: deionized water with 0.1% formic acid, B: acetonitrile, C: methanol: water (95:5), and D: ethyl acetate. The flow rate was 1.0 mL/min. Total run time was 45 min. Detection was set to DAD at 453 nm for β -carotene and to FLD at 290/335 nm (excitation/emission) for epicatechin and tocopherols. External calibration curves were built for all analytes using their respective standards. Concentrations were expressed in milligrams per kilogram (mg/kg) in wet weight.

The analytical method used was validated based on the parameters of linearity, trueness, precision, robustness, limit of quantification, uncertainty, and matrix effect. It met the linearity criteria, as there is a statistically significant linear relationship between the variables. Trueness was demonstrated with recoveries ranging from 70% to 130%. Precision was demonstrated with $RSD \leq 20\%$. Robustness was demonstrated by maintaining precision and trueness within the working range. Limits of quantification were 1.5 mg/kg for epicatechin, γ -tocopherol, δ -tocopherol, and α -tocopherol, and 25 mg/kg for β -carotene. Uncertainty was 16.62% for epicatechin, 15.91% for γ -tocopherol, 18.24%

Table 1 Gradient system with the mobile phases for analytical method by HPLC-DAD/FLD

Time (min)	A (%)	B (%)	C (%)	D (%)
0	95	5	0	0
1	95	5	0	0
4	70	30	0	0
8	5	95	0	0
9	5	95	0	0
10	0	0	40	60
13	0	0	40	60
28	0	0	0	100
30	0	0	0	100
31	95	5	0	0
45	95	5	0	0

Solvent A: deionized water with 0.1% formic acid, B: acetonitrile, C: methanol: water (95:5), and D: ethyl acetate. All solvents at 1.0 mL/min flow rate

for δ -tocopherol, 18.67% for α -tocopherol, and 18.38% for β -carotene. Regarding the matrix effect, which exceeded the 20% acceptance criterion, the quantification was corrected using a matrix curve and/or standard addition. The acceptance criteria were taken from EPA Method 8000D Determinative Chromatographic Separations.

Environmental and soil variables

During collection, environmental variables were recorded, including elevation by Timestamp Camera application, and ambient humidity and temperature by Halthen TTH-022 thermohygrometer. Also, the following soil properties were analyzed: humidity ψ by NTC 1886 (2013), temperature $\emptyset$ by Halthen Hi Precision punch thermometer, pH ψ by NTC 5264:2018, texture $\emptyset$ by Bouyoucos method NOM 021-SEMARNAT- 2000 As-09, conductivity ψ by NTC 5596 (2008), cation exchange capacity ψ by Normal NTC 5268, organic carbon content $\emptyset$ and organic matter ψ percentage by NTC 5403 B, available phosphorus $\emptyset$ by modified Bray II/UV/VIS Spectrophotometer-Evolution 300, and total Kjeldahl nitrogen ψ by NTC 5889. Additionally, the following metals ψ in soil were measured: aluminum (Al), antimony (Sb), arsenic (As)*, barium (Ba), beryllium (Be) $\ddagger$, boron (B)*, cadmium (Cd)*, calcium (Ca), chromium (Cr)*, copper (Cu)*, iron (Fe)*, lead (Pb)*, lithium (Li) $\ddagger$, magnesium (Mg), manganese (Mn)*, mercury (Hg)*, molybdenum (Mo)*, nickel (Ni), potassium (K), selenium (Se), silver (Ag), sodium (Na), tin (Sn) $\ddagger$, titanium (Ti) $\ddagger$, vanadium (V) $\ddagger$, and zinc (Zn)*.

ψ : validated method by GDCON; $\emptyset$: not validated method; *: toxic at high concentrations; $\ddagger$: the uncertainty value corresponds to 50% of the analyzed value.

Statistical analysis

All results are expressed as mean $\pm$ standard deviation (SD) from at least three biological replicates. The data censoring technique used was the average of the quantification limit and the detection limit. The results for β -carotene were

Table 2 Statistically significant differences between immature and mature *Physalis peruviana* L. fruits and their average concentrations in farms 1 and 2

Factor Metabolites	Farm	Fruit development stage	Sampling
Epicatechin	0.0047*	0.3292	0.1371
α -tocopherol	0.9507	0.0067*	-
δ -tocopherol	0.9835	0.0009*	0.0754
γ -tocopherol	0.2480	0.1218	-
β -carotene	0.9334	<0.0001*	0.1485

–: invalidity of the nonparametric analysis of variance model, lack of homoscedasticity

*: Kruskal-Wallis nonparametric analysis of variance test with a significance level of 0.05

transformed with natural logarithm to analyze the variation in its concentration in immature stage vs. mature stage fruits from farms 1 and 2, as were the results for epicatechin and α -tocopherol for the analysis of variance of the MeJA treatment. The transformation was done in order to reduce the impact of outlier data without eliminating them, review compliance with the assumptions of the method and thus facilitate the interpretation of the results. Results for farms 3 and 4 were not transformed. A nonparametric model using the Kruskal-Wallis test was chosen to determine statistically significant differences, with a significance level of 0.05 in metabolite concentrations (mg/kg) according to the farm, sampling, fruit development stage, and MeJA treatments. Differences were demonstrated using the multivariate analysis of variance (PERMANOVA) with the Pairwise Wilcoxon test. Spearman's correlation analysis without experimental control (observational research) was conducted to analyze the soil physicochemical variables in their natural environment without manipulation, to evaluate whether a statistical relationship exists between them. This was done by principal component analysis, considering the random behavior of the entire set of variables and the lack of control through the incorporation of factors. Data analysis was performed using R Studio 2024.12.1. For this, the physicochemical characteristics of the soil mentioned in Sect. 2.8 were considered as continuous quantitative variables, the analyzed fruit development stages and MeJA as explanatory variables, and the metabolite concentration as response variables. Meanwhile the immature and mature stages of the fruit, the concentrations of the MeJA treatments, the farms, and the sampling were considered as factors.

