

Article

Preharvest Ferulic Acid Spray Is Associated with Lignin-Related Outer Tissue Changes and Improved Fresh Weight Retention in Strawberry Fruit

Su-Hyun Choi ¹, Dae-Young Kim ², Seolah Kim ¹, Woo-Moon Lee ³ and Chan Saem Gil ^{4,*}

- ¹ Vegetable Research Division, National Institute of Horticultural and Herbal Science, Rural Development Administration, Wanju 55365, Republic of Korea; choishn94@korea.kr (S.-H.C.); sulah1234@korea.kr (S.K.)
² Allium Vegetable Research Center, National Institute of Horticultural and Herbal Science, Rural Development Administration, Muan 58877, Republic of Korea; young78@korea.kr
³ PHENOBOX Co., Ltd., Suwon 16643, Republic of Korea; wmllee65@gmail.com
⁴ Department of Horticulture, College of Industrial Science, Kongju National University, Yesan 32439, Republic of Korea
* Correspondence: csgil@kongju.ac.kr

Abstract

Strawberry fruit deteriorates rapidly after harvest due to its fragile surface tissues, and cultivation-based strategies that modulate phenolic-related responses may help improve selected postharvest-related traits. This study evaluated whether preharvest ferulic acid (FA) spray is associated with fruit surface penetration resistance (FSPR), lignin-related absorbance (LA) in the outer fruit tissue, outer tissue organization, and fresh weight retention in two strawberry cultivars, ‘Sulhyang’ and ‘Kuemsil’. Plants were sprayed with 0, 0.05, 0.2, and 0.4 g L^{−1} FA during fruit development, and fruit quality, surface-related traits, LA, light microscopic features, external appearance, and relative fresh weight during storage were assessed. FA treatment increased FSPR in both cultivars, with a significant cultivar × FA concentration interaction. LA decreased during ripening but was higher in mature red fruit treated with 0.2 and 0.4 g L^{−1} FA than in untreated fruit. The 0.4 g L^{−1} FA treatment showed better qualitative maintenance of outer tissue organization, improved external appearance, and higher fresh weight retention during short-term storage, without a consistent decrease in SSC and TA. These results indicate that preharvest FA spray is a practical cultivation-stage approach associated with improved surface-related postharvest responses in strawberry fruit and provides a basis for future metabolite-informed studies.

Keywords: strawberry; outer fruit tissue; ferulic acid; lignin-related absorbance; postharvest-related traits; fresh weight retention; fruit surface penetration resistance



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1. Introduction

Strawberry (*Fragaria* × *ananassa*) is one of the most commercially important crops worldwide and is highly valued due to its attractive appearance, sweetness, aroma, and nutritional quality [1,2]. However, strawberry fruit has a very short postharvest life because of its soft texture, high water content, active metabolism, and susceptibility to mechanical damage during handling, transportation, and storage [2]. It was suggested that the retail-level waste of strawberry fruit can range from 50% to 92% under inadequate or no precooling conditions [3]. In particular, the surface region, which is the outer fruit tissue including the epidermis, cuticle, and adjacent subepidermal parenchymatous tissues, is the first structural interface between internal tissues and the external environment. Its

stability is closely associated with water loss, surface collapse, mechanical injury, and visible deterioration in quality after harvest [4,5]. Therefore, practical strategies to improve the structural and biochemical properties of the surface region have been tried to maintain quality during postharvest distribution and retail handling [2,4,5].

The structural and biochemical properties of the surface region of strawberry fruit are influenced by metabolic changes that occur during fruit development and ripening [6,7]. In fleshy fruits, ripening is accompanied by coordinated changes in cell wall composition, phenolic metabolism, tissue softening, pigment accumulation, flavor formation, and stress responses [7–10]. Among these changes, cell wall-related metabolism is particularly important in determining texture, surface resistance, and tissue integrity [8,11]. In particular, lignin and related phenolic polymers contribute to cell wall rigidity, mechanical strength, and stress resistance in plant tissues [12,13]. Lignin biosynthesis is primarily derived from the phenylpropanoid pathway and involves enzymes such as phenylalanine ammonia-lyase, cinnamate 4-hydroxylase, 4-coumarate-CoA ligase, cinnamoyl-CoA reductase, cinnamyl alcohol dehydrogenase, and oxidative polymerization enzymes, including peroxidases and laccases [14]. Although lignification is generally more prominent in vegetative or vascular tissues, changes in lignin-associated phenolic compounds in fruit surface tissues may influence the physical stability of the fruit during ripening and postharvest storage [15].

Ferulic acid (FA; 4-hydroxy-3-methoxycinnamic acid) is a hydroxycinnamic acid derived from the phenylpropanoid pathway and is widely present in plant cell walls as a free, esterified, or cell wall-bound phenolic compound [16,17]. Ferulate residues can be ester-linked to cell wall polysaccharides and can participate in oxidative coupling reactions that contribute to cell wall cross-linking and structural reinforcement [18,19]. Furthermore, previous studies have suggested that FA or ferulate residues may participate in lignification-related cell wall processes by serving as precursor-related hydroxycinnamates in the monolignol pathway or as sites for oxidative coupling with lignin monomers in specific plant cell wall systems [20,21]. These multifunctional roles of FA provide a biochemical background for evaluating whether exogenous FA treatment is associated with lignin-related changes in the outer fruit tissue, without implying direct evidence of lignin biosynthesis in the present study. Previous studies have reported that exogenous FA treatment can enhance postharvest resistance or maintain quality in several fruit crops, such as tomato, banana, and kiwifruit, by affecting phenylpropanoid metabolism, antioxidant responses, defense-related enzyme activities, or cell wall-associated processes [22–24]. These findings suggest that FA may function not only as an antimicrobial or defense-related compound but also as a phenolic signal or substrate associated with structural reinforcement in fruit tissues [23,25,26].

From the perspective of metabolism-informed horticulture, preharvest application of phenolic compounds may offer a practical approach for steering quality-related metabolism during fruit development. Unlike postharvest treatments applied after quality decline has already begun, preharvest treatments can influence developing fruit tissues before harvest and may modify the physiological or biochemical status that determines postharvest performance. This cultivation-stage management may also reduce the need for additional handling after harvest and can be integrated into existing crop management practices. More broadly, sustainable cultivation-stage interventions, including microbial inoculation, humic products derived from agricultural waste, and foliar biostimulation, have been explored to improve crop physiological status and performance before harvest [27,28]. Although these examples are crop- and treatment-specific, they provide a broader context for evaluating preharvest interventions aimed at improving quality-related traits. In fact, several preharvest elicitor or biostimulant treatments, including salicylic acid, methyl jasmonate, chitosan,

and calcium-based sprays, have been reported to improve fruit firmness, cell wall integrity, and antioxidant responses in various horticultural crops [29–32]. These studies support the broader concept that cultivation-stage treatments can influence postharvest-related traits, although their efficacy is strongly governed by compound type, concentration, application timing, crop species, and cultivar. However, limited information is available on whether preharvest FA spray can modify lignin-associated characteristics in the outer tissue of strawberry fruit and whether these changes are linked to surface mechanical resistance and postharvest quality maintenance. In addition, cultivar-dependent responses to FA treatment remain unclear, although genotype-related differences in fruit texture and surface properties may influence the effectiveness of the treatment [33–35].

