

RESEARCH ARTICLE



Hexanal-Based Formulation Delays Softening in ‘Y368’ Kiwifruit Across Maturity Stages by Preserving Cell Wall Polysaccharides and Suppressing Cell Wall-Degrading Enzymes

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ABSTRACT

Kiwifruit has a limited storage life due to rapid softening, with harvest maturity playing a key role in softening rates, leading to substantial post-harvest losses. This study investigated the efficacy of a hexanal-based enhanced freshness formulation (EFF) in delaying the softening of “Y368” kiwifruit harvested at mid and late maturity stages, based on soluble solid content (7 and 9%, respectively). Kiwifruit were treated with 0.01 and 0.02% (v/v) EFF or left untreated (control), and stored for 8 weeks at 0 °C, followed by one week at 20 °C. Physicochemical properties, cell wall polysaccharides (CWPs), and cell wall-degrading enzymes (CWDEs) were assessed. EFF significantly delayed softening and optimized quality at both maturity stages, with late-harvested fruit exhibiting greater relative softening. Principal component analysis showed that EFF-treated fruit had higher firmness and CWP contents, whereas control fruit exhibited greater mass loss and higher CWDE activities. These results highlight the potential of EFF in delaying softening, preserving fruit quality, and enhancing the storage life of “Y368” kiwifruit, particularly for late-harvested fruit. The findings underscore the importance of harvest maturity and the potential of EFF to mitigate rapid softening, offering valuable insights for enhancing postharvest management in the kiwifruit industry.

KEYWORDS

Actinidia chinensis; hexanal; cell wall metabolism; firmness; postharvest storage

Introduction

Gold kiwifruit (*Actinidia chinensis*) is an economically valuable horticultural commodity that has dominated the global commercial market, owing to its unique flavor and high nutritional value (Tilahun et al., 2020). However, gold kiwifruit is extremely perishable and has a limited storage life due to rapid softening, leading to major postharvest losses (Cha et al., 2019). The postharvest losses of fruit due to rapid softening are estimated to be between 28 and 36% (Shafiee-Jood and Cai, 2016). Fruit firmness is a key quality attribute that directly influences grading, shelf life, marketability, and consumer acceptability of kiwifruit (Burdon et al., 2017), and is largely reliant on the integrity of the cell wall, which consists of polysaccharides including cellulose and hemicellulose Zhang et al. (2018); Fullerton et al. (2020). Fruit softening occurs when cell wall-degrading enzymes such as pectin

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methylesterase, polygalacturonase, β -galactosidase, and cellulase, catalyze the depolymerization of cell wall polysaccharides, weakening the adhesion between fruit cells (Li et al., 2024).

Low-temperature storage is the main technology used to suppress the metabolic changes that lead to kiwifruit softening during transit (Choi et al., 2022). However, kiwifruit can still undergo rapid softening at low temperatures (0–5 °C) due to the induction of softening-related genes (Asiche et al., 2018; Mitalo et al., 2019). Therefore, exploring postharvest treatments that can hinder softening under these conditions is crucial to optimize the storability of kiwifruit. Harvest maturity is another critical factor influencing the softening rate of kiwifruit (Choi et al., 2019). Tavarini et al. (2009) and Mahlaba et al. (2021) determined that later-harvested kiwifruit have a compromised postharvest performance, with Mahlaba et al. (2021) showing a 12% greater firmness loss in late-harvested kiwifruit during storage. This highlights the need to explore postharvest strategies to optimize firmness retention in kiwifruit harvested at different maturity stages.

Enhanced freshness formulation (EFF) is a hexanal-based formulation enriched with antioxidants, including geraniol, α -tocopherol and ascorbic acid (Paliyath and Padmanabhan, 2018). Hexanal (a natural volatile C6 aldehyde) is the active ingredient of EFF and the predominant compound that delays fruit softening by downregulating the expression of genes encoding cell wall-degrading enzymes (Tiwari and Paliyath, 2011). The ingredients of EFF are food additives approved by the United States Food and Drug Administration (FDA) with Generally Recognized as Safe (GRAS) status, underscoring the safety of this treatment for direct application on food. When supplemented with antioxidants, EFF optimizes firmness retention more effectively than hexanal alone (Sharma et al., 2010). EFF has been proven to optimize firmness retention of various fruit (Cheema et al., 2014; Gill et al., 2016; Qi et al., 2011). However, to our knowledge, no studies have evaluated the potential of EFF to delay rapid softening in gold kiwifruit, especially across different harvest maturity stages.

Given that South African gold kiwifruit destined for export are harvested at the mid and late maturity stages (Mahlaba et al., 2021), this study aimed to evaluate the efficacy of EFF in delaying softening at these stages under simulated export conditions. The capacity of EFF to delay softening by suppressing the activity of enzymes involved in the degradation of cell wall polysaccharides was assessed, as well as its impact on key physicochemical properties, including firmness, mass loss, total soluble solids and titratable acidity.

Materials and Methods

Fruit Source and Materials

Kiwifruit (*Actinidia chinensis* cv. “Y368”) were sourced from Roselands farm in Richmond, KwaZulu-Natal Province, South Africa. Harvesting was carried out at two maturity stages: mid (M1) and late (M2), determined by total soluble solid content of approximately 7 and 9%, respectively. After harvesting, the fruit were promptly transported to the Postharvest Laboratory at the University of KwaZulu-Natal. Only uniform fruit, without signs of damage, blemishes, or decay, were selected and assigned to the designated treatments. All chemicals used in this study were obtained from Sigma-Aldrich, South Africa.

Preparation of Postharvest Treatments and Storage

The enhanced freshness formulation (EFF) was prepared using a protocol described by Paliyath and Padmanabhan (2018). The formulation comprised of hexanal (10 mL), geraniol (10 mL), α -tocopherol (10 g), ascorbic acid (10 g), and Tween 20 (100 mL), all dissolved in 100 mL of ethanol (10%, v/v). To prepare hexanal concentrations of 0.01 and 0.02% (v/v), the stock solution was diluted with distilled water in ratios of 1:10 000 and 1:5000, respectively. The fruit were treated by immersing them in these solutions for 5 minutes, followed by air drying at ambient temperature. Untreated fruit served as the control. Each treatment included three replicates, with three fruit per replicate, per storage interval for

each maturity stage. The fruit were stored at 0 °C with 90% relative humidity for eight weeks, then transferred to 20 °C for one week to simulate shelf-life conditions.

Firmness and Mass Loss

Fruit firmness was determined using a penetrometer (Selectech, mod. FT 327, Italy) with an 8 mm diameter head. Firmness was recorded as kilogram-force (kgf) and converted to newtons (N), where 1 kilogram-force (kgf) is equal to 9.81 newtons (N).

