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The influence of electric field towards tomato cell wall degrading enzyme activities at low storage temperature

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Abstract

Tomato is a climacteric fruit with a short shelf-life, highly susceptible to softening and cell wall degradation during storage. Cold storage can slow these changes but may also induce chilling injury. Non-thermal technologies, such as electric field (EF) treatment, offer potential as alternative preservation methods. Electric fields are divided into two types: direct current (DC) and alternating current (AC). Alternating current (AC-EF) refers to electric fields in which the current's direction varies regularly, whereas direct current (DC-EF) maintains a constant flow in one direction. However, the application of electric fields in postharvest preservation remains underexplored, particularly under low-temperature storage conditions. Therefore, this study aimed to evaluate the effectiveness of alternating current (AC-EF) and direct current (DC-EF) electric field treatments in maintaining the postharvest quality of tomatoes grown in Kyushu Island during storage at 5 °C. Tomatoes at ripening index 2 were continuously exposed to 20 V/cm EF under AC, DC, or control (0 V) conditions for 21 days. Fruit was assessed at 7-day intervals for weight loss, colour, firmness, physicochemical properties, polygalacturonase (PG) activity, and relative gene expression. A completely randomized design (CRD) was used, with three replicates per treatment. Results showed that DC-EF treatment significantly maintained firmness and suppressed PG activity compared to the control ($p < 0.05$), although no significant differences were found in others parameters. The findings suggest that EF treatments particularly DC may contribute to texture preservation under cold storage, but their effects are limited compared to the impact of temperature alone.

Keywords: *electric field treatment, cold storage, firmness, polygalacturonase activity*

Introduction

Postharvest losses of fruits and vegetables remain a critical issue in global food systems. These losses are estimated at 5 – 25% in developed countries and up to 50% in developing regions, largely due to physiological degradation, microbial spoilage, and improper storage conditions (Sudheer & Indra, 2007). Tomatoes (*Solanum lycopersicum*), in particular, are susceptible to postharvest softening, water loss, and colour changes due to their climacteric nature and high metabolic activity. Ethylene production and respiration continue during storage, accelerating ripening and tissue breakdown (Saletnik et al. 2022).

Fruit softening is driven by the enzymatic disassembly of the cell wall. Two key enzymes, pectin methyl esterase (PME; EC 3.1.11) and polygalacturonase (PG; EC 3.2.1.15), work in tandem to depolymerise pectin: PME initiates de-esterification, facilitating PG-mediated hydrolysis of the homogalacturonan backbone (Carrillo-López et al. 2002; Carrillo-López et al. 2003). This process reduces fruit firmness, increases susceptibility to microbial infection, and limits marketability.

Among emerging preservation methods, high voltage electric field (HVEF) treatment has gained attention for its non-thermal, energy-efficient properties. It has been used to enhance drying efficiency, microbial safety, and extraction of valuable compounds in various fruits (Dalvi-Isfahan et al. 2016). Additionally, HVEF and pulsed electric fields have been shown to affect cellular structure and physiology in fresh produce such as apples, potatoes, and carrots, with potential impacts on texture and water retention (Puértolas et al. 2017; González-Casado et al. 2018).

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Recent studies have increasingly demonstrated that electric field (EF) treatments can serve as effective non-thermal methods for extending the postharvest shelf life of fruits and vegetables. High-voltage EF applications have been shown to reduce weight loss, delay firmness degradation, and suppress enzymatic activity responsible for softening such as polygalacturonase and cellulase in tomatoes and other climacteric fruits (Chang et al. 2023). For instance, cherry tomatoes treated with high-voltage electrostatic fields exhibited significantly lower weight loss and microbial growth, while maintaining better colour and vitamin C content during cold storage (Zhao et al. 2023). Additionally, EF exposure has been found to reduce respiration rates and ethylene production, thus delaying ripening and senescence without leaving chemical residues (Saletnik et al. 2022). These findings suggest that EF particularly in the form of direct current or pulsed treatments holds promise as a clean, energy-efficient approach to preserving the quality and extending the shelf life of fresh produce during storage and distribution.

However, despite its promising applications, the molecular mechanisms underlying electric field effects on fruit softening particularly enzyme activity and gene expression are not well understood. Recent work by Yang et al. (2021) demonstrated that externally applied oligogalacturonides suppressed PG-related gene expression and delayed tomato softening, highlighting the relevance of targeting molecular pathways to improve postharvest quality (Yang et al. 2021). To date, few studies have explored whether electric field exposure can similarly modulate gene expression and enzymatic activity during cold storage.

