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Cell wall and oxidative metabolisms of ripening 'Paluma' guava under potassium fertilization

Aline Priscilla Gomes da Silva [a,*], Silvanda de Melo Silva [b,**], Gerciane Cabral da Silva [c], Maria Auxiliadora Coelho de Lima [d], Rejane Maria Nunes Mendonça [e], Renato Lima Dantas [e], William Gustavo Sganzerla [f]

[a] Department of Biosystems and Agricultural Engineering, Michigan State University, East Lansing, MI, USA
[b] Department of Chemistry and Physics, Federal University of Paraíba, Areia, PB, Brazil
[c] State Agricultural Research Corporation, Joao Pessoa, PB, Brazil
[d] Brazilian Agricultural Research Corporation, Petrolina, PE, Brazil
[e] Graduate Program in Agronomy, Federal University of Paraíba, Areia, PB, Brazil
[f] University of Campinas (UNICAMP), School of Food Engineering (FEA), Campinas, SP, Brazil

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ABSTRACT

Guava (*Psidium guajava* L.) is an important tropical fruit crop, and its nutritional status is directly associated with the quality and postharvest conservation of the fruits. Several agronomic events are involved with changes in the flavor and texture of the fruits, which are associated with the postharvest delay of fruit maturation, especially cell wall loosening. In this study, 'Paluma' guava trees were treated with three doses of potassium fertilization (50 [producer dose - control], 100, and 150 g K_2O plant^{-1}) during the phenological phase of fruit growth, and the fruits were evaluated in three maturity stages (green yellow, yellow greenish, and yellow). The completely randomized design and fruits from three plants were used as replicates per treatment. The fruits were evaluated by the changes in pectin content and cell wall enzyme activity (pectin methylesterase and polygalacturonase) and oxidative metabolism enzymes (polyphenoloxidase and peroxidase activity). The results demonstrate that fruits from plants fertilized with 100 g K_2O plant^{-1} were firmer (59.24 N), in which the yellow-greenish stage presented higher total (3.69%) and insoluble pectin (2.58%) contents. Furthermore, fruits at yellow-greenish stage presented lower pectin methylesterase (370.9 mU g^{-1} FW) and polygalacturonase (110.1 mU g^{-1} FW) cell wall enzyme activity, reflecting the better resistance of the cell wall and possibly longer postharvest life. As a practical application, the use of 100 g of K_2O plant^{-1} during production and harvesting of "Paluma" guava at the yellow-greenish stage can maintain fruit firmness, improve quality, and reduce postharvest losses.

1. Introduction

Guava (*Psidium guajava* L.) is a widespread fruit in tropical and subtropical regions [1] and is cultivated especially in Brazil, Peru, Mexico, the Philippines, India, Pakistan, and Thailand. The global production in 2019 was approximately 55.85 million tonnes, representing an export value of approximately 3.74 billion USD [2]. This fruit is preferred due to its yearly availability, nutritional composition, medicinal value, and suitability for transport and handling [3]. Furthermore, guava has wide acceptance in the markets due to its pleasant flavor, strong aroma, and quality, being also recognized by its nutraceutical properties showing high levels of ascorbic acid, total phenolics, total carotenoids, and minerals [2,4]. However, agricultural practices and maturation processes can influence those characteristics, and studying these parameters is critical to improving the agronomical trails and postharvest conservation of guava. Previous research showed that increasing potassium doses improved fruit quality as related to increases in fresh mass, mesocarp thickness, soluble solids, soluble solids/titratable acidity ratio, reducing sugars, and ascorbic acid contents [5]. However, further studies need to be conducted focusing on the effect of potassium on cell wall metabolism.

Guava fruit maturation goes through different ripening stages during

* Corresponding author. 469 Wilson Rd., East Lansing, MI, 48824, USA.
** Corresponding author. Department of Chemistry and Physics, Areia, PB, 58397-970, Brazil.
E-mail addresses: alinepgsilva@gmail.com (A.P.G. da Silva), silvasil@cca.ufpb.br (S.M. Silva).

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its physiology that lead to changes in color, taste, and texture, involving disaggregation of cell wall polymers, such as cellulose, hemicelluloses, and pectin [6,7], making fruits more acceptable for fresh consumption [8,9]. Several enzymes are involved in pectin degradation, mainly the pectin methylesterase (PME), endo (EC 3.2.1.15) and exo (CE 3.2.1.67) types of polygalacturonase (PG), and β-galactosidase (EC 3.2.1.23) [10]. In the enzymatic reaction chain, PME prepares the substrate for the action of PG. PME catalyzes the demethylation of the six-carbon from the carboxylic group of galacturosyl, de-esterifying it. Thus, PG only catalyzes the hydrolysis of α-1,4 bonds of galacturonic acid when it is de-esterified [10]. In the oxidative metabolisms, polyphenoloxidase (PPO) (EC 1.10.3.1) and peroxidase (POD) (EC 1.11.1.7) are two oxidoreductase enzymes involved in browning process [11]. PPO and POD perform similar reactions that catalyzes the oxidation of the functional –OH group to o-quinones. However, PPO uses O_2, and POD uses H_2O_2 as a catalyst for the oxidation of phenolic compounds [12]. POD is considered the most heat-stable plant enzyme and its inactivation has been conventionally used as an indicator of the adequacy of the bleaching step in vegetable processing. Moreover, in vegetables, peroxidase induces changes in flavor, vitamin C content, among others during storage [13]. Furthermore, the membrane damage mechanism and tissue structure loss during ripening may also be considered similar to the characterized mechanisms in real senescent systems involving the accumulation of reactive oxygen species (ROS) and increased activity of the enzymes of oxidative metabolism [14].