Mass loss was measured using a calibrated Ohaus digital scale (± 0.01 g) (Model SKX2202, Switzerland). Mass loss was calculated using Eq. 1 and expressed as a percentage (%).

$$\text{Mass loss}(ML) = (IM - FM) / IM \times 100 \quad (1)$$

Where, IM, the initial mass of fruit (g) and FM, the final mass of fruit (g).

Total Soluble Solids (TSS) and Titratable Acidity (TA)

A desktop refractometer was used to quantify TSS of the fruit juice (Bellingham + Stanley Ltd, Model: RFM340+, UK). Titratable acidity was determined by titrating 10 mL of fruit juice with 0.1 M NaOH to a pH value of 8.1, using a Mettler Toledo Potentiometric compact titrator (Model G20S, Greifensee, Switzerland). Titratable acidity was expressed as the percentage of citric acid equivalent on a fresh weight (FW) basis using Eq. 2.

$$TA(\% \text{ citric acid}) = (0.0064 \times \text{titre (NaOH) mL}) / (10 \text{ mL juice}) \times 100 \quad (2)$$

Protopectin and Water-Soluble Pectin

Pectin extraction was performed as outlined by Wang et al. (2023). A 0.1 g sample of fruit pulp was homogenized in 2.5 mL of 95% ethanol, followed by incubation in a water bath (100 °C) for 30 min, with ethanol supplemented during the incubation process. The homogenate was centrifuged at $12\,000 \times g$ for 10 min at 4 °C. The supernatant was discarded, and 2.5 mL of 95% ethanol was added to the precipitate. This procedure was repeated three times. After centrifugation, the supernatant was discarded, and 1.5 mL of distilled water was added to the precipitate, incubated in a water bath at 50 °C for 30 min, and centrifuged at $12\,000 \times g$ for 15 min at 4 °C. The supernatant was collected as water-soluble pectin. Protopectin was extracted by adding 1.5 mL of 0.5 M sulfuric acid to the precipitate, boiling the homogenate for 1 h, and centrifuging at $12\,000 \times g$ for 15 min at 4 °C. One mL of each pectin solution (protopectin and WSP) was combined with 5 mL of concentrated sulfuric acid, and boiled for 20 min. Thereafter, 200 μ L of 0.15% carbazole-ethanol solution was added, and the reaction mixture was kept in the dark for 30 min. The absorbance was measured at 530 nm, and D-galacturonic acid served as the standard with results expressed as mg g^{-1} FW.

Cellulose and Hemicellulose

Cellulose content was analyzed following the method outlined by Sun et al. (2022). One gram of fruit pulp was mixed with 10 mL of 60% (v/v) sulfuric acid solution, and hydrolyzed at 4 °C for 12 h, and filtered through Whatman #4 filter paper. Subsequently, 200 μ L of filtrate was diluted to 10 mL, and 200 μ L of anthrone-sulfuric acid reagent was added to the mixture, which was heated in boiling water for 10 min. After cooling, the absorbance was measured at 620 nm, and cellulose content was calculated using glucose as a standard and expressed as mg g^{-1} FW.

Hemicellulose content was determined following the method outlined by Sun et al. (2022). One gram of fruit pulp was mixed with 6 mL of chilled distilled water and homogenized for 6 h. The mixture was then centrifuged at 8000 rpm for 15 min, and the supernatant was discarded.

The precipitate was homogenized with 6 mL of 0.5 M HCl for 6 h, followed by centrifugation, and the supernatant was discarded. The precipitate was extracted with 6 mL of 1 M KOH containing 0.02 M NaBH₄ for 6 h, followed by centrifugation. After the homogenate was centrifuged, the resulting supernatant was designated as hemicellulose. Hemicellulose was hydrolyzed with 60% (v/v) sulfuric acid at 100 °C for 1 h and diluted to 20 mL. Thereafter, 1.5 mL of 3,5-dinitrosalicylic acid (DNS) was added to 2 mL of the supernatant and boiled for 5 min and diluted to 25 mL after cooling. The absorbance was measured at 540 nm and hemicellulose was estimated using glucose as a standard and results were expressed as mg g⁻¹ FW.

Enzyme Extraction

The method for enzyme extraction followed the protocol outlined by Chen et al. (2017). One gram of fruit pulp was homogenized with 3.5 mL of 0.04 M sodium acetate buffer (pH 5.2), containing 5% polyvinyl pyrrolidone, 2% β-mercaptoethanol and 0.1 M NaCl. The homogenate was centrifuged at 15 000 × g for 30 min at 4 °C, and the resulting supernatant was used to measure polygalacturonase, β-galactosidase, and cellulase enzyme activity, following the protocol reported by Cao et al. (2021). All enzyme assays were run using a Shimadzu UV spectrophotometer (Model UV-1800 240 V, Kyoto, Japan).

Enzyme Assays

Polygalacturonase (PG, EC 3.2.1.15)

PG enzyme activity was assayed using the protocol described by Cao et al. (2021). The enzyme extract (500 µL) was added to 1 mL of 0.5 M sodium acetate buffer (pH 5.5), 500 µL of 1% polygalacturonic acid, incubated at 37 °C for 1 h. Thereafter, 1.5 mL of 0.63% DNS was added to the reaction mixture and boiled for 5 min. The concentration of the reducing groups was determined using D-galacturonic acid as a standard after measuring the absorbance at 540 nm. One unit of PG activity was expressed as nmol of galacturonic acid per min per mg protein.

β-galactosidase (β-Gal, EC 3.2.1.23)

β-Gal activity was assayed using the method described by Ali et al. (1995). The reaction mixture comprised of 400 µL of 13 mm 2-nitrophenyl-β-D-galactopyranoside, 400 µL of 0.1% bovine serum albumin, 500 µL of 0.1 M of sodium citrate (pH 4.1), and 100 µL of enzyme extract. The mixture was incubated at 37 °C for 15 min, and the reaction was stopped by adding 2 mL of 0.2 M sodium carbonate. The concentration of released 2-nitrophenol was measured at a wavelength of 415 nm, using 2-nitrophenol as a standard. One unit of β-Gal activity was expressed as nmol of 2-nitrophenol released per min per mg protein.

Cellulase (cx, EC 3.2.1.4)

Cx enzyme activity was assayed using the method described by Cao et al. (2021). The enzyme extract (100 µL) was added to 400 µL of 1% carboxymethyl cellulose, 500 µL of 0.1 M sodium acetate buffer (pH 5.0), followed by incubation at 37 °C for 1 hr. Thereafter, 1 mL of 1% DNS was added, and the assay mixture was boiled for 5 min. The concentration of reducing groups was measured at a wavelength of 540 nm using D-glucose as a standard. One unit of Cx activity was expressed as µmol of reducing groups per min per mg of protein.