Therefore, this study investigates the effects of continuous AC and DC electric field treatments on postharvest tomato quality at 5 °C, with emphasis on firmness, cell wall degradation (via PG activity), and relative gene expression. By integrating physiological and molecular data, this work aims to elucidate the mechanisms by which electric fields influence tomato softening and assess their potential as a tool for shelf-life extension.

Materials and method

Plant materials

Tomato fruits with index 2 (Pink means that more than 10 % but not more than 30 % of the surface, in the aggregate, by the USDA Colour Standard for tomato) were obtained from the local market in Kagoshima City and were brought to the laboratory. Fruits were selected for uniform size, colour and absence of physical defects. All experiments were performed at 5 °C. The study was conducted in a completely randomised design (CRD) with three replications, using tomatoes from the same supplier for each trial.

Electric field (EF) treatment

Figure 1 demonstrated electric field exposure was performed in a refrigerated incubator (PHCbi, MR-154, Japan) using an EF setup inside a desiccator (250 × 150 × 150 mm, VXL, AS ONE Corp., Japan). Two parallel stainless-steel electrode plates (90 × 190 mm) were spaced 10 cm apart. A high-voltage generator (NF Corporation EC750SA, Yokohama, Japan) applied a voltage of 200 V, resulting in an electric field strength of 20 V/cm between the plates. Fruits were continuously treated with alternating current (AC-EF) and direct current (DC-EF) electric fields for 21 days at 5 °C. Control fruits were stored under identical conditions without electric field exposure. Electric field strength was verified using a calibrated voltmeter, and electrode spacing was regularly checked to ensure consistency throughout the trials.

Texture analysis

Fruit firmness was measured using a digital texture analyser (RHEONER II RE2-3305C, YAMADEN Co., Tokyo, Japan) in compression mode. A 2 mm compression depth was applied at the equator of each fruit. Measurements were taken at three points/ fruit, across nine fruits/treatment and time point. Results are reported as mean maximum force (N) ± standard deviation.

Physicochemical properties

The weight of the fruits was measured using electronic balance at the initial and each assessment day. Weight loss (% fresh weight basis) was expressed as the percentage loss of the initial total weight loss calculated by considering the weight difference between the initial and final value of the tomatoes. The soluble solids content (SSC) and total titratable acidity (TTA) were measured using a digital refractometer (PAL-BX|ACID F5, ATAGO Co. Ltd., Tokyo). Whereas, the total soluble solids (TSS) were expressed as °Brix and the TTA results were expressed as % citric acid. The Hunter L*, a* and b* values of AC-EF, DC-EF treated, and control tomato fruit samples were measured before and during removal. Colorimeter Model CR-20 (KONICA MINOLTA JAPAN Inc., Tokyo) was used to measure the surface colour (a value: red = +a/green = -a; b value: yellow = +b/blue = -b) of the fruits. Observations on triplicate samples were taken at the equatorial region of the fruits followed by a calculation of the mean and standard deviation (SD) of the three observations.

Polygalacturonase (PG) activity

PG enzyme activity was assayed using modified protocols of Gross (1982) and Yoshida et al. (1984).1 g of frozen tomato tissue was ground in liquid nitrogen and extracted in 4 mL of 40 mM sodium acetate buffer (pH 5.5) containing 1 M NaCl and 10 g/L PVPP. After 3 h extraction at 4 °C, the sample was centrifuged at 10,143 × g for 20 min. The reaction mixture (1 mL) contained 0.2 mL buffer,

0.3 mL 1% polygalacturonic acid, 0.1 mL enzyme extract, and 0.4 mL water. After 1 h incubation at 37 °C, the reaction was terminated with 1 mL 3,5-dinitrosalicylic acid (DNS), boiled for 5 min, and cooled before dilution and absorbance measurement at 540 nm (UV1750, Shimadzu, Kyoto). Enzyme assays were validated using standard galacturonic acid curves. One unit of PG activity was defined as 1 µmol galacturonic acid released/minute.