As an essential element for all living organisms, potassium is one of the nutrients most needed by guava [15] due to its participation in many metabolic process mechanisms. Potassium has been recognized known as a determinant "quality element" for fruit quality, acting as an activator or cofactor of many other enzymes, neutralizing anion, cell swelling mechanism, and transport of carbohydrates, among others [16,17]. When present in proper quantities, it promotes increasing fruit weight through the transport of assimilates, intensifying the taste and aroma, and improving the storability [18]. In 'Paluma' guava, potassium rates can induce higher productivity, but they generally do not affect the chemical composition (sugar and protein contents) [18].

Some reports about changes in physical and physicochemical parameters, bioactive compounds, and storage techniques show that the quality of the fruit is deeply related to the maturity stage at harvest from the guava tree [1,19,20]. However, studies evaluating the interaction of mineral nutrition with the activity of the enzyme associated with cell wall and oxidative enzyme metabolism in guava fruits are still incipient. These subjects may contribute to a greater understanding of the rapid loss of firmness, and it may subsidize fertilizer adjustments to reduce the softening rates of guava, thus facilitating the adoption of technologies that extend the postharvest life of the fruit [16].

Therefore, this study brings the novelty of evaluating the changes in the cell wall and oxidative metabolism enzymes in 'Paluma' guava fruit harvested at different maturity stages under the influence of potassium fertilization, as an alternative to maintain firmness and increase its postharvest conservation.

2. Material and methods

2.1. Plant material

Guava trees (*Psidium guajava* L.) from the cultivar 'Paluma' at 16 months of age (commercial orchard in the year 2013), and whose plants were propagated by herbaceous cuttings were grown in a red–yellow podzolic loam soil of medium texture at a spacing of 5 × 6 m without irrigation, located in the city of Alhambra, Paraiba State, Brazil. Three different doses of potassium were used (50 [usual producer dose - control], 100, and 150 g of K_2O plant^{-1}), together with standard doses of nitrogen (150 g plant^{-1}) and phosphorus (140 g plant^{-1}). The doses used are in accordance with da Silva [5]. The nitrogen, phosphorus, and potassium sources were commercial urea, potassium chloride and monoammonium phosphate (MAP), respectively. Fertilizer applications were performed manually in the canopy projection. Phosphorus was applied in a single dose, while nitrogen and potassium were divided into three applications in the soil, the first right after pruning, at 45 days, and 75 days after pruning.

The fruits were manually harvested between January and March of 2013 early in the morning when the plants, and the fruits were harvested in three ripening stages, which were identified by the color of the fruits according to Cavalini et al. [21]: green yellow (GY), yellow greenish (YG), and yellow (Y) (Fig. 1). Three plants from each treatment were used as replications. From each plant, 12 fruits were harvested, totaling 36 fruits per treatment. The fruits were placed in polyethylene boxes previously sanitized and transported for analysis. Before analyses fruits were sanitized in sodium hypochlorite solution (1%) at room temperature for 5 min. For that, the fruits were chopped, and the endocarp (pulp with seeds) was removed and homogenized in a blender with the help of dry ice, avoiding grinding the seeds. The homogenized pulp with seeds was filtered through a nylon sieve (with pores of approximately 1 mm^2) to remove the seeds, and also all the material was washed and cooled before used. The pulp was stored at −80 °C for the analysis.

2.2. Analytical methods

2.2.1. Fruit firmness

For firmness determination, two measurements were made on opposite sides of fruits using a Texture Analyzer (6 mm diameter probe, force of 50 kg, speed range of 0.01–40 mm s^{-1}) (TA-XT2, Stable Micro Systems, UK). The results were expressed in Newtons (N).

2.2.2. Total and soluble pectin

The extraction of pectin was performed using 5.0 g of pulp homogenized in 80% ethanol, according to the procedure described by McCready and McComb [22]. After a leave overnight protected by the light for approximately 12 h, the sample was washed twice with 80% ethanol. Soluble pectin extraction was performed with filtration, dilution to 50 mL and agitation for 1 h. For total pectin, the pH was adjusted to 11.5 with a 1.0 M NaOH solution for later resting for 30 min. Then, the pH was adjusted to 5.0–5.5 with glacial acetic acid to allow ideal conditions for hydrolysis. The absorbance readings were taken by colorimetry in a spectrophotometer model (Genesys TM 10S UV-VIS, Thermo Electron Scientific Instruments, Madison, WI, USA) at a wavelength of 540 nm by the carbazole method, according to Bitter and Muir [23]. The results were expressed in the percentage of galacturonic acid. The insoluble pectin was obtained by the difference between total and soluble pectin.

