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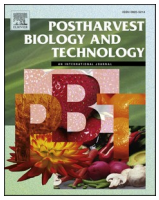

Cold storage extends mango postharvest life by modulating abscisic acid levels and sugar composition

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ABSTRACT

Mango is traditionally classified as a climacteric fruit, in which ethylene and abscisic acid (ABA) play central roles in ripening. Mango fruit is cultivated only in tropical and some subtropical regions, therefore, to meet global demand, cold storage is widely used during transport, followed by a ripening period. This study evaluated the effects of simulated commercial transit cold storage (9 °C, > 85% relative humidity [RH]) used during the sea freight supply chain from the Southern hemisphere to the UK, by comparing the two main mango fruit cultivars ('Keitt' and 'Kent') imported into the UK market. Fruit were ripened with and without prior cold storage (control) and the synthesis and catabolism of key ripening regulators (ABA and its metabolites) as well as associated changes in quality attributes (internal colour, firmness, individual sugar content) were investigated. Cold storage delayed firmness loss, extending the postharvest life from 10 to 12 days to 29 days. ABA accumulated throughout ripening in control fruit but was depleted in cold-stored fruit for both cultivars, indicating its central role in mango ripening; cold storage fundamentally altered ABA dynamics by suppressing accumulation and modifying spatial distribution and conjugation patterns in a cultivar and pulp dependent manner. Additionally, sugar metabolism was altered, likely affecting taste, and meaning that, in cold-stored fruit, sugar content no longer correlated with total soluble solids (TSS). These findings highlight ABA as a potential target for postharvest management and underscore the need for integrated quality indices beyond TSS to improve fruit evaluation and reduce losses in global supply chains.

1. Introduction

Mango (*Magnifera indica* L.) fruit has a short postharvest life (~10 days) with up to 19% losses during this period (Lalel et al., 2003; Zaharah et al., 2012, 2013; Food and Agriculture Organisation FAO, 2023). Mangoes are cold-stored during sea freight to enable transport from its tropical origins to non-tropical markets and subsequently ripened at final destination at a higher temperature (*ca.* 20 °C; González-Aguilar et al., 2000, 2001; Barman and Asrey, 2014; Rastegar et al., 2020). Despite the benefits of cold storage, exposure to low temperatures is often perceived as an abiotic stress in fresh produce, changing the biochemistry and physiology of the fruit (Hor et al., 2022). While most climacteric fruit increase ethylene production in response to cold temperatures (Lelièvre et al., 1995; Hewitt et al., 2020; Wang et al., 2021; Fernández-Cancelo et al., 2022), mango fruit has previously shown a decline in ethylene during low temperature storage (between 0 and 15 ºC; Nair et al., 2004). In addition, Nair et al. (2004) found that storing mango at lower temperatures (5 *vs.* 15 ºC) leads to lower ethylene production after the fruit is transferred to ripening conditions (22 ºC) due to lower activity in the ethylene synthesis enzymes aminocyclopropane-1-carboxylate (ACC) synthase (ACS), and ACC oxidase (ACO). Also, González-Aguilar et al. (2000) reported very low ethylene production from mangoes during ripening after cold storage. However, neither study included a comparison with fruit that had not undergone low-temperature storage before ripening, giving an incomplete view on the effects of this treatment.

Abscisic acid (ABA) is a central regulator of fruit development and ripening, particularly in non-climacteric species, where it acts as a primary hormonal signal initiating ripening-associated processes such as sugar accumulation, colour development, and softening (Li et al., 2011) and plays a critical role in temperature stress responses in plants (Gusta et al., 2005). In climacteric fruit, ABA has also been shown to play an important upstream role by modulating ethylene biosynthesis and sensitivity, thereby influencing the onset and progression of ripening

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(Zhang et al., 2009; McAtee et al., 2013). Accumulation of ABA during ripening has been reported in a range of fruit species, including tomato, strawberry, grape, and peach, where it is associated with transcriptional regulation of cell wall modification, sugar transport, and pigment biosynthesis pathways (Jia et al., 2016). In addition to its role in ripening, ABA is a key mediator of plant responses to abiotic stress, including low temperature stress, where it contributes to stress signalling, metabolic adjustment, and developmental regulation (Gusta et al., 2005). Cold storage has been shown to alter ABA accumulation and signalling in several fruit species, often leading to modified ripening behaviour following transfer to ambient temperatures (Wang et al., 2021). Despite mango being a climacteric fruit and being widely subjected to cold storage during commercial transport, the interaction between low-temperature storage, ABA metabolism, and subsequent ripening progression in mango remains poorly understood.

Besides PGRs such as ethylene and ABA, sugars can also function as signalling molecules; sucrose can promote ripening in both climacteric and non-climacteric fruits (Jia et al., 2016). However, sugars are best known for being a key determinant of sweetness, alongside acids (Beckles, 2012; Helstad, 2019). Total soluble solids (TSS) have been widely used as a fast, affordable, and easy method of approximating soluble sugar content in mango, which has led to TSS being widely used as a quality and ripeness measurement across supply chains (Munawar et al., 2013; Maraphum et al., 2022; Nordey et al., 2017; Pornprasit and Natwichai, 2013). Despite its high value, the impact of cold storage on sugar metabolism during ripening has not yet been investigated in mango.