RNA extraction and cDNA synthesis

Total RNA was isolated from 1 g of tomato pulp using the RNA Extraction Buffer Reagent (RNAs-ici-S, Rizo Inc., Ibaraki, Japan) according to the manufacturer's protocols. The RNA sample was dissolved in diethylpyrocarbonate (DEPC) treated water. The RNA was kept at 4 °C until used for complementary DNA (cDNA). RNA concentration and purity were determined using a nanophotometer (C40, Waken Btech Co. Ltd., Kyoto). Only RNA samples with a concentration between 0.5 µg to 1µg were used for cDNA analyses. For cDNA synthesis, sterile water was added and RNA equivalent to 1 µg to a 0.5 mL tube to a total volume of 4 µl. A mixture of 10 × DNase I reaction buffer and NAse was added and incubated at 20 °C for 15 minutes. Then, a mixture of oligo dT prime, 10 mM dNTP mix, and 25 mM EDTA was prepared and added followed by incubation in a thermal cycler (PC-708R, ASTEC Co. LtD., Fukuoka, Japan) at 65 °C for 10 minutes. Following that, a mixed solution of sterilised water, buffer, and reverse transcriptase was added and incubated in sequence using a thermal cycler: 30 °C for 10 minutes for annealing and bonding; 42 °C for 60 minutes for reaction, and 99 °C for 5 minutes for denaturation. TE (Tris-EDTA) Buffer was added at the final phase based on the amount of RNA used and stored at −20 °C until continuing with real-time PCR.

Quantitative Real-Time PCR (qPCR)

Gene expression analysis was performed using the AriaMx Real-Time PCR System (Agilent Technologies, USA) with SYBR Green Master Mix. Reactions were conducted in 96-well plates with a final volume of 20 µL containing 8 µL of diluted cDNA and 12 µL of SYBR Green mix. Thermal cycling conditions was subjected as followed; 95 °C for 3 min; 50 cycles: 95 °C for 5 s, 60 °C for 30 s and melt curve: 95 °C for 30 s, 65 °C for 30 s, 95 °C for 30 s. Each RT-qPCR analysis was performed in triplicate and the mean was used for RT-qPCR analysis. Expression levels are represented as ΔRn values, reflecting relative transcript abundance. The primer sequences for target and reference genes are listed in *Table 1*.

Table 1. Primer sequences used for quantitative real-time PCR analysis

Primer name	Sequence (5'–3')
LePGcat-F	AAGGGCCTTGTAAGTCAGCC
LePGcat-R	CACCATCGTTGACCATTGCC
LeActin-F	TCGGAATGGGACAGAAGG
LeActin-R	TCAGTCAGGAGAACAGGGTG

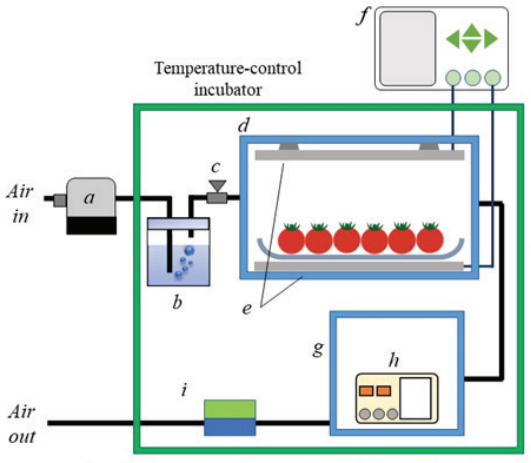
Statistical analysis

All data were analysed using ANOVA under a completely randomised design (CRD) framework in SAS 9.4 (SAS Institute Inc., Cary, NC, USA). Means were separated using Duncan's Multiple Range Test at a significance level of $p < 0.05$.

Results and discussion

Weight loss

Tomatoes in all treatments exhibited gradual weight loss during the 21 days storage period at 5 °C (*Figure 2*). Statistical analysis indicated that electric field (EF) treatments did not significantly reduce weight loss compared to the control ($p > 0.05$). However, a non-significant trend was observed, with DC-EF treated fruits consistently showing slightly lower cumulative weight loss approximately 15 – 20% less than the control at Day 21. This mild effect aligns with prior reports suggesting that electric fields may influence water retention by modulating membrane permeability (González-Casado et al. 2018; Nowacka et al. 2019).



a: air pump, *b*: water, *c*: flow regulator, *d*: electric field chamber, *e*: stainless steel plate, *f*: programmable power source, *g*: small desiccator, *h*: CO_2 sensor, *i*: gas flow meter

Figure 1. Schematic diagram of the electric field treatment system used in this experiment

Physiochemical properties (Firmness, soluble solid content, total acidity, reduction of ascorbic acid)

The changes in soluble solid content (SSC), sugar/acid ratio, total titratable acidity (TTA), and ascorbic acid reduction over 21 days of cold storage under electric field (EF) treatments are summarised in *Table 2*. No significant differences were observed among treatments for SSC or sugar/acid ratio ($p > 0.05$), although a significant effect of storage duration was observed ($p < 0.05$). SSC declined from 5.30°Brix on Day 0 to an average of 4.57 – 4.60°Brix by Day 21, consistent with previous findings that chilling temperatures can slow sugar accumulation in tomatoes (Kader et al. 2005).

