

Phosphorus and calcium nutrition influence potato tuber storability through effects on compositional and structural traits associated with bruising susceptibility

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Abstract

Potato tuber quality during storage is strongly influenced by susceptibility to mechanical damage, which depends on compositional and structural characteristics developed during tuber growth. This study evaluated the effects of phosphorus (P) and calcium (Ca) nutrition on potato tuber dry matter content, specific gravity, and bruising susceptibility during post-harvest storage, with the aim of clarifying their distinct contributions to storage-related quality. Phosphorus application significantly increased tuber dry matter content and specific gravity, reflecting greater dry matter accumulation during tuber development. Both traits were negatively associated with bruising incidence, suggesting that tubers with higher dry matter content and specific gravity may have greater resistance to mechanical damage. In contrast, calcium application had limited effects on tuber dry matter content and specific gravity but influenced bruising susceptibility through its interaction with phosphorus, suggesting a potential role in maintaining tissue integrity under mechanical stress. Regression analysis further demonstrated strong relationships between bruising incidence and both dry matter content and specific gravity, highlighting the importance of these compositional traits as predictors of mechanical susceptibility under the conditions of this study. Overall, the findings indicate that phosphorus and calcium may contribute to potato post-harvest quality through complementary pathways. Phosphorus primarily influenced tuber compositional development, whereas calcium had a stronger influence on bruising susceptibility in combination with phosphorus. These findings provide insights into the relationship between pre-harvest nutrient management and potato tuber quality and may help inform strategies for reducing mechanical damage and maintaining post-harvest quality during storage.

Introduction

Potato (*Solanum tuberosum* L.) is an important food crop worldwide because of its high productivity, nutritional value, and adaptability to diverse production environments. Beyond maximizing tuber yield, potato production increasingly focuses on tuber quality because physical, compositional, and physiological characteristics established during crop growth can influence subsequent handling, storage, and processing performance. Recent reviews emphasize that potato quality is determined by interacting preharvest and postharvest factors, including genotype, mineral nutrition, environmental conditions, maturity, handling, and storage environment (Keithellakpam et al., 2026).

Postharvest deterioration is a major constraint in potato production systems and can result in substantial economic losses during harvesting, transportation, storage, and processing (Campos & Ortiz, 2020). Mechanical damage, moisture loss, sprouting, physiological disorders, and pathogen infection can collectively reduce tuber marketability and processing quality. Among these factors, blackspot bruising is particularly important because it may develop internally following mechanical impact without causing obvious external damage, thereby reducing commercial value (Keithellakpam et al., 2026). Although bruising becomes apparent after mechanical impact, susceptibility to bruising is also influenced by preharvest characteristics, including tuber maturity, dry matter content, mineral nutrition, genotype, and tissue properties (Burton, 1989; Opara & Pathare, 2014; Alamar et al., 2017; Keithellakpam

et al., 2026). Thus, preharvest management may influence the capacity of tubers to withstand mechanical stress during subsequent handling and storage.

Dry matter content and specific gravity are widely used indicators of potato tuber quality because they are closely related to tuber composition, processing characteristics, and postharvest performance (Storey & Davies, 1992; Keithellakpam et al., 2026). These traits vary with genotype, environmental conditions, and nutrient availability and therefore represent important targets for crop management. Mineral nutrition can modify tuber development and quality attributes, although the magnitude and direction of these responses depend on nutrient supply, cultivar, and growing conditions (Westermann, 2005; Marschner, 2012). Because dry matter content and specific gravity can be readily determined, their relationships with bruising susceptibility may also provide useful information about tuber responses to mechanical stress.

Mineral nutrition is an important determinant of potato growth and tuber development, with phosphorus (P) and calcium (Ca) having distinct physiological functions that may influence different components of tuber quality (Marschner, 2012; Naumann et al., 2020). Phosphorus is involved in energy metabolism, photosynthesis, carbohydrate transport, and metabolic processes associated with tuber development (Rosen & Bierman, 2008). Adequate P availability can influence assimilate partitioning and carbohydrate metabolism in developing tubers and may consequently affect dry matter accumulation and specific gravity. However, potato responses to P supply vary with genotype and growing conditions. For example, Chea et al. (2021) reported morphological and metabolic responses of potato plants to different P levels, demonstrating that P availability can modify both plant development and tuber-associated metabolism.

Calcium (Ca) may affect a different but complementary component of tuber quality. Calcium has important structural and physiological functions in plants, including maintenance of cell wall and membrane integrity and regulation of cellular signaling. In potato, Ca status has also been associated with tuber quality and susceptibility to physiological disorders and mechanical injury (White & Broadley, 2003; Palta, 2010). Previous studies have reported associations between tuber Ca status and reduced blackspot bruising or improved postharvest quality (Palta et al., 2006; Palta, 2010; Wu & Huang, 2024). These observations suggest that Ca nutrition may influence the physical properties and stress responses of tuber tissues. However, the extent to which the response to Ca depends on P availability remains insufficiently understood.

In addition to their effects on primary metabolism and tissue properties, mineral nutrients can influence secondary metabolism and the accumulation of phenolic compounds involved in plant stress responses (Marschner, 2012; Fageria, 2009). Chlorogenic acid, caffeic acid, and ferulic acid are among the phenolic compounds detected in potato tissues and have been associated with responses to mechanical injury and postharvest stress (Friedman, 1997; André et al., 2007; Navarre et al., 2011; Wszelaczyńska et al., 2023). Previous studies have also shown that nutrient availability can modify phenolic metabolism and antioxidant-related responses (Akyol et al., 2016; Ngadze et al., 2014; Naumann et al., 2020). However,

changes in phenolic concentrations should not by themselves be interpreted as evidence of altered oxidative damage or antioxidant protection unless these processes are directly measured.

Although the effects of P and Ca on potato growth and quality have been investigated individually, their combined effects on tuber quality, phenolic composition, and susceptibility to mechanical damage remain insufficiently characterized. In particular, limited information is available on how different P × Ca combinations affect dry matter content, specific gravity, bruising incidence, and selected phenolic compounds within the same experimental framework. Furthermore, the relationships among these quality attributes under different postharvest storage conditions have rarely been examined simultaneously. Evaluating these traits together may help identify preharvest nutritional factors associated with tuber quality and bruising susceptibility while distinguishing empirical relationships from physiological mechanisms that require further investigation.

Therefore, this study investigated the effects of three P concentrations (21, 42, and 63 mg L⁻¹) and three Ca concentrations (120, 180, and 240 mg L⁻¹) on potato tuber dry matter content, specific gravity, selected phenolic compounds in tuber peel, and bruising incidence following simulated mechanical stress and storage under cold and ambient conditions. The relationships among tuber quality traits, phenolic compounds, and bruising incidence were also evaluated.

We hypothesized that P and Ca nutrition would differentially affect potato tuber quality and that their effects would interact. Specifically, we expected P supply to influence dry matter content and specific gravity, whereas Ca supply was expected to have a stronger association with bruising susceptibility. We further hypothesized that variation in selected phenolic compounds would be associated with differences in bruising incidence.

Materials and Methods

Experimental Timeline

The experiment was conducted in a greenhouse using certified potato minitubers of cv. Sante. Minitubers were first sprouted under dark conditions at 15–21°C for 12 days and subsequently transferred to indirect light for 7 days to promote the development of vigorous sprouts. Sprouted minitubers were then planted in pots containing a 1:1 (v/v) mixture of washed sand and perlite and grown under greenhouse conditions.

Throughout the growth cycle, plants received nutrient solutions containing the designated phosphorus (P) and calcium (Ca) concentrations. The nutrient solutions were renewed periodically to maintain nutrient availability and solution quality. Tubers were harvested at physiological maturity and subsequently washed, graded, and evaluated for tuber quality traits, including specific gravity and dry matter content. Tuber peel tissues were collected for phenolic compound extraction and HPLC analysis.

For the storage experiment, harvested tubers were subjected to simulated mechanical handling stress by repeated dropping from a height of 63 cm. The treated tubers were subsequently stored under either cold-storage conditions (5°C for 6 months) or ambient-storage conditions (20°C for 3 months). At the end of the respective storage periods, tubers were evaluated for bruising incidence and other storage-related traits.

Plant Material and Growth Conditions

The experiment was conducted in the greenhouse facilities of the Faculty of Agriculture, University of Tehran, Iran. Certified potato (*Solanum tuberosum* L.) minitubers of cv. Sante were used as plant material. Sante is a relatively early-maturing cultivar with high yield potential, good storage ability, moderate dry matter content, and relatively low production of undersized tubers. Virus-free minitubers were obtained from Isfahan Anbooh Kesht Company (Isfahan, Iran). The minitubers had been produced through micropropagation of stem cuttings and certified by the Iranian Seed and Plant Certification and Registration Institute. Tubers were uniform in physiological age and size, with a diameter of 20–25 mm.

Minitubers were sprouted under dark conditions at 15–21°C for 12 days and subsequently maintained under indirect light for 7 days. Sprouted minitubers were planted at a depth of approximately 6 cm in 20 × 20 cm plastic pots containing a 1:1 (v/v) mixture of washed sand and perlite. The substrate was placed to a depth of approximately 12 cm. To reduce excessive heating of the root zone under greenhouse conditions, all pots were painted white.

Experimental Design and Nutrient Treatments

The experiment was arranged as a 3 × 3 factorial based on a completely randomized design (CRD) with three replications. Nine treatment combinations were generated from three phosphorus concentrations (21, 42, and 63 mg L⁻¹ P) and three calcium concentrations (120, 180, and 240 mg L⁻¹ Ca). A total of 27 experimental units were established. Each pot contained one sprouted minituber and was considered a subsample within the experimental unit.

Plants were cultivated in an open hydroponic system using 20 × 20 cm plastic pots filled with a 1:1 (v/v) mixture of washed sand and perlite. Pots were filled to a depth of approximately 12 cm. Sprouted minitubers were placed on the substrate surface and covered with the same substrate mixture to achieve a planting depth of approximately 6 cm. To minimize root-zone heat stress, all pots were painted white.

Nutrient Solution Composition

A basal nutrient solution was prepared to provide all essential macro- and micronutrients required for potato growth (Table 1). The target phosphorus (P) concentrations were 21, 42, and 63 mg L⁻¹, whereas

calcium (Ca) concentrations were 120, 180, and 240 mg L⁻¹, resulting in nine P × Ca treatment combinations. The concentrations of the other macronutrients were maintained constant across all treatments at 160 mg L⁻¹ N, 239 mg L⁻¹ K, 38 mg L⁻¹ Mg, and 40 mg L⁻¹ S. Micronutrient concentrations were also maintained constant among treatments using a commercial oligoelement mixture (Oligo Azoron®), which provided Fe, Zn, Cu, Mo, Mn, and B at the required concentrations.

The target P and Ca concentrations were achieved by adjusting the proportions of H₃PO₄, KH₂PO₄, and Ca(NO₃)₂·4H₂O, respectively. Because KH₂PO₄ and Ca(NO₃)₂·4H₂O also supply K and N, respectively, the amounts of the other N- and K-containing fertilizer salts were adjusted correspondingly to compensate for these contributions and maintain constant final concentrations of N and K across all treatments. Specifically, K supplied by KH₂PO₄ was accounted for when determining the amounts of KNO₃ and K₂SO₄, while N supplied by Ca(NO₃)₂·4H₂O was accounted for when determining the amounts of KNO₃ and NH₄NO₃. The quantities of MgSO₄·7H₂O and sulfur-containing fertilizers were likewise calculated to maintain the target Mg and S concentrations.

All fertilizer quantities were calculated on an elemental nutrient basis, and the final nutrient concentrations were expressed as mg L⁻¹ of the respective elements. Analytical-grade fertilizer salts were dissolved separately and combined to prepare the final nutrient solutions. Phosphate-containing and calcium-containing stock solutions were prepared separately from concentrated stock solutions to minimize precipitation and undesirable chemical interactions. Nutrient solutions were prepared using purified water and renewed periodically throughout the experiment. The pH and electrical conductivity (EC) were maintained at 5.8–6.2 and 2–3 dS m⁻¹, respectively.

Table 1
Composition of the basal nutrient solution applied in the experiment

Component	B	Mn	Mo	Cu	Zn	Fe	S	Mg	Ca	K	P	N
Concentration in nutrient solution (mg L ⁻¹)	–	–	–	–	–	–	40	38	180	239	42	160
Concentration in micronutrient stock solution (w/w %)	1.5	3.0	0.05	0.6	4.0	4.0	–	–	–	–	–	–

Table 2
Fertilizer salts used for preparation of the nutrient solutions and the nutrients supplied by each source.

Nutrients supplied	Chemical formula	Fertilizer source
Ca, N	$\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	Calcium nitrate
K, N	KNO_3	Potassium nitrate
N	NH_4NO_3	Ammonium nitrate
K, P	KH_2PO_4	Monopotassium phosphate
K, S	K_2SO_4	Potassium sulfate
Mg, S	$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	Magnesium sulfate
P	H_3PO_4	Phosphoric acid
N	HNO_3	Nitric acid
S	H_2SO_4	Sulfuric acid
Fe, Zn, Cu, Mo, Mn, B	–	Oligo Azoron® micronutrient mixture

Extraction and Quantification of Phenolic Compounds

Four tubers from each experimental unit were pooled to form one composite sample for phenolic analysis. Tubers were washed, peeled, and the peel tissues were freeze-dried for 48 h. Dried tissues were ground to a fine powder and passed through a 1-mm sieve.

Approximately 200 mg of powdered sample was transferred into a 1.5-mL microcentrifuge tube. One milliliter of extraction solvent consisting of methanol:acetone:distilled water (7:7:1, v/v/v) was added to each tube. Samples were vortexed and sonicated for 5 min, followed by shaking at 160 rpm on ice for 20 min.

Samples were centrifuged at 5000 rpm for 5 min and the supernatant was collected. The extraction procedure was repeated three times. Combined extracts were evaporated under a laminar airflow hood at room temperature and the residue was re-dissolved in 1 mL sterile ultrapure water. Samples were filtered through 0.45- μm syringe filters and stored at 4°C until analysis.

HPLC Analysis

Phenolic compounds were identified and quantified using high-performance liquid chromatography (HPLC) following the method described by Negzad et al. (2014) with minor modifications. Analyses were performed using a Knauer HPLC system (Knauer GmbH, Berlin, Germany) equipped with a reverse-phase

C18 column (2.1 × 50 mm, 1.7 µm particle size) and a UV–Visible detector. The column temperature was maintained at 30°C throughout the analysis.

The mobile water (solvent phase consisted of ultrapure A) and acetonitrile (solvent B; Sigma-Aldrich, St. Louis, MO, USA). The flow rate was maintained at 0.20 mL min⁻¹. Prior to injection, extracts were diluted with ultrapure water (1:2, v/v) and filtered through 0.45-µm membrane filters. A 2-µL aliquot of each sample was injected into the HPLC system.

Detection was carried out at wavelengths of 325 and 340 nm. Chlorogenic acid, caffeic acid, and ferulic acid were identified by comparing the retention times and UV absorption spectra of sample peaks with those of authentic analytical standards (Sigma-Aldrich). Quantification was performed using external calibration curves prepared from standard solutions of each compound. The calibration curves showed good linearity over the concentration ranges used ($R^2 > 0.99$). Phenolic compound concentrations were expressed on a dry weight basis as mg g⁻¹ DW

Evaluation of Storage Performance

To investigate the effects of maternal phosphorus and calcium nutrition on tuber storability and resistance to mechanical damage, harvested tubers were subjected to simulated harvesting and handling operations based on the impact assessment approach described by Li et al. (2022). Twenty-four tubers from each treatment were repeatedly dropped from a height of 63 cm into a wooden container to induce mechanical stress similar to commercial handling conditions.

Following mechanical stress treatment, tubers produced under the nine P × Ca nutritional treatments were divided between two storage conditions: cold storage at 5°C for 6 months and ambient storage at 20°C for 3 months.

Storage temperature was included as an additional fixed factor in the statistical model for storage-related traits.

Assessment of Bruising Incidence

Twenty-four tubers per treatment were used for storage evaluation. Following storage, four randomly selected tubers from each replicate were assessed for bruising incidence. Tubers were cut longitudinally and visually inspected for symptoms of blackspot bruising and internal tissue damage. Bruising was defined as the presence of brown, gray, or black discoloration, hollow tissue, or abnormal starch deposition with a diameter of at least 3 mm, typically occurring outside the vascular ring (Hausladen, et al. 2009). Tubers exhibiting one or more symptoms were classified as bruised. Bruising incidence was expressed as the percentage of bruised tubers relative to the total number of tubers evaluated.

Statistical Analysis

All statistical analyses were performed using SAS version 9.4 (SAS Institute Inc., Cary, NC, USA). For tuber production and quality traits, data were analyzed using a two-way factorial analysis of variance with P concentration, Ca concentration, and their interaction as fixed effects. For storage-related traits, storage temperature was included as an additional fixed factor, resulting in a three-way factorial model with P concentration, Ca concentration, storage temperature, and their interactions as fixed effects. The experimental unit was considered the replicate used for each treatment. Where multiple tubers were evaluated within an experimental unit, measurements were summarized at the experimental-unit level before statistical analysis to avoid pseudoreplication.

When significant treatment effects were detected, means were compared using Duncan's multiple range test at the 5% probability level. Pearson's correlation coefficients (r) were calculated to evaluate linear associations among tuber quality traits, phenolic compounds, bruising incidence, and storage-related characteristics. Statistical significance was declared at $P \leq 0.05$.