To address these knowledge gaps, this study investigated the effects of cold storage on mango ripening, with particular emphasis on the role of ABA as a potential regulator of post-cold ripening behaviour, alongside associated changes in sugar composition and fruit quality attributes. This work aimed to improve our understanding of how commercial postharvest temperature regimes influence mango physiology and ripening outcomes.

2. Materials and methods

2.1. Plant material and experimental design

Mango fruit (*Mangifera indica*) of 'Keitt' and 'Kent', representing the two main cultivars imported to the UK (Orchard House Foods, personal communication) and which are closely related, were harvested following commercial practices, and transported to Cranfield University (Bedfordshire, UK) according to Table S1. Control fruit was directly stored at 20 ± 2°C, while the cold-stored fruit was first stored at 9 ± 1 °C for 21 days and then transferred to 20 ± 2 °C, to simulate commercial conditions recorded during shipments from UK-based tropical fruit importers (Orchard House Foods, personal communication). Mango fruit were sampled upon arrival to the UK (time zero measurement) and weekly thereafter during cold storage; whilst under ripening conditions (storage at 20 °C) fruit were sampled every 2 days - data is represented as 'Time under ripening conditions' (i.e. time at 20 °C; Fig. 1). In all cases, relative humidity of > 85% was maintained. Upon arrival to Cranfield University, fruit were evenly distributed across three 260 L boxes (Chiltern Industrial Machining Services Ltd.) per treatment, under controlled temperature conditions (9 *vs.* 20 °C), and supplied with a continuous air flow. Each box represented a biological replicate. For 'Keitt', ten fruits from each box were selected *ad hoc* at each sampling point (n = 3, ten fruit per replicate). For 'Kent', eight fruits from each box were selected *ad hoc* at each sampling point (n = 3, eight fruit per replicate). Fruit were checked for signs of chilling injury according to Brecht et al. (2012) and Cantre et al. (2017) including scald-like skin discolouration, brown spots, and lenticel pitting, and pulp discolouration. Representative pulp images are shown in Figure S2.

At each sampling point, firmness, objective colour, and TSS measurements were taken from the equatorial inner and outer pulp of individual fruits, according to Figure S1. For further biochemical and gene expression analyses, equatorial pulp samples from each replicate and treatment combination (ten or eight fruit per replicate for 'Keitt' and 'Kent', respectively) were pooled and then frozen in liquid nitrogen. The pooled samples were stored at −80 ℃, freeze dried (Sacanvac freeze-drier, Labogene, Denmark), ground into a fine powder, and then stored at −40 ℃ until biochemical and gene expression analyses were performed.

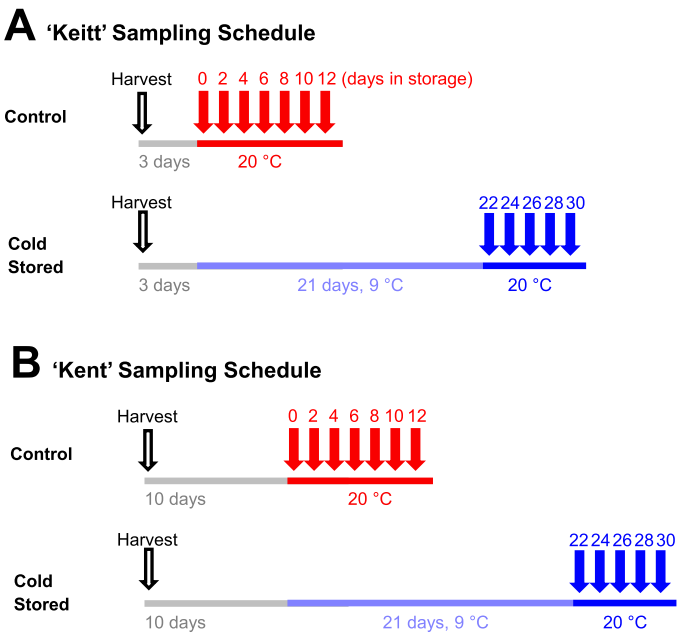

Fig. 1. Sampling schedule for 'Keitt' (A) and 'Kent' (B). Two postharvest treatments (Control, directly stored at 20 ± 2°C after transport; Cold-stored, placed at 9 ± 1 °C for 21 days after transport and then transferred to 20 ± 2 °C) are detailed. Colour key: grey: transport under uncontrolled conditions, light blue: storage time at 9 ± 2 °C, red and dark blue: storage time at 20 ± 2 °C.

2.2. Respiration rate

Respiration rate measurements were carried out according to Alamar et al. (2017) with minor modifications. Mango fruit (4 kg) was stored in 16 L airtight boxes (L&L Nordic OÜ) in triplicate, with continuous air flow at a rate of 12 L h^{-1}. Real time respiration rate (μmol kg^{-1} h^{-1}) as carbon dioxide (CO_2) production was determined for 'Keitt' mangoes throughout storage using a Sable Respirometry System (Model 1.3.8 Pro, Sable Systems International). The respiration rate measurements for 'Kent' were excluded due to instrumental error.