This study aimed to evaluate whether preharvest FA spray is associated with changes in selected postharvest-related traits in two strawberry cultivars, ‘Sulhyang’ and ‘Kuemsil’. The selected cultivars are commercially important Korean strawberry cultivars and were used to evaluate whether preharvest FA responses differ between cultivar backgrounds with different fruit texture- and surface resistance-related characteristics. The specific objectives were to determine whether FA treatment affects fruit surface penetration resistance (FSPR), lignin-related absorbance signals in the outer fruit tissue, qualitative organization of the outer tissue, external appearance, and relative fresh weight retention during short-term storage.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

The experiment was carried out from 1 May to 31 May 2023 using two strawberry cultivars, ‘Sulhyang’ and ‘Kuemsil’, grown on the elevated hydroponic system in a plastic greenhouse at the National Institute of Horticultural and Herbal Science (NIHHS), Wanju-gun, Republic of Korea. The substrate consisted of a commercial horticultural substrate (Hanareum type A, Sinsung Mineral, Seongnam, Republic of Korea) composed of coir (51.5%), perlite (15.0%), peat (13.0%), zeolite (10.0%), vermiculite (10.0%), and a trace amount of composted organic materials. The greenhouse environmental conditions were recorded at 1 h intervals throughout the experimental period. Each timestamped record represented the maximum air temperature, minimum air temperature, and mean relative humidity measured during the preceding 1 h interval. A total of 744 hourly records were used to summarize the greenhouse environment. Based on daily summaries calculated from the hourly records, the daily maximum air temperature averaged 27.4 °C and ranged from 20.7 to 34.0 °C, whereas the daily minimum air temperature averaged 6.6 °C and ranged from 2.6 to 10.0 °C. The daily mean relative humidity averaged 80.4% and ranged from 66.4 to 94.2%. To maintain uniform short-day conditions during the FA treatment period, plants were exposed to an 8 h photoperiod of natural sunlight from 09:00 to 17:00, and blackout curtains were used from 17:00 to 09:00 each day.

Plants were fertigated with a standard nutrient solution for strawberry cultivation as described by Choi et al. [36]. The nutrient solution contained the following macroelements: $\text{NO}_3\text{-N}$, 6.0 meq L^{-1} ; $\text{NH}_4\text{-N}$, 0.2 meq L^{-1} ; $\text{PO}_4\text{-P}$, 2.0 meq L^{-1} ; K, 3.5 meq L^{-1} ; Ca, 3.0 meq L^{-1} ; Mg, 1.0 meq L^{-1} ; and $\text{SO}_4\text{-S}$, 1.0 meq L^{-1} . The microelement composition was as follows: Fe, 1.30 mg L^{-1} ; B, 0.30 mg L^{-1} ; Mn, 0.30 mg L^{-1} ; Zn, 0.30 mg L^{-1} ; Cu, 0.02 mg L^{-1} ; and Mo, 0.01 mg L^{-1} . Irrigation was supplied six times per day via an automatic system, with the daily volume adjusted to 450 mL per plant. The nutrient solution was measured to have a pH range of 5.5–6.0 and an average EC of 1.0 dS m^{-1} .

Before FA treatment, all plants were standardized on 30 April by retaining five vigorous leaves per plant, removing all other leaves and visible flower clusters. Flowering and anthesis of newly emerged flower clusters began on 14 May and lasted for two days. Within

each flower cluster, only flowers located at the second node were retained, whereas flower buds at the first node and those at the third and subsequent nodes were removed. As a result, each plant retained two flowers at the second node. The experiment was arranged in a randomized block design with two blocks. The randomized block design was used to reduce potential positional effects within the greenhouse, including spatial variation in natural sunlight interception, air movement, and irrigation uniformity. The greenhouse bench area was divided into two blocks according to position, and FA treatments were randomized within each block. The block identity was maintained through the cultivation stage but could not be traced after harvest, as described in Section 2.3. For each cultivar, each FA concentration treatment consisted of 40 plants, with 20 plants per block. Thus, 160 plants were used per cultivar, for a total of 320 plants across the two cultivars.

2.2. Ferulic Acid Preparation and Treatment

As an experimental reagent, FA was used in the trans-isomeric form (trans-ferulic acid; (E)-4-hydroxy-3-methoxycinnamic acid, CAS No. 537-98-4, purity 99%, Sigma-Aldrich, St. Louis, MO, USA). FA aqueous solutions were prepared at concentrations of 0.05, 0.2, and 0.4 g L⁻¹, with distilled water as the untreated control (0 g L⁻¹). The concentration range was selected considering the relatively low aqueous solubility of FA, which was reported as 0.6729 g dm⁻³ [37]. Therefore, 0.4 g L⁻¹ was used as the highest concentration in this study, and the 0.05 and 0.2 g L⁻¹ treatments were used as low and intermediate concentrations to evaluate concentration-dependent responses under repeated preharvest spray conditions. FA powder was dissolved in distilled water preheated to 40 °C and sonicated until no undissolved particles were visible. Subsequently, the solutions were cooled to room temperature before application. Before application, the pH of each prepared solution was measured using a pH meter (HI 5221, Hanna Instruments, Woonsocket, RI, USA). The measured pH values ranged from 5.8 to 6.0 across the distilled water control and FA solutions, indicating that FA addition at the tested concentrations had little effect on solution pH. So, pH adjustment was not performed, and no other additives, such as buffer, alkali, surfactant, or wetting agent, were used.

FA treatment was initiated on 16 May. The solutions were sprayed onto leaves and developing fruits every 3 days at 16:00. At each application, 45–55 mL of FA solution or distilled water was applied per plant to ensure adequate wetting of all leaves and fruit surfaces. The spray application was not continued to a defined runoff point. The treatments were carried out six times until the fruit reached the mature red stage, resulting in a total spray volume of approximately 270–330 mL per plant. Based on this application volume, the estimated total FA dose per plant was 13.5–16.5 mg for 0.05 g L⁻¹, 54–66 mg for 0.2 g L⁻¹, and 108–132 mg for 0.4 g L⁻¹. Harvest was conducted on 1 June, 17 days after anthesis. Because each plant retained up to two fruits, a maximum of 80 fruits could be obtained for each cultivar × FA concentration combination (40 plants × 2 fruits per plant, pooled across both greenhouse blocks).

2.3. Measurement of Fruit Properties

After harvest, fruits from both blocks were pooled within each cultivar × FA concentration combination before sample selection. From this pooled harvest, fruits were screened using the same criteria across all treatments. Fruits were excluded if they showed visible surface injury during cultivation or harvest, visible symptoms of disease infection, abnormal morphology, excessive deviation from the average fruit size, or less than 90% red coloration. The exclusion rate could not be evaluated because the exact number of excluded fruits was not recorded. However, all treatments were screened using the same criteria,

and the number of selected fruits was sufficient for the planned analyses of fruit properties, as described below.

Fruit surface penetration resistance (FSPR), soluble solids content (SSC), and titratable acidity (TA) were measured using the same fruit samples because all three measurements were destructive analyses. For each treatment, three biological replicates were prepared, each consisting of four fruits. FSPR was first measured using a texture analyzer (DAIHAN Scientific Co., Wonju-si, Republic of Korea) equipped with a cylindrical probe measuring 5 mm in diameter and 10 mm in length. Because the achenes could not be removed from fresh strawberry fruit without damage, measurements were performed on intact fruit surfaces while carefully avoiding direct contact between the probe and visible achenes. The probe was advanced into the fruit surface at a constant loading speed of 2.5 mm s^{-1} , with a trigger force of 0.98 N until the depression limit of 5 mm was reached. Separate pre-test and post-test speeds were not available in the recorded instrument settings. The maximum force recorded during penetration was expressed in newtons (N) and used as an index of fruit surface penetration resistance. Each fruit was longitudinally bisected, and measurements from the two halves of the fruit were averaged to obtain one fruit-level value. The four fruit-level values within each replicate were then averaged to obtain one biological replicate value.