Results and discussion

Variation in selected functional metabolites in comparison to fruit developmental stages

Findings comparing fruit in two different stages of development revealed statistically significant differences. At farms 1 and 2, average α -tocopherol concentrations were 6.23 ± 1.16 mg/kg and 10.51 ± 1.96 mg/kg, δ -tocopherol concentrations were 19.60 ± 3.58 mg/kg and 34.88 ± 6.36 mg/kg, and β -carotene concentrations were 21.63 ± 3.97 mg/kg and 55.74 ± 10.25 mg/kg, respectively, in immature and mature *Physalis peruviana* fruits, with a significance level of 0.05 (Table 2; Fig. 1B-D; SI-1). Farms 1 and 2 also presented statistically significant differences for epicatechin (Table 2; Fig. 1A; SI-1), with average concentrations of 1.80 ± 0.30 mg/kg in immature fruits and 10.84 ± 1.80 mg/kg in mature fruits. For γ -tocopherol, concentrations were 7.02 ± 1.12 mg/kg and 6.74 ± 1.07 mg/kg, respectively,

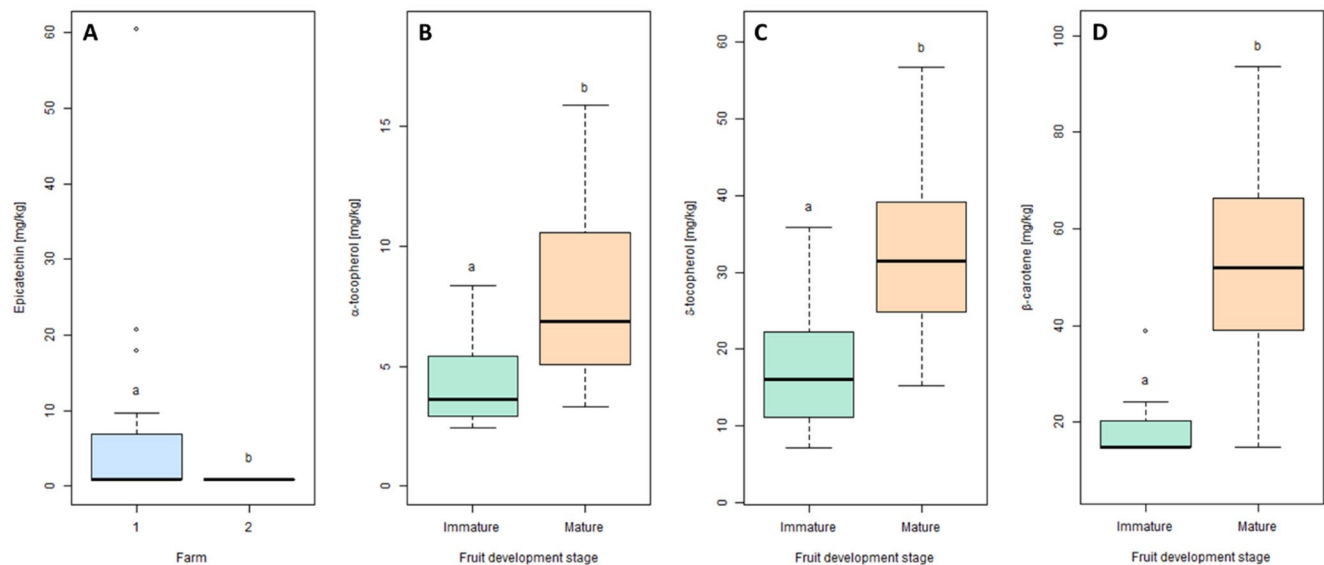


Fig. 1 Boxplot of Pairwise comparisons using the Wilcoxon rank sum test with continuity correction, with a significance level of 0.05 between farms 1 and 2 for (A) epicatechin, and between immature (green boxes) and mature (orange boxes) fruit development stages in

(B) α -tocopherol, (C) δ -tocopherol, and (D) β -carotene. Fruit development stages and farms that share the same letter(s) correspond to non-significant statistical differences

Table 3 Statistically significant differences between immature and mature *Physalis peruviana* L. fruits and their average concentrations in farms 3 and 4

Factor	Metabolites	Farm	Fruit development stage	Sampling
Epicatechin	0.0793	0.8852	0.0115	
α -tocopherol	1.0000	<0.0001*	-	
δ -tocopherol	0.3441	<0.0001*	-	
γ -tocopherol	0.1312	-	0.0820	
β -carotene	0.5616	-	0.6263	

–: invalidity of the nonparametric analysis of variance model, lack of homoscedasticity

*: Kruskal-Wallis nonparametric analysis of variance test with a significance level of 0.05

which is not a statistically significant difference (Table 2; SI-1).

Farms 3 and 4 also presented statistically significant differences in α -tocopherol concentrations, with 1.70 ± 0.32 mg/kg in immature fruits and 6.44 ± 1.20 mg/kg in mature fruits, and δ -tocopherol, with 14.08 ± 2.57 mg/kg and 29.27 ± 5.34 mg/kg, respectively, in immature and mature *P. peruviana* fruits, with a significance level of 0.05 (Table 3; Fig. 2A-B; SI-2). On the other hand, the average epicatechin concentrations found were 0.93 ± 0.15 mg/kg in immature fruits and 0.93 ± 0.15 mg/kg in mature fruits, without statistical significance between fruit development stages. The values were excluded at a specific threshold where the measured concentrations fell below the limit of quantification. As a result, the same concentrations were

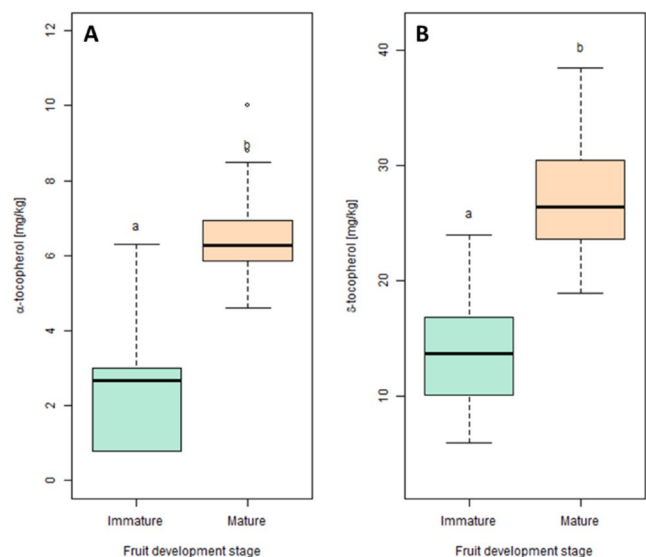


Fig. 2 Boxplot of Pairwise comparisons using the Wilcoxon rank sum test with continuity correction with a significance level of 0.05 between immature (green boxes) and mature (orange boxes) fruit development stages in (A) α -tocopherol and (B) δ -tocopherol, on farms 3 and 4. Fruit development stages and samplings that share the same letter(s) correspond to non-significant statistical differences

reported for epicatechin in both developmental stages, since in both cases measurements were below this threshold and therefore corresponded to the value assigned at the detection limit (Table 3; SI-2). This also occurred between farms and between samplings (Table 3; SI-2).

The variation of specific functional metabolites during the ripening of *P. peruviana* fruits is poorly documented, and total quantifications of some chemical families, without monitoring of the different stages of the fruit development, are mainly found. Therefore, there was insufficient data in the literature about the target metabolites of this research, making it difficult to make a more detailed comparison of our results with previous findings.