Although the electric field treatments did not significantly alter SSC or sugar/acid ratio, a significant interaction was observed between treatment and storage duration for titratable acidity ($p < 0.05$). DC-EF treated fruits maintained a more stable acidity level (0.48 – 0.54% citric acid) compared to AC-EF and control, which may reflect improved biochemical stability under direct current exposure. These findings suggest that while EF does not directly enhance sugar accumulation or acid degradation, it may contribute to maintaining metabolic homeostasis under cold stress, as proposed in studies involving electric field influence on ion transport and stress response in plant tissues.

Skin colour

Tomato skin colour parameters which is lightness (L*), redness (a*), and yellowness (b*) were evaluated to assess ripening changes under electric field (EF) treatments during cold storage (*Figure 3*). The L* value, representing lightness, decreased slightly across all treatments, indicating minimal darkening over time, with no significant difference between control, AC-EF, and DC-EF treatments ($p > 0.05$). However, the a* value, indicative of red pigmentation and lycopene accumulation, increased more rapidly in the AC-EF and DC-EFgroups than in the control, particularly between Day 7 and Day 21. This suggests that EF may stimulate lycopene biosynthesis or modify pigment development pathways under cold conditions. Nevertheless, since the control also maintained stable colouration, EF treatment did not provide a statistically significant advantage in colour preservation. This may reflect a mild acceleration of ripening processes or lycopene synthesis under electric stimulation, as previously observed in other produce like cherry tomatoes treated with electrostatic fields (Zhao et al. 2023). The b* value (yellow/blue chromaticity) remained relatively stable, with minor decreases observed in all treatments. Wang et al. (2010) also found that both static and alternating electric fields delayed the loss of firmness and enhanced colour change from green to red in tomatoes, suggesting stimulation of the ripening process (Wang et al. 2010). Additionally, low-intensity pulsed electric field (LIPEF) treatment was found to significantly increase a value by as much as 40.78% indicating enhanced red coloration and lycopene content in tomatoes (Prakasha et al. 2024). *Figure 4* showed colour changes of tomatoes treated with different EF conditions during storage at 5 °C.

Table 2. Changes in soluble solid content (SSC), sugar/acid ratio, total titratable acidity (TTA), and reduction of ascorbic acid of tomatoes treated with electric field at 5 ^{o}C of storage temperature.

Main effects	SSC (^{0}Brix)	Sugar/Acid ratio	TTA (% citric acid)
EF treatments (T)			
Control	4.93a	11.08a	0.53a
AC	4.63a	10.96a	0.46ab
DC	4.70a	10.59a	0.48ab
F-Test Sig	ns	ns	ns
Storage period (D)			
0	5.30a	10.53ab	0.50a
7	4.57b	11.24a	0.42b
14	4.55b	9.15b	0.51a
21	4.60b	9.12b	0.54a
F-Test Sig	*	*	*
T x W Interaction	ns	ns	*

Each value was the mean of three replicates
Means separation within columns and main effect by DMRT at $p \leq 0.05$
ns,*, ** Non-significant or significant or highly significant at $p \leq 0.05$, respectively

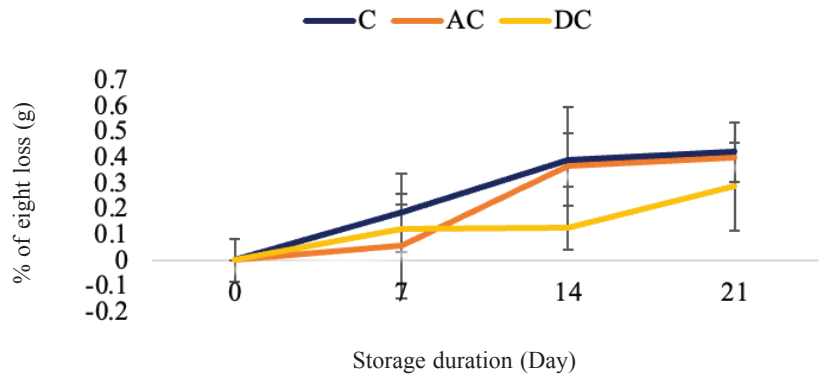


Figure 2. Changes in weight loss with and without electric field conditions on tomatoes during storage duration. (A) colour lightness (L), (B) a value, and (C) b* value. The bars represent the standard deviation of the mean, n=3, C: Control, AC: Alternating current, DC: Direct current*