After FSPR measurement, the same four fruits from each replicate were pooled, and juice was extracted by squeezing the pooled fruit sample. The extracted juice sample from each replicate was used for both SSC and TA measurements. SSC was measured using a portable digital refractometer (PAL-1, ATAGO Co. Ltd., Tokyo, Japan) and expressed as °Brix. TA was determined using an automatic titrator (TitroLine easy, SCHOTT Instruments GmbH, Mainz, Germany) and expressed as a percentage of citric acid equivalent (%).

For fresh weight retention analysis, six fruits were placed in each transparent PET container, and three PET containers were used for each cultivar $\times$ FA concentration combination. The tare weight of each container was subtracted before analysis; therefore, each recorded fresh weight value represented the total weight of six strawberry fruits in one container. The initial fruit mass per container ranged from 90.0 to 92.0 g for ‘Sulhyang’ and from 87.0 to 90.0 g for ‘Kuemsil’. The containers were covered with lids; however, they were not completely airtight, as gaps remained between the lids and the container bodies, allowing exposure to the surrounding storage environment. The containers were not perforated, and ventilation occurred only through natural gaps between the lid and container body. The containers were stored in darkness at 20–22 °C and 53–57% relative humidity. Relative humidity inside individual PET containers was not measured. The fresh weight was measured on days 0, 2, 4, 6, and 8 of storage. For each replicate, relative fresh weight (%) was calculated as a percentage of the initial fruit fresh weight recorded on day 0. Data are presented as the mean with the standard error of three replicate containers.

2.4. Light Microscopic Observation

Light microscopic observation of the surface region was conducted using fruit samples obtained immediately after harvest and stored for 4 days at 20–22 °C and 53–57% relative humidity. The outer tissue structure was compared between the untreated control group and the 0.4 g L^{-1} FA-treated group because the latter group exhibited the most apparent maintenance of external appearance. Therefore, microscopic observation was conducted to qualitatively compare the untreated control and the highest-response treatment, rather than as a concentration-dependent anatomical analysis.

Each replicate included three fruits, and three replicates were conducted. From each fruit, one tissue block was excised from the equatorial surface region. At least three sections per fruit and three microscopic fields per section were examined. Representative images

were selected from sections showing the typical tissue organization observed for each treatment. Tissue sections were prepared with modifications of the plant histological staining protocol described by Park et al. [38]. Samples were cut into approximately 5 mm pieces, and each fragment contained subepidermal parenchyma adjacent to the epidermis, without physical separation of the epidermal layer itself. The fragments were then fixed in a solution containing 4% paraformaldehyde and 1% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2) for 24 h at room temperature. The fixed tissues were dehydrated through a graded ethanol series, embedded using a historesin embedding kit, and sectioned at 5 μm with a microtome (Leica RM 2065, Leica Microsystems, Wetzlar, Germany).

To visualize polysaccharide-rich cell wall regions, the sections were subjected to the periodic acid-Schiff (PAS) reaction, in which PAS-positive regions appeared red, following the staining conditions of Park et al. [38] with minor modifications: sections were sequentially treated with 1% (*w/v*) periodic acid for 30 min and Schiff's reagent for 40 min, followed by 5% (*w/v*) sodium bisulfite for 35 min, with intervening distilled water rinses between each step. The PAS-stained sections were used to evaluate qualitative organization of the epidermal and subepidermal tissues rather than lignin deposition. A negative control omitting the periodic acid oxidation step was not performed in this study; therefore, the specificity of the PAS reaction for polysaccharide detection under the present staining conditions was not independently verified in our samples, and this is acknowledged as a limitation of the microscopic analysis. The stained sections were washed in distilled water for 1 h, mounted in ClearSee solution, and observed under a light microscope (Leica universal DM LB, Leica Microsystems, Wetzlar, Germany). Images were captured using the microscope-mounted imaging system.

2.5. Thioglycolic Acid-Reactive Lignin-Related Absorbance

Lignin-related absorbance (LA) was measured using a thioglycolic acid assay described by Suzuki et al. [39]. For the maturity-stage analysis, additional fruits that were untreated with the FA solution were harvested at the immature green (IMG), immature white (IMW), and mature red (MR) stages. For the FA treatment analysis, mature red fruits were sampled from each FA concentration treatment. For each maturity stage or FA treatment, 10 fruits were pooled as one biological replicate, and three biological replicates were prepared ($n = 3$).

The assay was conducted in five steps as follows. (1) Acquisition of alcohol-insoluble residue (AIR): After removal of achenes, the outer fruit tissue fraction of the freeze-dried strawberry fruits was obtained by removing the inner flesh using a cork-borer of 2 cm diameter. This fraction contained the epidermal layer, the surface region, and adjacent outer parenchymatous tissues. The epidermal layer alone was not physically isolated; therefore, the sample used for LA analysis was consistently defined as the outer fruit tissue fraction. Each sample was pooled and finely ground using a mortar and pestle. The powder (50 mg) was dissolved in 2 mL of distilled water. After centrifugation at 12,000 *g* for 15 min, the residue was mixed with 1.8 mL of methanol and incubated in a water bath at 60 °C for 20 min. After the incubation, the mixture was centrifuged at 12,000 *g* for 15 min, and the supernatant was discarded. This process was conducted twice. (2) Derivatization: The dried pellet (30 mg) was mixed with 1 mL of 3N HCl solution and 0.1 mL of thioglycolic acid solution. The mixture was placed in a water bath at 80 °C for 3 h. (3) Extraction of the lignin-thioglycolate using an alkaline solution: The incubated mixture was centrifuged at 12,000 *g* for 15 min, and then the supernatant was removed. The residual pellet was washed with 1 mL of distilled water. The washed pellet was mixed with 1 mL of 1N NaOH and placed in a shaking incubator at 80 rpm for 16 h. (4) Acidification: The incubated sample was centrifuged at 12,000 *g* for 15 min, and 1 mL of the supernatant was inoculated into a

1.5 mL tube filled with 0.2 mL of concentrated HCl solution. The mixture was incubated in a refrigerator at 4 °C for 4 h. (5) Detection: Through centrifugation of the cooled mixture at 12,000 g for 15 min, a brown-colored pellet was obtained. The pellet was thoroughly dried at room temperature and then dissolved in 1 mL of 1 N NaOH. Absorbance at 280 nm was measured using 1 N NaOH as the spectrophotometric blank because the final pellet was dissolved in 1 N NaOH before measurement. No calibration curve using purified lignin or lignin-thioglycolate standard was prepared, and assay linearity, recovery, and independent validation by another lignin-specific method were not assessed in this study. Therefore, the data were not expressed as absolute lignin concentration. Instead, the results were reported as thioglycolic acid-reactive lignin-related absorbance (LA), normalized to the dry weight of the outer fruit tissue fraction and expressed as $OD_{280} \text{ g}^{-1}$ dry weight (DW).

2.6. Statistical Analysis

Although plants were arranged in two spatial blocks during cultivation, fruits from both blocks were pooled within each cultivar $\times$ FA concentration combination before sample selection for quality and storage analyses. Therefore, the block identity of the selected fruit samples was not retained, and the block was not included as a statistical factor.