2.3. Physiological tests

Flesh firmness and colour were measured on individual mangoes at each timepoint for both the inner (closer to the stone) and outer (closer to the skin) pulp from the equator of each fruit (Figure S1 **A, B**). Firmness was analysed according to Landahl and Terry (2020) with slight modifications. A 4 mm flat head cylindrical probe was mounted onto a Universal Testing Machine (Series 68SC-05, Instron) and inserted into the sample to a depth of 5 mm at a speed of 120 mm min^{-1}, with the maximum load used to represent firmness. Colour was quantified using ImageJ (v. 1.53, NIH) on images captured using a Lumenera Infinity 3 high-definition digital camera, with samples illuminated using a Photo-e-Box plus 1419. RGB values for areas between 3 – 6 mm^2 were converted to CIEL*a*b*, and lightness (L*), chroma (C*) and hue angle (h°) values . Figure S1. TSS (%) were measured from the juice of each fruit using a digital Palette refractometer.

2.4. Biochemical analyses

Individual sugars were extracted from 50 ± 0.5 mg dry weight (DW) powder using one mL of a methanol/water (62.5:37.5 v/v) solution (O'Brien, 2025). The mixture was heated to 55 °C while shaking at 2000 rpm for 15 min, before being passed through a 0.2 μm nylon filter (Agilent, Berkshire, United Kingdom). Sugars were quantified using a High-Performance Liquid Chromatograph (HPLC) binary pump (Agilent, Berkshire, United Kingdom) equipped with an evaporative light scattering detector (Agilent 1260 Infinity II) and a Shodex Asahipak polymer-based column (4.6 ×250 mm, 10 nm particle size [part number NH2P-50 4E]). HPLC-grade water (A) and acetonitrile (B) were used as mobile phases with a flow rate of 1 mL min^{-1} programmed to the following ratios: 0 min, 20% A and 80% B; 20 min, 50% A and 50% B; 23.5 min, 20% A and 80% B; and held until a total run time of 25 min was reached. The identity and abundance of glucose, sucrose, and fructose were determined by comparing to a calibration curve constructed from Sigma-Aldrich authentic standards (Dorset, UK). Sugar concentrations were expressed as mg g^{-1} DW.

ABA and related compounds were quantified as per Fernández--Cancelo et al. (2023) with minor modifications. The targeted compounds were ABA, ABA-glucose ester (ABA-GE), 7'-hydroxy-ABA (7'OH-ABA), phaseic acid (PA), dihydrophaseic acid (DPA), and neophaseic acid (neoPA). Briefly, an internal standard mixture containing 1 ng of each labelled (deuterated) compound was added to 15 ± 0.5 mg DW of each sample. Endogenous PGRs were extracted using a methanol/water/formic acid (35:50:5 v/v/v) solution (1 mL) and reconstituted in water/methanol/formic acid (9:1:0.1% v/v/v) solution (0.5 mL). Detection of compounds was carried out using a Triple Quad™ 6500 liquid chromatography-mass spectroscopy (LC-MS/MS) system (SCIEX). Separation was achieved using a Hypersil GOLD C4 High-performance liquid chromatography (HPLC) Column (25002–052130, Thermofisher). The identity and abundance of PGRs were determined by comparing to a calibration curve constructed from internal standards and unlabelled standards containing 12 points ranging from 0.1 to 250 ng mL^{-1} . PGR concentrations were expressed as ng g^{-1} DW. (±)-ABA was purchased from Sigma-Aldrich; the rest of labelled and unlabelled standards were obtained from the National Research Council of Canada-Plant Biotechnology Institute.

2.5. Gene expression profiling

Three timepoints from the 'Keitt' fruit were selected for gene expression analysis: day 0 (under ripe), day 4, and day 8 (overripe). Both the inner and outer pulp of control and cold-stored fruit were included. RNA extraction and cDNA synthesis were carried out on lyophilised pulp samples using the RNeasy Plant Mini Kit and the QuantiTect Reverse Transcription Kit (Qiagen) according to manufacturer specifications. An on-column DNase digestion step was added during RNA extraction, as per manufacturer specifications (Qiagen). Quantification of target mRNAs was carried out using QuantiNova SYBR Green PCR Kit (Qiagen) and target-specific primers (0.7 μM each, Merk, sequences listed in Table S2), and 50 ng cDNA. The reaction was performed in a CFX96 Touch Real-Time PCR Detection System (Bio-Rad) with the following cycling conditions: an initial 2 min denaturation step at 95 °C, 35 cycles of 5 s denaturation (95 °C), then 10 s for annealing and extension (60 °C), followed by melt-curve analysis (65–95 °C at 0.5 °C increments). Results were expressed as normalised gene expression according to Muller et al. (2002) using glyceraldehyde-3-phosphate dehydrogenase (GAPDH) as a reference gene, with 3 technical replicates per sample.

2.6. Statistical analyses

Analysis of variance (ANOVA) was used to identify significant differences ($p < 0.05$) between the main factors (ripening time, tissue) and their interactions. The Fisher's test was subsequently used as *post-hoc* analysis and the least significant differences (LSDs) shown where appropriate. Repeated measures ANOVAs were used where the same fruit were measured at multiple timepoints (respiration rate measurements). Unbalanced designs were used where two treatments without equal timepoints were compared (e.g. control *vs*. cold-stored). ANOVA assumptions were tested in each case, and the datasets that violated any assumption were transformed by either taking the $\log_e$ or the square root of the data before analysis. Statistical analysis was carried out using Genstat (23rd Edition) and R.