Results

Effects of phosphorus and calcium nutrition on tuber physical quality

Analysis of variance showed that phosphorus significantly affected tuber specific gravity ($P \leq 0.01$), dry matter content ($P \leq 0.001$), and bruising incidence following storage at both 5 and 20°C ($P \leq 0.05$). In contrast, calcium had no significant main effect on these variables. A significant phosphorus × calcium interaction was detected for bruising incidence after storage at 5°C, indicating that the response of bruising incidence to calcium depended on the phosphorus treatment. No significant phosphorus × calcium interaction was detected for the other physical quality traits evaluated (Table 3).

Table 3
Analysis of variance (mean squares) for tuber quality, and storability of seed potato as affected by phosphorus and calcium nutrition.

Source of variation	df	Specific gravity	Dry matter(%)	Bruising (%) at 5°C	Bruising(%) at 20°C
Phosphorus (P)	2	0.001	27.43	7500.00	8611.11
Calcium (Ca)	2	0.00003 ^{ns}	0.96 ^{ns}	0.00 ^{ns}	1111.11 ^{ns}
P × Ca	4	0.00036 ^{ns}	3.06 ^{ns}	5000.00	277.78 ^{ns}
Error	24	0.0028	3.26	1041.67	1828.70
Note: ns, not significant;; and significant at $P \leq 0.05$, 0.01, and 0.001, respectively.					

Mean comparisons further showed that phosphorus significantly affected tuber specific gravity, dry matter content, and bruising incidence (Table 4). Tubers supplied with 42 mg L⁻¹ phosphorus had the

highest specific gravity (1.114) and dry matter content (28.25%), whereas both the 21 and 63 mg L⁻¹ treatments resulted in lower values. Compared with the 21 mg L⁻¹ treatment, application of 42 mg L⁻¹ phosphorus increased specific gravity by approximately 1.18% and dry matter content by 10.99%. Bruising incidence showed an inverse response to phosphorus supply. Under the 21 mg L⁻¹ phosphorus treatment, bruising incidence was 58.33% and 91.67% after storage at 5 and 20°C, respectively. Increasing phosphorus to 42 mg L⁻¹ reduced bruising incidence to 8.33% at 5°C and 41.67% at 20°C. At 63 mg L⁻¹ phosphorus, bruising incidence increased relative to the 42 mg L⁻¹ treatment but remained lower than that observed under phosphorus deficiency.

Table 4
Effects of phosphorus concentration in nutrient solution on tuber specific gravity, dry matter content, and bruising incidence of seed potato tubers.

Phosphorus (mg L ⁻¹)	Specific gravity	Dry matter (%)	Bruising (%) at 5°C	Bruising (%) at 20°C
21	1.101 b	25.45 b	58.33 a	91.67 a
42	1.114 a	28.25 a	8.33 b	41.67 b
63	1.106 b	26.66 b	33.33 ab	50 b

. Means followed by different letters within a column are significantly different according to LSD test at $P \leq 0.05$.

The phosphorus × calcium interaction significantly affected bruising incidence after storage at 5°C (Fig. 1). Among the treatment combinations, P2C2 resulted in the lowest bruising incidence, whereas treatments receiving 21 mg L⁻¹ phosphorus showed the highest bruising incidence across calcium levels. Under the 42 mg L⁻¹ phosphorus treatment, the intermediate calcium level was associated with lower bruising incidence than the deficient or excessive calcium treatments.

(P1, P2 and P3, Phosphorus concentration of 21, 42 and 63 PPM; C1, C2 and C3, calcium concentration of 120, 180 and 240 PPM in nutrient solution)

Within each chart, treatments with at least one letter in common do not differ significantly at the 5% probability level according to the LSD test

Relationships among dry matter content, specific gravity, and bruising incidence

Linear regression analysis revealed a strong negative relationship between dry matter content and bruising incidence (Fig. 2A; $R^2 = 0.994$), indicating that bruising incidence decreased consistently with increasing dry matter content across the phosphorus treatments. Similarly, bruising incidence showed a strong negative linear relationship with specific gravity (Fig. 2B; $R^2 = 0.983$). A strong positive linear relationship was also observed between specific gravity and dry matter content (Fig. 2C; $R^2 = 0.997$),

indicating that these two measures of tuber composition changed closely together across the phosphorus treatments.

Figure 2A. Linear relationship between tuber dry matter content (%) and bruising incidence (%) of seed potato tubers as affected by phosphorus nutrition. The fitted regression equation was $y = 508.74 - 17.75x$ ($R^2 = 0.994$).

Figure 2B. Linear relationship between tuber specific gravity and bruising incidence (%) of seed potato tubers as affected by phosphorus nutrition. The fitted regression equation was $y = 4216.76 - 3779.07x$ ($R^2 = 0.983$).

Figure 2C. Linear relationship between tuber specific gravity and dry matter content (%) of seed potato tubers as affected by phosphorus nutrition. The fitted regression equation was $y = -209.93 + 213.84x$ ($R^2 = 0.997$).

Pearson correlation analysis supported the regression results (Table 5). Dry matter content was positively correlated with specific gravity ($r = 0.970$) and negatively correlated with bruising incidence. Chlorogenic acid and caffeic acid were positively correlated with dry matter content and specific gravity and negatively correlated with bruising incidence. The strongest correlation was observed between chlorogenic acid and caffeic acid ($r = 0.981$), indicating that their concentrations showed closely related patterns across the nutrient treatments.

Table 5
Pearson correlation analysis between dry matter content, specific gravity, bruising, chlorogenic and caffeic acid.

Trait	Dry Matter	Specific Gravity	Bruising	Chlorogenic Acid	Caffeic Acid
Dry Matter	1.000				
Specific Gravity	0.970	1.000			
Bruising	-0.534	-0.393	1.000		
Chlorogenic Acid	0.406	0.335	-0.650	1.000	
Caffeic Acid	0.427	0.341	-0.633	0.981	1.000

Correlation analysis confirmed these findings (Table 5). Dry matter content was positively correlated with specific gravity and negatively correlated with bruising incidence. Together, these results suggest that dry matter content and specific gravity may serve as reliable physiological indicators of tuber storability and resistance to postharvest mechanical damage.

Effects of phosphorus and calcium nutrition on phenolic compounds

Analysis of variance revealed significant effects of phosphorus, calcium, and their interaction on chlorogenic acid and caffeic acid concentrations ($P \leq 0.001$), whereas ferulic acid concentration was not significantly affected by the nutrient treatments (Table 6). The significant phosphorus $\times$ calcium interactions indicated that the effects of phosphorus and calcium on chlorogenic acid and caffeic acid concentrations depended on the level of the other nutrient.

Table 6
Analysis of variance (mean squares) for phenolic traits of seed potato as affected by phosphorus and calcium nutrition.

Source of variation	df	Chlorogenic acid	Caffeic acid	Ferulic acid
Phosphorus (P)	2	0.0369	0.0348	0.00003 ^{ns}
Calcium (Ca)	2	0.0183	0.0201	0.00013 ^{ns}
P $\times$ Ca	4	0.0202	0.0162	0.00007 ^{ns}
Error	16	0.0003	0.0002	0.00005
Note: ns, not significant;, and significant at $P \leq 0.05$, 0.01, and 0.001, respectively.				

Mean comparisons further showed that the phosphorus $\times$ calcium interaction significantly affected both chlorogenic acid and caffeic acid concentrations (Fig. 3). The highest concentrations of both compounds were observed under the P2C2 treatment, whereas the lowest concentrations generally occurred under phosphorus-deficient treatments. Increasing phosphorus beyond the intermediate level reduced both chlorogenic acid and caffeic acid concentrations relative to P2. For caffeic acid, the highest concentration was also observed under P2C2, while phosphorus-deficient and excessive-phosphorus treatments resulted in lower concentrations across calcium levels. Differences among calcium levels were more evident under P2 than under phosphorus-deficient conditions.

(P1, P2 and P3, Phosphorus concentration of 21, 42 and 63 PPM; C1, C2 and C3, calcium concentration of 120, 180 and 240 PPM in nutrient solution)

Within each chart, treatments with at least one letter in common do not differ significantly at the 5% probability level according to the LSD test.

Overall treatment response

Collectively, the results presented in Tables 3–6 and Figs. 1–3 showed that phosphorus had significant effects on several measured tuber quality traits, including specific gravity, dry matter content, and bruising incidence. Calcium did not show significant main effects on these physical quality traits but significantly interacted with phosphorus for bruising incidence after storage at 5°C. The intermediate phosphorus treatment (42 mg L⁻¹), particularly when combined with the intermediate calcium treatment (P2C2), was associated with the highest specific gravity and dry matter content, the highest chlorogenic acid and caffeic acid concentrations, and the lowest bruising incidence under the conditions evaluated

Discussion

Phosphorus regulation of dry matter accumulation and specific gravity

The present study demonstrated that phosphorus nutrition significantly affected tuber dry matter content and specific gravity and was associated with lower bruising incidence. These findings indicate that phosphorus availability during tuber development can influence tuber compositional characteristics and, consequently, quality traits relevant to postharvest handling. This interpretation is consistent with recent evidence showing that phosphorus supply can affect multiple potato tuber quality attributes, including dry matter, starch, and soluble sugar concentrations, and that the response of yield and quality to phosphorus supply may not be linear (Kong et al. 2026).

Phosphorus is involved in energy metabolism, photosynthetic carbon assimilation, carbohydrate transport, and processes associated with tuber development. Adequate phosphorus availability can influence assimilate partitioning toward developing tubers and affect carbohydrate metabolism and starch formation (López-Arredondo et al. 2014; Sonnewald and Fernie 2018). In potato, cultivar-dependent responses to phosphorus availability have also been associated with changes in tuber yield, dry matter, starch concentration, and carbon metabolism (Chea et al. 2021). More recently, organ-specific transcriptomic and metabolic responses to limited phosphate availability have demonstrated that phosphate status modifies metabolic processes before and after tuberization (Nasr Esfahani et al. 2025). Consistent with these observations, a recent three-year field study showed that phosphorus application significantly affected potato dry matter and starch content, supporting the importance of phosphorus management for balancing tuber yield and quality (Kong et al. 2026).

These physiological relationships provide a plausible basis for the higher dry matter content and specific gravity observed under the optimum phosphorus treatment in the present study. However, starch content and starch biosynthetic activity were not directly measured. Therefore, the increases in dry matter content and specific gravity should not be interpreted as direct evidence of enhanced starch biosynthesis. Rather, the observed response is consistent with previous evidence linking phosphorus nutrition with tuber starch accumulation and dry matter formation (Chea et al. 2021; Kong et al. 2026). Recent research has further shown that phosphorus fertilizer reduction can alter starch accumulation characteristics and the activities of enzymes involved in starch biosynthesis, although these responses are strongly dependent on the experimental environment and fertilizer regime.

The non-linear response observed at the highest phosphorus level is also consistent with the cultivar- and nutritional-status-dependent response of potato to phosphorus availability (Chea et al. 2021). Importantly, the recent work of Kong et al. (2026) similarly demonstrated that phosphorus application rates affected different quality traits in different ways and that an optimum phosphorus supply should be considered in relation to the simultaneous effects on yield and quality. Thus, the intermediate

phosphorus level producing the highest dry matter and specific gravity in the present experiment should be interpreted as an experimental optimum rather than as a universal phosphorus recommendation.

Calcium nutrition and tuber bruising susceptibility

Calcium had a comparatively limited effect on dry matter accumulation but was more closely associated with bruising susceptibility through its interaction with phosphorus. The significant phosphorus × calcium interaction indicates that the response of tuber bruising to calcium depended, at least in part, on phosphorus nutritional status. Such an interaction is biologically plausible because mineral nutrition can influence tuber tissue properties and quality through multiple, interconnected processes rather than through independent effects of individual nutrients (Naumann et al. 2020; Palta 2010).

Calcium is an important structural and signaling element in plant tissues and contributes to cell-wall organization, membrane stability, and cellular regulation (White and Broadley 2003; Wang et al. 2023). In potato, targeted calcium nutrition has been proposed as an important component of tuber quality management, and increased tuber calcium concentration has previously been associated with reduced blackspot bruise incidence (Palta 2010; Karlsson et al. 2006). These observations provide a plausible physiological basis for the association between calcium nutrition and bruising susceptibility observed in the present study.

Nevertheless, the mechanisms responsible for the observed calcium response cannot be established from the present measurements. Cell-wall composition, pectin structure, calcium–pectate interactions, membrane integrity, and tissue mechanical properties were not directly measured. Therefore, the present results support an association between calcium nutrition and bruising response rather than demonstrating a specific structural mechanism. This distinction is particularly important because bruising susceptibility is influenced not only by tissue properties but also by cultivar, impact conditions, and temperature during the postharvest period (Hendricks et al. 2026).

The phosphorus × calcium interaction may therefore reflect the combined influence of nutrient status on tuber development and tissue characteristics. However, this interpretation remains a physiological hypothesis and requires direct measurements of calcium distribution, cell-wall properties, tissue firmness, membrane integrity, and mechanical resistance to confirm the underlying mechanism.

Relationships among dry matter, specific gravity, and bruising

The strong relationships among dry matter content, specific gravity, and bruising incidence provide quantitative evidence that tuber compositional characteristics were associated with bruising susceptibility under the conditions of the present experiment. Dry matter and specific gravity are widely used indicators of potato tuber composition and processing quality, and their relationship with starch concentration is well established (Simmonds 1977; Naumann et al. 2020). Recent research continues to identify dry matter as an important trait for potato processing quality and productivity, while specific gravity remains a practical indicator of tuber composition (Kaur et al. 2026).

In the present study, higher dry matter content and specific gravity were associated with lower bruising incidence. This pattern suggests that differences in tuber composition and physical properties may contribute to variation in bruising susceptibility. However, the correlation and regression analyses do not establish causality between phosphorus nutrition, carbon allocation, and reduced bruising. Because starch concentration was not directly determined, these relationships should be interpreted as associations among measured quality traits rather than as direct evidence that phosphorus-induced starch accumulation increased resistance to bruising.

Moreover, bruising susceptibility is affected by several factors beyond tuber composition. Recent experimental work demonstrated that cultivar, impact height, and temperature after impact can substantially influence the development and expression of blackspot and shatter bruises (Hendricks et al. 2026). Therefore, the negative relationships between dry matter or specific gravity and bruising observed in the present study should be considered specific to the tested cultivars, nutritional treatments, storage conditions, and experimental bruising assessment.

The particularly strong relationship between dry matter content and specific gravity supports their use as complementary indicators of tuber composition. Their negative relationships with bruising suggest that these readily measurable traits may have potential as indicators of bruising susceptibility under the conditions evaluated. However, further studies combining these measurements with direct mechanical and structural assessments would be required before using dry matter or specific gravity as predictive indicators of bruising risk across cultivars and production environments.

Phosphorus and calcium effects on tuber phenolic composition

Phosphorus and calcium significantly affected chlorogenic acid and caffeic acid concentrations, and the phosphorus × calcium interaction was also significant, whereas ferulic acid was not significantly affected by the nutrient treatments. These results indicate that phenolic accumulation in potato tubers responded selectively to phosphorus and calcium nutrition rather than showing a uniform response across all measured phenolic compounds.

Chlorogenic acid and caffeic acid are important phenolic compounds in potato, with chlorogenic acid generally representing a major phenolic component of tubers (Friedman 1997; Navarre et al. 2011). Phenolic metabolism is also closely associated with responses to tissue injury. Following mechanical wounding, potato tubers can accumulate phenolic compounds, including chlorogenic and ferulic acids, as part of the wound-response and protective metabolism (Dogramaci et al. 2024).

The increases in chlorogenic and caffeic acids observed under particular phosphorus × calcium combinations may therefore reflect changes in secondary metabolism associated with nutritional status. However, the present study measured phenolic concentrations rather than antioxidant capacity, enzyme activities, reactive oxygen species, or other direct indicators of oxidative stress. Consequently, higher

chlorogenic and caffeic acid concentrations cannot by themselves be interpreted as evidence of enhanced antioxidant protection or reduced oxidative damage.

Recent evidence supports the functional relevance of chlorogenic acid in potato wound and postharvest responses. You et al. (2024) reported that exogenous chlorogenic acid inhibited browning in fresh-cut potato tissue and was associated with activation of ROS-scavenging responses, suggesting that chlorogenic acid can participate in mechanisms related to oxidative protection and quality preservation. Nevertheless, because chlorogenic acid was not externally applied and oxidative responses were not measured in the present study, these findings should be used only as physiological context rather than as evidence of causality.

The negative correlations of chlorogenic acid and caffeic acid with bruising incidence further indicate an association between phenolic composition and bruising susceptibility. Mechanical injury is known to initiate biochemical changes involving phenolic compounds and oxidation processes in potato tissues, and recent work has demonstrated substantial changes in phenolic metabolites following tuber wounding (Dogramaci et al. 2024). However, the correlations observed here do not establish that higher phenolic concentrations directly reduced bruising. Establishing a functional contribution would require measurements of polyphenol oxidase activity, antioxidant capacity, ROS accumulation, and temporal changes in phenolic metabolites following mechanical injury.

The absence of a significant response in ferulic acid further suggests that nutrient effects on phenolic metabolism were compound-specific. This selective response may reflect differences among phenolic biosynthetic pathways, their metabolic regulation, or their roles during tuber development and wound responses. Direct measurement of pathway-related enzymes and metabolites would be necessary to determine the basis of this differential response.