Statistical analyses were mainly performed using SAS Enterprise Guide 7.1 (SAS Institute Inc., Cary, NC, USA). Data are presented as the mean $\pm$ standard error (SE) of three biological replicates ($n = 3$). For SSC, TA, FSPR, and LA, pooled fruit samples within each replicate were used as the experimental unit, and individual fruits within a pooled replicate were not treated as independent statistical units. These data were analyzed by two-way analysis of variance (ANOVA) to evaluate the effects of cultivar, FA concentration, and their interaction. When a significant cultivar $\times$ FA concentration interaction was detected, the effect of FA concentration was interpreted separately within each cultivar. When the interaction was not significant, the main effects were used for interpretation. Mean comparisons were performed using Tukey's honestly significant difference (HSD) test at $p < 0.05$.

Relative fresh weight retention data were reanalyzed using a repeated-measures mixed model with the statsmodels package (version 0.14.6) in Python (version 3.13.5). Cultivar, FA concentration, storage day, and their interactions were treated as fixed effects, while the PET container served as the repeated experimental unit. Because relative fresh weight was normalized to the initial value at day 0, day 0 was retained as the baseline but was excluded from inferential statistical analysis. Therefore, the repeated-measures analysis was performed using data from days 2, 4, 6, and 8.

3. Results

3.1. Soluble Solids Content and Titratable Acidity

Soluble solids content (SSC) and titratable acidity (TA) were evaluated at harvest as basic edible and marketable quality attributes, rather than as direct indicators of tissue firmness or structural integrity (Table 1). Two-way ANOVA showed that SSC was significantly affected by cultivar, whereas the effect of FA concentration and the cultivar $\times$ FA concentration interaction were not significant. TA was significantly affected by FA concentration, whereas the cultivar effect and cultivar $\times$ FA concentration interaction were not significant. Overall, FA treatment did not cause a consistent concentration-dependent decrease in SSC or TA, indicating that preharvest FA spray did not markedly compromise these basic fruit quality traits under the present experimental conditions.

Table 1. Soluble solids content (SSC) and titratable acidity (TA) of strawberry fruit treated with different concentrations of ferulic acid (FA).

Cultivar	FA Concentration (g L ⁻¹)	SSC (°Brix)	TA (%)
Sulhyang	0	10.33 ± 0.33	0.740 ± 0.006
	0.05	9.97 ± 0.37	0.810 ± 0.006
	0.2	11.47 ± 0.27	0.763 ± 0.015
	0.4	9.70 ± 0.26	0.740 ± 0.015
Kuemsil	0	11.77 ± 1.08	0.737 ± 0.015
	0.05	11.73 ± 0.95	0.810 ± 0.006
	0.2	12.70 ± 0.71	0.773 ± 0.033
	0.4	12.30 ± 0.53	0.790 ± 0.015
Significance ¹	Cultivar	**	NS
	Concentration	NS	**
	Cultivar × Concentration	NS	NS

¹ Significance of cultivar, FA concentration, and their interaction was determined through two-way ANOVA, exhibiting NS (no significant) and ** ($p < 0.01$).

3.2. Fruit Surface Penetration Resistance

Fruit surface penetration resistance (FSPR) was significantly influenced by cultivar [$F(1,16) = 136.9$, $p < 0.001$], FA concentration [$F(3,16) = 32.0$, $p < 0.001$], and their interaction [$F(3,16) = 8.22$, $p = 0.0016$]. Due to the significant interaction between cultivar and FA concentration, the effect of FA concentration was separately compared within each cultivar (Figure 1). In ‘Sulhyang’, FA concentration significantly affected FSPR [$F(3,8) = 22.6$, $p < 0.001$]. FSPR increased from 2.01 N in the untreated control to 2.04, 2.08, and 2.11 N in the 0.05, 0.2, and 0.4 g L⁻¹ FA treatments, respectively (Figure 1). The 0.2 and 0.4 g L⁻¹ FA treatments described significantly higher FSPR values than the untreated control and the 0.05 g L⁻¹ treatment, whereas the 0.05 g L⁻¹ treatment did not significantly differ from the untreated control. In ‘Kuemsil’, mean FSPR values were consistently measured higher than those of ‘Sulhyang’ across all FA concentrations (Figure 1). Although few notable responses were observed, FA concentration had a significant effect on FSPR [$F(3,8) = 10.1$, $p = 0.004$]. The FSPR values were increased from 2.11 N in the untreated control to 2.11, 2.13, and 2.14 N in the 0.05, 0.2, and 0.4 g L⁻¹ treatments, respectively. Among the concentrations, the 0.2 g L⁻¹ FA treatment showed an intermediate value and did not differ significantly from either the lower-concentration treatments or the 0.4 g L⁻¹ treatment.

3.3. Lignin-Related Absorbance in the Outer Fruit Tissue

LA in the fruit outer tissue was significantly affected by cultivar [$F(1,12) = 9.96$, $p < 0.01$] and maturity stage [$F(2,12) = 169.7$, $p < 0.001$], whereas the cultivar × maturity stage interaction was not significant [$F(2,12) = 2.64$, $p = 0.112$], as determined by two-way ANOVA. Meanwhile, as shown in Figure 2A, the LA markedly decreased as the fruit maturity progressed from the IMG stage to the MR stage in both cultivars. In ‘Sulhyang’, the LA decreased by 49.4%, from 21.60 OD₂₈₀ g⁻¹ DW in IMG fruit to 10.93 OD₂₈₀ g⁻¹ DW in MR fruit. Similarly, in the case of ‘Kuemsil’, it decreased by 54.6%, from 24.97 OD₂₈₀ g⁻¹ DW in IMG fruit to 11.33 OD₂₈₀ g⁻¹ DW in MR fruit.