3. Results

3.1. Chilling injury and respiration rate

No symptoms of chilling injury were observed for any of the cultivars or sampling points, matching commercial expectations (Figure S2). Neither of the treatments showed a climacteric peak in the respiration rate during ripening (Fig. 2). After being transferred from cold storage conditions (9 ºC) to ripening conditions (20 ºC), the respiration rate of the fruit increased *ca*. 5-fold. Only minor changes were seen in the respiration rate of control fruit.

3.2. Firmness

During the 21-day cold storage period the fruit firmness decreased, such that on day zero of ripening 'Keitt' were *ca*. 70% less firm than the control fruit, while 'Kent' were half as firm (Fig. 3**, A and B**). Spatially, the outer pulp was firmer than the inner pulp at the beginning of ripening across all cultivars and treatments. In 'Keitt', these spatial differences were maintained in the control but diminished through ripening in the cold-stored fruit. Conversely, the control 'Kent' fruit had no spatial differences after six days of ripening, but in the cold-stored fruit the inner pulp was less firm at every timepoint.

3.3. Colour

The L* of 'Kent' fruit decreased through ripening in both the inner and outer pulp, and in both treatments (Fig. 4**, A**). A difference between the treatments only existed when the cold-stored fruit were overripe, with 9% lower L* values in the cold=stored than control on day 8. The C* values steadily increased by 7% in the control fruit through ripening (Fig. 4**, B**). By the end of the ripening process, the C* had decreased in cold-stored fruit to be 13% lower than the control treatment. The hº decreased by 30% in the control fruit through ripening, with a lower hº in the inner pulp compared to the outer. No significant difference between the treatments was found for hº (Figure S3).

3.4. Sugar profiles

Sucrose, the most abundant sugar, accumulated through ripening in the pulp of both mango cultivars under control conditions, with a two-fold and 1.5-fold increase through ripening in 'Keitt' and 'Kent', respectively (Fig. 5**, A and B**). This likely comes from the breakdown of starch and dominates the expected sugar accumulation for sweetening during ripening (Castrillo et al., 1992; Fuchs et al., 1980). However, the two cultivars had contrasting sucrose accumulation profiles in fruit pulp subjected to cold storage prior to ripening, where sucrose increased through ripening in 'Keitt' and decreased in 'Kent'. Glucose was the only sugar where different accumulation patterns were seen in 'Kent' and 'Keitt' through ripening in the control fruit (Fig. 5**, E and F)** increasing by 5.8-fold in 'Keitt' pulp and falling by half in 'Kent' pulp. Through the ripening process, fructose levels increased by 37% in the 'Kent' control pulp positions, while 'Keitt' had equivalent levels on days zero and 12 (Fig. 5**, C and D**). After cold storage, the fructose levels in the 'Keitt' and 'Kent' pulp were higher than in their respective controls.

Given the changes in sugar metabolism between treatments, we

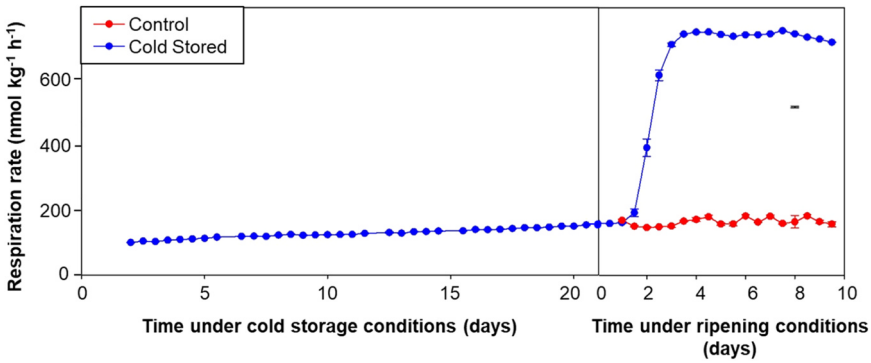

Fig. 2. Postharvest changes in respiration rate of mango fruit. Respiration rate (nmol kg^{-1} h^{-1}), as carbon dioxide (CO_2) production of 'Keitt' mangoes during ripening and cold storage. The Least Significant Difference at $p < 0.05$ ($LSD_{0.05}$) bar is shown for the interaction between treatment and time. Error bars represent standard error, n = 3, five fruit per replicate.