Pectin Methylesterase, PME (EC 3.1.1.11)

The PME activity was analyzed using the method described by Amnuaysin et al. (2012). The reaction mixture contained 2 mL of 0.5% citrus pectin, 200 µL of 0.01% of bromothymol blue (3 mM potassium phosphate buffer pH 7.5), 300 µL of distilled water and 500 µL of enzyme

extract. The reaction was initiated by adding the enzyme extract, and the absorbance was measured at 620 nm and recorded for 3 min. One unit of PME activity was expressed as nmol of methyl ester hydrolyzed per min per mg protein.

Protein Concentration

The protein content in the enzyme extracts was determined using the Bradford (1976), with bovine serum albumin serving as the standard. The enzymes' specific activity was expressed as U mg⁻¹ protein.

Statistical Analysis

All experiments were conducted using a completely randomized factorial design with three factors: treatment, harvest maturity and storage period. Statistical analysis, Pearson correlation and Principal component analysis were carried out in R software version 4.3.1 (R Development Core Team, 2023). The data were analyzed using analysis of variance (ANOVA) and are presented as mean values $\pm$ standard error (SE). Duncan's multiple range test, with the least significant difference (LSD) at the 5% significance level, was used to separate the mean values.

Results and Discussion

Physicochemical Properties

Retaining firmness is critical for mitigating fruit deterioration and is a key parameter affecting fruit texture (Xu et al., 2023). Fruit firmness declined as the storage period progressed, with control fruit exhibiting the greatest loss in firmness (Figure 1A). At week 9 of storage, firmness was approximately 5, 8, and 10 N for the control, 0.01 and 0.02% EFF treatment levels, respectively. The sensory rejection point for kiwifruit is considered to be below 4 N; fruit with firmness levels below this threshold is regarded as unsuitable for further storage (Zhang et al., 2021).

The firmness values of treated fruit remained well above the sensory rejection point, suggesting that the reduction in firmness for treated fruit was within an acceptable limit for continued storage, illustrating the efficacy of EFF in delaying softening. These results are comparable to those reported by Silué et al. (2022), who showed that hexanal optimized firmness retention of mango fruit. Additionally, firmness declined with the advancement of harvest maturity, with fruit harvested at M1 exhibiting approximately 62% greater firmness than fruit harvested at M2 by the end of the storage period (Figure 1B).

Mass loss contributes significantly to fruit deterioration which leads to a loss of marketability (Shiri et al., 2016). The interaction among treatments, maturity stage, and storage duration had no significant ($p > .05$) effect on mass loss (Supplemental Table S1). However, the effect of treatments and harvest maturity significantly ($p < .05$) influenced the mass loss of fruit (Figure 1c,d). Fruit treated with 0.01 and 0.02% EFF had approximately 22 and 27% lower mass loss compared to the control, respectively. The findings are similar to those obtained by Cheema et al. (2018), who found that hexanal reduced mass loss of bell peppers. EFF can reduce the mass loss of fruit by preserving membrane integrity, which lowers moisture loss (Tiware and Paliyath, 2011). The mass loss of fruit harvested at M1 and M2 was approximately 6 and 7%, respectively. These findings suggest that late-harvested fruit deteriorate quicker than earlier-harvested fruit.

TSS is used as a maturity index and contributes to the flavor of kiwifruit (Meena et al., 2018). The interaction between treatments and storage duration significantly affected TSS ($p < .01$), with the 0.02% EFF-treated fruit exhibiting lower TSS than the control and the 0.01% treatment level (Figure 2a). These results are in accordance with those reported by Jincy et al. (2017), who showed that hexanal delayed the accumulation of TSS in mango fruit. As fruit ripen, TSS increases due to the conversion of polysaccharides into soluble sugars (Kaur et al., 2013). Additionally, a rise in

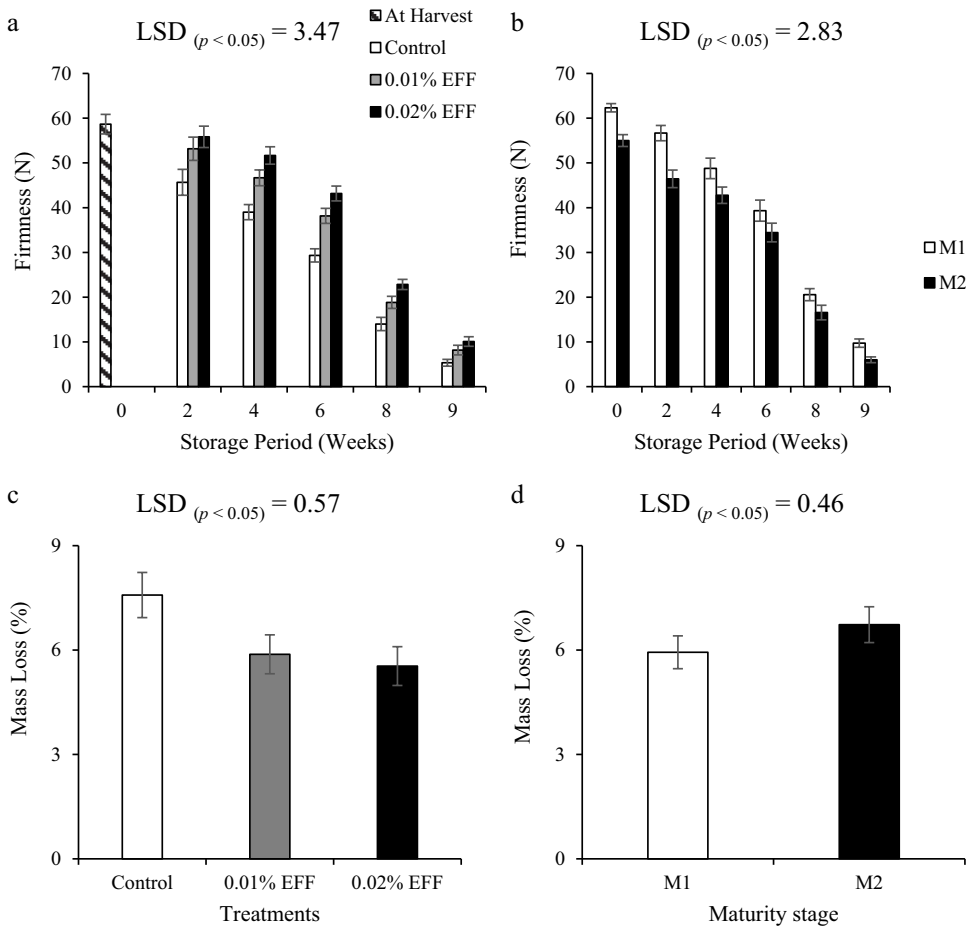


Figure 1. Effect of interaction between treatments and storage time (a), and the effect of interaction between maturity stage and storage time (b) on the firmness of kiwifruit. Effect of treatments (c) and maturity stage (d) on the mass loss of kiwifruit. Values are the means $\pm$ SE ($n = 3$).