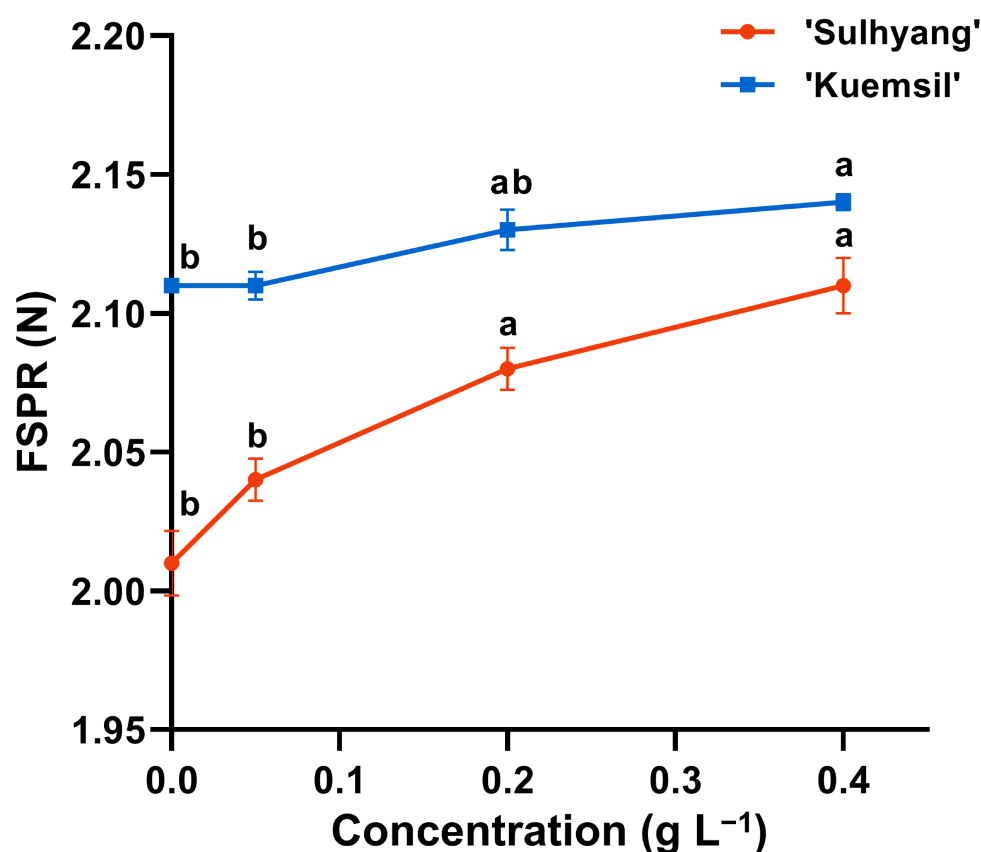


Figure 1. Mean values $\pm$ SE ($n = 3$) of fruit surface penetration resistance (FSPR) in strawberry 'Sulhyang' and 'Kuemsil' treated with 0, 0.05, 0.2, and 0.4 g L⁻¹ of ferulic acid (FA) during fruit development. Different letters within each cultivar indicate significant differences among FA concentrations according to Tukey's HSD test at $p < 0.05$.

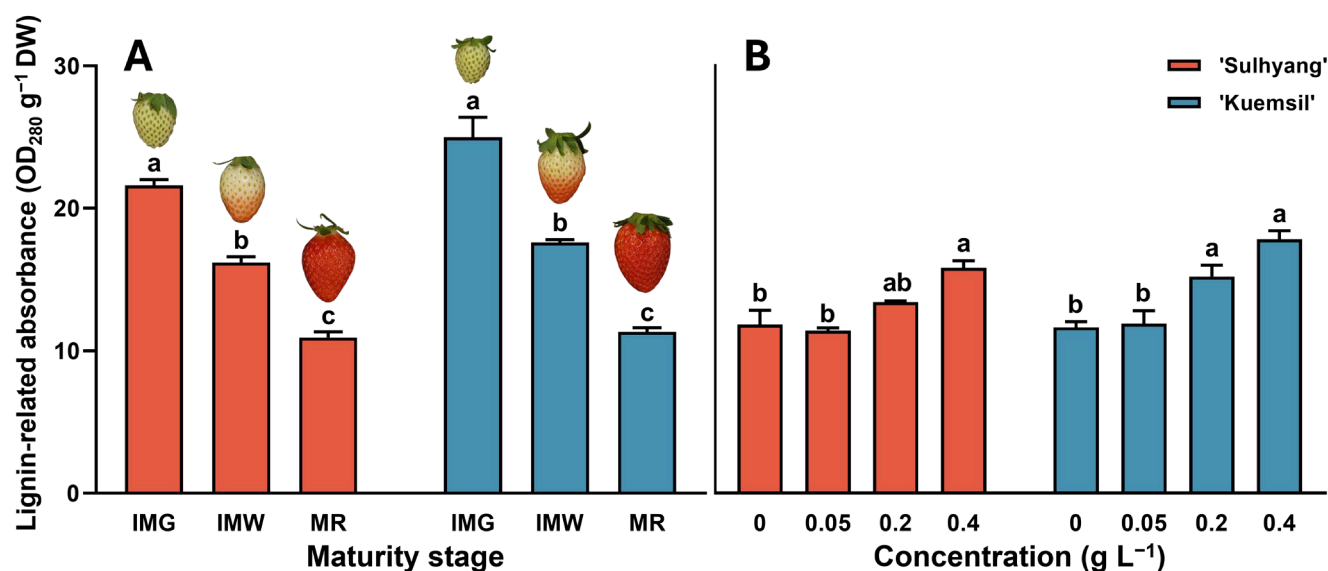


Figure 2. Mean value $\pm$ SE ($n = 3$) of thioglycolic acid-reactive lignin-related absorbance (LA) in the outer fruit region in strawberry 'Sulhyang' and 'Kuemsil', depending on fruit maturity, including immature green (IMG), white (IMW), and mature red (MR) (A) and according to ferulic acid (FA)-treated concentrations (B). Values are expressed as OD₂₈₀ g⁻¹ dry weight. Different letters within each cultivar indicate significant differences among FA concentrations according to Tukey's HSD test at $p < 0.05$.

The effect of FA treatment on LA was evaluated in MR fruit harvested after spray treatment during fruit ripening. Two-way ANOVA described significant effects of cultivar [$F(1,16) = 4.81, p = 0.043$] and FA concentration [$F(3,16) = 29.2, p < 0.001$], whereas the cultivar $\times$ FA concentration interaction was not significant [$F(3,16) = 1.29, p = 0.312$]. Because the cultivar $\times$ FA concentration interaction was not significant, the FA concentration effect was interpreted as a main effect across the two cultivars (Figure 2B). In ‘Sulhyang’, the LA increased with increasing FA concentration. The untreated control had a low LA of $11.84 \text{ OD}_{280} \text{ g}^{-1} \text{ DW}$, whereas the 0.4 g L^{-1} FA treatment increased the LA value to $15.81 \text{ OD}_{280} \text{ g}^{-1} \text{ DW}$. Similar to ‘Sulhyang’, the LA of ‘Kuemsil’ also increased in response to FA treatment (Figure 2B). The highest LA value was observed as $17.52 \text{ OD}_{280} \text{ g}^{-1} \text{ DW}$ by the 0.4 g L^{-1} FA treatment, which is about 1.5 times higher than the LA of $11.65 \text{ OD}_{280} \text{ g}^{-1} \text{ DW}$ in the untreated control. As a result, the overall pattern of FA-induced changes in LA was not statistically different between the two cultivars.

3.4. External Appearance and Outer Fruit Tissue Integrity

After 4 days of storage at room temperature, visible differences in external fruit appearance were observed among FA-treated concentrations (Figure 3). In both ‘Kuemsil’ and ‘Sulhyang’, untreated control fruit showed reduced surface gloss and visible calyx wilting. Fruit treated with FA showed better maintenance of external appearance than the untreated control, and this visual difference was more apparent in 0.2 and 0.4 g L^{-1} FA-treated groups. In particular, fruit treated with 0.4 g L^{-1} FA retained a glossier surface appearance and less wilted calyx tissue compared with the untreated control in both cultivars.