Integrated interpretation and practical implications

Taken together, the results indicate that phosphorus and calcium influenced different but interconnected aspects of potato tuber quality. Phosphorus had clearer effects on dry matter content and specific gravity, whereas calcium was more closely associated with bruising susceptibility through its interaction with phosphorus. The combined nutrient treatments also influenced chlorogenic acid and caffeic acid concentrations.

These findings support an integrated interpretation in which phosphorus nutrition was primarily related to tuber compositional characteristics, whereas calcium modified selected responses related to bruising depending on phosphorus availability. This interpretation is consistent with recent evidence showing that phosphorus fertilization can simultaneously influence potato yield, dry matter, starch, sugars, and other quality traits, emphasizing the need to optimize rather than simply maximize phosphorus supply (Kong et al. 2026).

The significant phosphorus × calcium interactions indicate that the two nutrients should not necessarily be considered independently when interpreting tuber quality responses. Nevertheless, the present

experiment does not allow the determination of whether the interaction resulted from direct nutrient antagonism or synergy, altered nutrient uptake, changes in nutrient partitioning, or indirect effects on tuber development. Such mechanisms should be investigated through measurements of tissue nutrient concentrations and nutrient-use efficiency.

Although the results are consistent with physiological roles for phosphorus in carbon and carbohydrate metabolism and for calcium in tissue structure and stability, the underlying molecular and structural mechanisms were beyond the scope of the present measurements. In particular, measurements of starch-related traits, cell-wall properties, membrane integrity, tissue mechanical strength, and oxidative responses would be needed to test these mechanisms directly.

From an applied perspective, the results suggest that balanced phosphorus and calcium nutrition may contribute to improvement of selected potato tuber quality traits and may be associated with lower bruising susceptibility. However, the intermediate phosphorus level that produced the most favorable response in the present experiment should be regarded as an experimental optimum rather than a general fertilizer recommendation. Recent research similarly indicates that the optimal phosphorus supply depends on the desired balance between yield and multiple quality traits (Kong et al. 2026). Validation across cultivars, soil types, production systems, and environmental conditions is therefore necessary before broader agronomic recommendations can be made.

Study limitations and future perspectives

Several limitations of the present study should be acknowledged. The experiment established relationships between nutrient treatments and tuber quality traits, but the physiological and biochemical mechanisms underlying these responses were not directly assessed. In particular, starch and carbohydrate partitioning, cell-wall and membrane properties, tissue mechanical characteristics, and oxidative responses were not measured. Likewise, the relationships between phenolic concentrations and bruising susceptibility cannot be interpreted as evidence of direct causality.

Future studies should integrate phosphorus and calcium treatments with measurements of tuber nutrient concentrations, starch accumulation, carbohydrate partitioning, cell-wall composition, calcium localization, tissue mechanical properties, polyphenol oxidase activity, antioxidant capacity, and ROS metabolism. Temporal sampling following mechanical injury would also help distinguish pre-existing nutritional differences from biochemical responses induced by bruising. Recent work on wounded potato tissue demonstrates the value of combining phenolic profiling with antioxidant and structural measurements to understand postharvest wound responses (Dogramaci et al. 2024).

Future experiments should also evaluate multiple cultivars and environmental conditions. This is particularly important because both phosphorus-use responses and bruising susceptibility can be cultivar-dependent (Chea et al. 2021), while recent bruising research has demonstrated substantial effects of cultivar, impact conditions, and temperature on bruise development (Hendricks et al. 2026).

Such validation would help determine the consistency and practical relevance of the nutrient responses observed in the present experiment.

Conclusion

This study demonstrated that phosphorus and calcium nutrition influenced potato tuber quality, with distinct effects and significant interactions between the two nutrients. Phosphorus had the clearest effects on tuber dry matter content and specific gravity, with the intermediate phosphorus level (42 mg L⁻¹) producing the highest values and lower bruising incidence after storage. Dry matter content and specific gravity were strongly and negatively associated with bruising incidence, suggesting that these readily measurable traits may serve as useful indicators of bruising susceptibility under the conditions evaluated.

Calcium had limited effects on dry matter content and specific gravity as a main factor, but its effects were more evident through interactions with phosphorus, particularly for bruising incidence after storage at 5°C and for chlorogenic and caffeic acid concentrations. The highest concentrations of these phenolic compounds were generally observed under the intermediate phosphorus and calcium combination, whereas ferulic acid was not significantly affected by the nutrient treatments.

Overall, phosphorus nutrition was primarily related to tuber compositional characteristics, while calcium modified selected responses depending on phosphorus availability. These findings highlight the importance of considering phosphorus and calcium nutrition together when evaluating potato tuber quality and bruising susceptibility. Further studies incorporating direct measurements of starch accumulation, tissue mechanical properties, cell-wall characteristics, nutrient partitioning, and oxidative responses are needed to clarify the physiological mechanisms underlying these nutrient effects.

Declarations

Author Contribution

A wrote the main manuscript B and C reviewed the manuscript

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Figures

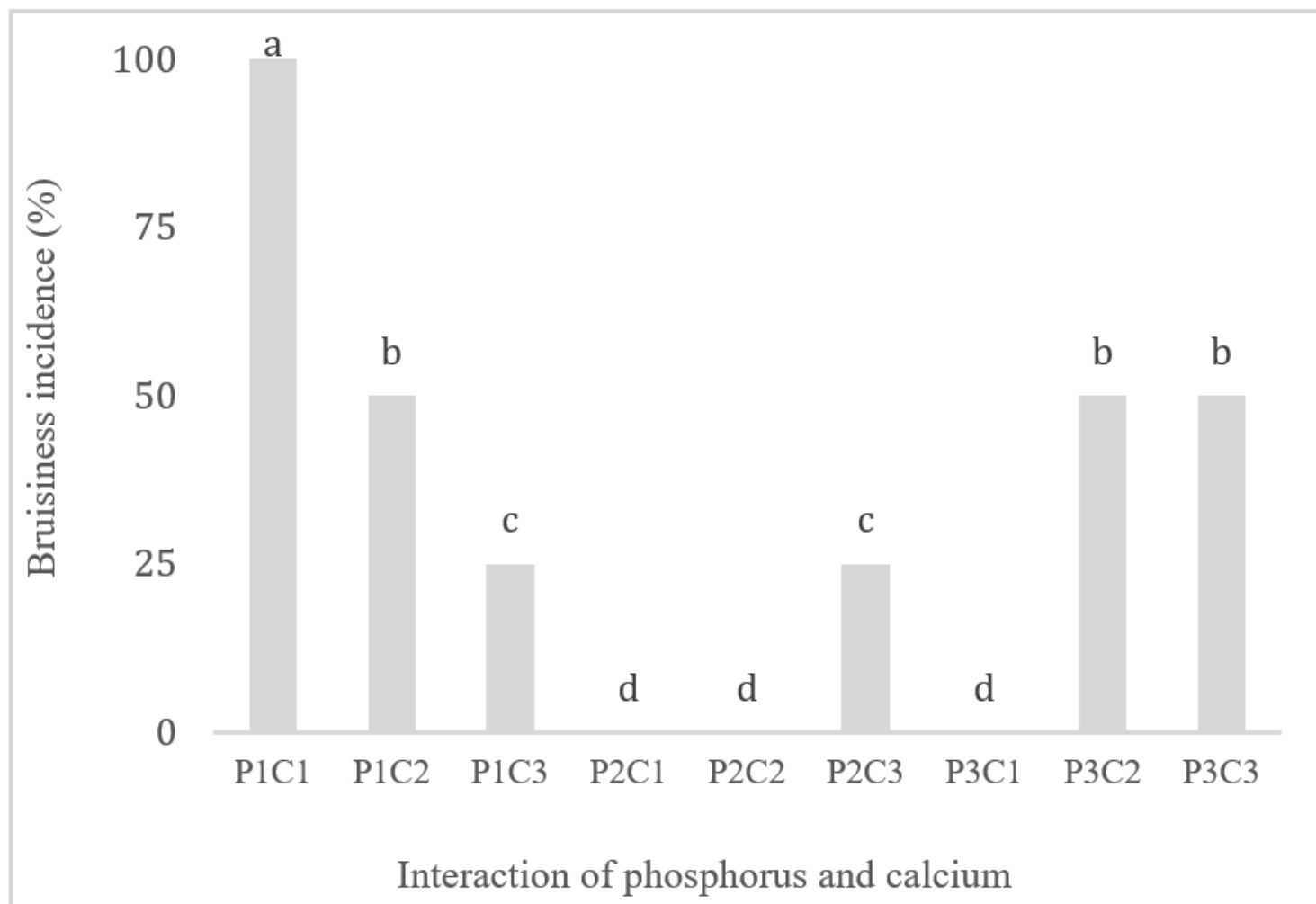


Figure 1

Interaction effects of phosphorus and calcium nutrition on bruising incidence of seed potato tubers after storage at 5°C.

(P1, P2 and P3, Phosphorus concentration of 21, 42 and 63 PPM; C1, C2 and C3, calcium concentration of 120, 180 and 240 PPM in nutrient solution)

Within each chart, treatments with at least one letter in common do not differ significantly at the 5% probability level according to the LSD test

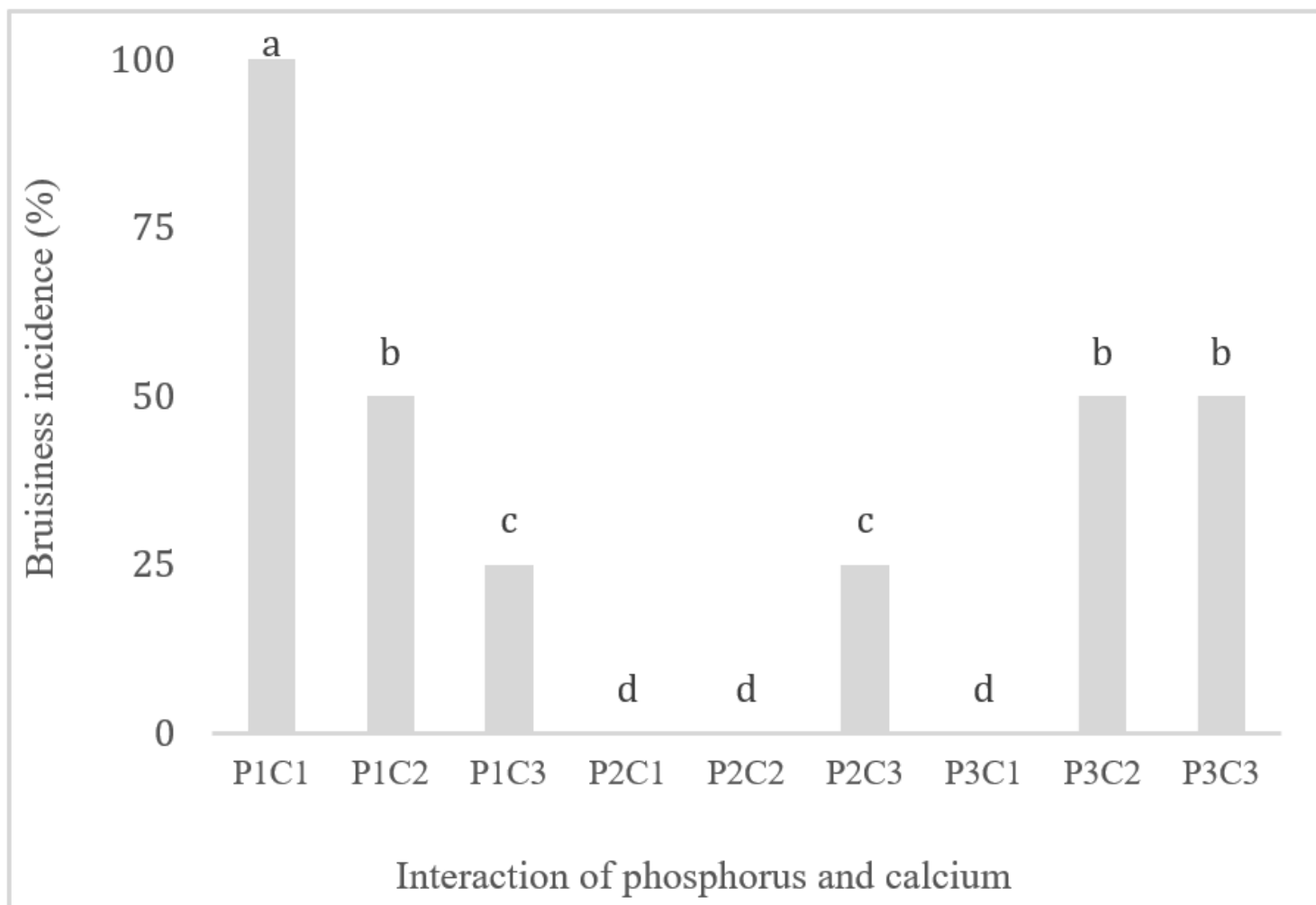


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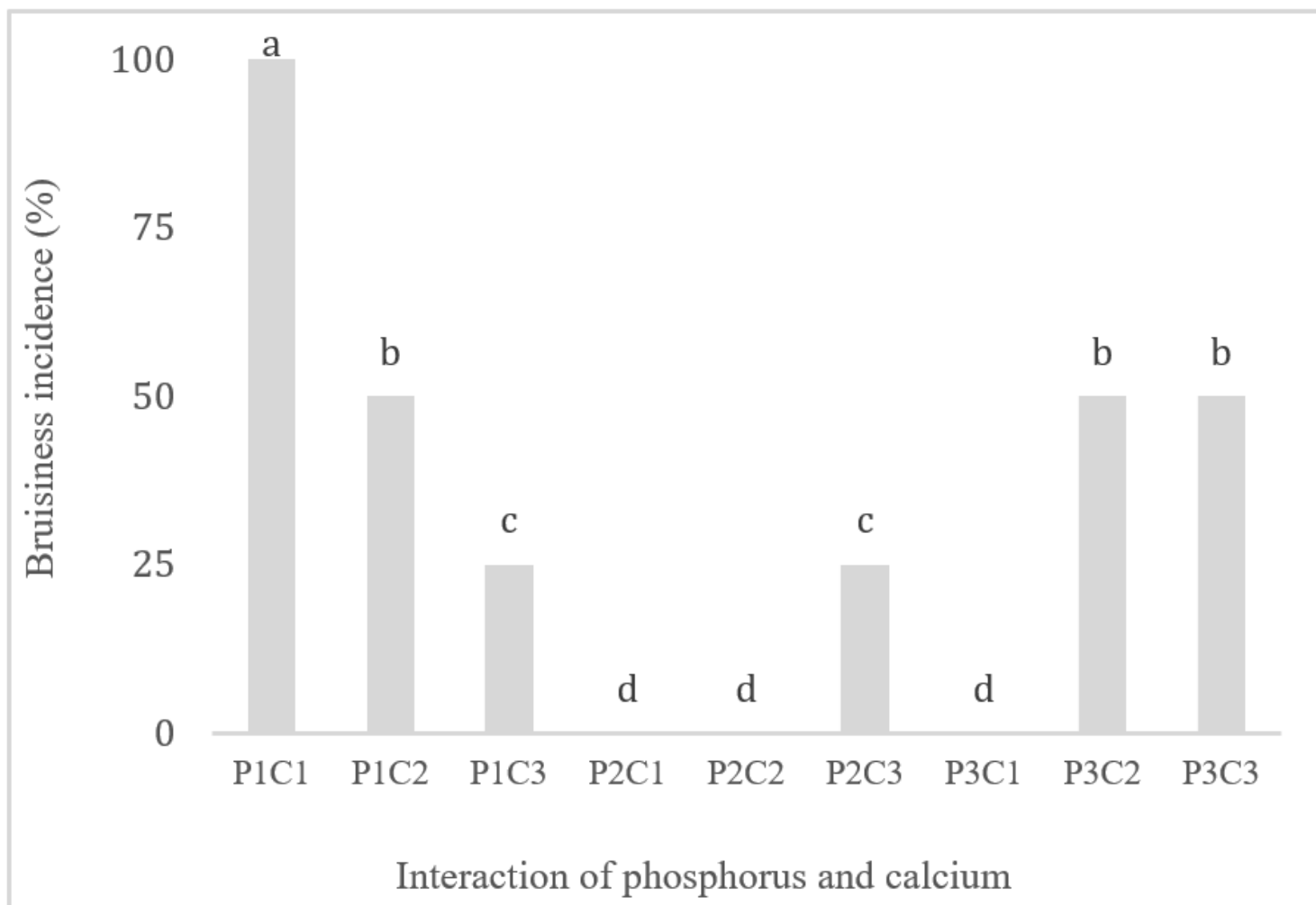