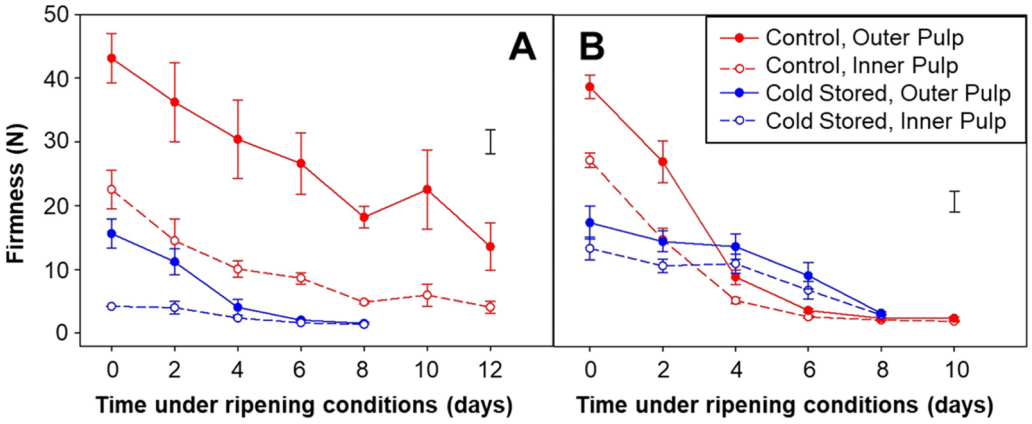

Fig. 3. Postharvest changes in firmness of mango fruit. Firmness changes (N) in 'Keitt' (A) and 'Kent' (B) fruit were measured in the inner pulp (dashed) and outer pulp (solid) of the fruit through ripening. Control fruit (red) were ripened at 20 °C immediately on reception, while cold-stored fruit (blue) were stored at 9 °C for 21 days before ripening. Timepoint zero in the cold-stored fruit corresponds to 21 days after cold storage. Standalone Least Significant Difference bars at $p < 0.05$ ($LSD_{0.05}$) are shown for the interaction between time, pulp position, and treatment. Error bars represent standard error, n = 3, (A) ten fruit per replicate, (B) eight fruit per replicate.

investigated whether TSS correlated with sugar content in control and in cold-stored fruit. A strong positive correlation was found between the TSS and sum of individual sugars (glucose, sucrose, and fructose content of the outer pulp added together) in the control fruit of both cultivars (r = 0.86 for the outer pulp, and r = 0.88 for the inner pulp), while in the cold-stored no correlation was found (Fig. 5**, G and H,** Figure S4).

3.5. Regulatory systems

ABA levels increased through ripening in both pulp positions and cultivars in control fruit (Fig. 6**, A-B**), accumulating steadily to *ca.* 3 times the initial concentration for 'Keitt' pulp, and *ca.* 1.5 times for 'Kent' pulp. By contrast, in the cold-stored fruit ABA decreased through storage at 20 °C in both cultivars, halving in 'Keitt' pulp and dropping *ca.* 7-fold in 'Kent' pulp. 'Kent' showed no differences in ABA-GE content between treatments or spatially (Fig. 6, **C**). In cold-stored 'Keitt' fruit, ABA-GE accumulated through ripening, doubling in the outer pulp and increasing by two fifths in the inner pulp, while no change was seen in control fruit (Fig. 6**, D**). In these 'Keitt' fruit, *NCED* transcript levels were similar in cold-stored and control fruit until the final sampling point (day 8; Fig. 6**, E**).

Spatial differences were also seen in ABA content and synthesis. In 'Keitt', the inner pulp had higher levels of ABA in both treatments, with 51% more ABA in the inner pulp of control fruit, but only 6% more in cold-stored fruit. The expression of *NCED* was *ca.* 20% higher in the inner pulp than the outer, although no significant interaction was observed between pulp position and treatment. In 'Kent', the inner pulp also had a higher ABA content, nearly double than that of the outer pulp in the cold-stored treatment. In the control 'Kent', only a 10% difference was seen, which is only evident in the final sampling point.

Despite the lack of ethylene detection, expression of the key genes involved in ethylene biosynthesis (*ACS* and *ACO*) were identified in 'Keitt'. Both *ACS* isoforms showed similar expression profiles, where the inner pulp had lower *ACS* expression on day zero, and equivalent levels after four days of storage (Fig. 7). No difference was seen between the control and cold-stored fruit. *ACO* levels were lower in the cold-stored fruit than the control, but only at the overripe stage (day 8). In the cold-stored fruit, *ACO* expression followed the same pattern as *ACS*, with lower expression levels in the inner pulp on day zero compared to the outer pulp, and expression decreasing through ripening. By contrast, the control fruit showed an increase in *ACO* transcripts between days 4 and 8, such that the inner pulp has higher *ACO* levels when overripe.

4. Discussion

4.1. Cold storage altered mango ripening

In control fruit, loss of firmness, change in pulp colour, and accumulation of soluble sugars (glucose, sucrose, and fructose) was observed, matching the descriptions of ripening throughout the literature (Zaharah et al., 2012, 2013; Nordey et al., 2014). Cold storage slowed down the loss of firmness, more than doubling the postharvest