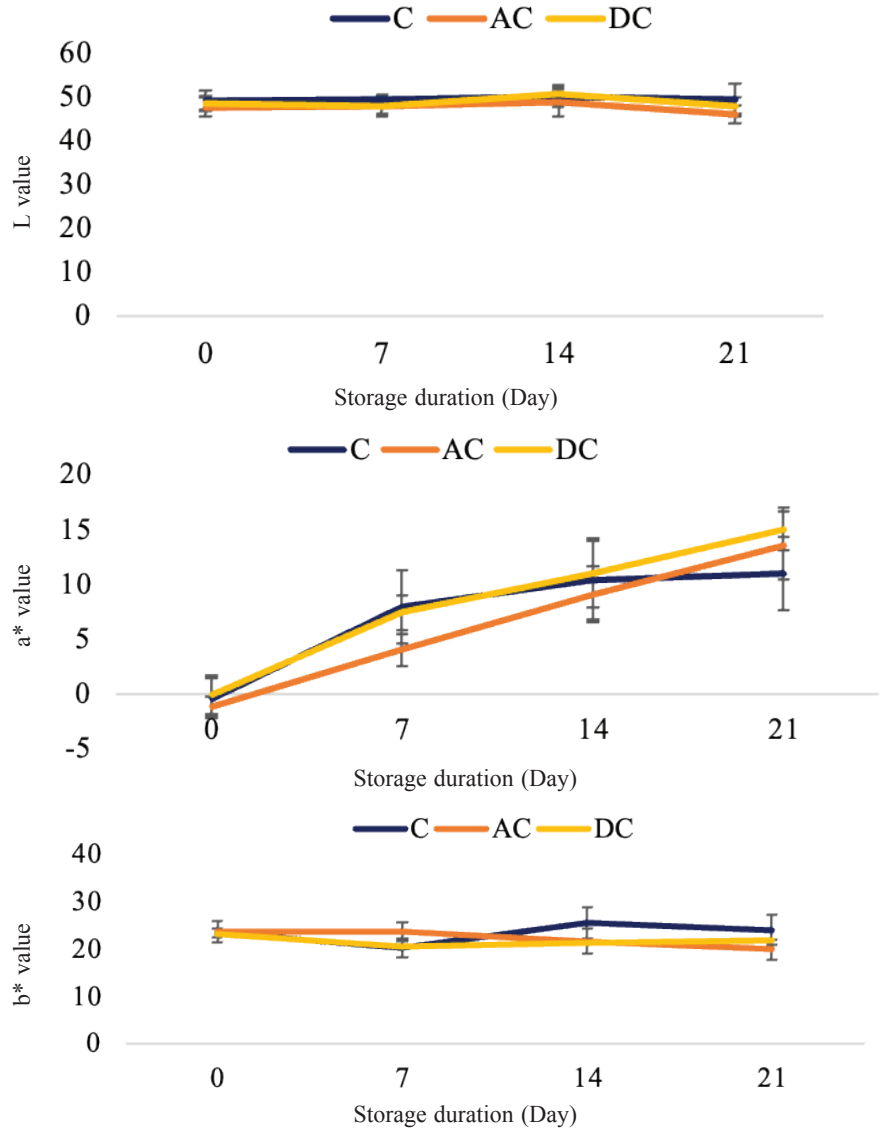


Figure 3. Skin colour index with and without electric field conditions on tomatoes during storage duration. The bars represent the standard deviation of the mean, n=3, C: Control, AC: Alternating current, DC: Direct current

Firmness

Tomato firmness was measured in Newtons (N) over a 21-day storage period to assess the impact of electric field treatments on textural quality (*Figure 5*). At Day 0, all samples had high firmness, with DC-EF treated tomatoes showing the highest initial values (~12 N), followed by AC-EF and control groups. This trend aligns with findings from prior research. Wang et al (2010) reported that electric field treatments (both static and alternating) significantly delayed the softening of tomatoes during storage, likely by slowing down enzymatic degradation of cell walls (Wang et al. 2010). Similarly, Kishore & Hamanaka (2019) found that tomatoes treated with high-voltage electric fields retained greater firmness after one week compared to untreated samples, suggesting enhanced structural preservation under electric treatment (Kishore & Hamanaka, 2019).

By Day 7, a significant reduction in firmness was observed across all treatments. The firmness declined sharply in all groups to approximately 6 – 7 N, indicating rapid softening early in storage. However, from Day 7 to Day 21, the firmness of electric field-treated tomatoes (both AC-EF and DC-EF) either stabilised or slightly increased, whereas the control group showed a more gradual and continuous decline.

Statistical analysis using two-way repeated-measures ANOVA revealed a significant effect of storage duration on firmness ($p < 0.01$), but no significant main effect of treatment ($p > 0.05$). However, the interaction between treatment and time approached significance ($p = 0.07$), suggesting a possible influence of electric field exposure on the firmness trend over time.