TSS can also be attributed to moisture loss, which increases the concentration of soluble sugars (Nath et al., 2012). This corroborates the results of this study, demonstrating that fruit with the highest TSS also had the highest mass loss. Therefore, EFF can effectively delay TSS accumulation by reducing mass loss. The combined effect of maturity stage and storage duration on TSS was significant ($p < .01$), with fruit harvested at M2 exhibiting substantially higher levels of TSS than fruit harvested at M1 (Figure 2b). These findings suggest that the ripening rate of kiwifruit increases with an advancement in fruit maturity.

TA is linked to the concentration of organic acids in fruit and are important for the maintenance of fruit quality (Shiri et al., 2016). The treated fruit exhibited significantly ($p < .05$) higher TA than the control fruit (Figure 2c). TA for the 0.01 and 0.02% treatment levels were approximately 5 and 8% higher than the control, respectively. The combined effect of maturity stage and storage duration on TA was significant ($p < .05$), with fruit harvested at M1 showing a 12% higher TA than those harvested at M2 at week 9 of storage (Figure 2d). When fruit respire, organic acids are used as substrates in the respiratory cycle, which leads to a decrease in acidity (Kaur et al., 2013). Past research has shown that EFF improves retention of TA by reducing the respiration rate (Yumbya et al., 2018). Thus, we hypothesize that the retention of TA exhibited by treated fruit could be due to the ability of EFF to suppress respiration rates.

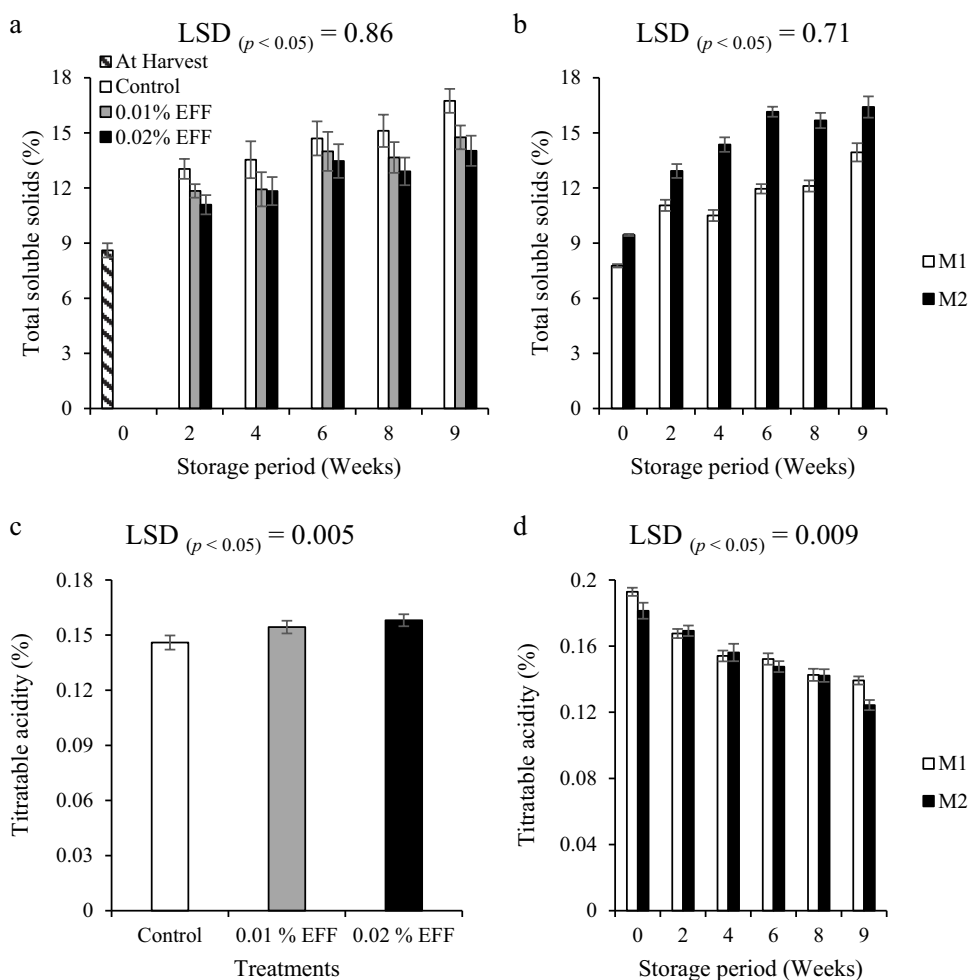


Figure 2. Effect of interaction between treatments and storage time (a), and the effect of interaction between maturity stage and storage time (b) on the total soluble solids of kiwifruit. Effect of treatments (c) and the effect of interaction between maturity stage and storage time (d) on the titratable acidity of kiwifruit. Values are the means $\pm$ SE ($n = 3$).

Cell Wall Polysaccharides (CWPs)

Protopectin is a water insoluble form of pectic substances that contributes to the firmness and texture of fruit and degrades into water-soluble pectin (WSP) during fruit ripening (Zhang et al., 2019). The interaction between treatments and storage duration significantly affected protopectin content ($p < .001$), with treated fruit maintaining substantially higher content than the control during storage (Figure 3a). These results are corroborated by those obtained by Gill et al. (2016), who showed that EFF reduced the degradation of pectin in guava fruit. The combined effect of maturity stage and storage duration on protopectin content was significant ($p < .001$), with M1 fruit exhibiting considerably higher content than M2 fruit (Figure 3b). The WSP content increased as the storage period progressed; however, treated fruit had substantially lower WSP content than the control, with the 0.02% treatment level showing the most pronounced effect (Figure 3c). The WSP content of fruit harvested at M1 was approximately 16% lower than fruit harvested at M2 (Figure 3d). These results support the theory that the degradation of protopectin is characterized by the increase in WSP (Wang et al., 2023).

Cellulose is a structural polysaccharide of the cell wall that is involved in supporting and protecting the cell structure (Wang et al., 2021). The interaction between treatments and storage duration