In the words of Añibarro-Ortega et al. (2025) [6], the nutritional and functional qualities of *P. peruviana* fruit are directly associated with its tocopherol (vitamin E) content, which also improves its antioxidant activity. The results obtained in this research showed statistically significant differences in α -tocopherol and δ -tocopherol between immature and mature developmental stages of goldenberry fruits, in both groups of farms (Tables 2 and 3). This is consistent with a recent report by Añibarro-Ortega et al. (2025) [6], which shows a total tocopherol concentration = 2.34 mg/100 g, with γ -tocopherol (0.86 mg/100 g wet weight (ww)) being the most dominant isoform, followed by α -tocopherol (0.58 mg/100 g ww), β -tocopherol (0.59 mg/100 g ww), and δ -tocopherol (0.31 mg/100 g ww). The predominant isoform is also α -tocopherol.

However, the few reports found on tocopherols in *P. peruviana* fruits have mainly focused on the oil fractions of different parts of the fruit, such as peel, pulp, and/or seed, rather than the content in the whole fruit. In this context, γ -tocopherol (73%) and α -tocopherol (19%) were predominant in the peel oil, while the seed oil had similar contents of β -tocopherol (34%), δ -tocopherol (33%), and γ -tocopherol (31%) [18]. Similar findings are reported in a previous study, where γ -tocopherol (45.5 mg/kg) and α -tocopherol (28.3 mg/kg) were the main constituents in the pulp/peel oil, respectively, and β -tocopherol and γ -tocopherol were the main constituents in the seed oil [19].

Regarding epicatechin, although there are no specific studies on the variation in its concentration during the ripening of *P. peruviana* fruits, there are reports of an increase in phenolic compounds (including flavonoids such as epicatechin in some studies) during the ripening process in these fruits [20–22]. However, our results for epicatechin in the two groups of farms evaluated, which do not show statistical significance between fruit development stages (Tables 2 and 3) due to most of the measurements being below the limit of quantification, are consistent with the findings of Choco Matute (2014) [23], who found no significant changes in the variation in total phenol content, concluding that the concentration of phenolic compounds does not appear to be associated with physiological variations in fruit ripening. Meanwhile, de la Vega et al. (2019) [24] found that the total polyphenol content (129.9 to 124.9 mg GAE/100 g ww) decreased with maturation. Corrales Bernal et al. (2015)

[25] found the same for total flavonoid content (131.9 to 65.9 mg catechin/100 g pulp dry weight (dw)). This behavior may be associated with multiple enzymatic reactions, to which these compounds are highly susceptible, and that can give rise to organoleptic characteristics such as the color, smell, bitterness, and astringency of the fruit [26–27].

The results obtained in this research found statistically significant differences in β -carotene between immature and mature developmental stages of *P. peruviana* fruits, between farms 1 and 2 (Table 2). Regarding farms 3 and 4, according to the nonparametric analysis of variance, there are no statistically significant differences (Table 3). This result is consistent with what has been reported in other studies on cape gooseberries. This is to be expected because the carotenoid content tends to increase during ripening in most fruits, as they are responsible for the yellow to red pigments in photosynthetic organisms [28].

For their part, Mier & Cáez (2011) [20] reported that these compounds reached their highest concentration, of 310 μ g of β -carotene/100 g ww, in *P. peruviana* fruits in the most advanced ripening stage tested. Similar values had already been reported by Fisher & Martínez (1999) [29], Fisher et al. (2000) [30], and Bravo et al. (2014) [27] for Colombian cape gooseberries. Olivares-Tenorio et al. (2016) [22] also reported that β -carotene contents are directly proportional to the ripeness stage. Etzbach et al. (2018) [2] reported a variation in total carotenoid content from 27.22 μ g/g ww to 204.5 μ g/g ww between immature and mature fruit developmental stages, respectively. Also, they identified 20 types of carotenoids in the immature state and 42 in the mature state, which also explains the increase in these compounds during fruit development. Additionally, de la Vega et al. (2019) [24] reported an increase in the carotenoid content during the fruit ripening (136.96 to 149.26 μ g/g ww), and found a direct correlation between these metabolites and the antioxidant capacity attributed to these fruits.

However, Corrales Bernal et al. (2015) [25] reported the highest total carotenoid content during the transition from immature to mature stage, when the fruit has orange pigments with green overtones around the cup, with 3961.6 μ g β -carotene/100 g dry pulp. However, they suggest that this is due to an increase in xanthophyll pigments such as lutein, which have a yellow color. They also clarify that the ripe stage does not correspond to the point at which the fruit has a completely bright orange color, where the highest concentration of β -carotene, responsible for this pigment, is expected to be found.

Certainly, environmental elements such as light, temperature, and oxidative stress also affect how these metabolic pathways are regulated [12]. According to Borges et al. (2016) [13], Carmona-Hernandez et al. (2019) [31], and Sun & Li (2020) [32], they are essential for the activation or

repression of the genes involved in the biogenesis of functional metabolite pathways, microbial metabolism, intestinal absorption rates, and for the stability of these compounds during laboratory analysis, even after ingestion and during digestion. However, direct studies analyzing the relationship between soil conditions and the content of functional metabolites in the fruit are lacking.

In this regard, in the present study, groups of soil physicochemical variables associated with some of the metabolites analyzed were observed, applying Spearman's correlation analysis (Figs. 3 and 4). The same results or an inverse trend were found in both developmental stages of fruit evaluated, or only in one of them, i.e., immature and/or mature. These relationships are explained below, considering the assessment of physicochemical parameters and metals examined in the soil in sample 0. It is important to clarify that these results are exploratory, not causal.

In immature fruits (Fig. 3A; SI-3), based on the descriptive analysis of Spearman's correlation, it can be observed that in the initial stages of the study (sampling 0), at farms 1 and 2 there is a correlation between Be, soil temperature (T), soil humidity (H), total Kjeldahl nitrogen (N_{total}), cation exchange capacity (IC), organic carbon content (C_{org}), and organic matter percentage (MO; blue cluster; Fig. 3A). There was also a correlation between epicatechin (E), α -tocopherol (A), and β -carotene (B) concentration, and the concentrations of the following metals: Al, Cu, Fe,

Li, Mn, Ni, Pb, Se, Sb, Ti, and Zn (green cluster; Fig. 3A). There was also a correlation between the concentrations of δ -tocopherol (D), available phosphorus (P_{disp}), As, Ba, Cr, K, Mg and Mo (violet cluster; Fig. 3A). The relationships between the variables of the first two clusters mentioned are inverse.