2.2.3. Pectin solubilization

The percentage of pectin solubilization was calculated according to **Eq. (1)** [20], considering the quantification of pectin described in the previous section.

$$\text{Pectin solubilization } (\%) = \frac{\text{Soluble pectin}}{\text{Total pectin}} \times 100 \quad (1)$$

2.2.4. Cell wall enzymatic activity

2.2.4.1. Pectin methylesterase (PME). PME activity was determined according to Jen and Robinson [24]. One gram of pulp was weighed, and then 10 mL of 0.2 M NaCl was added and homogenized for 1 min. Afterwards, the material was filtered. From this mixture, 5 mL was removed and added to 20 mL of 1% citrus pectin dissolved in 0.2 M NaCl (titrated with 0.1 N NaOH to pH 7.5). The mixture was transferred to a 50 mL beaker and kept under constant stirring. The pH of the solution was immediately adjusted to 7 using a 0.01 N NaOH solution and maintained at this value by adding 0.01 N NaOH for 10 min. One unit of PME was defined as the amount of enzyme capable of catalyzing the

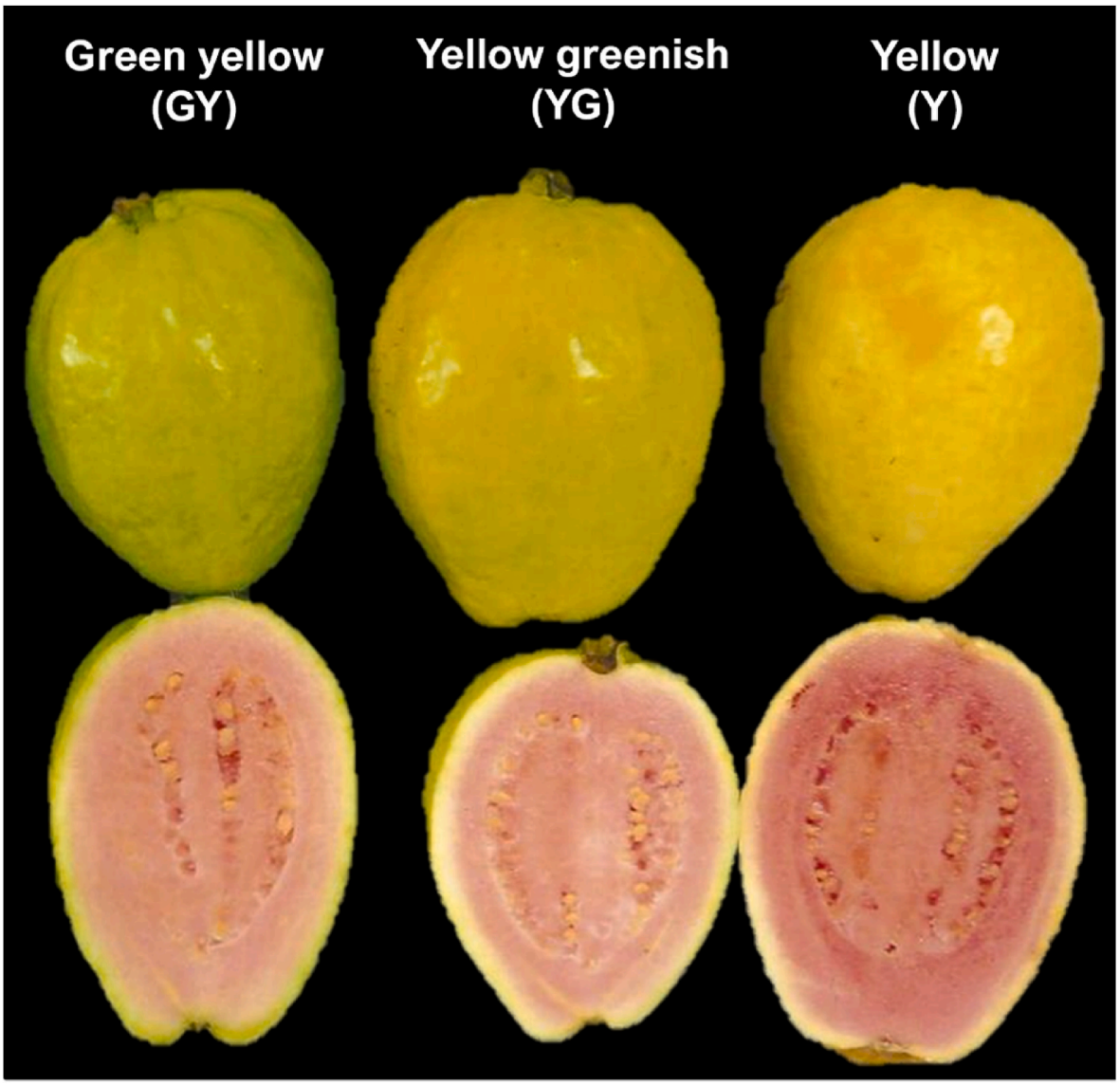

Fig. 1. Ripening stages of 'Paluma' guava.

demethylation of pectin corresponding to the consumption of 1 μM NaOH per min per g of tissue. The analysis was conducted in triplicate, and the results were expressed as mU g^{-1} Fresh Weight (FW).

2.2.4.2. Polygalacturonase (PG). The enzymatic activity of PG was determined according to Markovic et al. [25]. The extract was incubated in a 0.25% solution of galacturonic acid (washed with 80% ethanol before use) in 37.5 mM sodium acetate buffer, pH 5, for 3 h. The reaction was interrupted in a boiling water bath. The reducing groups released were according to the Somogy technique using glucose as a standard [26]. The thermally inactivated extract was used and incubated under the same conditions as a blank. A unit of PG activity was considered the amount of enzyme capable of catalyzing the formation of 1 μM reducing groups per minute under the assay conditions. The analysis was conducted in triplicate, and the results were expressed as U g^{-1} FW.