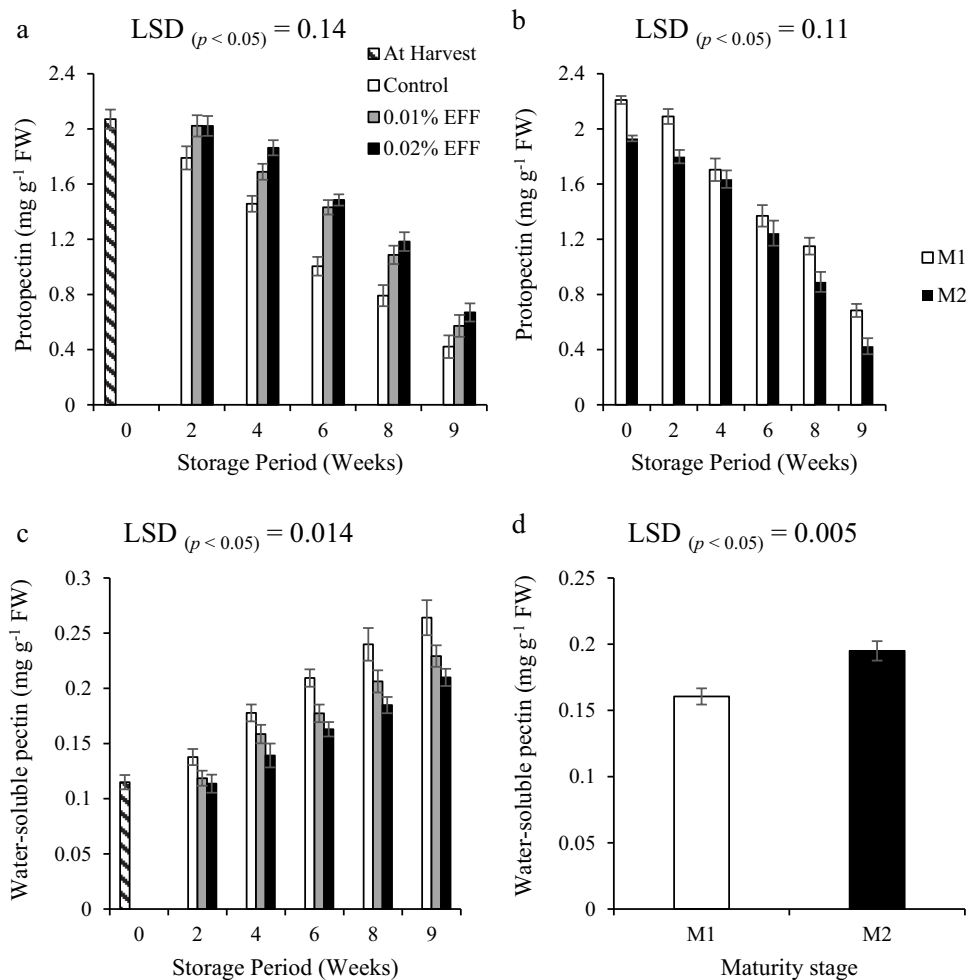


Figure 3. Effect of interaction between treatments and storage time (a), and the effect of interaction between maturity stage and storage time (b) on the protopectin content of kiwifruit. Effect of interaction between treatments and storage time (c) and the effect of maturity stage (d) on the water-soluble pectin content of kiwifruit. Values are the means $\pm$ SE ($n = 3$).

significantly affected ($p < .001$) cellulose content, with treated fruit maintaining substantially higher levels throughout the storage period, particularly at the 0.02% treatment level (Figure 4a). Additionally, harvest maturity had a significant ($p < .001$) effect on cellulose content, with fruit harvested at M1 showing approximately 1.2 times greater content than those harvested at M2 (Figure 4b).

Hemicellulose is a heteropolysaccharide comprised of xyloglucan and xylose, which is connected with cellulose by hydrogen bond (Posé et al., 2019). The interaction between treatments and storage duration significantly affected hemicellulose content ($p < .05$) (Figure 4c). At week 9 of storage, the hemicellulose content of treated fruit was approximately 33 and 48% greater than the control, for the 0.01 and 0.02% EFF treatment levels, respectively. The hemicellulose content decreased as the storage period progressed, with fruit harvested at M1 showing significantly ($p < .05$) greater hemicellulose content compared to those harvested at M2 (Figure 4d).

Given that fruit softening is attributed to the degradation of CWPs, these results suggest that the effectiveness of EFF in delaying softening (Figure 1a) is due to its ability to preserve the contents of CWPs (Figures 3a and 4a,c). This underscores the potential of EFF to prevent the

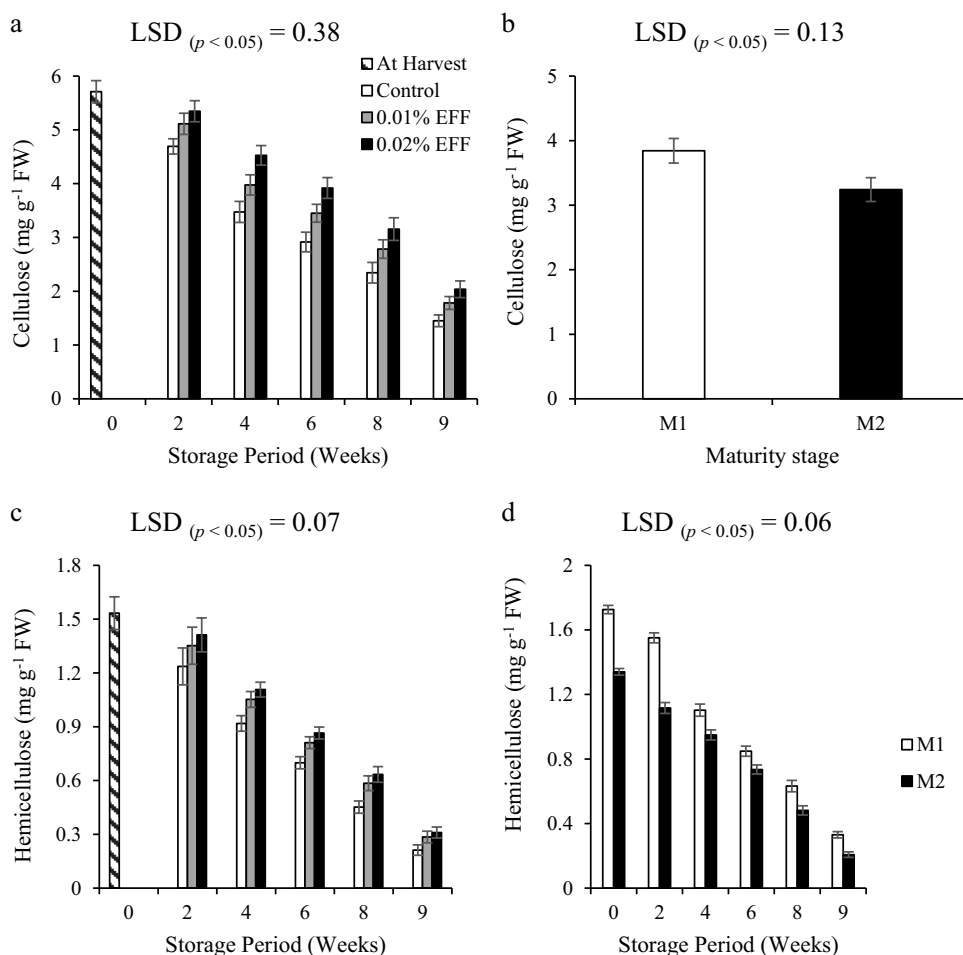


Figure 4. Effect of interaction between treatments and storage time (a), and the effect of maturity stage (b) on the cellulose content of kiwifruit. Effect of interaction between treatments and storage time (c) and the effect of interaction between maturity stage and storage time (d) on the hemicellulose content of kiwifruit. Values are the means $\pm$ SE ($n = 3$).

deterioration of kiwifruit by hindering rapid softening. Additionally, the significantly lower levels of CWPs exhibited by fruit harvested at M2 suggest that the content of CWPs decreases with an advancement in maturity. This may explain why fruit harvested at M2 were softer compared to those harvested at M1 (Figure 1b). This observation highlights the impact of harvest maturity on the firmness of kiwifruit, as softer fruit may be more prone to deterioration during storage.