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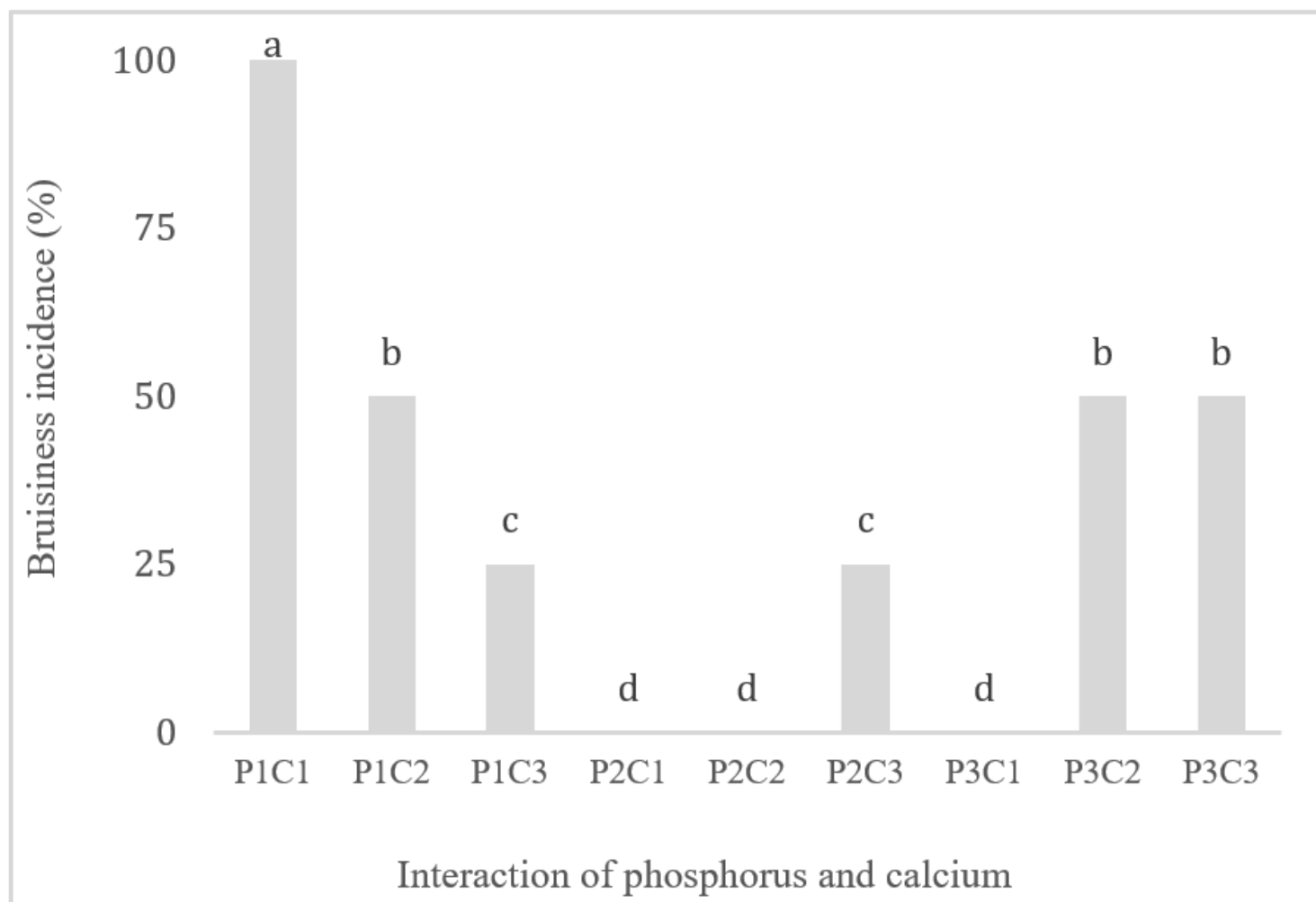


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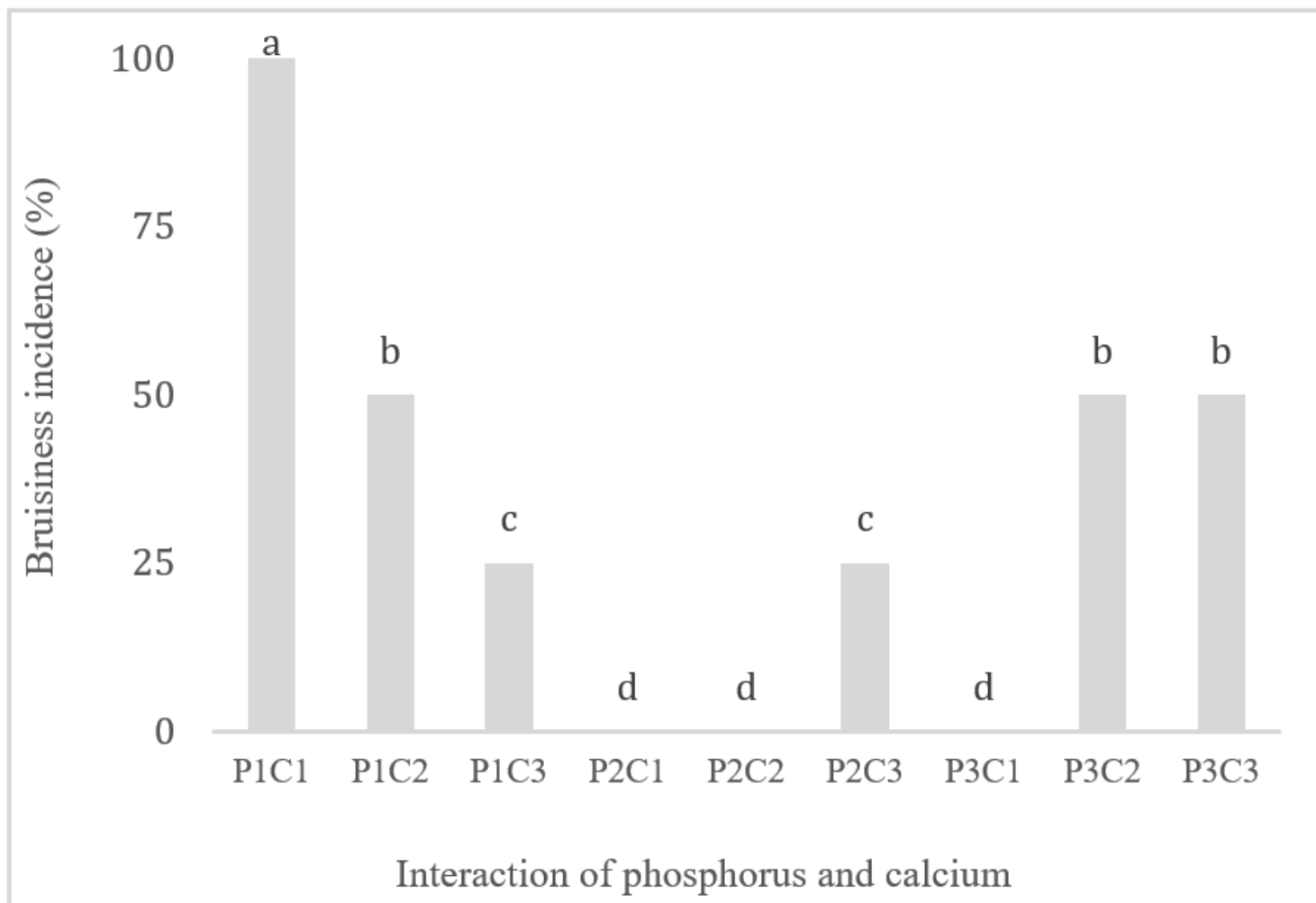


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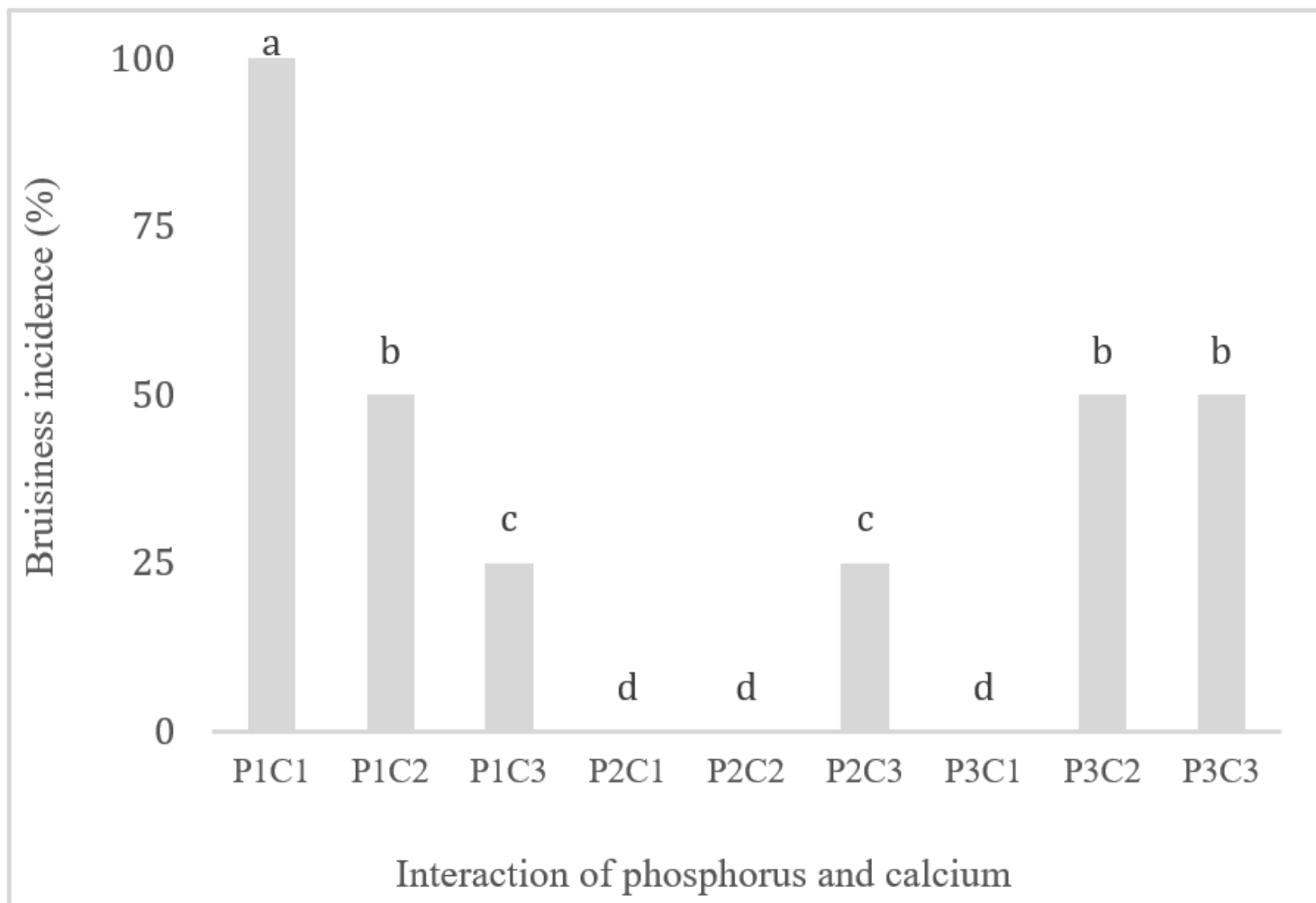


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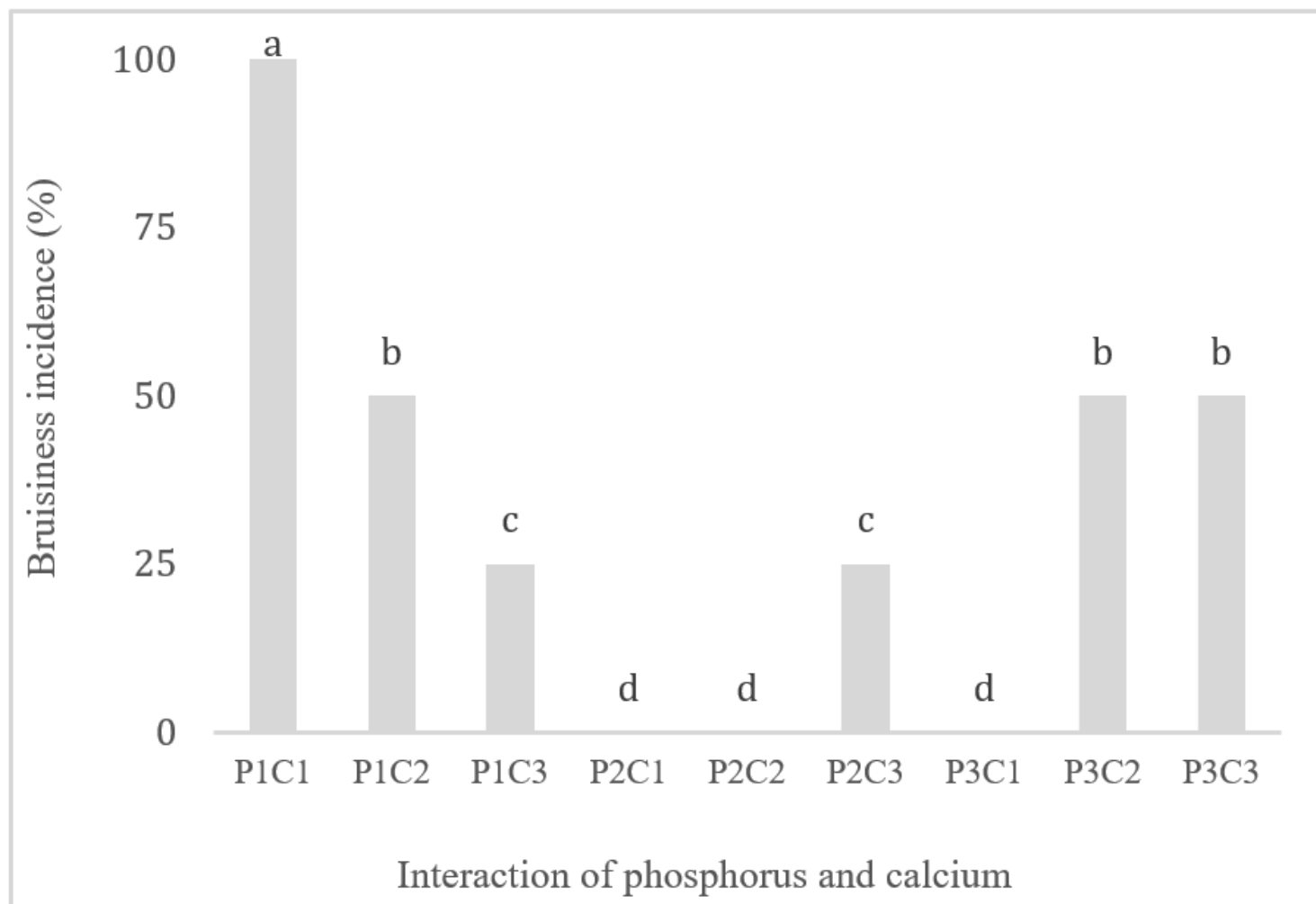


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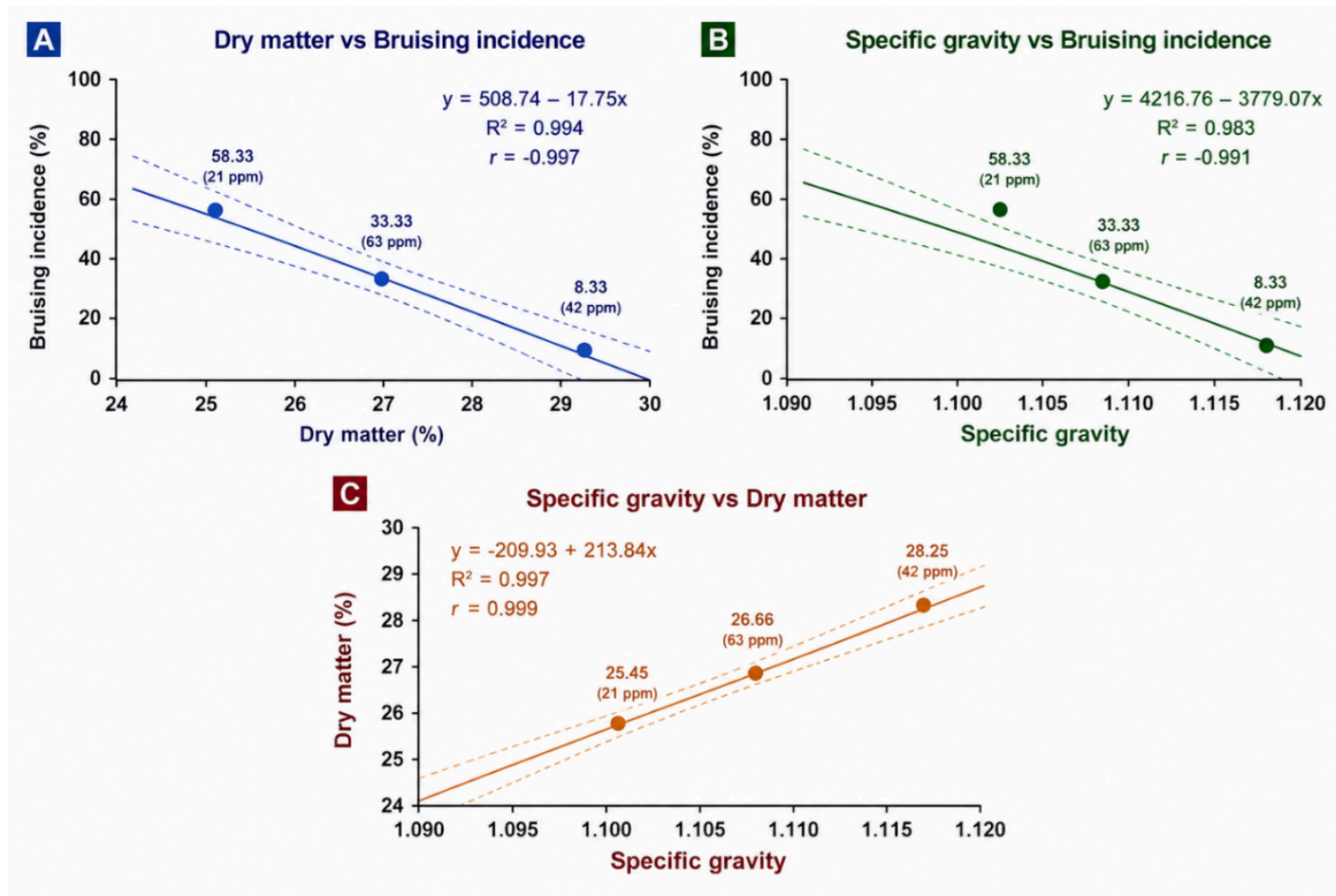


Figure 2

A. Linear relationship between tuber dry matter content (%) and bruising incidence (%) of seed potato tubers as affected by phosphorus nutrition. The fitted regression equation was $y = 508.74 - 17.75x$ ($R^2 = 0.994$).