In mature fruits (Fig. 3B; SI-4), correlations were found between Be, soil temperature (T), soil humidity (H), total Kjeldahl nitrogen (N_{total}), cation exchange capacity (IC), organic carbon content (C_{org}), organic matter percentage (MO; blue cluster; Fig. 3B). The same was found in the immature fruit stage (blue cluster; Fig. 3A). Also, γ -tocopherol (G) concentration, pH and Hg concentrations (pink cluster; Fig. 3B). Also, there were correlations between concentrations of epicatechin (E), δ -tocopherol (D) and the following metals: Al, Cu, Fe, Li, Mn, Ni, Pb, Se, Sb, Ti, V and Zn (green cluster; Fig. 3B). Additionally, there were correlations between concentrations of available phosphorus (P_{disp}), As, Ba, Cr, K, Mg and Mo (violet cluster; Fig. 3B), the same physicochemical variables as in the immature fruit stage (violet cluster; Fig. 3A). Once again, inverse relationships are found between the variables of the blue and green cluster (Fig. 3B), as in immature fruits (Fig. 3A).

In immature fruits (Fig. 4A; SI-5), based on the descriptive analysis of Spearman's correlation, it can be observed that in the initial stages of the study (sampling 0), at farms

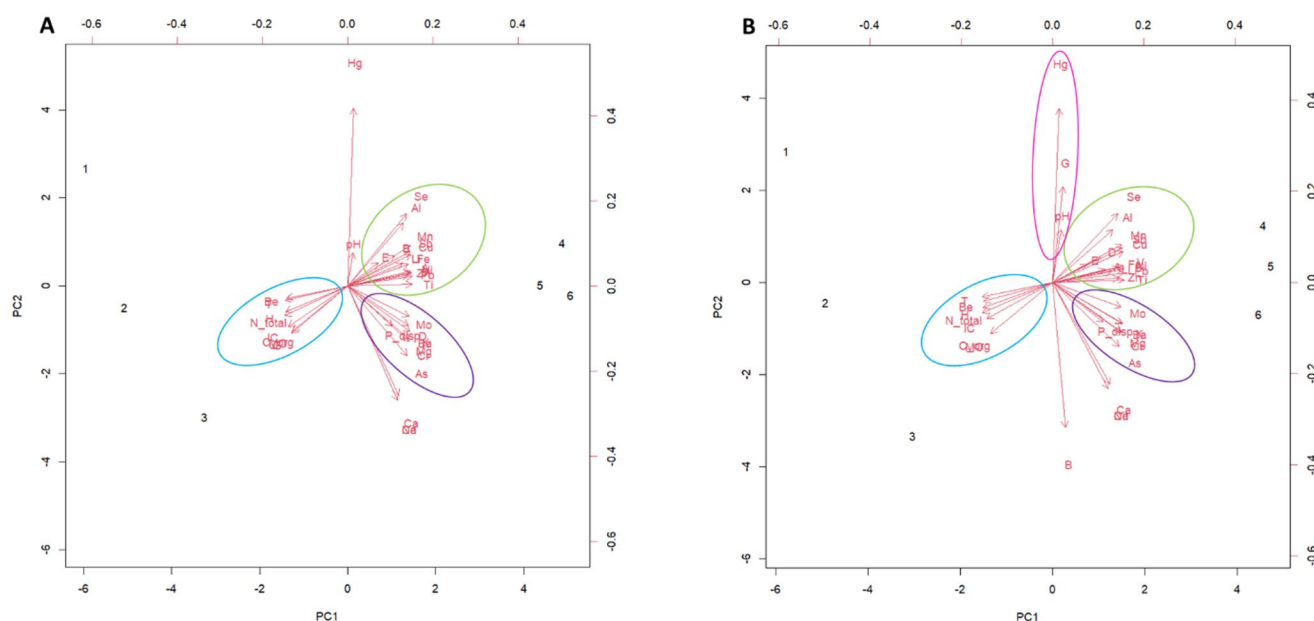


Fig. 3 Principal component analysis based on Spearman's correlation showing analysis of functional metabolites (epicatechin (E), α -tocopherol (A), δ -tocopherol (D), γ -tocopherol (G), and β -carotene (B)) was performed on *Physalis peruviana* L. fruits, at farms 1 and 2, evaluating metals (Al, Fe, Cu, Zn, Mn, Mo, Ba, Cd, Cr, Ca, K, Mg, Na,

Pb, Ni, Sn, Be, V, Li, Ti, As, Sb, Se, Hg) and physicochemical soil variables (humidity (H), temperature (T), pH, cation exchange capacity (IC), organic carbon content (C_{org}), organic matter percentage (MO), available phosphorus (P_{disp}) and total Kjeldahl nitrogen (N_{total})). (A) Immature fruits stage. (B) The mature fruit stage

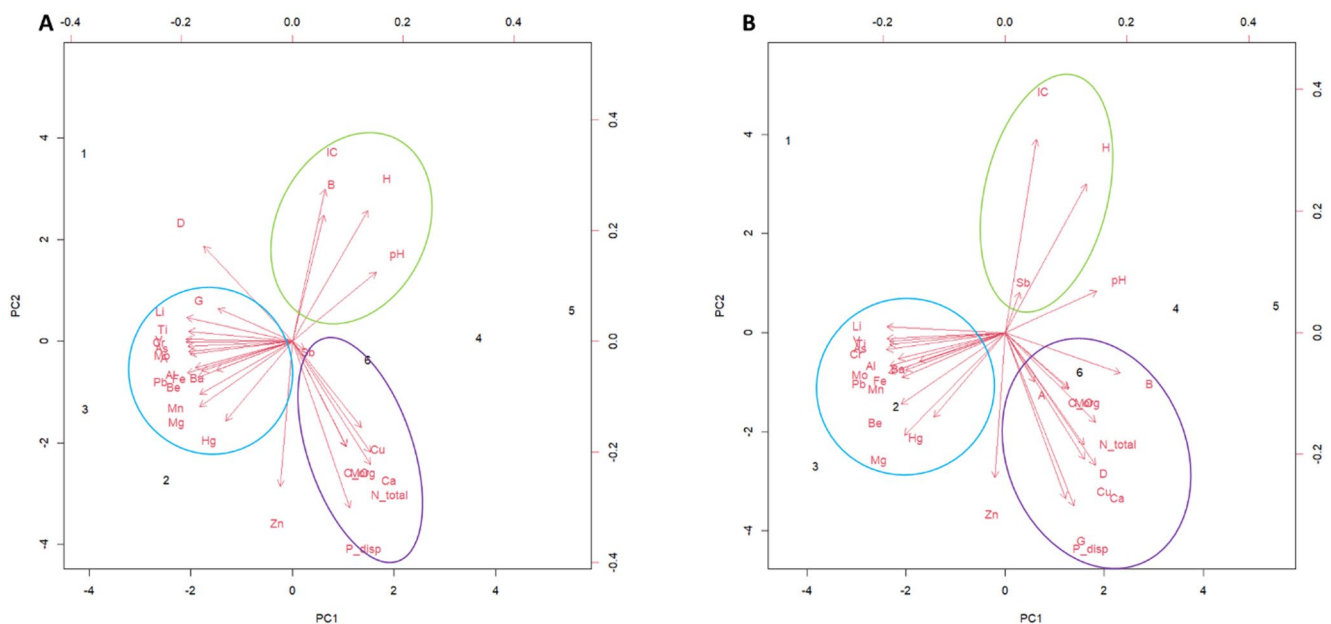


Fig. 4 Principal component analysis based on Spearman's correlation showing analysis of functional metabolites (epicatechin (E), α -tocopherol (A), δ -tocopherol (D), γ -tocopherol (G), and β -carotene (B)) was performed on *Physalis peruviana* L. fruits, at farms 3 and 4, evaluating metals (Al, Fe, Cu, Zn, Mn, Mo, Ba, Cr, Ca, Mg, Pb, Be, V,