2.2.5. Oxidative metabolism enzymatic activity

2.2.5.1. Extraction procedure. Oxidative metabolism enzymes were extracted according to Zanatta et al. [27], with modifications. All extraction procedures were conducted at 4 °C in an ice bath. Guava extracts were prepared by a mixture of 5 g pulp with 10 mL of sodium phosphate buffer (100 mM, pH 6.3) for peroxidase or sodium phosphate buffer (100 mM, pH 6.8) for polyphenol oxidase. Polyvinylpyrrolidone (PVPP) and calcium chloride (5%) (1% (w\v) were added to the extract to prevent the action of phenols and pectin. The extract was filtered through filter paper, and the liquid fraction was centrifuged (9000 rpm, 4 °C, and 20 min). The supernatant was used to determine the polyphenoloxidase and peroxidase activity.

2.2.5.2. Polyphenoloxidase (PPO). The PPO activity was determined according to Fujita et al. [28]. Briefly, 0.5 mL of PPO substrate was mixed with 0.8 mL of 100 mM sodium phosphate buffer, pH 6.8, and 0.05 mL of 10 mM catechol solution; then, the mixture was incubated for 30 min at 30 °C in a water bath. After the incubation period, 0.8 mL of 2 M perchloric acid solution was added, and the tubes were immersed in an ice bath. The activity was determined at a wavelength of 395 nm using a spectrophotometer model (Genesys TM 10S UV-VIS, Thermo Electron Scientific Instruments, Madison, WI, USA). The analysis was conducted in triplicate, and the results were expressed as min^{-1} g^{-1} FW.

2.2.5.3. Peroxidase activity (POD). The POD activity was determined by the method described by Campos and Silveira [29]. Briefly, 1.5 mL of enzyme extract, 2.5 mL of buffer with phosphate-citrate containing

sodium phosphate solution 0.2 M dibasic and 0.1 M citric acid (pH 5.0) and 0.25 mL of 0.5% guaiacol were mixed by vortexing (VWR International, PA, USA). Then, 0.25 mL of 3% H_2O_2 was added to this mixture. The extract was incubated at 30 °C for 15 min. After incubation, the extract was placed in an ice bath, and 0.25 mL of sodium metabisulfite (2%) was added. After vortexing, the tube was left to rest for 10 min. The absorbance reading was performed in a spectrophotometer at a wavelength of 450 nm. Enzyme activity is expressed in enzymatic units (EU). An enzyme unit is defined as the amount of enzymatic extract that showed an increase at an absorbance of 0.001 units per minute. The enzyme activity was calculated by using the same formula used for polyphenol oxidase, and the whole procedure was performed at 4 °C. The analysis was conducted in triplicate, and the results were expressed as min^{-1} g^{-1} FW.

2.3. Statistical analysis

The experimental design was completely randomized in a factorial design composed of 3 potassium doses × 3 maturity stages with the replication of three plants. Data were subjected to analysis of variance (ANOVA), and means were compared by Tukey's test at 5% significance. The statistical analysis and correlation were conducted using SAS® (SAS 9.1) software.

3. Results and discussion

3.1. Fruit firmness

Potassium nutrition statistically affected the firmness of guava fruits (Table 1). The guava trees fertilized with 100 g K_2O $plant^{-1}$ (intermediate dose) produced firmer fruits at the GY maturity stage (59.24 N), maintaining firmness until stage Y (33.96 N). This demonstrated that K would not be pumped out of the cell but would be retained to trigger a metabolic response or to provide primary iso-osmotic conditions across the membrane and work on the maintenance of firmness [30]. Therefore, the results for firmness are in agreement with those obtained by Lima et al. [31], who reported that potassium levels applied in the field delayed the postharvest loss of firmness of fresh guavas. Loss of texture is dependent on both cell wall degradation and loss of turgidity of the tissue. In general, firmness loss during maturation is associated with intensive solubilization of pectin from the cell wall, starch breakdown, and turgor reduction [32]. However, softening in the pulp and fruit yellowing were associated with other factors in addition to pectin solubilization. The reduction in protein content and the increase in water content are also related to fruit softening [32].

3.2. Total and insoluble pectin

The results revealed an interaction between ripening stages and doses of K_2O applied (Table 2). For 100 g K_2O $plant^{-1}$, the maturity stage YG (intermediate ripening point) had distinct effects on total and insoluble pectin contents among the doses applied, since YG was the ripening stage with higher content. Therefore, in addition to no significant difference for the Y stage, the dose of 100 g K_2O $plant^{-1}$ resulted in fruits with higher pectin content in ripened fruits, and the pectin solubilization was lower for this potassium dose (Table 3). The higher total pectin contents in fruits at the YG stage and fertilized with 100 g of K_2O $plant^{-1}$ resulted in firmer fruits, which was possibly achieved due to increased deposition of sublayers of potassium [33,34]. This fact is associated with increased pressure potential of fruit tissue, resulting in a greater accumulation of potassium and other osmoelectrolytes [9,35]. Similar to our results, Braga et al. [18] obtained total pectin levels of approximately 1.80% galacturonic acid when analyzing cv. Pedro Sato guava during 8 days under room conditions.