B. Linear relationship between tuber specific gravity and bruising incidence (%) of seed potato tubers as affected by phosphorus nutrition. The fitted regression equation was $y = 4216.76 - 3779.07x$ ($R^2 = 0.983$).

C. Linear relationship between tuber specific gravity and dry matter content (%) of seed potato tubers as affected by phosphorus nutrition. The fitted regression equation was $y = -209.93 + 213.84x$ ($R^2 = 0.997$).

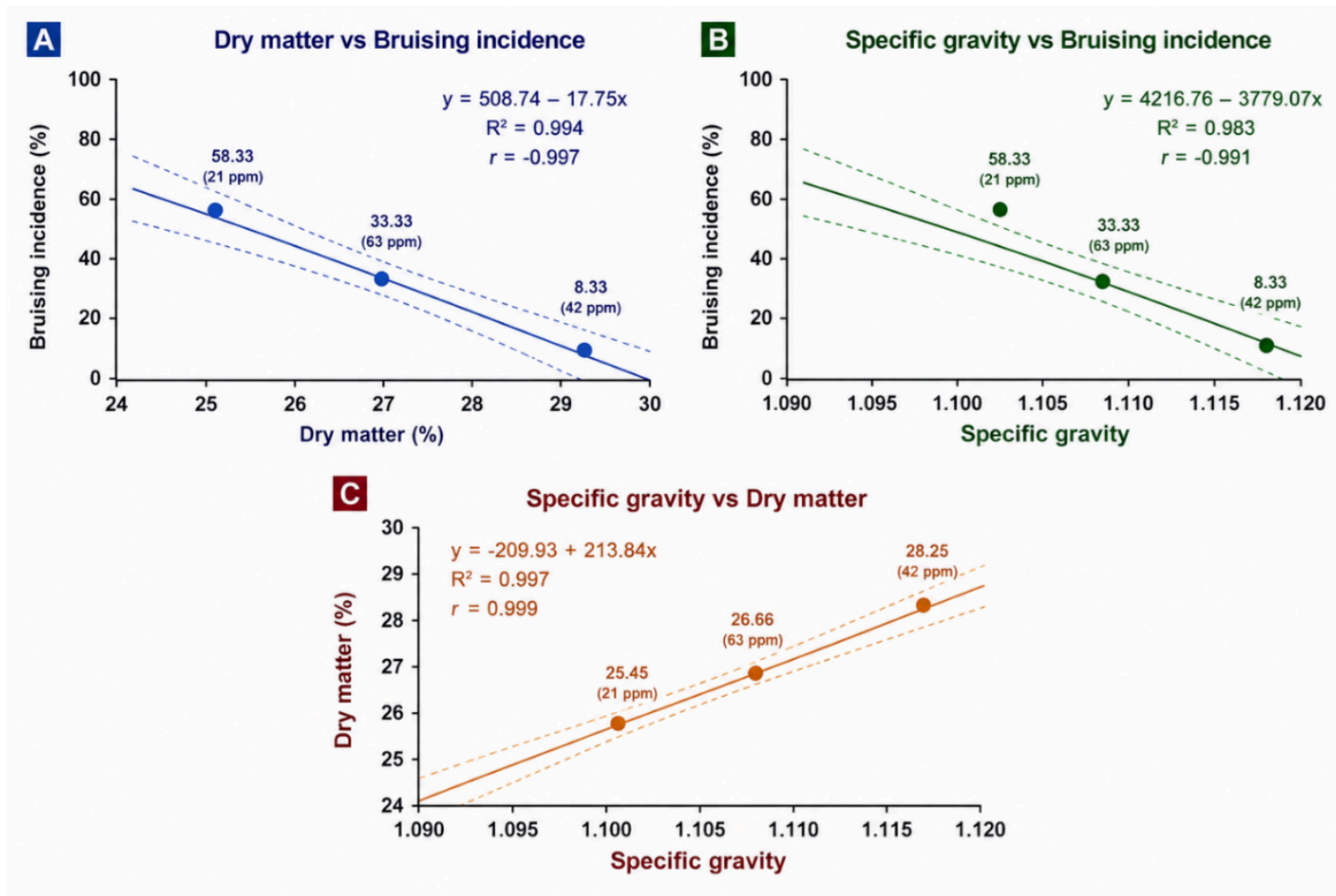


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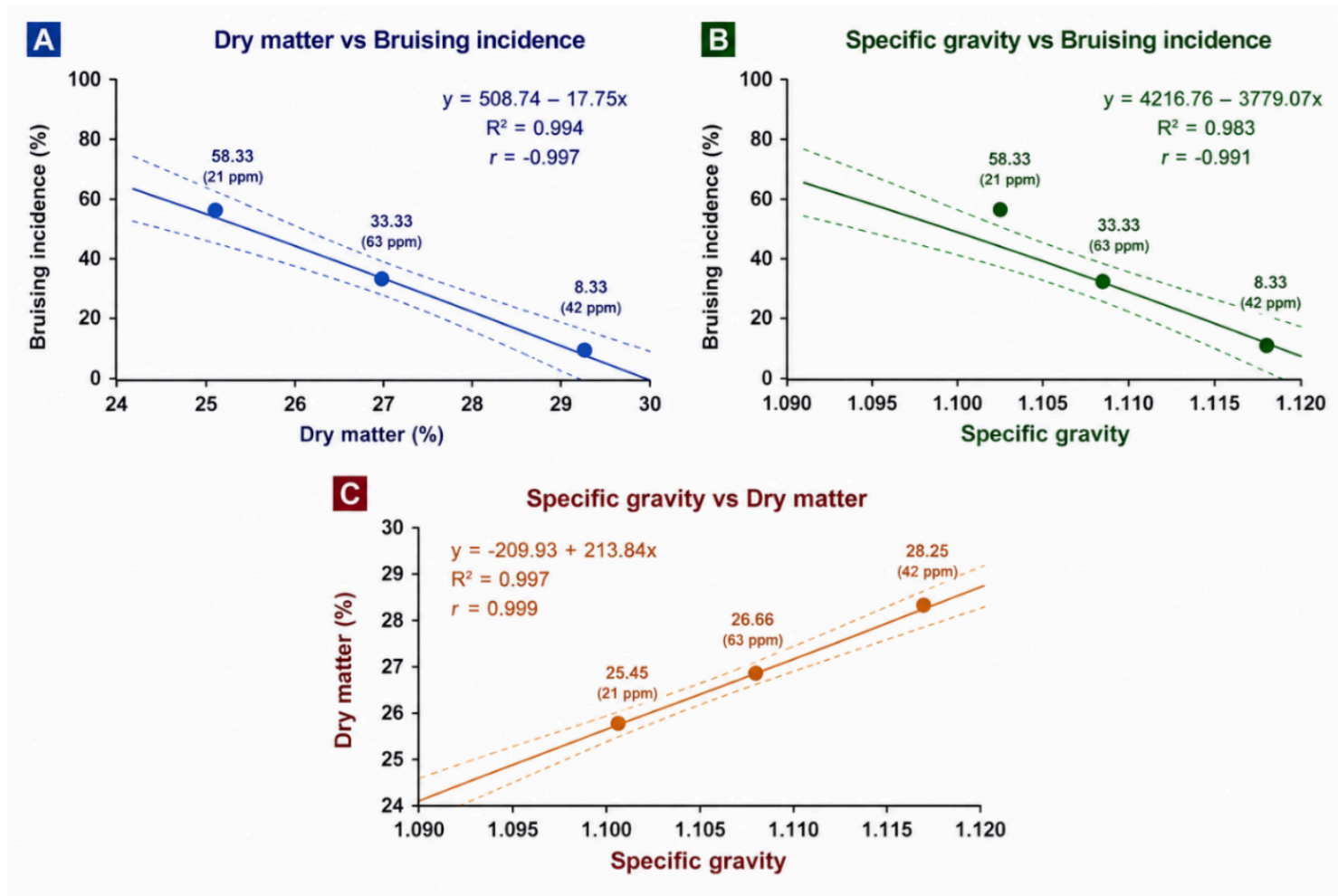


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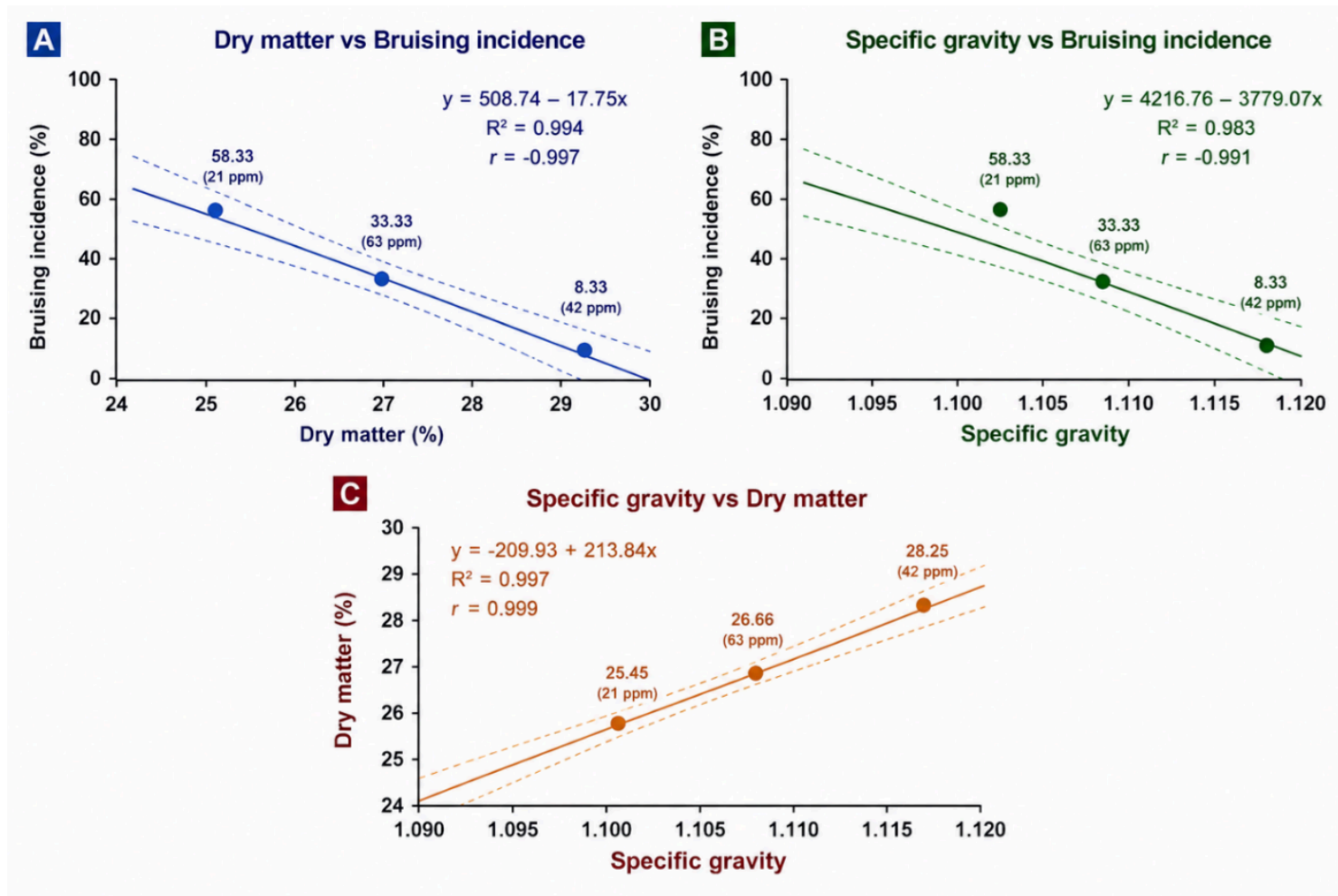


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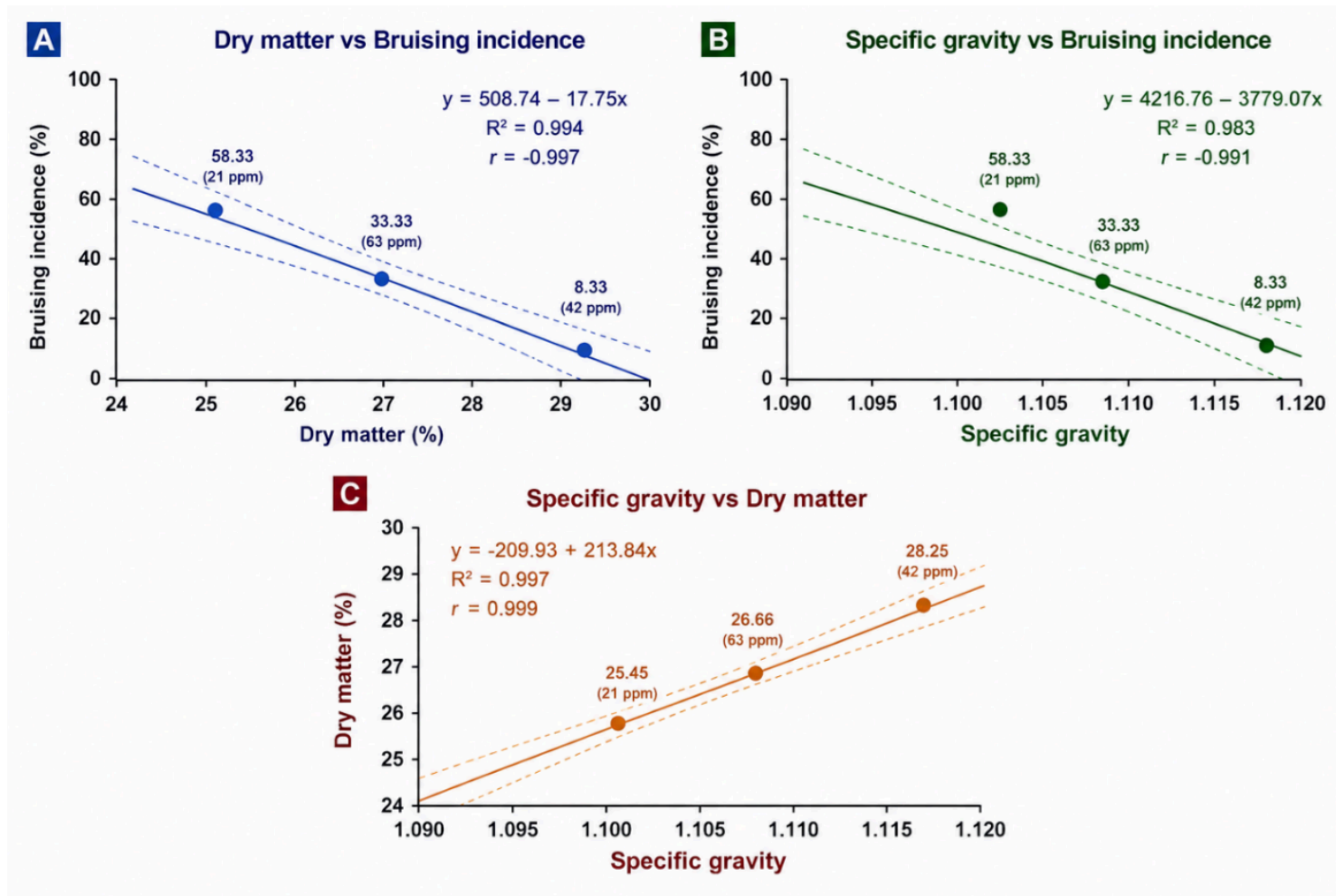