Li, Ti, As, Sb, Hg) and physicochemical soil variables (humidity (H), pH, cation exchange capacity (IC), organic carbon content (C_org), organic matter percentage (MO), available phosphorus (P_disp) and total Kjeldahl nitrogen (N_total)). (A) Immature fruits stage. (B) The mature fruit stage

3 and 4 there is a correlation between the concentrations of α -tocopherol (A), γ -tocopherol (G) and the following metals: Al, As, Ba, Be, Cr, Fe, Hg, Li, Mg, Mn, Mo, Pb, Ti, and V (blue cluster; Fig. 4A). There was also a correlation between β -carotene (B) concentration, cation exchange capacity (IC), pH, and soil humidity (H) (green cluster; Fig. 4A). Additionally, there is a correlation between the concentrations of Ca, Cu, available phosphorus (P_disp), total Kjeldahl nitrogen (N_total), organic carbon content (C_org), and organic matter percentage (MO; violet cluster; Fig. 4A). The relationships between δ -tocopherol and the variables of the violet cluster is inverse.

In mature fruits (Fig. 4B; SI-6), correlations were found between the following metals: Al, As, Ba, Be, Cr, Fe, Hg, Li, Mg, Mn, Mo, Pb, Ti, and V (blue cluster; Fig. 4B), which was also the case in the immature fruit stage (blue cluster; Fig. 4A). Also, cation exchange capacity (IC), soil humidity (H), and Sb concentration (green cluster; Fig. 4B). There was also a correlation between the concentrations of α -tocopherol (A), δ -tocopherol (D), γ -tocopherol (G), β -carotene (B), Ca and Cu, and available phosphorus (P_disp), total Kjeldahl nitrogen (N_total), organic carbon content (C_org), and organic matter percentage (MO; violet cluster; Fig. 4B). The same was found for the physicochemical variables in the immature fruits (violet cluster; Fig. 4A). The relationship between the soil pH and the variables of the blue cluster is inverse, as is the relationship between Zn concentration and the variables of the green cluster.

Interestingly, in farms 1 and 2, it was observed that the green clusters (Fig. 3A-B) containing the functional metabolites epicatechin, α -tocopherol, and β -carotene in immature fruits (Fig. 3A), and epicatechin and δ -tocopherol in mature fruits (Fig. 3B), correlated with the same metals present in the soil, specifically Al, Cu, Fe, Li, Mn, Ni, Pb, Se, Sb, Ti, and Zn, except for V in immature fruits. This highlights the presence of epicatechin in both stages of development.

As with farms 3 and 4, in the violet clusters (Fig. 4A-B), an inverse correlation is observed for immature fruits (Fig. 4A) between the soil variables grouped in the cluster (Ca, Cu, available phosphorus, total Kjeldahl nitrogen, organic carbon content, and organic matter percentage) and δ -tocopherol. Meanwhile, in mature fruits (Fig. 4B), the cluster contains the same soil variables, in addition to the three tocopherol isomers and β -carotene.

These exploratory and descriptive results suggest that these variables could have a positive or negative impact on the synthesis of some of the functional metabolites evaluated, also depending on the stage of fruit development. However, more rigorous experiments and robust analyses are needed to determine these correlations, given that in terms of physicochemical variables, studies on the physicochemical characteristics of *P. peruviana* fruit are common [20, 33–34], partly to analyze their organoleptic characteristics or to associate them with the presence or absence of functional metabolites families or specific compounds responsible for biological activities [1, 20, 33, 35–36].

Some studies of *P. peruviana* also analyze the variation in the concentration of functional metabolites with respect to the origin of the seeds, variety, the different ripeness stages of fruit, crop conditions, and/or geographical origin. Fischer et al. (2000) [30] suggested that the higher temperature at 2300 m.a.s.l. enhanced the provitamin A content when comparing two tropical altitudes. Olivares-Tenorio et al. (2016) [22] evaluated the content of total phenolic compounds and flavonoids, including catechin, epicatechin and β -carotene, at consumption stage, considering the incidence of harvest stage (pre- or post-) processing (thermal and non-thermal), storage steps, origin, growing conditions, analytical methods employed and ripeness. Furthermore, multivariate statistical analysis by Bravo et al. (2015) [1] suggested that β -carotene, phenolic content, and oxygen radical absorbance capacity (ORAC) values were mainly affected by harvest time, and ascorbic acid content and radical-scavenging activity were mainly affected by genotype. Consequently, the harvest time must be scheduled carefully to gain the highest proportion of bioactive compounds according to the specific cultivar and the environment where it is grown. Grigolo et al. (2020) [33] evaluated storage temperature (fresh, refrigerated, and frozen fruits) and found that it affects the concentration of phenolic compounds in the fruit (77 and 75 mg GAE/100 g ww without statistical significance, for fresh and refrigerated fruits, respectively; and 39 mg GAE/100 g ww for frozen fruits). Muñoz et al. (2021) [37] also showed that cultivated Cape gooseberry from the Andean region of the Atacama Desert had total polyphenol content (26.24 mg GAE/100 g ww) that was higher than that reported for the same species (15.20 mg GAE/100 g ww) grown in Argentinean northern Andean region under similar conditions, and similar to that of fruits grown in Mediterranean climates. From this, the incidence of external factors on the concentration of metabolites in the fruit could be inferred.

Meanwhile, Oney Montalvo et al. (2021) [38] found that both the stage of ripeness and the type of soil

exhibited a significant effect ($p < 0.05$) on the concentration of α -tocopherol and β -carotene, albeit not in *P. peruviana* but in *Capsicum chinense*, another Solanaceae. They compared unripe (green pepper), half ripe (green-orange pepper) and ripe (orange pepper) stages of fruits. Additionally, they compared the following two types of soils: red soil, with higher concentration of calcium (2075.28 mg/kg), magnesium (779.23 mg/kg), phosphorus (11.00 mg/kg), and iron (6.27 mg/kg) and lower concentration of organic matter (5.16%); and black soil, with higher concentration of nitrogen (52.01 mg/kg), organic matter (10.93), and manganese (5.24 mg/kg). The concentration of α -tocopherol showed statistically significant differences between the two soil types at different stages of fruit ripeness. The same was found for β -carotene, although only in the first two stages of ripeness. However, in the analysis of interactions, they reported that soil types did not show a significant effect on the concentration of the metabolites studied, possibly because the predominant effect of the ripening stage could mask possible effects of the soil.