Cell Wall-Degrading Enzymes (CWDEs)

The PME activity increased substantially during storage; however, EFF-treated fruit exhibited significantly ($p < .05$) lower enzyme activity than the control fruit (Figure 5a). These outcomes are in alignment with those reported by Kaur et al. (2019), who showed that EFF suppressed PME activity in grapes. The combined effect of maturity stage and storage duration significantly affected PME activity ($p < .05$), with fruit harvested at M2 showing substantially higher enzyme activity than fruit harvested at M1 throughout the storage period (Figure 5b). PG activity was significantly influenced ($p < .001$) by the interaction between treatments and storage duration, with treated fruit displaying reduced enzyme

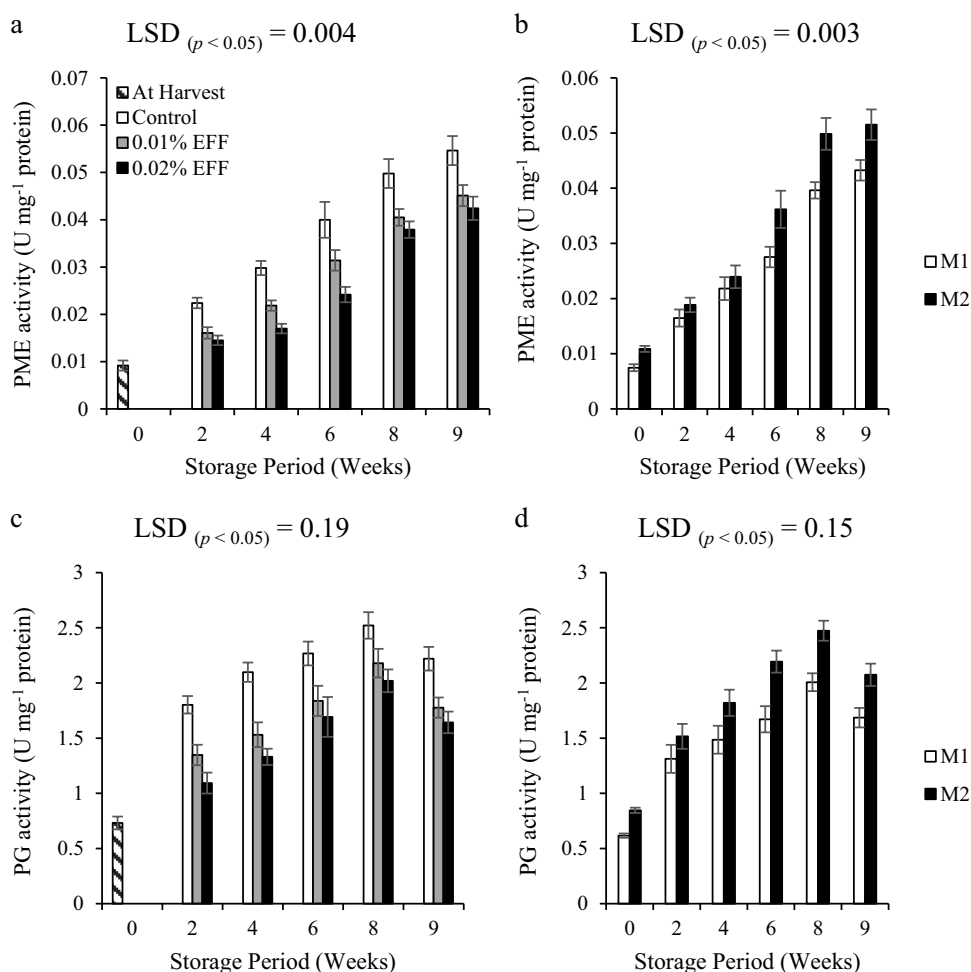


Figure 5. Effect of interaction between treatments and storage time (a), and the effect of interaction between maturity stage and storage time (b) on the pectin methylesterase (PME) activity of kiwifruit. Effect of interaction between treatments and storage time (c) and the effect of interaction between maturity stage and storage time (d) on the polygalacturonase (PG) activity of kiwifruit. Values are the means $\pm$ SE ($n = 3$).

activity compared to the control (Figure 5b). These findings are comparable to those obtained by Preethi et al. (2021), who showed that EFF suppressed PG activity in mango fruit. The combined effect of maturity stage and storage duration significantly affected PG activity ($p < .05$), with M1 fruit maintaining lower enzyme activity than M2 fruit (Figure 5d).

At week 9 of storage, β -Gal activity in the 0.01 and 0.02% EFF-treated fruit was reduced by approximately 1.2-fold and 1.4-fold, respectively, compared to the control (Figure 6a). β -Gal activity increased as the storage period progressed, with fruit harvested at M2 exhibiting significantly ($p < .001$) higher enzyme activity than fruit harvested at M1 (Figure 6b). The combined effect of treatments and storage duration significantly affected ($p < .05$) Cx activity, with treated fruit showing markedly reduced enzyme activity during storage (Figure 6c). Additionally, harvest maturity had a significant effect ($p < .001$) on Cx activity, with fruit harvested at M1 exhibiting approximately 7% lower enzyme activity than those harvested at M2 (Figure 6d).

CWDEs facilitate the degradation of CWP's resulting in fruit softening (Rao et al., 2011). In the cell wall, PME hydrolyzes methoxylated pectin by hydrolyzing the methyl group on the galacturonic acid, leading to the production of demethylated pectin that is further hydrolyzed by PG (Zhang et al., 2019).