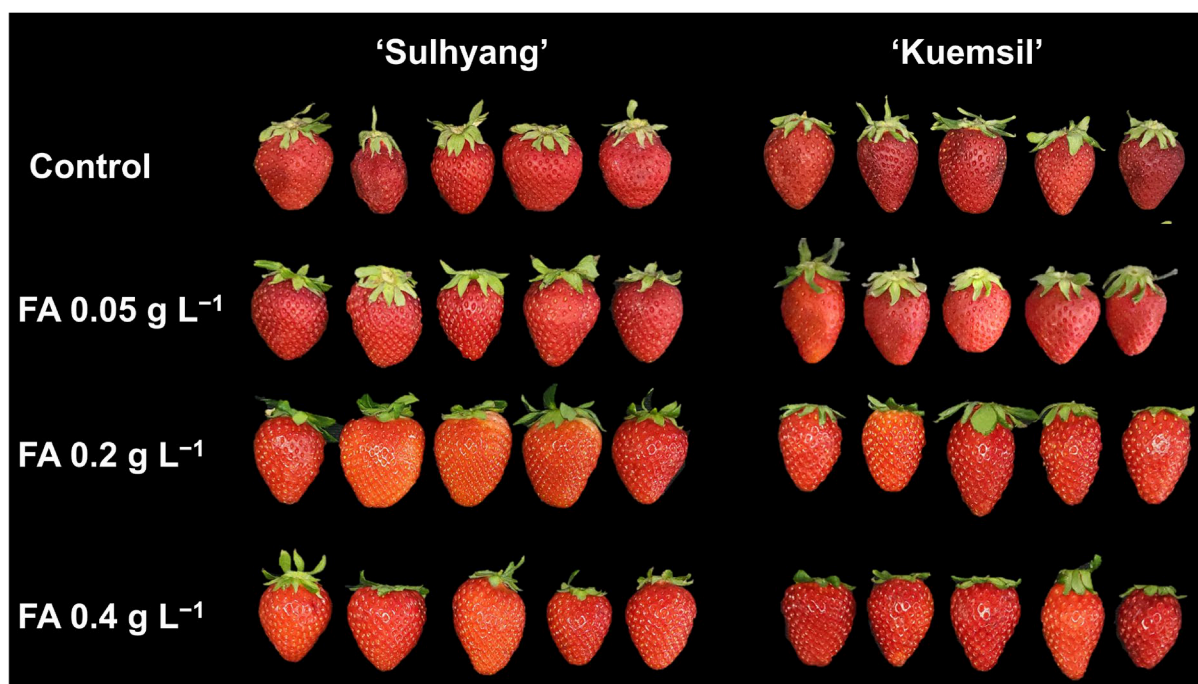


Figure 3. Morphological images of the external appearance of strawberry ‘Sulhyang’ and ‘Kuemsil’ fruit after 4 days of storage. Fruits were treated with 0 (untreated control), 0.05, 0.2, and 0.4 g L^{-1} of ferulic acid (FA) during fruit development.

Light microscopic observation was conducted to qualitatively compare the outer tissue organization of untreated control fruit and 0.4 g L^{-1} FA-treated fruit at harvest and after 4 days of storage using PAS-stained sections (Figure 4). Because PAS staining visualizes polysaccharide-rich cell wall regions rather than lignin deposition, Figure 4 was interpreted as qualitative evidence of tissue organization. At harvest, both cultivars showed a relatively

continuous epidermal surface region and organized adjacent subepidermal tissues. After 4 days of storage, the untreated control showed visible disruption of the epidermal and subepidermal tissue organization. In contrast, fruit treated with 0.4 g L^{-1} FA exhibited a more continuous epidermal surface region and better-organized adjacent tissues after storage compared with the untreated control.

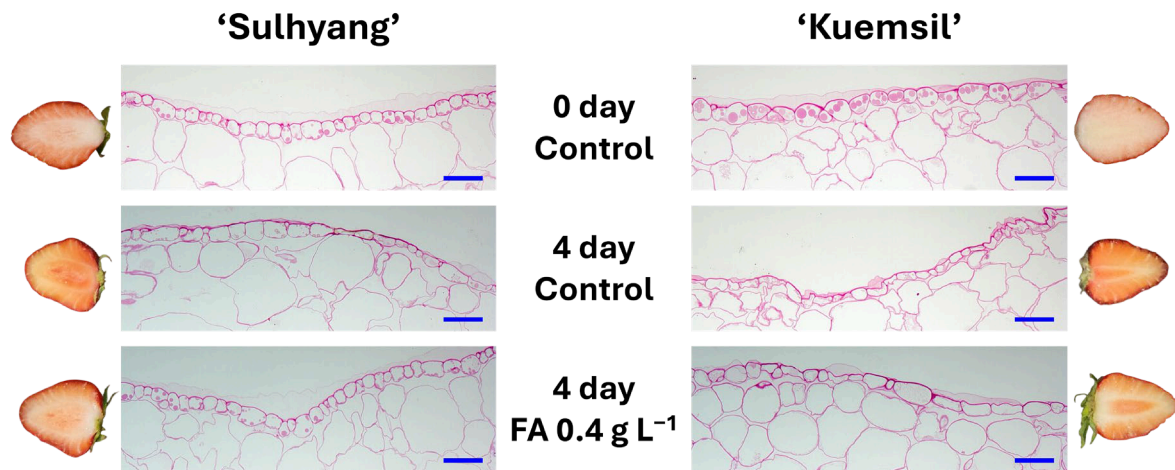


Figure 4. Representative light micrographs showing outer fruit tissue structure of ‘Sulhyang’ and ‘Kuemsil’ strawberry fruit at harvest and after 4 days of storage. Blue bars in each image indicate 100 μm .

3.5. Fresh Weight Retention During Storage

Relative fresh weight retention decreased progressively during storage in both cultivars (Figure 5). Because the same PET containers were weighed repeatedly over the storage period, the data from days 2, 4, 6, and 8 were analyzed using a repeated-measures mixed model with PET container as the repeated experimental unit. The analysis showed significant effects of cultivar (Wald $\chi^2 = 7.23$, $p = 0.0072$), FA concentration (Wald $\chi^2 = 204.71$, $p < 0.001$), storage day (Wald $\chi^2 = 1085.59$, $p < 0.001$), FA concentration $\times$ storage day interaction (Wald $\chi^2 = 176.96$, $p < 0.001$), and cultivar $\times$ FA concentration $\times$ storage day interaction (Wald $\chi^2 = 26.47$, $p = 0.0017$). In contrast, the cultivar $\times$ FA concentration interaction (Wald $\chi^2 = 2.15$, $p = 0.542$) and cultivar $\times$ storage day interaction (Wald $\chi^2 = 3.72$, $p = 0.293$) were not significant.

Because the cultivar $\times$ FA concentration $\times$ storage day interaction was significant, the temporal patterns of fresh weight retention were described separately by cultivar and FA concentration. In ‘Sulhyang’, the 0.2 and 0.4 g L^{-1} FA treatments maintained higher relative fresh weight retention than the untreated control and the 0.05 g L^{-1} treatment throughout storage. At 8 days of storage, relative fresh weight retention was highest in the 0.4 g L^{-1} FA treatment (88.2%), followed by the 0.2 g L^{-1} treatment (82.1%), whereas the untreated control and 0.05 g L^{-1} treatment retained 68.1 and 71.3%, respectively (Figure 5A).

In ‘Kuemsil’, FA-treated fruit also tended to retain higher relative fresh weight than the untreated control during storage, particularly at 0.2 and 0.4 g L^{-1} treatments (Figure 5B). At 8 days of storage, the untreated control retained 64.5% of its initial fresh weight, whereas the 0.05, 0.2, and 0.4 g L^{-1} FA treatments retained 69.4, 82.9, and 86.8%, respectively. The difference between the untreated control and higher FA concentrations became more apparent as storage progressed, especially from 4 to 8 days of storage (Figure 5B). These results indicate that preharvest FA treatment was associated with improved fresh weight retention during short-term storage, although the magnitude of the response varied depending on cultivar, FA concentration, and storage day.