At Day 21, tomatoes in the DC-EF and AC-EF treatment groups maintained slightly higher firmness (7.3 N and 7.0 N, respectively) compared to the control group (6.6 N), though the differences were not statistically significant ($p > 0.05$). This work is consistent with the findings of (Pang et al. 2021), who discovered that electric field treatment can delay the loss of luscious firmness in fruit by preserving cellular structural integrity. This trend indicates that electric field treatments may help maintain firmness during extended storage, potentially by slowing down cell wall degradation processes. Its effectiveness depends on the electric field's strength (Nowacka et al. 2019). This supports the hypothesis that DC-EF can moderate cell wall degradation and softening.

Relative gene expression

To investigate the physiological impact of electric field exposure at the molecular level, changes in relative gene expression were assessed in tomatoes stored at 5 °C under control (C), AC-EF, and DC-EF treatments over a 21-day period (*Figure 6*). Expression levels are represented as ΔRn values, reflecting relative transcript abundance.

At Day 0, baseline expression was highest in the control group (~1.0 ΔRn), while both AC-EF and DC-EF groups showed minimal or undetectable expression. By Day 7, gene expression declined in the control group and remained low in all treatments, with no significant differences observed ($p > 0.05$).

A notable increase in gene expression occurred at Day 14, particularly in the AC-EF and DC -EF groups, reaching average ΔRn values of approximately 1.5 – 2.0, although large standard deviations were observed. In contrast, the control group maintained relatively stable and lower expression (~0.6 ΔRn). Despite these increases, the large variability in expression resulted in no statistically significant differences among the treatment groups at any time point ($p > 0.05$).

At Day 21, expression levels in AC-EF and DC-EF groups remained elevated compared to the control, though again not significantly. These trends suggest that electric field treatments, especially DC-EF, may induce an upregulation of gene expression related to stress

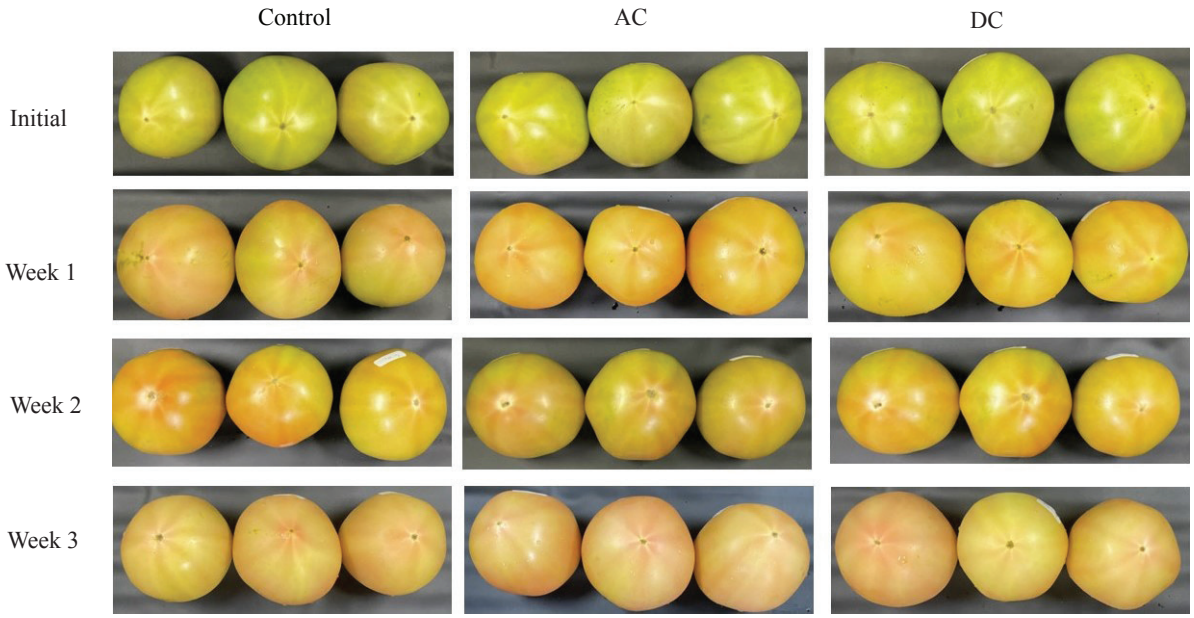


Figure 4. Colour changes of tomatoes treated with different EF conditions during storage at 5 °C

response or metabolic activity, though further replicates and validation would be required to confirm significance.

Further studies should focus on optimising EF parameters and exploring other related genes and enzymes (e.g., PME, cellulase) to fully understand the biological pathways affected by EF exposure during postharvest storage.