For their part, Muñoz et al. (2021) [37] showed that cultivated *P. peruviana* from the Andean region of the Atacama Desert had higher contents of calcium, sodium, and phosphorus than those reported for the same fruit grown in other producing areas such as the Argentinean northern Andean region. Meanwhile Popova et al. (2021) [18] found high levels of important macro- and microminerals (K, Mg, Na, Zn, Cu, Fe) in seeds and peels, a discarded material from juice production. Due to its nutritional importance, it would be very interesting to explore in greater detail the correlation between the physicochemical characteristics of the soil and the bioactive compounds stored in the fruits.

Effect of methyl jasmonate treatment on mature fruits

Overall, under the experimental conditions evaluated, statistically significant differences were not observed in the concentrations of epicatechin, tocopherol isoforms, or β -carotene in mature *P. peruviana* fruits with preharvest MeJA foliar spray in the tested concentrations of 0.5, 2.5, 5.0 $\mu\text{L/mL}$ (Table 4; SI-7). There was one exception to this, which was α -tocopherol in farms 3 and 4, whose concentration showed a statistically significant increase in response to the low MeJA treatment (0.5 $\mu\text{L/mL}$) compared to control and higher concentrations (Table 5; Fig. 6B; SI-8).

Likewise, significant differences were observed between farms 1 and 2 for α -tocopherol concentration (Table 4; Fig. 5A; SI-7). Significant differences were also observed for α -tocopherol and δ -tocopherol between sampling times, particularly when comparing the initial samplings (0 and 1) with the later ones (2 and 3), for the concentrations of

Table 4 Statistically significant differences between methyl jasmonate treatments of *Physalis peruviana* L. fruits and the average concentrations from farms 1 and 2

Factor	Farm	Methyl Jasmonate Treatments	Sampling
Metabolites			
Epicatechin	0.7504	0.5443	0.2077
α -tocopherol	0.0284*	0.8310	<0.0001*
δ -tocopherol	0.7666	0.8433	<0.0001*
γ -tocopherol	0.7887	0.6922	-
β -carotene	0.8317	0.6407	-

–: invalidity of the nonparametric analysis of variance model, lack of homoscedasticity

*: Kruskal-Wallis nonparametric analysis of variance test with a significance level of 0.05

The treatment factor was applied at 3 levels of methyl jasmonate: low [0.5 $\mu\text{L/mL}$], medium [2.5 $\mu\text{L/mL}$], and high [5.0 $\mu\text{L/mL}$]

Table 5 Statistically significant differences between methyl jasmonate treatments of *Physalis peruviana* L. fruits and the average concentrations from farms 3 and 4

Factor	Farm	Methyl Jasmonate Treatments	Sampling
Epicatechin	-	0.9871	-
α -tocopherol	0.0434*	0.0003*	-
δ -tocopherol	0.0929	0.4328	<0.0001*
γ -tocopherol	-	0.1012	-
β -carotene	0.5059	0.4925	0.0269

–: invalidity of the nonparametric analysis of variance model, lack of homoscedasticity

*: Kruskal-Wallis nonparametric analysis of variance test with a significance level of 0.05

The treatment factor was applied at 3 levels of methyl jasmonate: low [0.5 μ L/mL], medium [2.5 μ L/mL], and high [5.0 μ L/mL]

both tocopherol (Table 4; Fig. 5B–C, respectively; SI-7). In farms 3 and 4, significant differences were also found for α -tocopherol (Table 5; Fig. 6A; SI-8), as well as between sampling 3 and the other samplings for δ -tocopherol (Table 5; Fig. 6C; SI-8). However, these differences between farms and sampling days do not directly reflect the impact of fruit development stages or MeJA application on the concentration of the functional metabolites evaluated, which is the aim of this research.

Fruit ripening processes frequently result in high α -tocopherol levels at the expense of γ -tocopherol [39–40].

This is the case for citrus [39–40], mango [39, 41], tomato, peach, strawberry, and pepper [39, 42]. In tomato (*Solanum lycopersicum*), exogenous application of MeJA during ripening induced an increase of approximately 80% in α -tocopherol content compared to untreated controls, alongside broader metabolic changes involving amino acids and fatty acids [43–44]. Similar effects have been observed in plant cell cultures, where MeJA treatment altered tocopherol levels and enzymatic activities linked to their biosynthetic pathway, suggesting a direct influence on key metabolic steps [45].

The above is due to the fact that α -tocopherol is the most biologically active form in terms of antioxidant capacity, neutralizing reactive oxygen species (ROS) generated by intensified cellular respiration and senescence-related metabolic changes, particularly during the final developmental stages of fruit [40, 46–53]. Additionally, tocopherols themselves are not only antioxidants but may also participate in signaling processes that interact with jasmonate pathways, suggesting a bidirectional relationship between these molecules [46]. The capacity of MeJA to alter lipid metabolism further reinforces this connection, as studies have shown significant changes in fatty acids, carotenoids, and tocopherols following its application, particularly during later stages of fruit ripening [43, 54]. This indicates that MeJA