At a dose of 50 g K_2O $plant^{-1,}$ there was a decrease in total pectin levels, indicating higher rate of cell wall metabolism of fruits. In turn, at a dose of 150 g K_2O $plant^{-1,}$ the total pectin contents did not differ among maturity stages; however, the firmness declined sharply for stage Y. Based on these results, it can be stated that fruit from plant undergoing fertilization with 50 g K_2O $plant^{-1}$ showed higher pectin solubilization (Table 3), implying earlier ripening fruit and a shorter postharvest life. For the contents of insoluble pectin, an interaction between maturity stages and doses of K_2O applied was observed (Table 2). Fruits in the maturity stage YG from plants treated with 100 g K_2O $plant^{-1}$ resulted in higher levels of insoluble pectin (2.58% galacturonic acid), which decreased in yellow fruit, corroborating the behavior of the total pectin. At a dose of 50 g K_2O $plant^{-1}$, fruits of stage YG had the lowest content of insoluble pectin, which increased in the Y stage. This fact can be associated with protopectinase activities, which do not act among stages due to the effect of K_2O doses. It is expected that the levels of insoluble pectin decrease over-ripening due to the increase in pectin solubilization as a result of enzymatic and physical mechanisms [36]. However, this study showed that only fruits obtained at a dose of 150 g K_2O $plant^{-1}$ showed a decline in insoluble pectin. Several factors influence this response, including the maturity stage and growing conditions [37,38].

Regarding the higher total and insoluble pectin contents at a dose of 100 g K_2O $plant^{-1}$, this may indicate that this dose of potassium would be sufficient to produce firmer fruit of the YG stage and that the dose of

Table 1
Firmness in 'Paluma' guavas harvested at maturity stages green yellow (GY), yellow greenish (YG), and yellow (Y) from plants treated to different doses of K_2O.

Parameter	Doses (g K_2O $plant^{-1}$)	Maturity Stage		
		GY	YG	Y
Firmness (N)	50	32.34 ± 2.61^{Ab}	30.14 ± 4.78^{Ab}	8.07 ± 4.02^{Bb}
	100	59.24 ± 4.64^{Aa}	39.35 ± 13.11^{Ba}	33.96 ± 9.99^{Ba}
	150	34.64 ± 10.18^{Ab}	32.97 ± 9.68^{Ab}	5.71 ± 3.46^{Bb}

The results are expressed as mean ± standard deviation (n = 3). Different capital letters in the same line (dose) and lowercase in the same column (maturity stage) are significantly different by the Tukey test at 5% of error probability. Doses $plant^{-1}$: 150 g of N + 50 g of K_2O + 140 g of P_2O_5; 150 g of N + 100 g of K_2O + 140 g of P_2O_5; 150 g of N + 150 g of K_2O + 140 g of P_2O_5.

Table 2
Total Pectin – TP and Insoluble Pectin – IP in 'Paluma' guavas harvested at maturity stages green yellow (GY), yellow greenish (YG), and yellow (Y) from plants treated to different doses of K_2O.

Parameters	Doses (g K_2O $plant^{-1}$)	Maturity Stage		
		GY	YG	Y
Total pectin (% galacturonic acid)	50	2.52 ± 0.07^{Aa}	1.55 ± 0.15^{Bc}	2.39 ± 0.03^{Aa}
	100	2.62 ± 0.16^{Ba}	3.69 ± 0.19^{Aa}	2.09 ± 0.13^{Ca}
	150	2.33 ± 0.18^{Aa}	2.34 ± 0.37^{Ab}	2.18 ± 0.07^{Aa}
Insoluble Pectin (% galacturonic acid)	50	1.41 ± 0.25^{Aa}	0.48 ± 0.17^{Bc}	1.31 ± 0.13^{Aa}
	100	1.78 ± 0.08^{Ba}	2.58 ± 0.06^{Aa}	1.33 ± 0.19^{Ba}
	150	1.59 ± 0.20^{Aa}	1.21 ± 0.09^{Ab}	0.67 ± 0.21^{Bb}

The results are expressed as mean ± standard deviation (n = 3). Different capital letters in the same line (dose) and lowercase in the same column (maturity stage) are significantly different by the Tukey test at 5% of error probability. Doses $plant^{-1}$: 150 g of N + 50 g of K_2O + 140 g of P_2O_5; 150 g of N + 100 g of K_2O + 140 g of P_2O_5; 150 g of N + 150 g of K_2O + 140 g of P_2O_5.

Table 3
Soluble pectin and percentage of pectic solubilization in 'Paluma' guavas harvested at maturity stages green yellow (GY), yellow greenish (YG), and yellow (Y) from plants treated to different doses of K_2O.

Parameters	Maturity Stages			Doses (g K_2O plant^{-1})			S × D **
	GY	YG	Y	50	100	150	
Soluble pectin (%)	1.05 ± 0.29^{a}	1.19 ± 0.21^{a}	1.00 ± 0.28^{a}	1.22 ± 0.32^{a}	0.91 ± 0.12^{a}	1.11 ± 0.35^{a}	n.s.
Pectin solubilization (%)	42.05 ± 12.45^{a}	55.3 2 ± 13.20^{a}	45.15 ± 13.19^{a}	59.20 ± 15.01^{a}	34.00 ± 6.24^{b}	49.22 ± 17.59^{ab}	n.s.