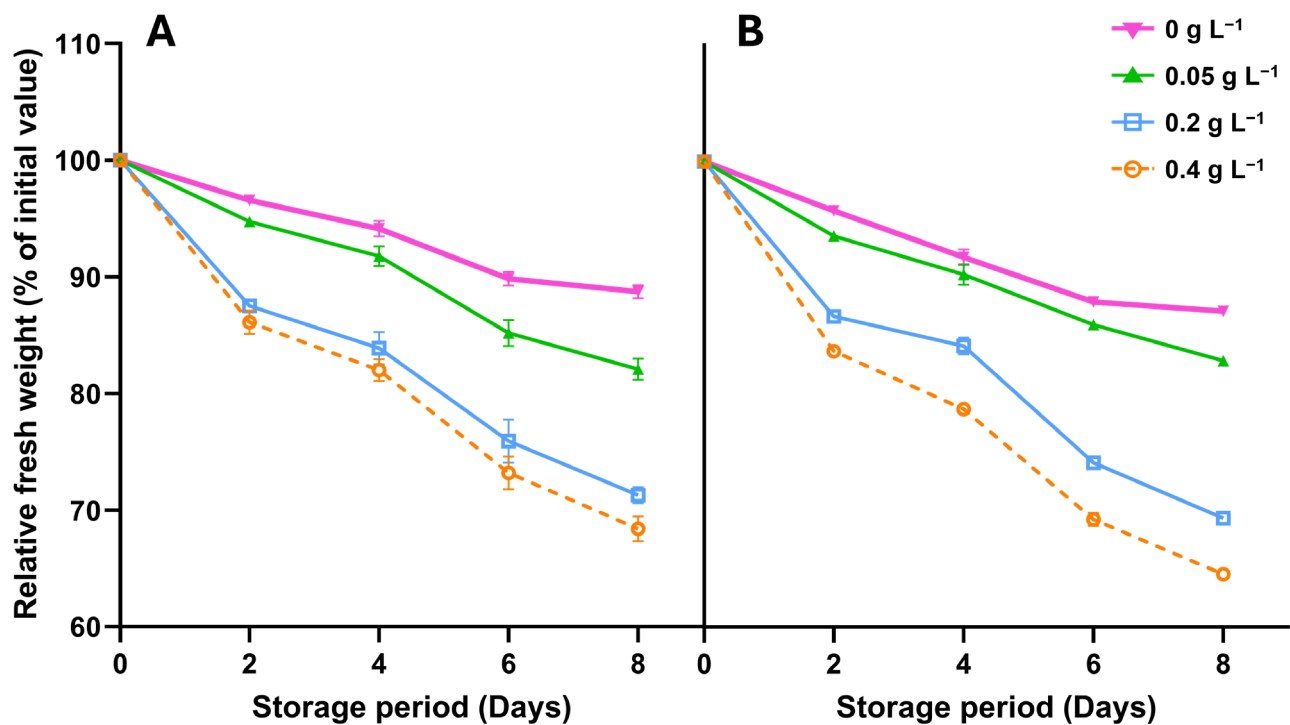


Figure 5. Changes in relative fresh weight retention of strawberry fruit during storage at room temperature (A) ‘Sulhyang’ and (B) ‘Kuemsil’ fruit were treated with 0, 0.05, 0.2, and 0.4 g L⁻¹ ferulic acid (FA) during fruit development. Values are expressed as a percentage of the initial fresh weight recorded on day 0 and are presented as the mean $\pm$ SE of three replicate PET containers ($n = 3$). Statistical effects of cultivar, FA concentration, storage day, and their interactions are described in the Results section.

4. Discussion

SSC and TA were included as basic fruit quality attributes because they are commonly used to evaluate strawberry eating quality and marketability. However, these parameters are not direct indicators of outer tissue integrity, fruit surface resistance, or cell wall structure. Therefore, the absence of a consistent concentration-dependent decrease in SSC and TA should be interpreted only as evidence that FA treatment did not markedly compromise these basic soluble solids- and acidity-related traits under the present experimental conditions.

The increase in FSPR observed in FA-treated fruit indicates that preharvest FA application was associated with higher resistance to surface penetration in both cultivars. Because FSPR was measured on the intact fruit surface, this response should not be interpreted as an increase in whole-fruit firmness or as a direct measurement of the mechanical stability of an isolated epidermal layer. Instead, FSPR represents a surface-level puncture resistance trait that reflects the combined mechanical response of the epidermal surface region and adjacent outer tissues. The significant cultivar $\times$ FA concentration interaction indicates that the magnitude of the FA response differed between the two cultivars, suggesting that cultivar-specific surface properties may influence responsiveness to FA treatment. Importantly, the increase in FSPR at higher FA concentrations was statistically significant in both cultivars, supporting the interpretation that preharvest FA treatment improved surface penetration resistance, a surface-level trait relevant to mechanical injury during harvest, packaging, handling, and transportation.

The FSPR response was accompanied by higher lignin-related absorbance (LA) signals in the outer fruit tissue, suggesting that FA-treated fruit showed coordinated changes in surface-level mechanical resistance and lignin-associated outer tissue responses. Lignin and related phenolic polymers are major structural components that contribute to cell wall

rigidity and mechanical strength in plant tissues [40–42]. Indeed, the regulation of the phenylpropanoid pathway and lignin-associated cell wall matrices has been identified as a critical determinant of mechanical firmness in strawberry fruits [40,42]. The developmental decline in LA signals from immature to mature fruit indicates that ripening was accompanied by reduced lignin-associated responses in the outer fruit tissue, which may contribute to the structural vulnerability of mature strawberry fruit. In this context, the FA-associated increase in LA signals in mature fruit provides a plausible physiological basis for the higher surface penetration resistance observed in FA-treated fruit. Because the LA response was broadly consistent across the two cultivars, whereas the FSPR response showed cultivar-dependent magnitude, the relationship between lignin-associated outer tissue responses and surface mechanical phenotype may be modified by cultivar-specific fruit surface properties.

The relevance of FA-associated LA responses is supported by studies in other fruit crops. In postharvest apple fruit, 0.80 g L⁻¹ FA soaking increased phenylpropanoid pathway enzyme activities, enhanced total phenol and flavonoid accumulation, affected lignin biosynthesis-related enzymes, and reduced gray mold development, indicating that FA can function as an elicitor of phenolic- and lignin-associated defense responses in fruit tissue [43]. Similarly, in tomato fruit, a 100 µM FA treatment reduced *Botrytis cinerea* disease incidence and lesion area while increasing PAL, PPO, chitinase, and β-1,3-glucanase activities, as well as NO-related defense signaling [24]. These studies differ from the present work because they focused mainly on postharvest disease resistance, whereas the present study evaluated preharvest FA application and surface-related postharvest traits in strawberry. Nevertheless, they support the broader concept that FA can modulate phenylpropanoid-, defense-, and cell wall-associated responses in fruit crops.

Additional evidence from berry and vegetable crops further indicates that FA-containing or phenolic acid-based treatments can influence postharvest or stress-related physiology beyond strawberry. In blackberry fruit, a combined treatment of FA and natamycin was associated with transcriptomic and proteomic changes in carbohydrate metabolism, energy metabolism, stress responses, and fruit defense capability, thereby improving preservation-related traits [44]. Although that study used a combined postharvest treatment rather than FA alone, it is relevant because it shows that FA-containing preservation systems can alter molecular processes associated with berry fruit storage performance. In Chinese cabbage, foliar application of FA and salicylic acid at 10–100 µM modified phenolic compound accumulation, antioxidant activity, and photosynthetic performance under salt stress, indicating that phenolic acid treatments can regulate stress-related metabolism in vegetable crops as well [45]. Taken together, these studies suggest that the effects of FA or related phenolic acid treatments are highly dependent on crop species, treatment timing, concentration, and target trait. The present study extends this broader framework to a cultivation-stage FA spray strategy aimed at improving selected surface-related postharvest traits in strawberry fruit.