Cell wall degrading enzymes activities

Polygalacturonase (PG) activity, a key enzyme involved in pectin degradation and fruit softening, was measured in tomatoes during a 21-day storage period under control, AC-EF, and DC-EF electric field treatments (*Figure 7*). All treatments began with comparable PG activity levels (~0.30 μmg^{-1}) at Day 0. A significant decline in activity was observed by Day 7 in all groups, with the DC-EF treated tomatoes showing the lowest PG activity, suggesting a potential suppressive effect of the DC-EF on early enzymatic degradation.

Between Day 7 and Day 14, PG activity increased again in all groups, but the DC-EF consistently exhibited lower activity levels than the control and AC-EF groups. This trend persisted through Day 21, where PG activity in the DC-EF group remained reduced relative to the control. Although differences were not statistically significant ($p > 0.05$), the consistent suppression of PG activity in the DC-EF group may contribute to delayed softening.

These observations are supported by recent findings that external treatments can modulate PG-related softening in tomato. For instance, application of fungal polygalacturonase-generated oligogalacturonides was shown to restrain fruit softening by downregulating PG-related gene expression and maintaining firmness during storage (Yang et al. 2021). These results align with our findings, suggesting that DC-EF treatment may suppress PG activity and enhance textural preservation, offering a promising non-chemical method to extend shelf life.

The preservation of firmness under DC-EF appears to be primarily linked to suppressed PG enzymatic activity, rather than delayed pigment development or changes in soluble solids. While EF had little impact on most physiochemical traits, the observed reduction in PG activity under DC-EF treatment highlights a novel mechanism by which electric fields can influence ripening at the enzymatic level. Compared to other studies employing electrostatic or space electric fields, which have also demonstrated improved firmness and reduced enzymatic activity in fruits like strawberries and tomatoes (Chang et al. 2023; Xiyun et al. 2024; Nie et al. 2024), the results herein contribute new insight into the application of continuous EF exposure under cold storage. This positions EF, particularly DC-EF based systems, as a potential non-thermal intervention for postharvest management. Given that PG plays a key role in cell wall disassembly and fruit softening, these results suggest that DC-EF may help extend postharvest shelf life of tomatoes by modulating softening at the molecular level.

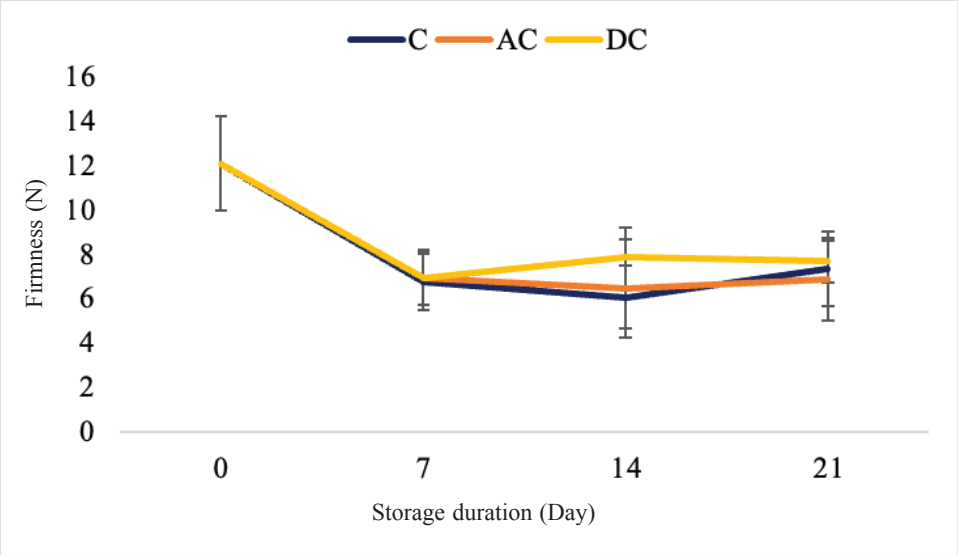


Figure 5. Changes in the firmness (N) of tomatoes with and without electric field conditions during storage duration at 5 ^{o}C. The bars represent the standard deviation of the mean, n=3,C: Control, AC: Alternating current, DC: Direct current