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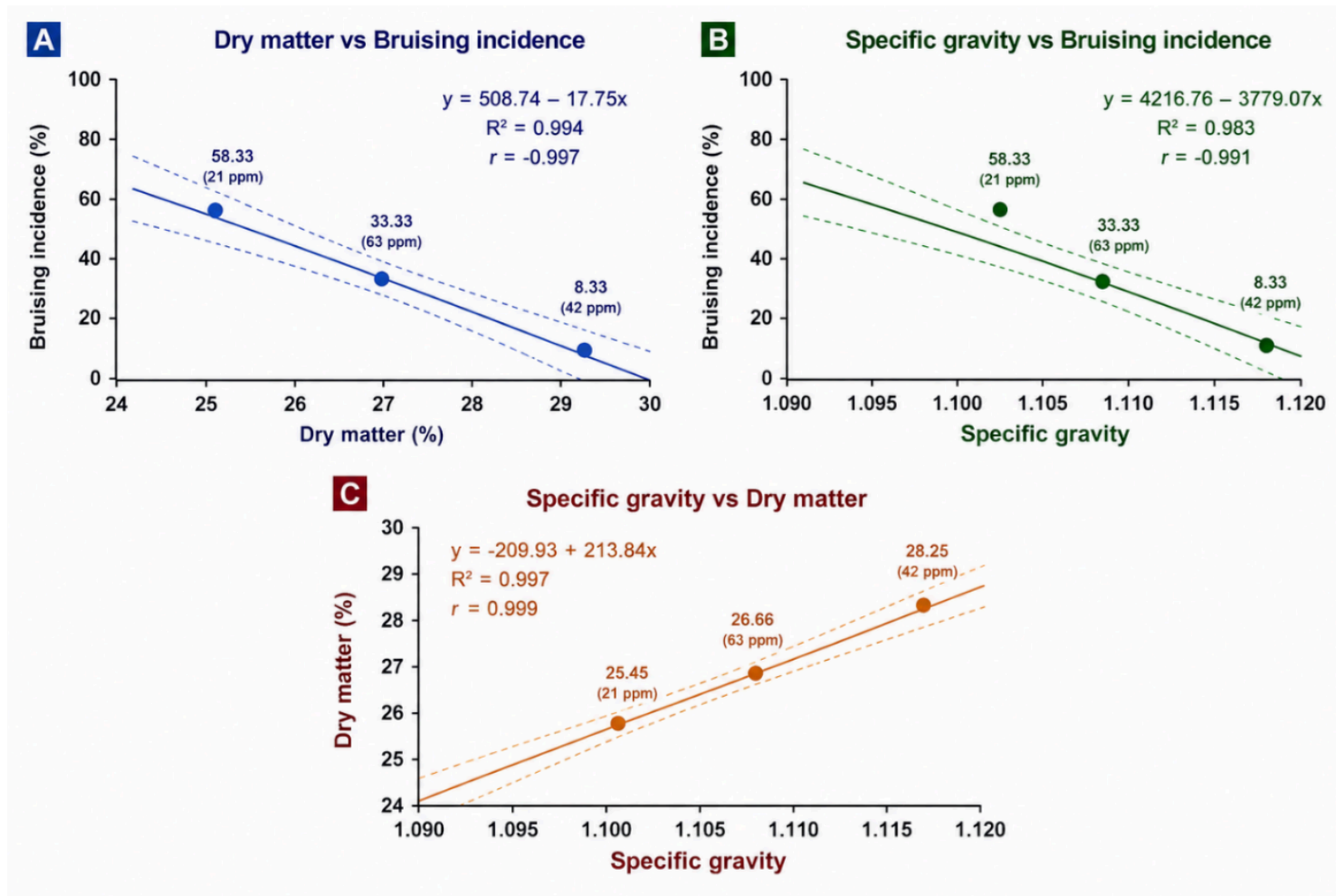


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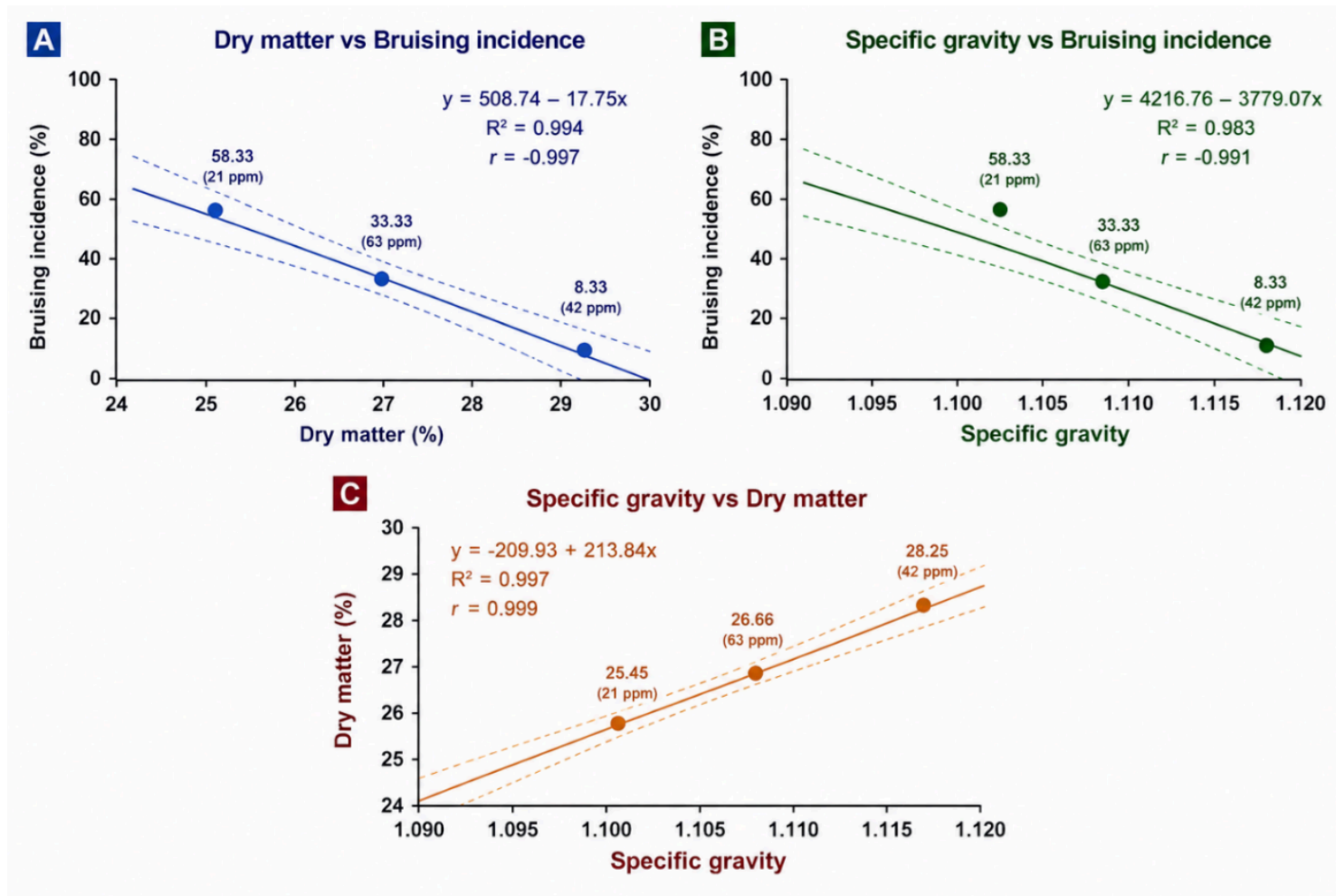


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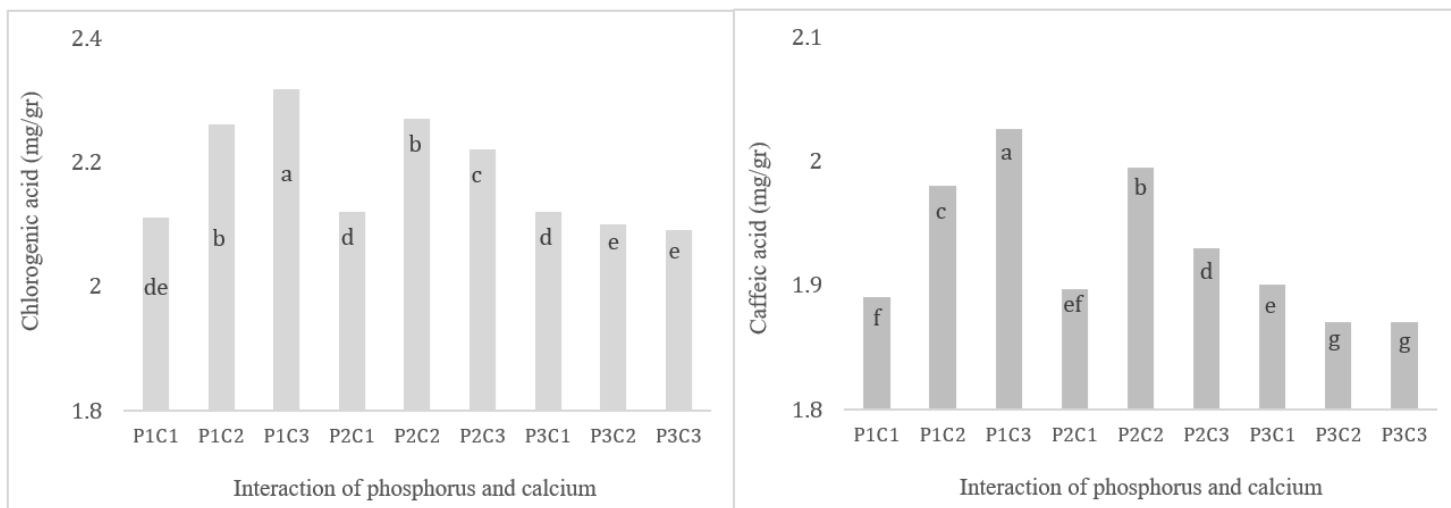


Figure 3

Interaction of phosphorus and calcium on caffeic and chlorogenic acid content of potato tuber skin

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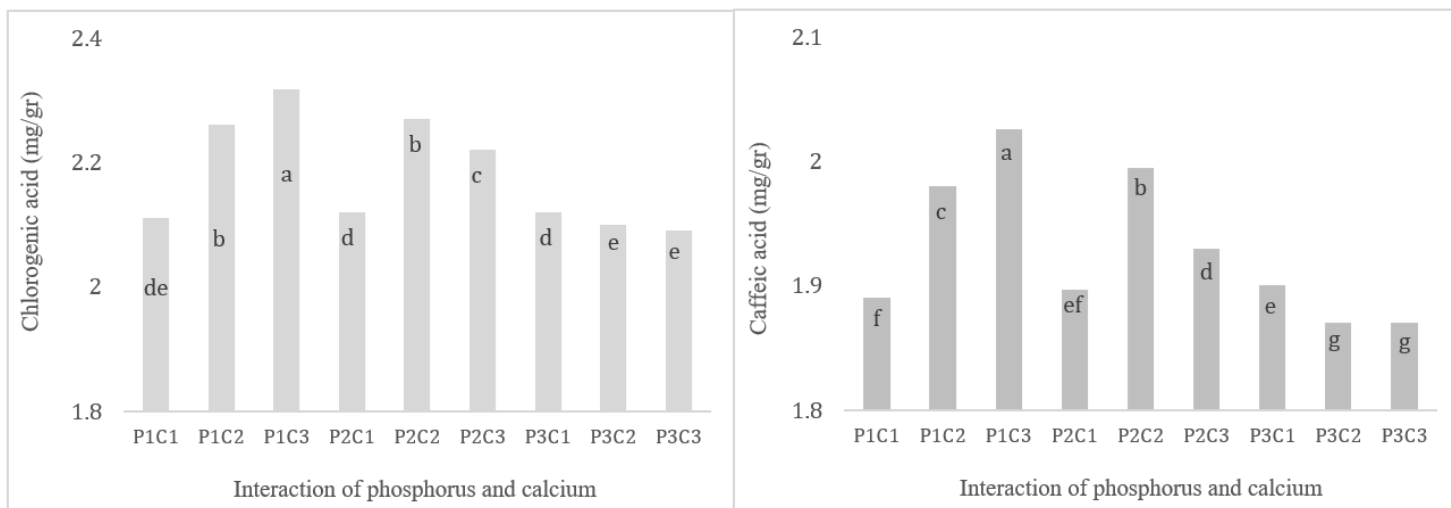


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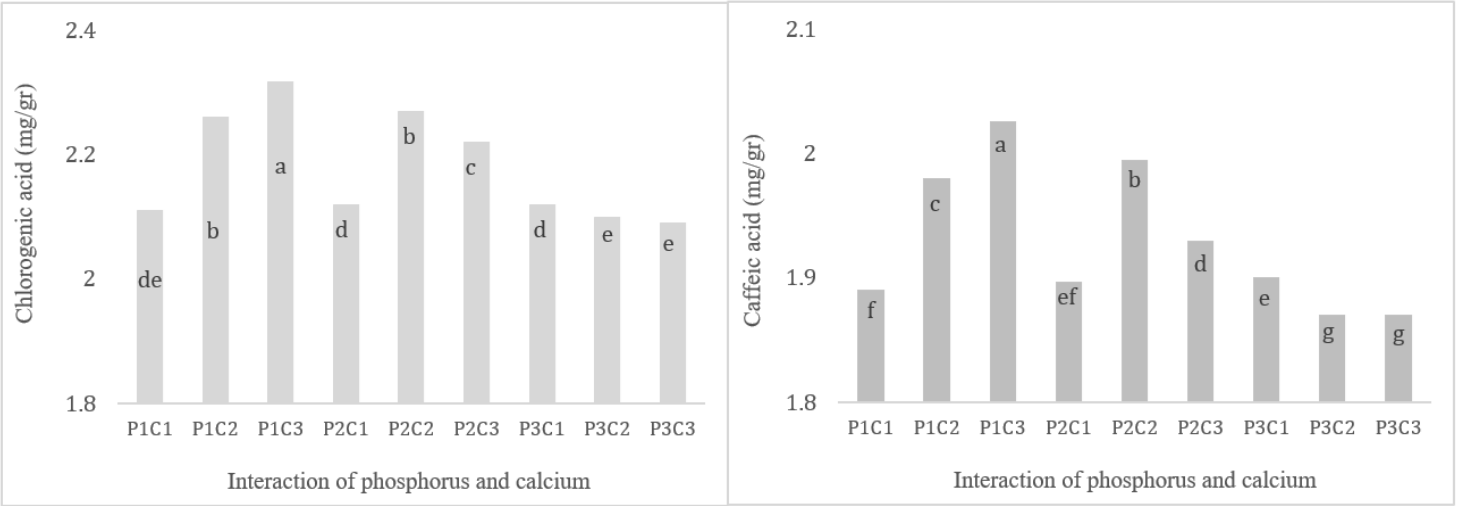


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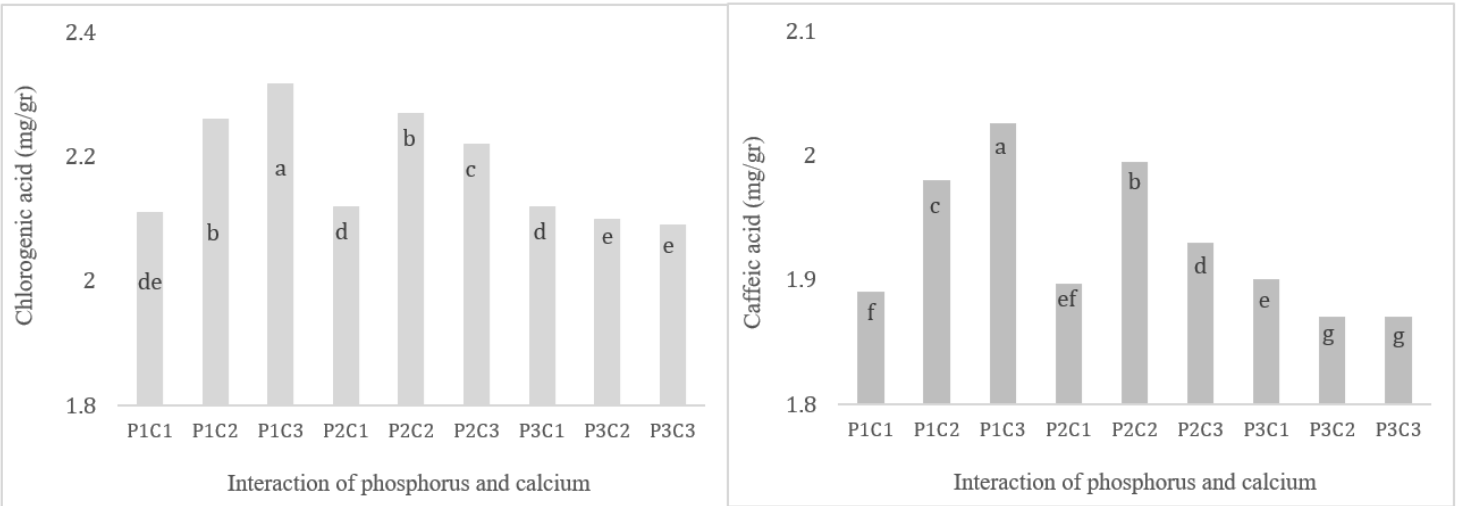