From a metabolic perspective, FA is particularly relevant because it is a hydroxycinnamic acid derived from the phenylpropanoid pathway and is closely associated with cell wall-bound phenolics, polysaccharide cross-linking, and lignin-related metabolism [42,46]. Ferulate residues can participate in cross-linking reactions within the cell wall matrix and are associated with structural reinforcement and defense-related responses in plant tissues [16,19]. Therefore, the higher LA signals observed in FA-treated strawberry fruit are consistent with the possibility that exogenous FA supplied during fruit development influenced phenolic- and lignin-associated cell wall responses in the outer fruit tissue. This interpretation is supported by the coordinated increases in FSPR and LA signals, together with the improved external appearance and fresh weight retention observed in

FA-treated fruit during short-term storage. However, this study did not directly measure phenylpropanoid enzyme activities, lignin biosynthetic gene expression, metabolic flux, or the incorporation of exogenous FA into cell wall-bound fractions. Thus, while the present results provide physiological evidence linking preharvest FA treatment with surface-related postharvest responses, the specific biochemical pathway underlying this response requires further validation.

The external appearance and microscopic observations further support the interpretation that FA treatment was associated with better maintenance of outer tissue organization during storage. Because PAS staining visualizes polysaccharide-rich cell wall regions rather than lignin deposition, the microscopic observations do not provide direct evidence of lignification. Rather than restating treatment-specific visual differences, these observations should be interpreted as qualitative evidence that FA-treated fruit maintained a more continuous epidermal surface region and better-organized adjacent tissues during short-term storage. According to a previous study, some exogenous treatments applied to strawberry fruits can trigger cell distortion, breakdown, or the formation of microscopic channels [47]. In contrast, the representative micrographs in the present study were consistent with the overall pattern of improved FSPR and fresh weight retention, suggesting that FA-treated fruit maintained better organization in the surface region during storage. However, because microscopic observation was conducted only for the untreated control and the 0.4 g L⁻¹ FA treatment, these observations should be interpreted as qualitative support for tissue organization rather than quantitative anatomical evidence across all FA concentrations.

Fresh weight retention during storage was also improved by FA treatment. Water loss is a major cause of postharvest deterioration in fresh strawberry fruit and is closely associated with the structural and barrier properties of the fruit surface [48–50]. Strawberry fruit skin is highly susceptible to postharvest water loss because of its permeable surface, extremely thin cuticle, and the presence of microcracks or polar pathways that facilitate water movement [48,49]. In addition, cuticle deposition in strawberry fruit does not keep pace with rapid fruit surface expansion during development, resulting in cuticle thinning, increased strain, and greater susceptibility to microcracking as the fruit approaches maturity [50]. These structural characteristics provide a physiological basis for linking outer tissue organization with fresh weight retention during storage. In the present study, the higher relative fresh weight retained by FA-treated fruit was consistent with better external appearance and qualitative maintenance of outer tissue organization, suggesting that FA-associated outer tissue responses contributed to improved storage performance. However, because this study did not directly measure cuticular permeability, transpiration rate, wax deposition, cutin composition, or cuticle thickness, the higher relative fresh weight should be interpreted as improved fresh weight retention rather than as direct evidence of altered cuticular water permeability. Taken together, the coordinated responses of higher FSPR, increased LA signals in the outer fruit tissue, and improved relative fresh weight retention suggest that preharvest FA treatment was associated with surface-related structural responses that contributed to better storage performance. Because these variables were measured using different analytical sample sets, this relationship should be interpreted as a treatment-level physiological association rather than individual fruit-level causal evidence.

Overall, the cultivar-dependent responses observed in this study indicate that FA treatment did not affect all traits uniformly across the two cultivars. ‘Kuemsil’ showed higher FSPR values than ‘Sulhyang’ across FA concentrations, indicating inherent cultivar differences in surface resistance. In contrast, the FA-associated increase in LA showed no significant cultivar × FA concentration interaction, suggesting that the FA-associated lignin-related response did not differ significantly between the two cultivars tested. This contrast suggests that lignin-associated outer tissue responses may contribute to surface

resistance, but the final mechanical phenotype is also likely influenced by cultivar-specific anatomical or structural characteristics. Further studies using a wider range of cultivars are required to determine whether FA responsiveness is associated with inherent differences in epidermal anatomy, fruit texture, or phenylpropanoid metabolism.

5. Conclusions

This study showed that preharvest FA treatment was associated with higher fruit surface penetration resistance, increased lignin-related absorbance signals in the outer fruit tissue, better qualitative organization of epidermal and subepidermal tissues, and improved fresh weight retention during short-term storage. To our knowledge, this is among the first studies to evaluate preharvest FA spray in strawberry fruit in terms of lignin-related outer tissue responses, surface penetration resistance, and fresh weight retention during storage. These results indicate that preharvest FA spray may serve as a practical cultivation-stage strategy to improve selected postharvest-related traits in strawberry fruit. Because the treatment was applied during fruit development, this approach may be compatible with existing cultivation practices and help improve surface-related storage performance before fruit enters postharvest handling, packaging, transportation, and distribution. Future studies should examine total phenolic and flavonoid content, antioxidant activity, calcium status, cell wall-modifying enzyme activities, phenylpropanoid pathway activity, and cuticular barrier properties to clarify the mechanisms underlying FA-associated responses. Further validation across multiple harvests, a wider range of cultivars, commercial production systems, and actual postharvest distribution conditions will also be important for determining the practical applicability of preharvest FA treatment and its potential contribution to reducing postharvest quality deterioration in strawberry fruit.

6. Patents

A Korean patent application has been filed based on the results reported in this manuscript. The patent application, entitled “Method for Ferulic acid Treatment and Its Application for Strawberry Storage and Improved Shelf Life,” was filed with the Korean Intellectual Property Office under application number (10-2024-0193000) on 20 December 2024. The authors of this manuscript are included among the inventors or applicants of the patent application.

Author Contributions: Conceptualization, S.-H.C. and C.S.G.; methodology, C.S.G.; software, S.-H.C. and C.S.G.; validation, D.-Y.K.; formal analysis, S.K.; investigation, S.-H.C. and C.S.G.; resources, D.-Y.K., W.-M.L. and S.K.; data curation, S.-H.C.; writing—original draft preparation, S.-H.C.; writing—review and editing, C.S.G.; visualization, C.S.G.; supervision, C.S.G.; project administration, S.-H.C. and D.-Y.K. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: All data presented in this study are available from the corresponding author upon reasonable request. The raw and replicate-level datasets supporting the findings of this study are not publicly available at the revision stage because the study was conducted at the National Institute of Horticultural and Herbal Science, Rural Development Administration, Republic of Korea, and the data are subject to institutional data management restrictions prior to publication. Data may be made available from the corresponding author upon reasonable request and with permission from the relevant institution. Full-resolution images are available from the corresponding author upon reasonable request.

Conflicts of Interest: W.-M.L. is affiliated with PHENOBOX Co., Ltd., which had no role in the research design, data collection, data analysis, interpretation of results, or decision to publish. A Korean patent application has been filed based on the results reported in this manuscript, and all authors are included among the inventors or applicants of this patent application. The authors declare no other commercial, financial, or personal conflicts of interest related to this manuscript.

Abbreviations

The following abbreviations are used in this manuscript:

FA	Ferulic Acid
FSPR	Fruit Surface Penetration Resistance
LA	Lignin-Related Absorbance
IMG	Immature Green
IMW	Immature White
MR	Mature Red
SSC	Soluble Solids Content
TA	Titrateable Acidity
PET	Polyethylene Terephthalate

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