The results are expressed as mean ± standard deviation (n = 3). Different lowercase letters in the same line (comparing maturity stage and dose separately) are significantly different by the Tukey test at 5% of error probability. Doses plant^{-1}: 150 g of N + 50 g of K_2O + 140 g of P_2O_5; 150 g of N + 100 g of K_2O + 140 g of P_2O_5; 150 g of N + 150 g of K_2O + 140 g of P_2O_5. **Interaction effect between stage (S) × doses (D), n.s. = non-significant.

150 g K_2O could be avoided, decreasing the cost of production of 'Paluma' guava. Moreover, the soluble fraction of pectin did not differ among maturity stages or K_2O doses applied (Table 3). The percentage of pectic substances solubilization did not differ among maturity stages; however, a difference between the doses of K_2O was observed. The percentage of solubilization showed a lower value of 34% for the dose of 100 g K_2O plant^{-1}, characterizing the stabilization of the cell wall at this level of potassium. However, compared to the dose of 100 g K_2O plant^{-1}, the pectin solubilization was higher for the dose of 50 g K_2O plant^{-1} (59.2%) and did not differ from 150 g K_2O plant^{-1} (34%), characterizing a more intensive solubilization rate of pectin from the cell wall. The values of insoluble pectin obtained are consistent with those of Tsai et al. [39], who evaluated the insoluble fraction of 'Jen-Ju-Bar' guava fruit at ripe stage. The changes in pectin content and pectinase activity reported by Ali et al. [32] showed a nonsignificant reduction in the 'Kampuchea' guava pectin content and significant values for 'Beaumont', which verified a decline in the levels. However, when analyzing the pattern of fruit ripening, the loss of firmness occurs not only by modification of cell wall pectin but also by degradation of other components, such as starch and cellulose [38,40]. For soluble pectin, Das and Majumder [36] reported that 'Allahabad Safeda' guava presented an increase in the soluble fraction of pectin during ripening, a process attributed to the action of pectolytic enzymes. The increase in the soluble pectin fractions indicates the softening of the fruit due to the pectic substances degradation into fractions of soluble galacturonic acid.

3.3. Cell wall enzymatic activity

Table 4 presents the results of the enzymatic activity. There was a significant interaction between the maturity stage and the dose of K_2O for PME activity. For the dose of 50 g K_2O plant^{-1}, the PME activity did not differ among stages. However, for fruits fertilized with 100 and 150 g K_2O plant^{-1}, the PME activities were higher in the GY stage and declined in the following maturity stages, suggesting that the degradation rates of pectic polysaccharides were reduced at these doses of potassium. The stages YG and Y for fruits treated with 100 g K_2O plant^{-1} presented the lowest PME activity.

A significant interaction was observed between the ripening stage and the dose of K_2O for PG activity (Table 4). Independent of the dose of K_2O, the activity of PG was lower in Y fruits. For doses of 50 and 100 g K_2O plant^{-1}, the activity of PG did not differ between the GY and YG stages. However, fruits from the dose of 150 g K_2O plant^{-1} harvested at the YG stage and subsequently Y showed decreased PG activity, indicating a possible reduction of the substrate for this enzyme.

The decrease in the apoplastic pH is required to activate the enzymes involved in cell wall degradation. Therefore, the higher stability of the cell wall at the dose of 100 g K_2O plant^{-1} may be due to the accumulation of potassium in the cells, which is required to stabilize the pH in the apoplast and cytoplasm, increasing the osmotic potential in the vacuole [41]. Additionally, potassium is also necessary to offset the electrochemical ATPase enzymes to support the cell wall's energy metabolism [42].

This demonstrates that the higher the total pectin content is the greater the insoluble fractions and the lower the rate of solubilization of pectic substances, implying higher cell wall stability. In turn, the soluble fraction was positively correlated with the pectic substances solubilization. In contrast, when correlated the percentage of pectic substances solubilization with the total and insoluble pectin contents, a significant negative correlation was revealed, indicating that, at least in part, the higher the levels of these pectic polysaccharides, the smaller the percentages of solubilization (Table 5). In addition, it is expected that with advancing maturity, the content of soluble pectin increases [41], which will increase the percentage of solubilization, explaining this negative correlation.

The most common function of PME is demethylesterification of pectic polysaccharides, triggering the process of pulp softening [6]. Thus, the lower PME activity resulted in reduced pectin demethylation and, therefore, decreased the substrate's availability for PG [41]. Consequently, this may result in a decline in the subsequent action of polygalacturonase, reflecting the stabilization of the cell wall by

Table 4
Pectinmethylesterase and polygalacturonase activity in 'Paluma' guavas harvested at maturity stages green yellow (GY), yellow greenish (YG), and yellow (Y) from plants treated to different doses of K_2O.