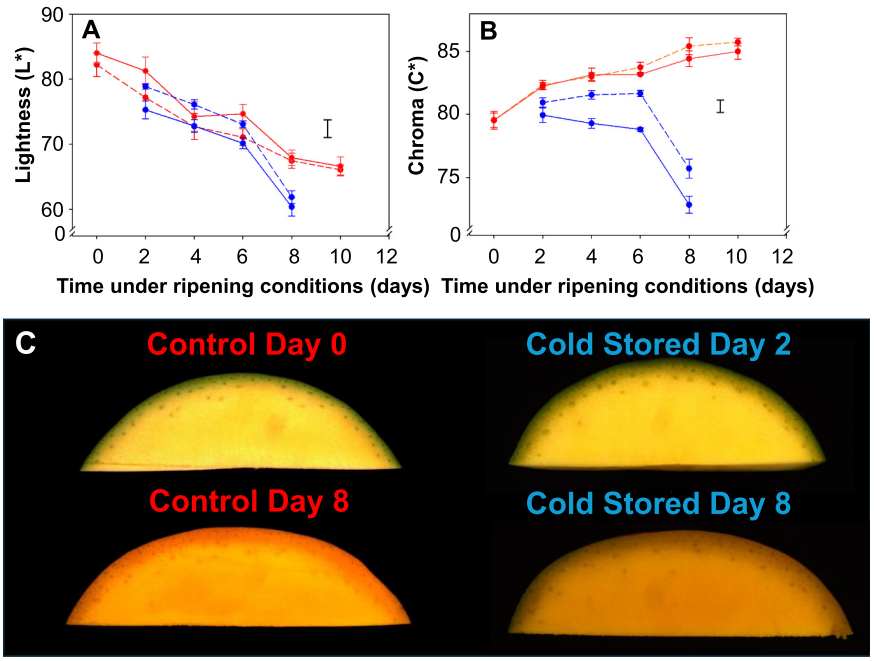

Fig. 4. Colour changes in 'Kent' mango through ripening. (A) Changes in the lightness (L*) and (B) chroma (C*) in the inner (dashed) and outer (solid) pulp. Control fruit (red) were ripened at 20 °C immediately on reception, while cold-stored fruit (blue) were stored at 9 °C for 21 days before ripening. Timepoint zero in the cold-stored fruit corresponds to 21 days after cold storage. Error bars represent standard error, n = 3, eight fruit per replicate. Standalone Least Significant Difference bars at $p < 0.05$ ($LSD_{0.05}$) are shown for the interaction between time and treatment. Timepoint zero for the cold-stored fruit was excluded due to instrumental error. Figure legends as per Fig. 3. (C) Examples of fruit at different ripening times are shown.

life in both cultivars. This extension is critical for enabling transport from the tropical production areas to non-tropical markets. However, cold storage also altered key ripening and quality characteristics. The lower L* and C* values in cold-stored 'Kent' fruit mean the pulp will appear darker and less vibrant than in the fruit ripened without cold storage and may be less attractive to consumers (examples shown in Fig. 4**, D**). The effects of cold storage on the spatial firmness differences were inconsistent between 'Keitt' and 'Kent', preventing firm conclusions about its impact on product homogeneity. Although similar changes have been previously reported after short term (4 day) cold storage of mango fruit (Montalvo et al., 2007), the present study is the first to quantify the differences under storage durations relevant to non-tropical markets.

The contrasting ABA profiles between cold-stored and control fruit strongly suggest that ABA contributes to the divergent ripening physiologies observed between treatments. During postharvest storage, there are three mechanisms for the fruit to control its endogenous free ABA concentration: 1) *de novo* synthesis through NCED, 2) catabolism, and 3) storage as inactive ABA-GE, which can be hydrolysed back to free ABA (Jadhav et al., 2008; Weng et al., 2016; Diretto et al., 2020). In 'Keitt' the levels of ABA-GE increased as free ABA was depleted in the cold-stored treatment, whereas no increase was seen in the control. Together with the absence of a decrease in *NCED* expression during early ripening (days 0–4), these findings suggest that the reduced ABA levels in cold-stored fruit result from greater sequestration in its inactive form, ABA-GE. This pattern was not seen in 'Kent', where ABA and ABA-GE levels did not track one another. Instead, elevated concentrations of ABA catabolites, including 7'OH-ABA and neoPA (Fig. 8), indicate that enhanced catabolism contributed to the decline in ABA levels in cold-stored 'Kent'.

The expected climacteric respiration and ethylene production peaks were not present in either cultivar or treatment. One possible explanation is that the climacteric peak may have occurred between harvest and day 0 of storage, given the four- and eleven-day transport period for 'Keitt' and 'Kent', respectively. However, previous reports place the climacteric peak 3–6 days after harvest, with ethylene production exceeding 140 nmol kg^{-1} h^{-1} (limit of detection = 107 nmol kg^{-1} h^{-1}; Lalel et al., 2003; Zaharah et al., 2012; Zerbini et al., 2015; Liu et al., 2021). Thus, some ethylene should still be detectable using a more advanced and sensitive system, at least in 'Keitt'.

An alternative explanation is that these fruits did not exhibit a climacteric peak. Lalel et al. (2003) found that mangoes harvesting at certain maturities can suppress both the ethylene production and the associated respiration peak. Industry sources indicate that fruit destined for local markets are typically harvested at a later stage than those intended for export and cold-storage (Orchard House Foods, personal communication), supporting this hypothesis. Additional support comes from the variability in molecular responses to ethylene inhibition (Zhang et al., 2020). Moreover, ethylene-independent ripening has been documented in other climacteric species, including melon (Ayub et al., 1996; Pech et al., 2008), fig (Qiao et al., 2021), and tomato (Jeffrey et al., 1984). In fact, it has long been proposed that fruit ripening is governed by both ethylene-dependent and ethylene-independent pathways, a view reinforced by evidence for multiple independent origins of the climacteric type (Lelièvre et al., 2006; Lü et al., 2018).