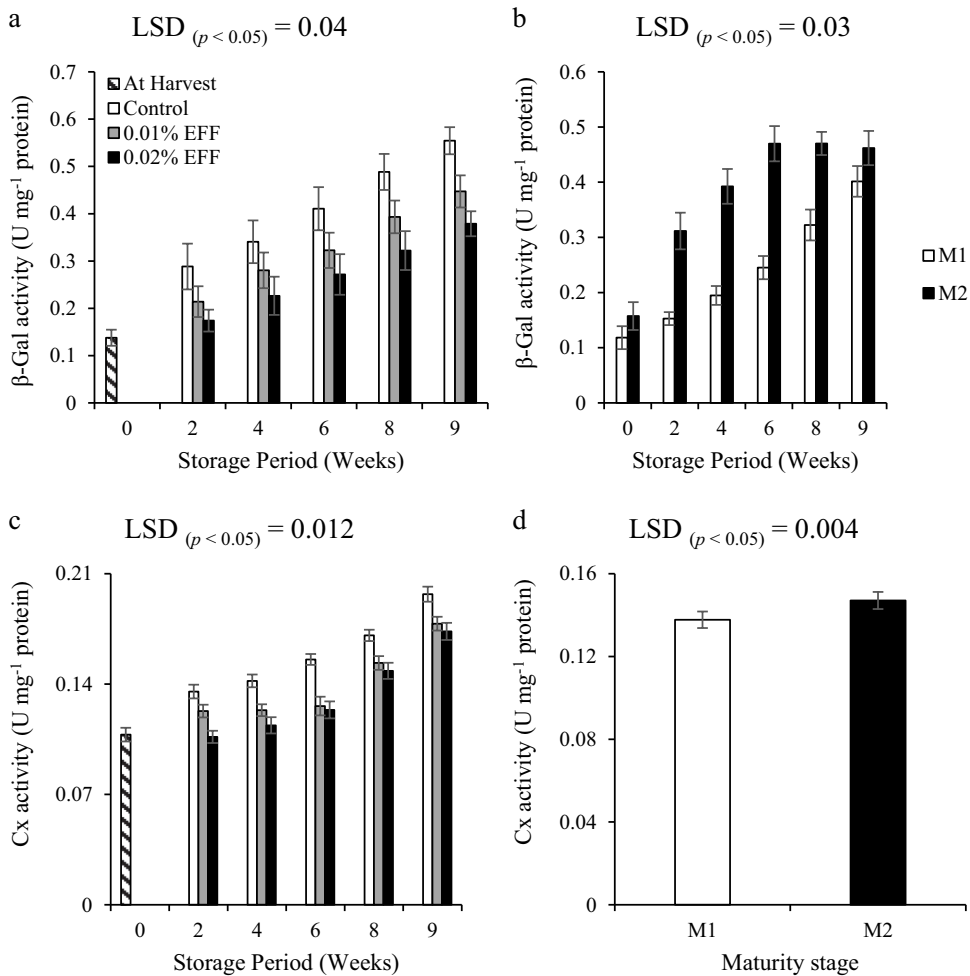


Figure 6. Effect of interaction between treatments and storage time (a), and the effect of interaction between maturity stage and storage time (b) on the β -galactosidase (β -gal) activity of kiwifruit. Effect of interaction between treatments and storage time (c) and the effect of maturity stage (d) on the cellulase (Cx) activity of kiwifruit. Values are the means $\pm$ SE ($n = 3$).

PG catalyzes the hydrolysis of α (1 $\rightarrow$ 4) galacturonan linkages of demethylated pectin, resulting in the depolymerization and dissolution of pectin (Zhou et al., 2011). β -Gal hydrolyzes pectin and hemicellulose by cleaving the galactosidic bonds in the CWPs and removing galactose residues (Lin et al., 2018). Cx plays a role in degrading cellulose and the β -1,4-glucan backbone of xyloglucan, hemicellulosic polysaccharide (Zhou et al., 2011).

Thus, the significantly higher levels of firmness (Figure 1a) and CWPs (Figures 3a and 4a,c), along with the substantially lower activities of CWDEs (Figures 5a,c and 6a,c) observed in treated fruit, suggest that EFF delayed softening by preserving CWPs through the suppression of CWDEs. These results reinforce the potential of EFF to optimize storage life of “Y368” kiwifruit by hindering rapid softening. Findings by Tiwari and Paliyath (2011) showed that EFF treatment downregulated genes for cell wall softening enzymes (PME, PG, and β -Gal) in tomato fruit.

Therefore, the suppression of CWDEs in treated kiwifruit may be linked to the downregulation of genes encoding these enzymes. However, further investigations are needed to evaluate the molecular mechanisms by which EFF affects cell wall degradation in kiwifruit to validate this hypothesis. The activities of CWDEs were significantly higher in fruit harvested at M2 compared

to M1. This increased enzyme activity may have contributed to the lower contents of CWPs observed in M2 fruit (Figures 3b and 4b,d), suggesting that elevated CWDE activity accelerated softening in late-harvested fruit.

This is further supported by the results in Figure 1b, which show that fruit harvested at M2 exhibited greater relative softening than those harvested at M1, suggesting that higher CWDE activity may contribute to more rapid softening in late-harvested fruit. These results are comparable to those reported by Tilahun et al. (2020), who found that later-harvested kiwifruit exhibited higher PG activity, and lower levels of pectin, which correlated with greater softening compared to earlier-harvested fruit.

Pearson Correlation Coefficient and Principal Component Analysis

A correlation analysis conducted to evaluate the relationships among the measured parameters (Figure 7). TSS showed positive correlations with WSP ($r = 0.79$; $p < .001$), mass loss ($r = 0.67$; $p < .001$) and negative correlations with firmness ($r = 0.68$; $p < .001$), protopectin ($r = 0.70$; $p < .001$), cellulose ($r = 0.76$; $p < .001$), hemicellulose ($r = 0.73$; $p < .001$) and TA ($r = 0.64$; $p < .001$). As previously mentioned, the accumulation of TSS increases due to moisture loss and the conversion of polysaccharides into soluble sugars (Nath et al., 2012, Kaur et al., 2013).

These findings therefore provide further evidence supporting the contention that the increase in mass loss and the degradation of CWPs contributes to the accumulation of TSS (Li et al., 2024; Wang