Parameters	Doses (g K_2O plant^{-1})	Maturity Stages		
		GY	YG	Y
Pectinmethylesterase activity (mU g^{-1} FW)	50	472.91 ± 50.30^{Ab}	387.85 ± 16.20^{Bb}	538.79 ± 5.17^{Aab}
	100	583.49 ± 50.45^{Aab}	370.92 ± 8.32^{Bb}	425.90 ± 49.86^{Bb}
	150	617.77 ± 11.04^{Aa}	459.22 ± 25.41^{Ba}	575.15 ± 70.38^{ABa}
Polygalacturonase activity (U g^{-1} FW)	50	116.75 ± 8.94^{Aa}	107.02 ± 2.60^{Aa}	55.94 ± 1.76^{Ba}
	100	113.91 ± 8.53^{Aa}	110.12 ± 6.37^{Aa}	57.80 ± 6.49^{Ba}
	150	111.80 ± 5.84^{Aa}	65.30 ± 13.98^{Bb}	46.47 ± 7.83^{Ba}

The results are expressed as mean ± standard deviation (n = 3). Different capital letters in the same line (dose) and lowercase in the same column (maturity stage) are significantly different by the Tukey test at 5% of error probability. Doses plant^{-1}: 150 g of N + 50 g of K_2O + 140 g of P_2O_5; 150 g of N + 100 g of K_2O + 140 g of P_2O_5; 150 g of N + 150 g of K_2O + 140 g of P_2O_5.

Table 5
Correlation coefficients for the fractions of the total, soluble and insoluble pectin, and percentage of pectic substances solubilization in 'Paluma' guavas harvested at maturity stages green yellow (GY), yellow greenish (YG), and yellow (Y) from plants treated to different doses of K_2O.

r	Total pectin	Soluble pectin	Insoluble pectin
Soluble pectin	−0.08 ^{NS}		
Insoluble pectin	0.87 **	−0.30 ^{NS}	
Percentage of pectin solubilization	−0.56 **	0.82 **	−0.66 **

^{NS}($P > 0.05$); **($P \leq 0.05$).

reducing the rate of pectic substances degradation and, thus, in the higher firmness of fruits of maturity stage YG, as observed herein for the dose of 100 g K_2O plant^{-1}. In addition, as PME presented notably less activity for the interaction of the maturity stage of YG with the dose of 100 g K_2O plant^{-1}, this clearly indicates that this level of potassium nutrition associated with levels of nitrogen and phosphorus tested herein played a role in stabilizing the cell wall. This might happen because balanced fertilization of nitrogen and phosphorus with potassium enhanced better efficiency in using nitrogen and phosphorus by plants, including environmental effects, with lower losses of nitrate and phosphate by leaching, improving this interaction and, consequently, the cell wall stability [43].

Fruits from plants fertilized with 100 g K_2O plant^{-1} presented lower activities of PME in the YG guava, a maturity stage recognized for having high metabolic activity due to ripening of this fruit [20]. Lower activity of this enzyme directly implies delayed fruit maturity [32]. Thus, it indicates that this potassium dose (100 g K_2O plant^{-1}) would be sufficient for plants producing firmer fruits of the YG stage, which could probably be maintained for a longer postharvest period. For the dose of 150 g K_2O plant^{-1}, this greater supply resulted in the highest uptake rates, called 'luxury absorption' [43], which raises production costs and reduces the quality and postharvest life of the fruit.

This behavior showed that PME demethylesterified of the polygalacturonic acids at 150 g K_2O plant^{-1}, allowed the hydrolytic action of PG by providing its substrate. However, the pectic substances remained solubilized after lowering the enzymatic activity, indicating that other enzymes may be involved in the softening process of guava pulp, such as cellulases and β-galactosidases [44]. It has been proposed that methylesterification can prevent the PG-mediated cell wall degradation of some fruits, and partial de-esterification of the PME is necessary for the PG to perform continuous pectin depolymerization [45]. Therefore, the degree of methylesterification of pectins may be a factor regulating guava maturation process [32]. Additionally, for some fruits in which no softening of the pulp occurs, this behavior has been related to failures in demethoxylation, which, again, decreased the action of PG [46].

However, Ali et al. [32] reported an increase in PG activity when evaluating 'Beaumont' and 'Kampuchea' guava cultivars in advanced maturity, in contrast to that observed in 'Paluma' guava. It is likely that other enzymes act together to modify the texture of this fruit, considering that cell wall-degrading enzymes are probably not the only main factor responsible for the guava softening, taking into account the complex structure of the cell wall [39].

3.4. Oxidative metabolism enzymatic activity

The PPO activity increased as maturation advanced (Table 6). Regarding potassium doses, fruits from plants fertilized with 100 g K_2O plant^{-1} had lower PPO activity. This dose resulted in the lowest conversion of phenolic compounds to melanin [46], which may reflect lower oxidative browning of the pulp. For POD activity, a significant interaction was observed between the maturity stage and dose (Table 7), and the activity was reduced for doses of 100 and 150 g K_2O plant^{-1} from the Y stage. Regarding the dose, in general, the lowest enzyme activity was observed at 100 g K_2O plant^{-1} in yellow fruits. This implies that there was probably a decline at a cellular level in the oxidation process resulting from this enzyme activity. It is known that potassium is the cofactor of several enzymes, including peroxidase. It also acts as an activator of the enzyme phenylalanine ammonia-lyase (PAL), which triggers the and reactions leading to the production of several phenolic compounds [47], and then participates as a cofactor of the enzyme peroxidase, coupled with the polymerization of alcohols for the formation of lignin at the end of the shikimic acid pathway [48]. The lower values of oxidation, according to these authors, may be due to a bypass of phenolic production by the shikimic acid pathway, using the glycolysis intermediates toward the synthesis of ascorbic acid.