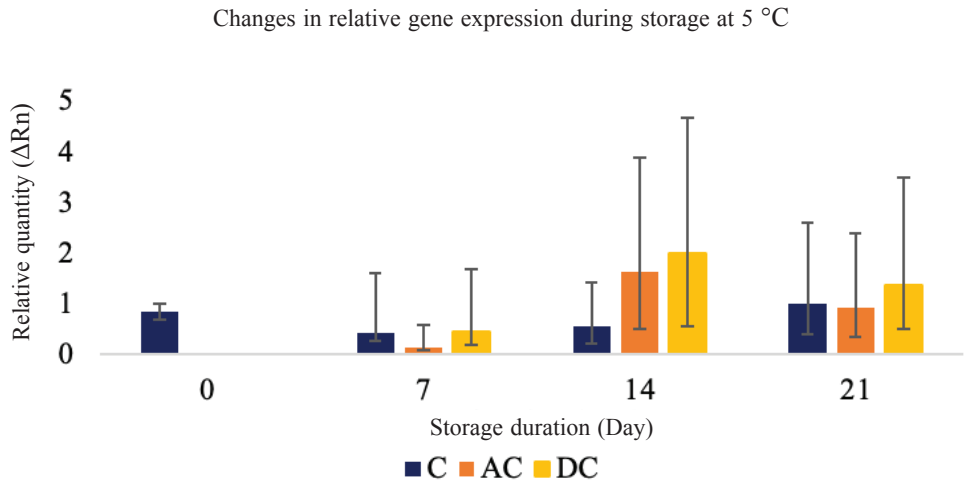


Figure 6. Changes in PG gene expression with and without electric field treatment during storage duration. The bars represent the standard deviation of the mean, n=3, C: Control, AC: Alternating current, DC: Direct current

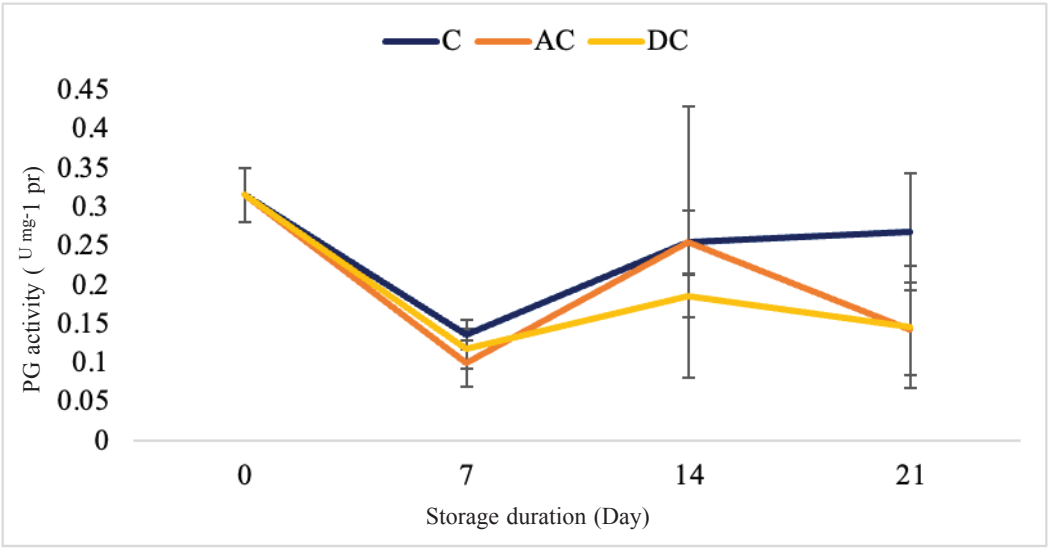


Figure 7. The polygalacturonase activity in pericarp tissue from tomatoes stored at 5 ºC after 20 V/cm of EF exposure. The bars represent the standard deviation of the mean, n=3, C: Control, AC: Alternating current, DC: Direct current

Conclusion

DC-EF treatment showed modest but statistically significant retention of fruit firmness and a notable reduction (~35%) in polygalacturonase (PG) enzyme activity at Day 21, compared to untreated controls. However, EF treatment did not significantly influence other physiochemical attributes, such as soluble solids, titratable acidity, or skin colour, under cold storage conditions.

Importantly, although EF treatment did not significantly reduce overall weight loss, DC-EF consistently trended toward lower water loss than control and AC-EF treatments. These outcomes suggest that DC-EF may play a role in modulating enzymatic activity related to cell wall degradation specifically by reducing PG activity which contributes to maintaining firmness. The divergence between PG gene expression and enzymatic activity also suggests that EF effects may involve post-transcriptional regulation or stress-induced enzymatic inhibition.

Further research should explore the synergy between EF and other storage technologies (e.g., modified atmosphere, coatings), evaluate a broader range of enzyme markers (e.g., PME, cellulase), and clarify the biophysical mechanisms by which EF influences tissue integrity and metabolic regulation during cold storage.

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