Additional studies on the changes in both physical traits and biochemical composition of mango fruit during cold storage (where this work focused on ripening after cold storage) would be valuable in deciphering at what stages the sugar metabolism and PGR accumulation of control and cold-stored fruit diverge. Additionally, exogenous treatment with ABA or ABA inhibitors could be used to demonstrate the causative effects seen on the ripening of cold-stored fruits observed in this study.

4.2. New strategies are needed for postharvest management of cold-stored mango

The results of this study found evidence of ABA playing a central role in the ripening differences between control and cold-stored fruit. This is critical, as most postharvest management strategies for mango focus on promoting or inhibiting ethylene signalling (Wang et al., 2009; Lü et al., 2018; Jaimun and Sangsuwan, 2019; Li et al., 2020). Supplemental ABA

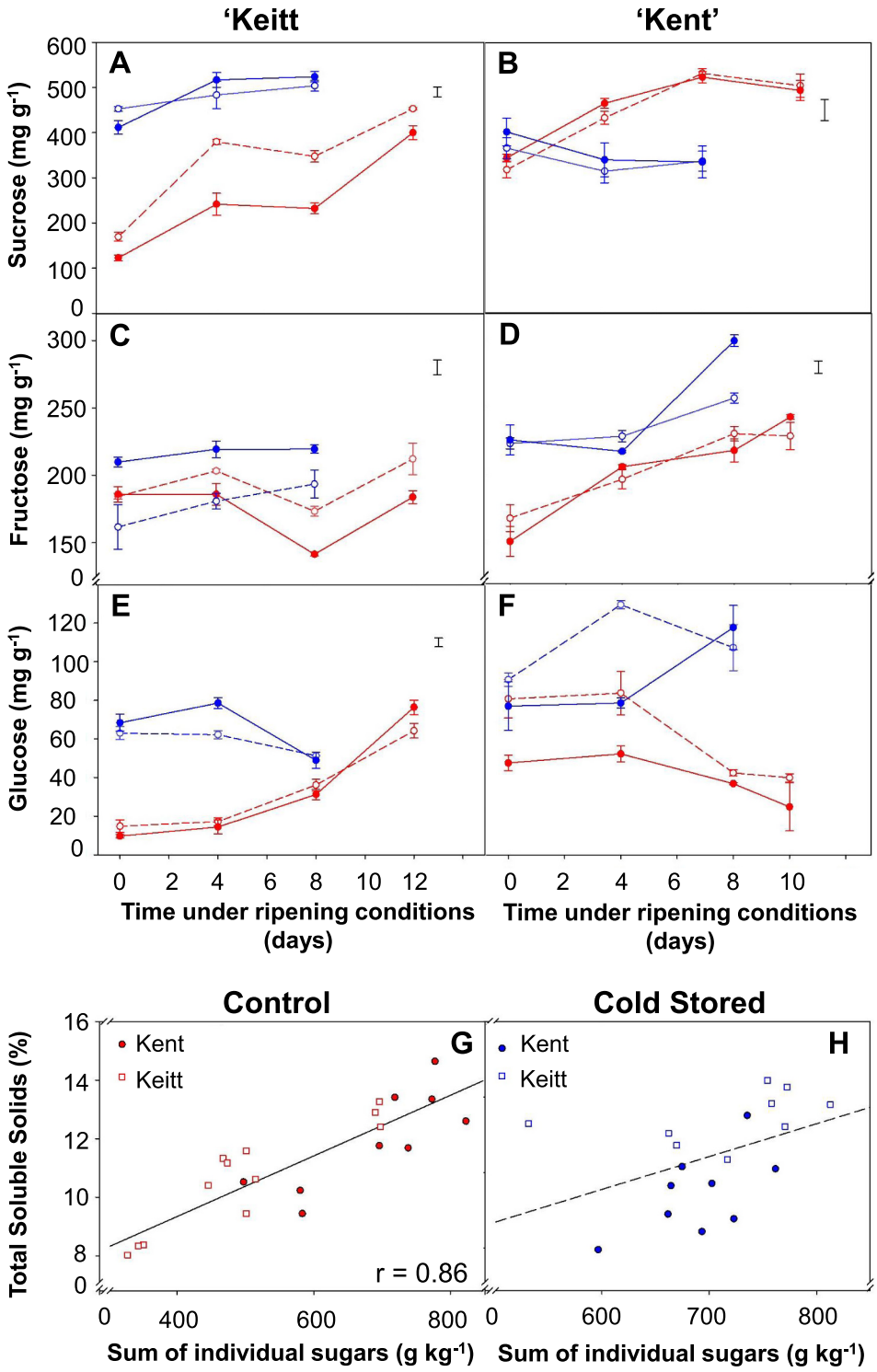

Fig. 5. Changes in the sugar profile of mango fruit through ripening. (A-F) Changes in individual sugar concentrations (mg g^{-1}) per dry weight in the inner (dashed) and outer (solid) pulp of 'Keitt' and 'Kent' mango fruit. Control fruit (red) were stored at 20 °C immediately on reception, while cold-stored fruit (blue) were stored at 9 °C for 21 days before transferring to 20 °C (ripening conditions). Least Significant Difference at $p < 0.05$ ($LSD_{0.05}$) bars are shown for the interaction between pulp position and treatment. The LSD for (F) is not shown as the square root of the glucose content was used for significance calculations, where $LSD_{0.05} = 0.3597$. Error bars represent standard error, n = 3, where each replicate contained ten ('Keitt') or eight ('Kent') fruit. Figure legend as per Fig. 3. (G and H) Correlation between total soluble solids and the sum of individual sugars in the outer pulp of control and cold-stored mango fruit. The sum of the individual sugars is the sum of the glucose, sucrose, and fructose, contents in the outer pulp. n = 12 for control, n = 9 for cold-stored, where each replicate (each point on the graph) contained ten ('Keitt') or eight ('Kent') fruit.