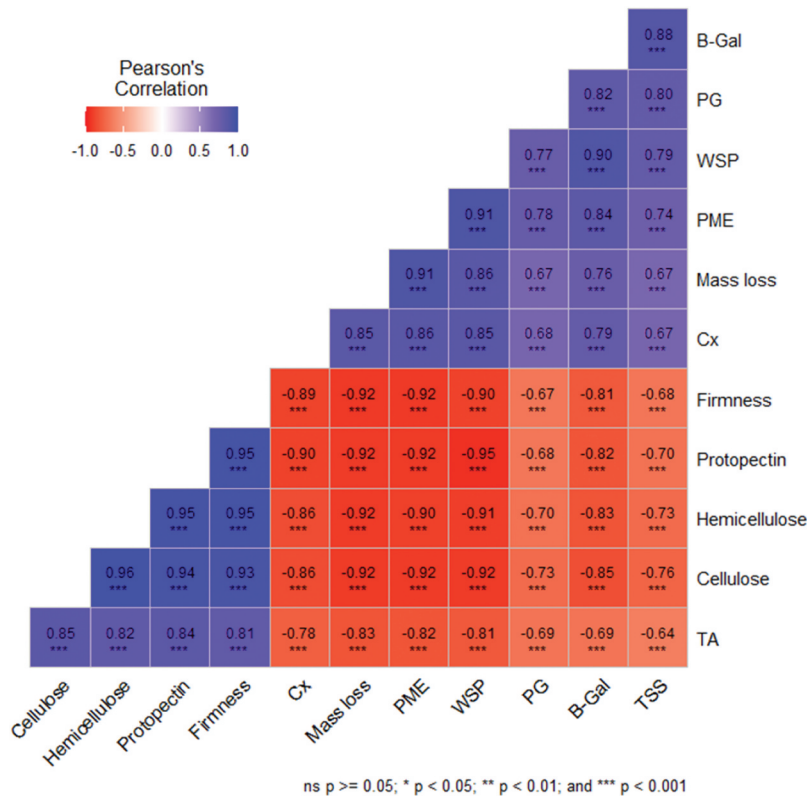


Figure 7. Pearson correlation matrix between physicochemical properties (firmness, mass loss, total soluble solids (TSS), and titratable acidity (TA)), cell wall polysaccharides (protopectin, cellulose, hemicellulose), water-soluble pectin (WSP), pectin methylesterase (PME), polygalacturonase (PG), β -galactosidase (β -gal), and cellulase (cx). The correlation coefficients are proportional to the color intensity. Positive correlation is displayed in blue and negative correlation is displayed in red.

et al., 2021). The activity of CWDEs was negatively ($p < .001$) correlated with firmness and CWP, and positively ($p < .001$) correlated with WSP. This suggests that kiwifruit softening may be delayed by inhibiting CWDEs, thereby reducing the degradation of CWPs and loss of firmness, which could enhance storability and fruit quality.

Principal component analysis (PCA) was performed to distinguish which parameters were more dominant in categorizing the fruit from the treatments/maturities (Figure 8). PCA was produced for the first two dimensions where Dim1 and Dim2 accounted for 91.2 and 6.9% of the total variance, respectively. Factor loadings are categorized as strong, moderate, or weak, when corresponding to loading values: > 0.75 , $0.75-0.50$ and $0.50-0.30$, respectively (Liu et al., 2003). In addition, factor loadings represent the correlation between the principal component and the original variable (Mooi et al., 2018). Dim1 exhibited positive correlations for PME (0.98), PG (1.00), β -Gal (0.96), Cx (0.96), WSP (0.99), TSS (0.90) and mass loss (0.89), and negative correlations for protopectin (-1.00), cellulose (-0.99), hemicellulose (-0.95), firmness (-1.00) and TA (-0.85) (Supplemental Table S2).

These results demonstrate that control fruit harvested at both M1 and M2, exhibited higher levels of mass loss, TSS, WSP, and CWDEs (PME, PG, β -Gal, and Cx), compared to EFF-treated fruit, which maintained greater firmness, CWPs (protopectin, cellulose, and hemicellulose), and TA. In contrast, M2 fruit treated with 0.01% EFF showed higher levels of mass loss, TSS, WSP, and CWDEs. These findings suggest that the 0.01% EFF treatment level was not as effective as the 0.02% level in optimizing firmness retention and quality in fruit harvested at both the mid and late maturity stages. Given that fruit harvested at M2 exhibited greater softening (Figure 1b) due to higher enzyme activities (Figures 5b,d and 6b,d), it can be deduced that the increased softening observed in late-harvested fruit can be mitigated by increasing the EFF dosage.

Previous studies on hexanal formulations for delaying fruit softening have primarily focused on their application at a singular maturity stage. In contrast, the current study broadens the understanding of EFF by demonstrating its ability to effectively delay rapid softening in “Y368” kiwifruit harvested at both mid and late maturity stages, in a dose-dependent manner. These findings underscore the potential of EFF as a postharvest strategy to impede rapid softening across different harvest maturities. Thus, the application of EFF to delay softening in kiwifruit during prolonged storage is

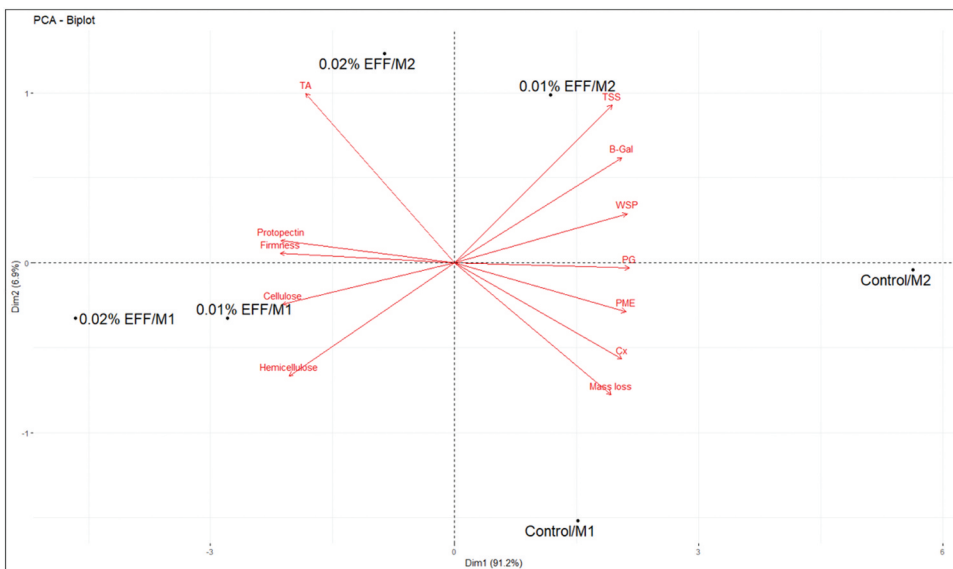


Figure 8. Principal component analysis biplot showing the correlations between the measured variables and factors (treatment and maturity stage). Dimension one (Dim1), dimension two (Dim2), total soluble solids (TSS), and titratable acidity (TA), pectin methylesterase (PME), polygalacturonase (PG), β -galactosidase (β -gal), cellulase (cx), and water-soluble pectin (WSP).

a promising preservation strategy that could benefit the kiwifruit industry by reducing postharvest losses attributed to rapid softening.

Conclusion

The findings of this study demonstrated the efficacy of EFF in delaying kiwifruit softening by suppressing CWDEs, thereby facilitating the retention of CWPs essential for maintaining fruit firmness. This was further substantiated by the pronounced clustering in the PCA biplot, underscoring the role of EFF in optimizing kiwifruit quality and storability. Among the treatments, the 0.02% (v/v) EFF dosage was most effective in delaying softening, especially in late-harvested fruit that are more prone to rapid postharvest deterioration. The adoption of this treatment has the potential to reduce postharvest losses in the kiwifruit industry. Ethylene production triggers fruit softening, which in turn regulates the activities of CWDEs. Therefore, future research should investigate how EFF affects ethylene biosynthesis and cell wall metabolism-related genes to elucidate the molecular mechanisms by which EFF inhibits cell wall degradation.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author, AM, upon reasonable request.

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Hexanal-based formulation delays softening in 'Y368' kiwifruit across maturity stages by preserving cell wall polysaccharides and suppressing cell wall-degrading enzymes

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