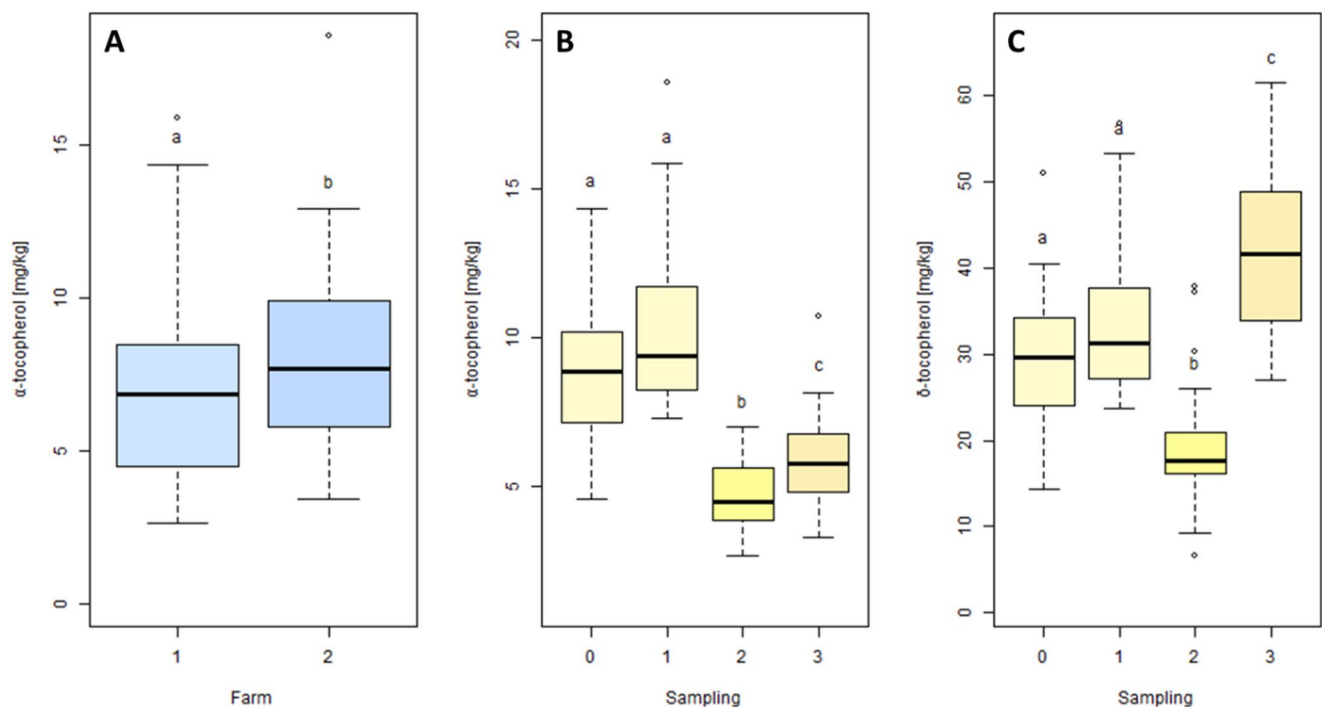


Fig. 5 Boxplot of Pairwise comparisons using the Wilcoxon rank sum test with continuity correction, with a significance level of 0.05 between farms 1 and 2 in (A) α -tocopherol. Also, between the initial samplings (0 and 1) and the later ones (2 and 3) for (B) α -tocopherol

concentrations, and between the initial samplings (0 and 1) and samplings 2 and 3 for (C) δ -tocopherol. Farms and samplings that share the same letter(s) correspond to non-significant statistical differences

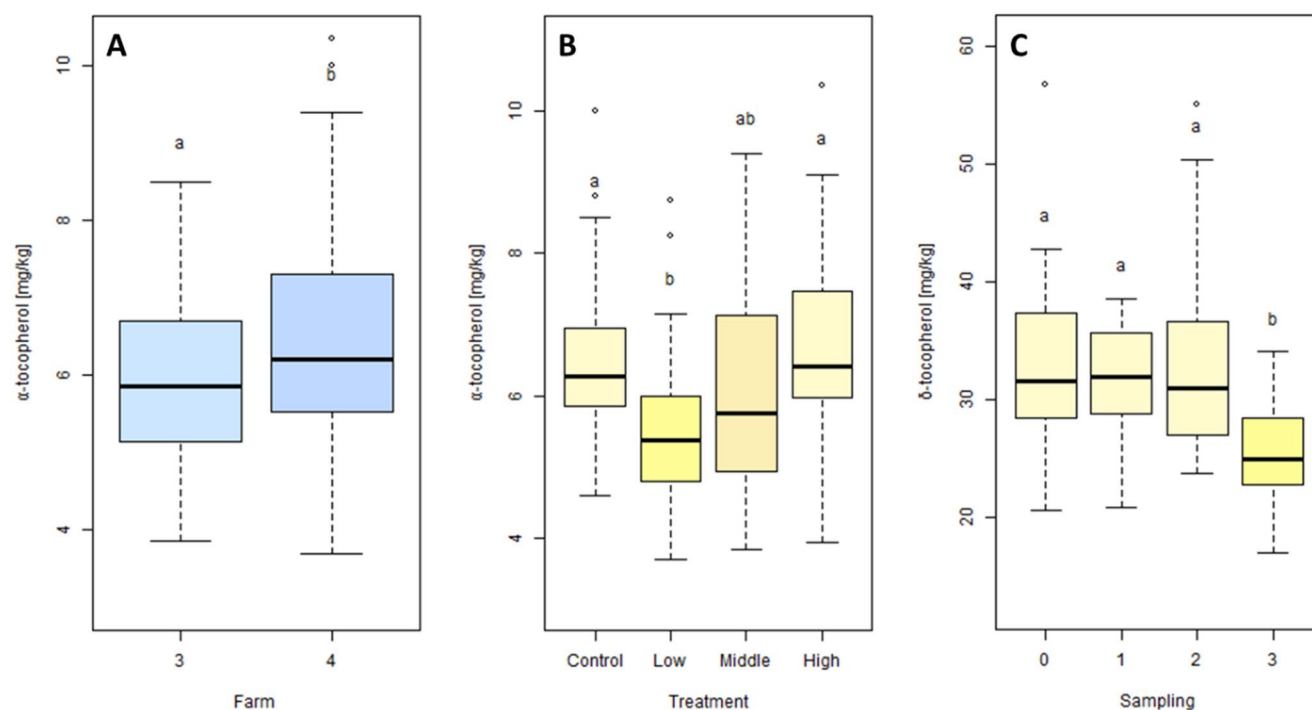


Fig. 6 Boxplot of Pairwise comparisons using the Wilcoxon rank sum test with continuity correction, with a significance level of 0.05 between farms 3 and 4 in (A) α -tocopherol. Also, for α -tocopherol (B), between low MeJA treatment and the control and high MeJA concen-

tration, and between the initial samplings (0, 1, and 2) and sampling 3 for (C) δ -tocopherol. Farms and samplings that share the same letter(s) correspond to non-significant statistical differences

may act as a central regulator coordinating multiple metabolic pathways linked to fruit quality and stress adaptation.

Despite this substantial amount of evidence, a critical gap remains in the specific case of *P. peruviana*. While studies in related systems demonstrate that MeJA enhances secondary metabolites and increases α -tocopherol content, no direct experimental research has confirmed this effect in *P. peruviana* fruits. This is particularly relevant given that species within the Solanaceae family often share conserved metabolic pathways, suggesting that similar responses could occur in goldenberry.

MeJA foliar spray, on the other hand, has been shown to improve fruit quality by raising levels of antioxidant chemicals, such tocopherols. The fact that some phytohormones, such jasmonates and abscisic acid, spontaneously increase in response to abiotic stressors and promote synthesis of secondary metabolites with antioxidant activity is also widely established. This regulatory function suggests that MeJA acts not only as a stress signal but also as a tool to improve the nutraceutical quality of horticultural products. Also, α -tocopherol (isoform of vitamin E) aids in protecting oxidative damage to plant cells, especially from ROS. Similar reactions have been noted under abiotic stress conditions or after the introduction of exogenous phytohormones [55].

In this regard, increased synthesis of tocopherols has been reported under such treatments [8].