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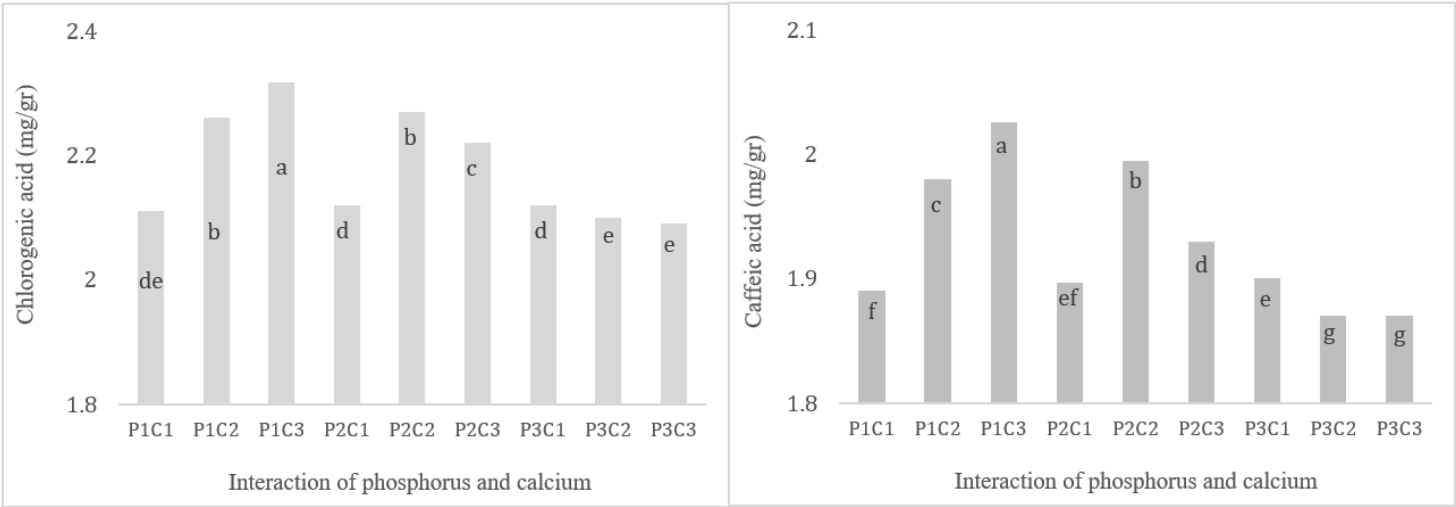


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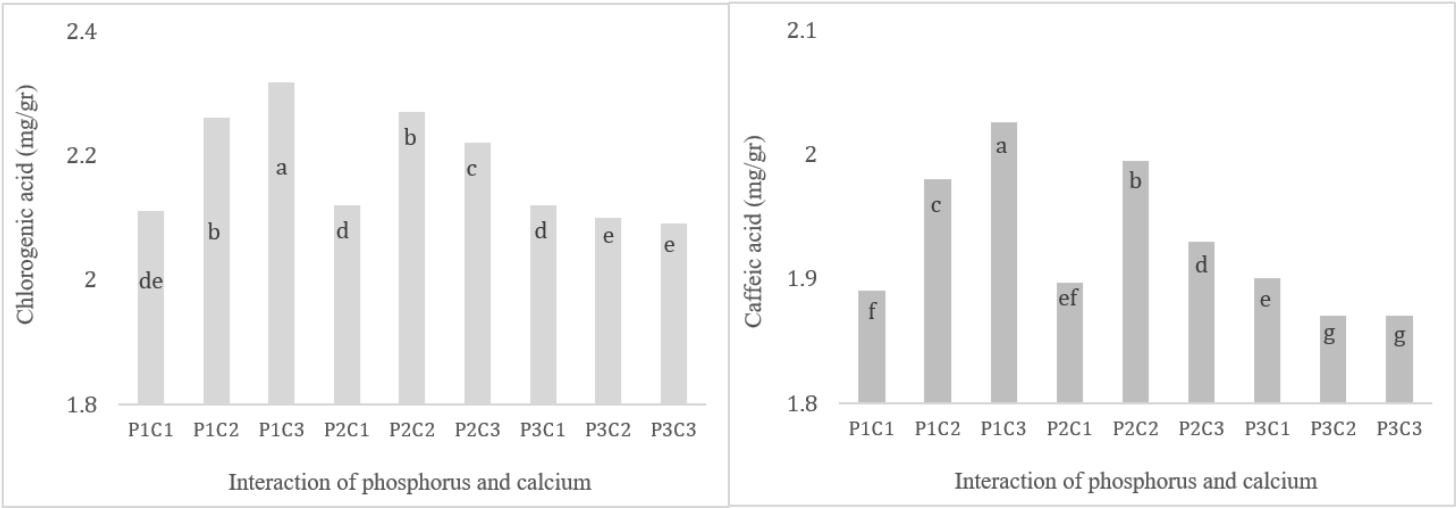


Figure 3

Interaction of phosphorus and calcium on caffeic and chlrogenic acid content of potato tuber skin

(P1, P2 and P3, Phosphorus concentration of 21, 42 and 63 PPM; C1, C2 and C3, calcium concentration of 120, 180 and 240 PPM in nutrient solution)

Within each chart, treatments with at least one letter in common do not differ significantly at the 5% probability level according to the LSD test.

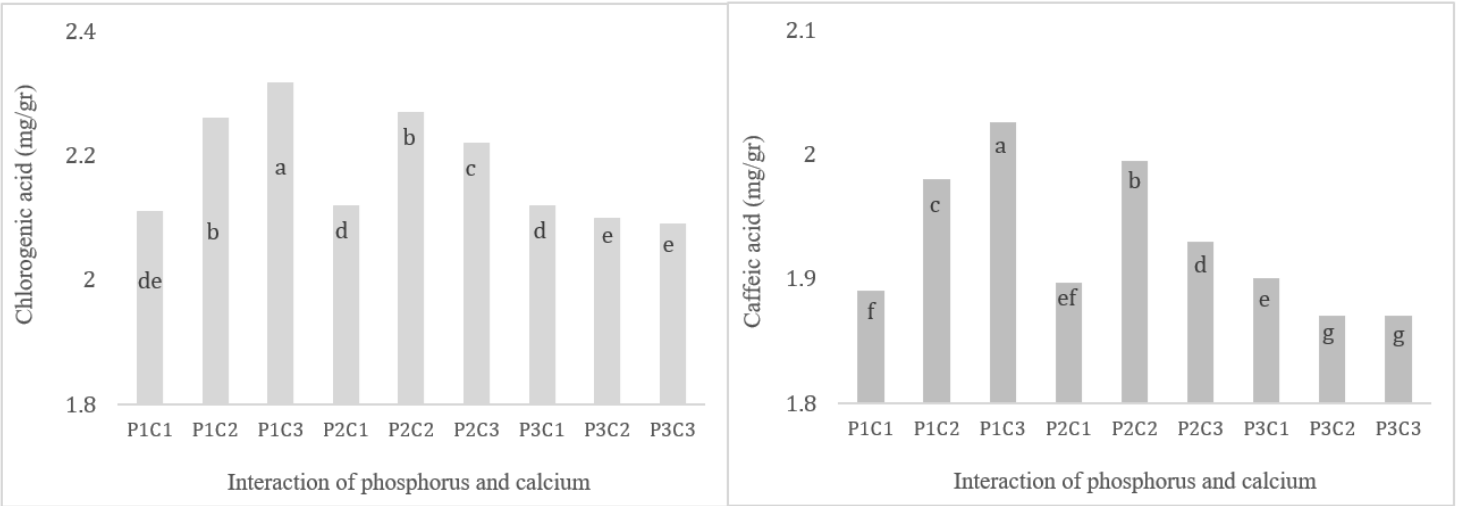


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(P1, P2 and P3, Phosphorus concentration of 21, 42 and 63 PPM; C1, C2 and C3, calcium concentration of 120, 180 and 240 PPM in nutrient solution)

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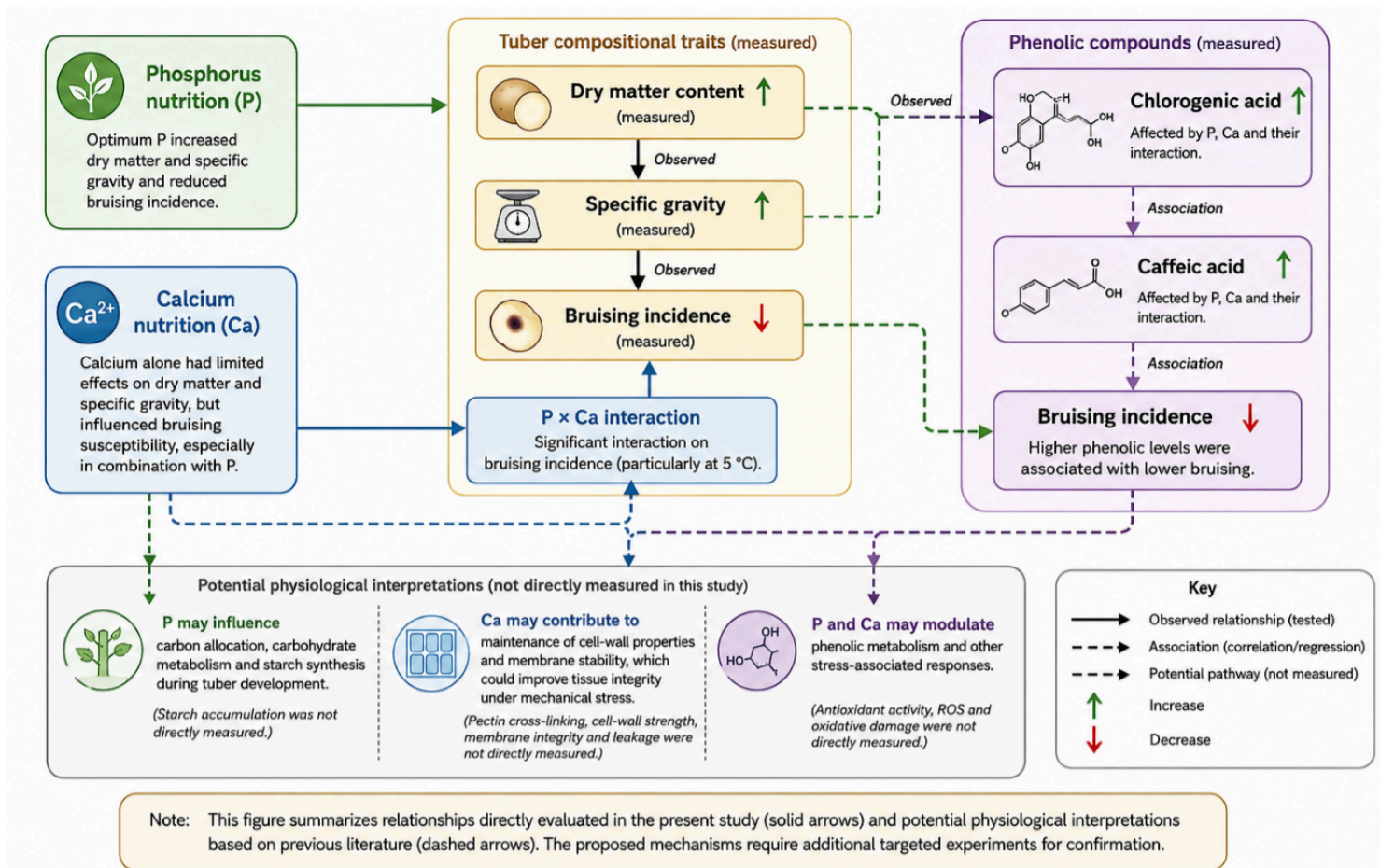


Figure 4

Conceptual interpretation of the observed relationships among phosphorus and calcium nutrition, tuber composition, phenolic compounds, and bruising susceptibility. The model integrates relationships directly observed in the present study with potential physiological interpretations. Solid arrows represent relationships or associations evaluated directly through analysis of variance, mean comparisons, regression, or correlation analyses. Dashed arrows represent potential physiological pathways that are consistent with previous physiological knowledge but were not directly measured in the present study. Phosphorus significantly affected tuber dry matter content, specific gravity, and bruising incidence, while the phosphorus × calcium interaction significantly affected bruising incidence after storage at 5 °C. Phosphorus and calcium also influenced chlorogenic acid and caffeic acid concentrations, which were associated with bruising incidence. Potential roles of carbohydrate allocation, tissue structural properties, and phenolic metabolism are therefore presented as interpretations rather than demonstrated mechanisms. Starch accumulation, pectin cross-linking, membrane leakage, and oxidative damage were not directly measured and should not be interpreted as experimentally demonstrated pathways.

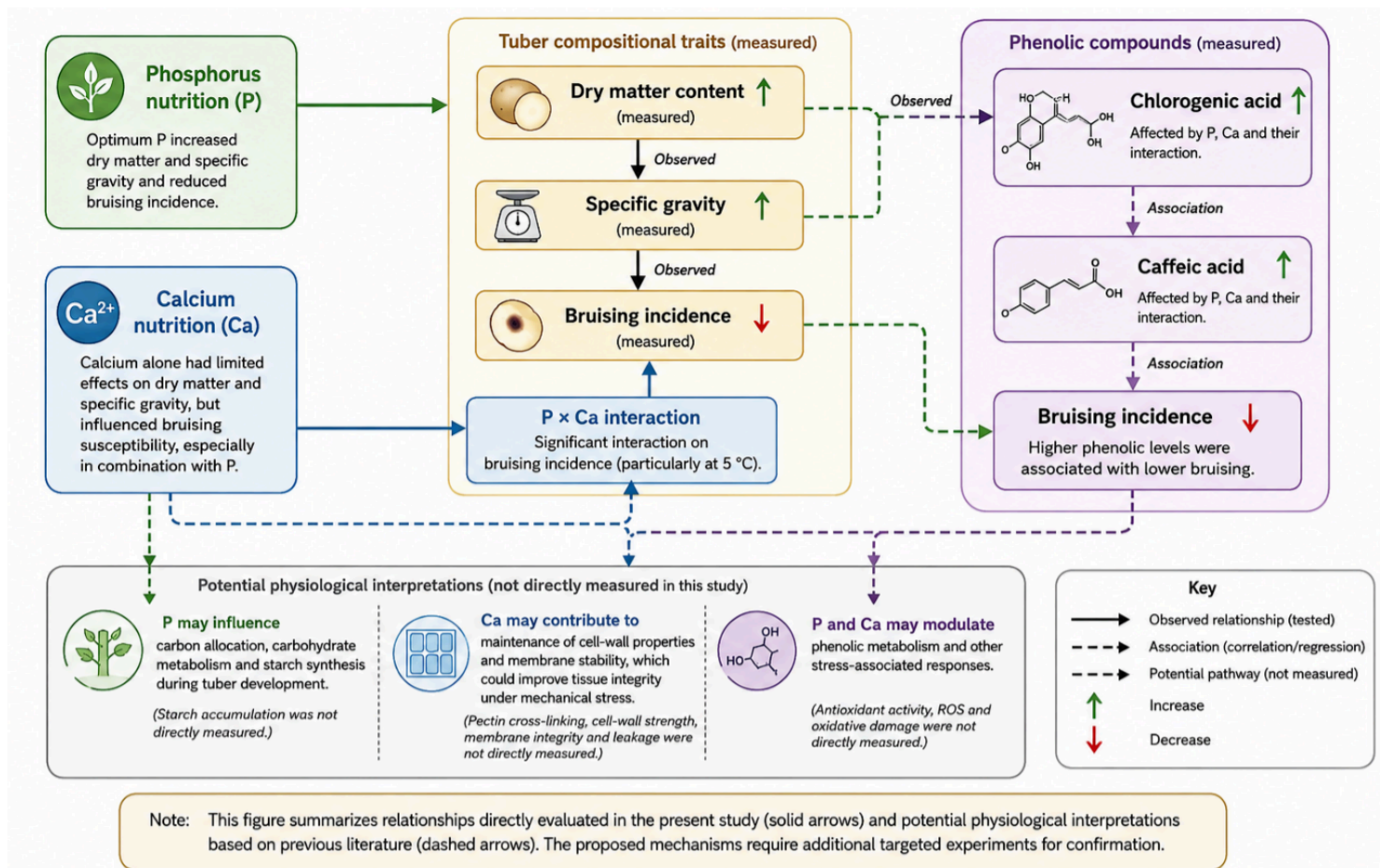


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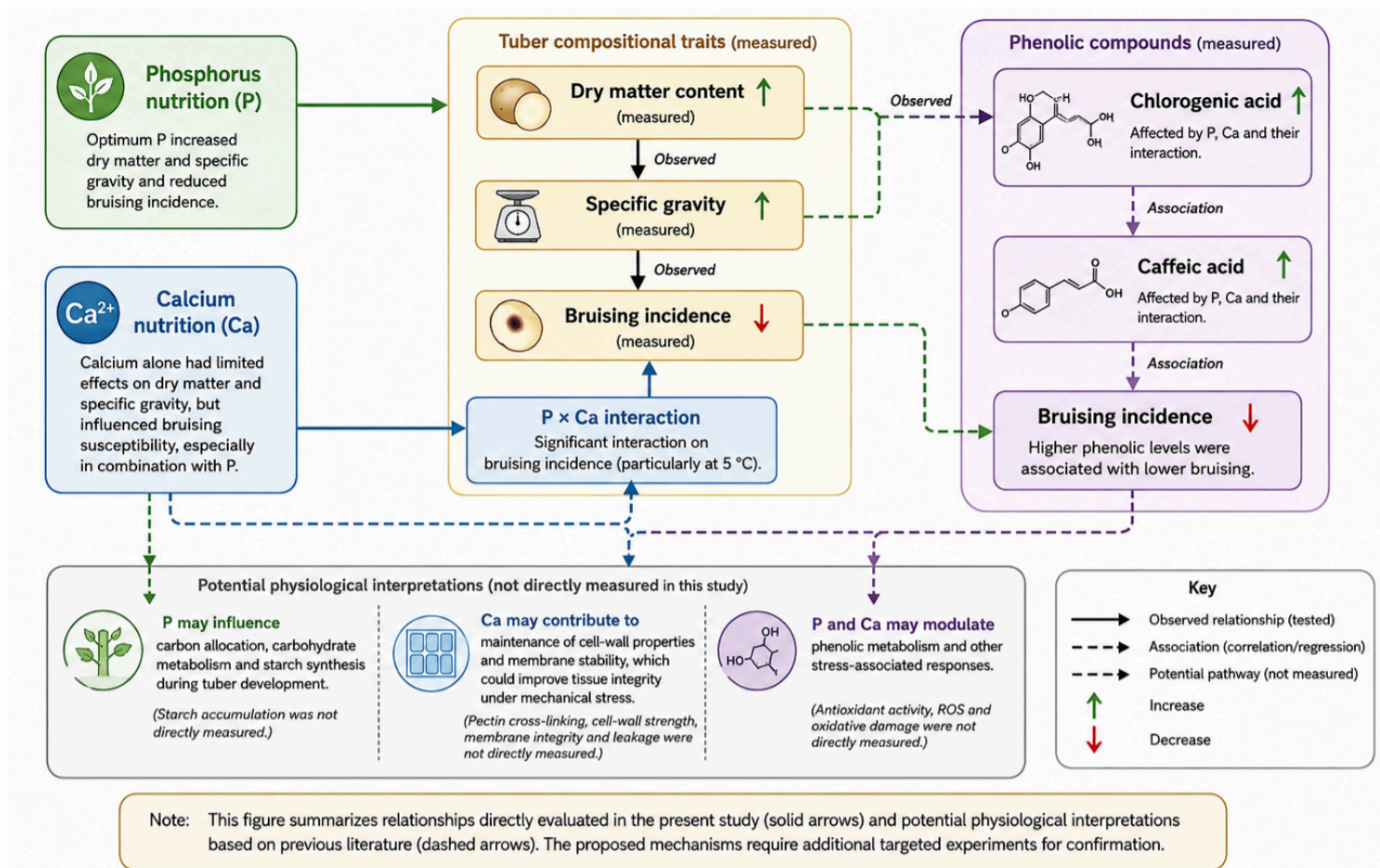