Oxidases, such as PPO, exhibit greater activity in tissues deficient in potassium, which accumulates soluble nitrogen compounds, such as amino acids, diamines, and nitrate [43]. This may explain the lower PPO activity, as these changes in enzyme activity in tissues with an adequate supply of potassium lead to typical changes in metabolite contents, especially an increase in soluble carbohydrates, reducing the levels of positively charged amino acids, nitrate, organic acids, negatively charged amino acids, and pyruvate [47].

Fruits are less susceptible to oxidative stress and have reduced degrading enzyme activities of cell wall components when they present a suitable nutritional balance [48]. Then, when the plant is subjected to stress, an optimal nutritional status of K is critical for the stress resistance of plants. Thus, one of the defense mechanisms to increase stress resistance under potassium deficiency is an increased production of ROS that results in oxidative stress [49]. In turn, these compounds are related to the increased resistance of plants to pathogens, which provides greater stability to the tissues [50]. Despite this efficient defense system, plant cells suffer from oxidative damage under abiotic and biotic stress conditions [50]. The accumulation of ROS occurs due to either excess production or dysfunction of the antioxidant defense system, making the tissues unable to remove those species completely [50–53]. Therefore, this may be an indication that yellow fruits produced by plants fertilized with 100 and 150 g K_2O plant^{-1} presented lower oxidative stress.

Mondal et al. [14] reported an increase in POD activity for two guava varieties at advancing maturity and a subsequent decline in this oxidation due to the accumulation of lipid hydroperoxides and other reactive oxygen species during fruit ripening. Thus, the results obtained in this study indicate that the ripening of guava may be followed by a progressive increase in the oxidative/peroxidative stress that induces the antioxidant system [51], but that does not proceed to the more advanced

Table 6
Enzyme polyphenoloxidase activity – PPO in 'Paluma' guavas harvested at maturity stages green yellow (GY), yellow greenish (YG), and yellow (Y) from plants treated to different doses of K_2O.

Parameter	Maturity Stages			Doses (g K_2O plant^{-1})			S × D **
	GY	YG	Y	[1]50	100	150	
PPO (g^{-1} min^{-1} FW)	0.46 ± 0.09^{c}	0.93 ± 0.14^{b}	1.27 ± 0.25^{a}	0.85 ± 0.17^{ab}	0.78 ± 0.17^{b}	1.03 ± 0.13^{a}	n.s.

The results are expressed as mean ± standard deviation (n = 3). Different lowercase letters in the same line (comparing maturity stage and dose separately) are significantly different by the Tukey test at 5% of error probability. Doses plant^{-1}: 150 g of N + 50 g of K_2O + 140 g of P_2O_5; 150 g of N + 100 g of K_2O + 140 g of P_2O_5; 150 g of N + 150 g of K_2O + 140 g of P_2O_5. **Interaction effect between stage (S) × doses (D), n.s. = non-significant.

Table 7
Peroxidase activity in 'Paluma' guavas harvested at maturity stages green yellow (GY), yellow greenish (YG), and yellow (Y) from plants treated to different doses of K_2O.

Parameters	Doses (g K_2O plant^{-1})	Maturity Stages		
		GY	YG	Y
Peroxidase activity (min^{-1} g^{-1} FW)	50	1226.64 ± 348.80^{Aa}	1132.26 ± 380.75^{Aa}	1079.08 ± 110.94^{Aa}
	100	920.67 ± 55.83^{Aa}	1000.13 ± 49.60^{Aa}	316.46 ± 70.70^{Ba}
	150	1438.22 ± 336.39^{Aa}	1167.28 ± 31.72^{Aa}	105.09 ± 0.39^{Bb}

The results are expressed as mean ± standard deviation (n = 3). Different capital letters in the same line (dose) and lowercase in the same column (maturity stage) are significantly different by the Tukey test at 5% of error probability. Doses plant^{-1}: 150 g of N + 50 g of K_2O + 140 g of P_2O_5; 150 g of N + 100 g of K_2O + 140 g of P_2O_5; 150 g of N + 150 g of K_2O + 140 g of P_2O_5.

stages of maturation. In turn, the postclimacteric decrease in the activity of antioxidant enzymes may reflect dysfunction in the cell or even in specific organelles by altering the processes of synthesis and/or degradation in response to suppression of ethylene action [54,55].

4. Conclusion

The intermediate dose of 100 g K_2O plant^{-1} (associated with the applied levels of nitrogen and phosphorus) at yellow greenish maturity stage resulted in higher total pectin and insoluble pectin contents. In addition, PME and PG, and also the oxidative enzymes PPO and POD showed lower activities, indicating higher stability of the cell wall and firmer 'Paluma' guava fruits, therefore, with more extensive postharvest life. Furthermore, the results herein can be exploited as a strategic alternative for adjustment of the nutritional recommendations for guava trees cultivation. This will certainly provide fruits more resistant to postharvest handling, maintaining quality, and increasing the shelf life, reducing the postharvest losses and, thus, enhancing the financial return for the producer. However, further investigations are necessary to verify whether these doses influence consumers' sensory perception, fruit storage potential, and changes in bioactive compound profiles through potassium fertilization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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