The findings of this study contrast with previous reports in other fruit species, where preharvest or postharvest MeJA application has been shown to enhance the accumulation of antioxidant metabolites, including phenolic compounds [15, 56–57], tocopherols [7, 43, 58], and carotenoids [30, 59]. Such responses have been reported in preharvest application to raspberry with 0.01 mM and 0.1 mM MeJA concentrations [60], pomegranate with 1.5 mM and 10 mM MeJA concentrations [61], grape with 0.01 mM, 0.1 mM, 1.0 mM, 1.5 mM and 10 mM MeJA concentrations [62–63], strawberry with 250 μ M/L MeJA concentration [16], cherry with 0.5 mM MeJA concentration [64–65], and pear with 0.5 mM/L, 1.0 mM/L and 2.0 mM/L MeJA concentrations [66]. In postharvest application, the response has been found for strawberry with 0.06 μ L/mL MeJA concentration [9, 14], mango with 30 ppm MeJA concentration [67], cherry tomato with 0.01 μ M and 0.05 μ M MeJA concentrations [54], and tomato with 100 ppm MeJA concentration [43–44].

However, the effectiveness of MeJA treatments is known to vary based on multiple factors, including species, cultivar, ripening stage, treatment, cultivation conditions, management practices and other variables of context, and positive

responses reported for other crops cannot be directly extrapolated to *P. peruviana* [15, 22, 55, 59].

The limited response observed in this study may be explained not only by the concentration of MeJA applied and the spray volume, but also by environmental conditions and intrinsic physiological factors that could have constrained the effectiveness of the elicitor [15, 35]. Under field conditions, the efficacy of foliar-applied elicitors is strongly influenced by post-application weather, particularly precipitation and wind, which can significantly reduce compound retention and absorption on the leaf surface. Rainfall occurring shortly after application can wash off exogenous elicitor before it penetrates the leaf surface, while wind can alter droplet deposition and distribution, thereby limiting uptake efficiency [68]. These factors may have reduced the effective dose of MeJA reaching the target tissues, contributing to the limited response observed.

In addition, the physicochemical properties of the spray solution, including viscosity and surface tension, influence its interaction with the leaf surface and ultimately determine the efficiency of foliar uptake. While the plant cuticle is often described as a major barrier to diffusion, in species with a well-developed indumentum, trichomes may play a decisive role in modulating the retention and absorption of exogenously applied compounds. Leaf trichomes can intercept spray droplets, altering their distribution and reducing direct contact with the epidermal surface; depending on their density and morphology, they may either enhance retention or promote runoff and evaporation [68]. In the case of *Physalis peruviana*, which presents pubescent leaves, the indumentum may therefore have acted as a physical barrier limiting MeJA penetration. Although Tween was included in the spray solution as a surfactant to reduce surface tension and improve spreading, its effectiveness can vary depending on leaf surface characteristics, and may not fully overcome the constraints imposed by dense trichome coverage [69]. Consequently, limited absorption of MeJA due to surface-related factors remains a plausible explanation for the weak physiological response.

Beyond environmental constraints, the physiological stage of the fruit at the time of elicitor application is likely a critical determinant of responsiveness. The treatments in this study were applied at a fully mature stage, a condition in which metabolic activity related to growth and secondary metabolite biosynthesis is often reduced. It is well established by Wasternack & Hause (2013) [70] that the effectiveness of MeJA depends on the developmental stage of the tissue, with earlier stages typically showing greater sensitivity due to higher metabolic plasticity and active gene expression related to defense and secondary metabolism. During fruit ripening, metabolic processes shift toward maturation and senescence, which may limit the capacity

of tissues to respond to elicitation signals. For example, in tomato (*Solanum lycopersicum*), MeJA-induced increases in antioxidant compounds are more pronounced at earlier ripening stages, whereas responses tend to diminish as fruits reach full maturity [54, 71].

Furthermore, the regulation of secondary metabolite pathways, including those associated with antioxidant production, is tightly controlled by developmental cues. In mature fruits, key biosynthetic enzymes may be downregulated, reducing the potential for elicitor-induced enhancement. This is particularly relevant for compounds such as tocopherols, whose biosynthesis occurs in plastids and may decline as chloroplasts transition into chromoplasts during ripening [72]. As a result, late-stage application of MeJA may fail to trigger significant metabolic changes, even if the elicitor is successfully absorbed.

Taken together, these findings suggest that the lack of a significant MeJA effect in this study likely reflects a combination of environmental limitations, surface-related barriers associated with the indumentum, and intrinsic physiological constraints linked to fruit maturity. While the inclusion of Tween may have improved spray performance to some extent, it may not have been sufficient to ensure effective uptake under the prevailing conditions.

In addition, differences in jasmonate-mediated signaling sensitivity during fruit development have been reported between species, suggesting that *P. peruviana* may exhibit a reduced responsiveness to MeJA during the evaluated developmental window [14, 55]. The absence of targeted studies therefore represents a significant opportunity for research. Evaluating the effect of MeJA on other functional metabolites accumulation, including higher or repeated MeJA doses; optimizing application timing across fruit developmental stages, even postharvest treatments; evaluating different adjuvant formulations; and exploring alternative elicitation strategies and more controlled environmental conditions, could contribute to both the understanding of its metabolic regulation and the development of strategies to enhance the nutraceutical value of *P. peruviana*.

Conclusions

This work provides one of the first reports describing correlations between soil composition and bioactive compound content in *P. peruviana* fruits. Likewise, it reports on assays with different concentrations of methyl jasmonate sprayed on leaves during pre-harvest, which did not affect the concentration of metabolites targeted in the fruits, likely due to the low concentration tested, and/or the applied volume not being enough. Overall, the results confirm that mature fruits accumulate higher concentrations of antioxidant

metabolites, particularly α -tocopherol, δ -tocopherol, and β -carotene than immature fruits, with important implications for the nutritional, health-promoting properties and functional quality of the fruit. This pattern reflects a coordinated regulation of antioxidant metabolism during fruit ripening. The findings obtained in this research, by contributing to knowledge about *P. peruviana* fruit in terms of its metabolomics, also provide relevant information applicable to agronomic processes in the fruit production and post-harvest chain to ensure fruit quality and safety, providing opportunities to optimize cultivation and harvest strategies. Interestingly, some of the reports found correspond to degree theses in producing countries. This is an incentive for further research into the metabolomics of these fruits, which are attracting increasing interest from other parts of the world due to their nutraceutical potential. Moreover, expanding knowledge from a scientific perspective in order to solve the challenges faced by farmers during cultivation, as well as optimizing conditions during the transport chain, will also contribute to food security in the territories where this plant is native. Future research should explore alternative elicitors; treatment timings, concentrations, and volumes; and storage conditions, to optimize the accumulation of bioactive compounds postharvest. Meanwhile, understanding the genetic and biochemical regulation, and the impact of the environment, in these pathways in *P. peruviana* could support breeding programs aimed at improving the nutraceutical potential of the fruit.

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Data availability All relevant data are within the paper and its supporting information files.

Declarations

Conflict of interest The authors declare no competing interests.

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