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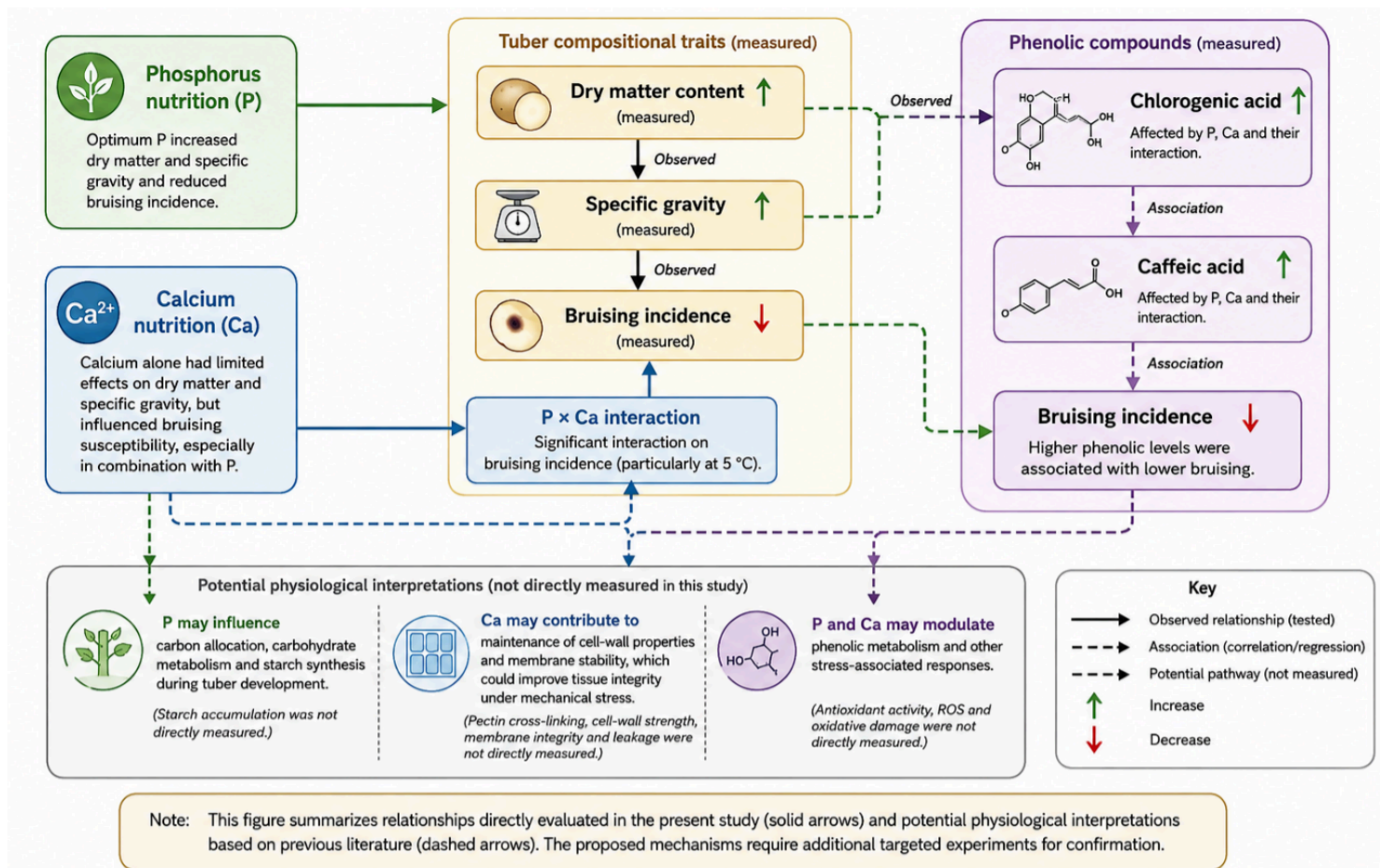


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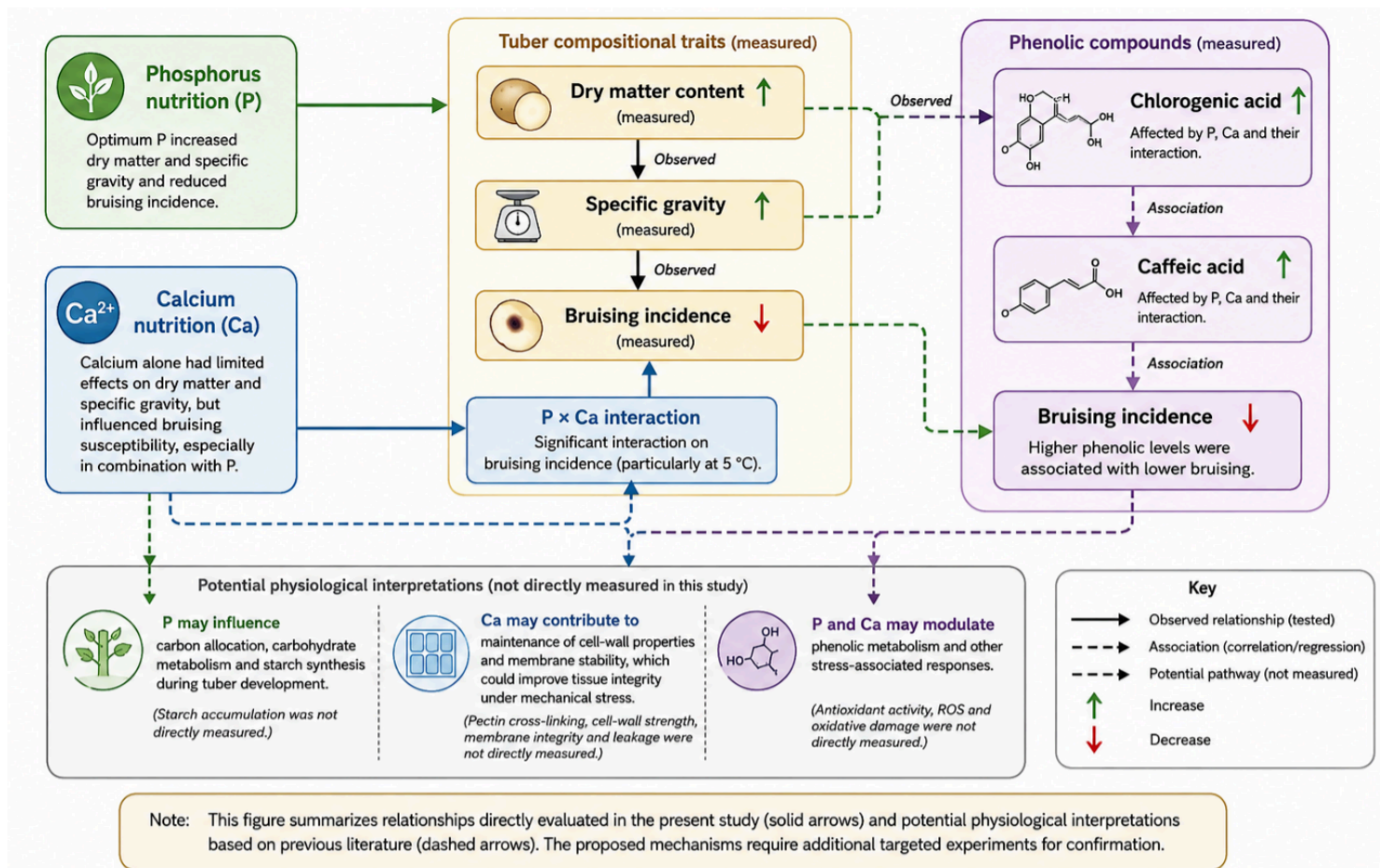


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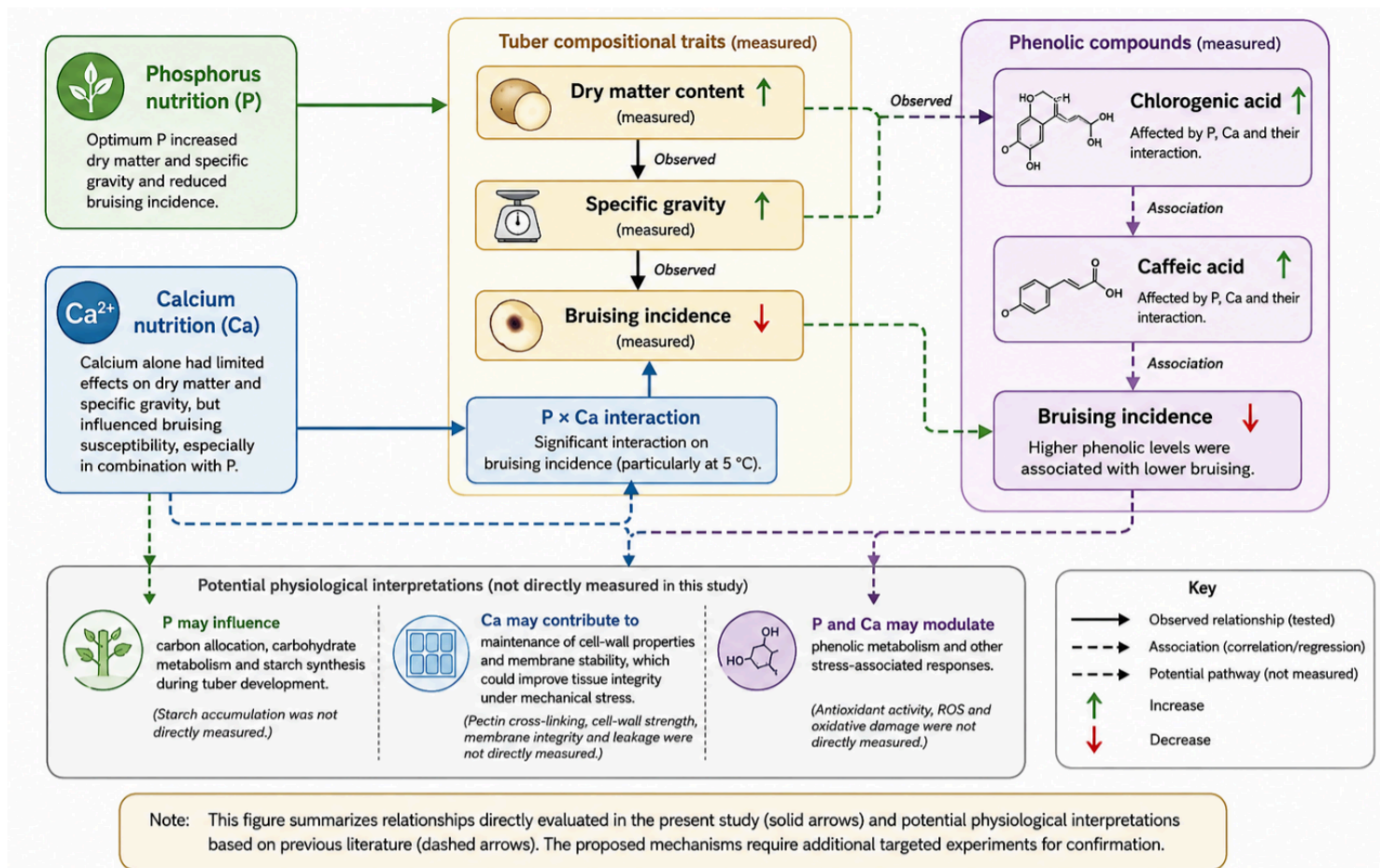


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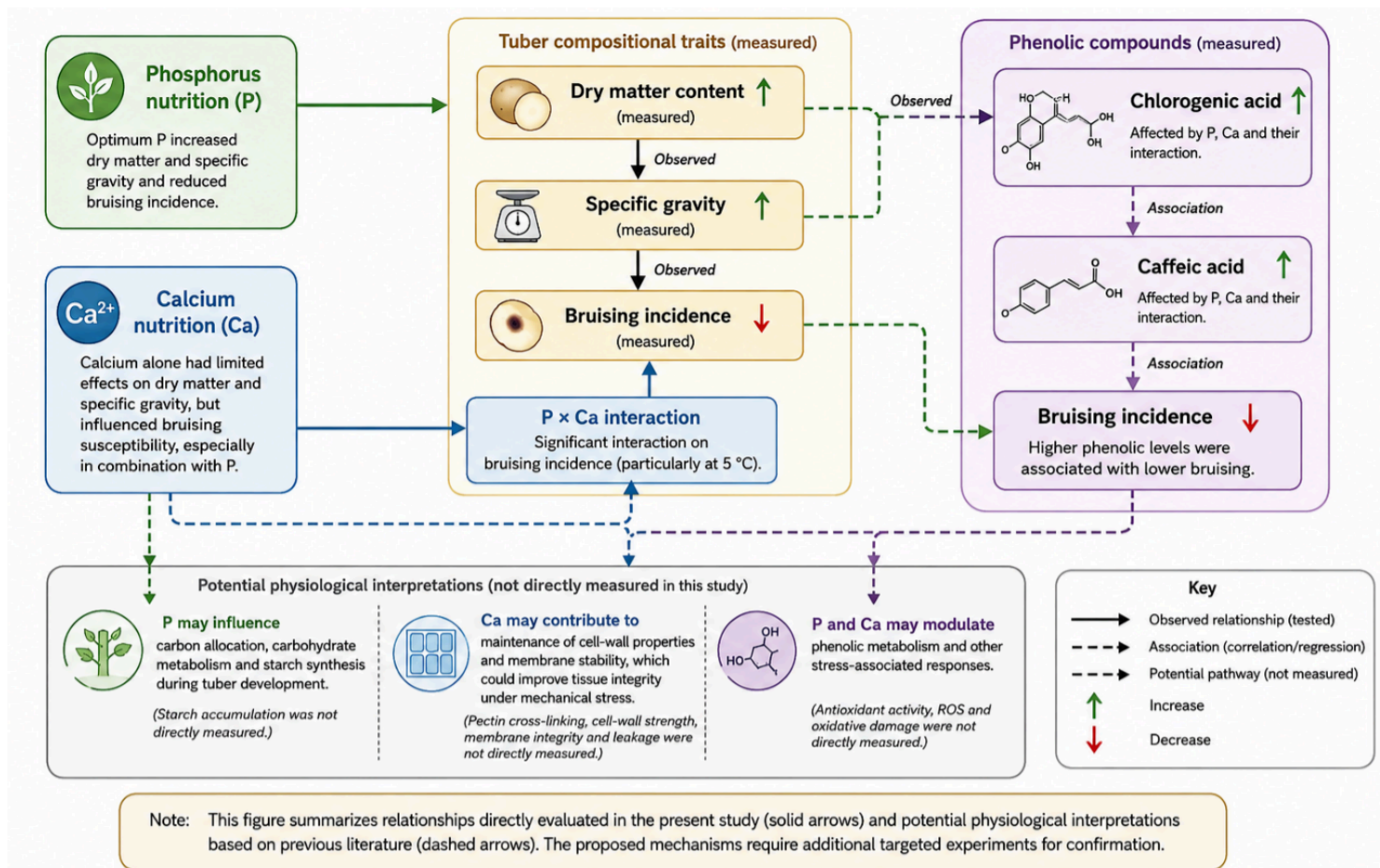


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