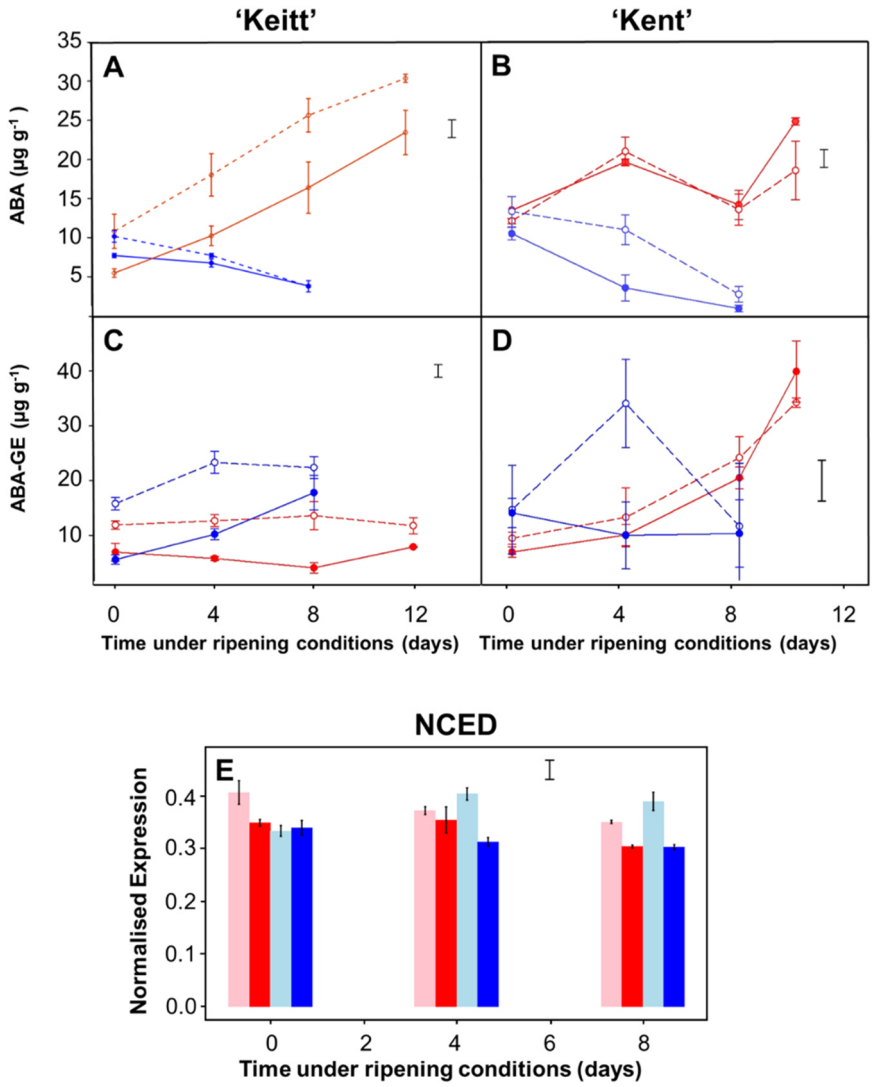

Fig. 6. Changes in abscisic acid (ABA)-related compounds (mg g^{-1} per dry weight) and gene expression. (A-B) Abscisic acid (ABA) levels in 'Keitt' and 'Kent'. (C-D) ABA-glucose ester (ABA-GE) levels in 'Keitt' and 'Kent'. (E) Relative expression of 9-*cis*-epoxycarotenoid dioxygenase (NCED) in 'Keitt'. The Least Significant Difference at $p < 0.05$ ($LSD_{0.05}$) bars are shown for the interaction between the factors pulp position and treatment (A, B, C), time (D), or pulp position. Figure legend as per Fig. 3. (E) The $LSD_{0.05}$ bars are shown for the interaction between the factors time and treatment, where relevant. Error bars represent standard error, n = 3. Each replicate contained ten ('Keitt') or eight ('Kent') fruit. Figure legend as per Fig. 3.

or supporting its signalling may also mitigate the quality changes seen between cold-stored and control fruit. Additionally, strategies such as controlled atmosphere and graduated controlled atmosphere (Falagan et al., 2020), which have been shown to be effective for both climacteric and non-climacteric fruit, may further enhance fruit storability by delaying senescence, reducing oxidative stress, and preserving sensory and nutritional quality. However, the classical classification of fruits as climacteric or non-climacteric is being challenged. Earlier studies have described a third postharvest physiological behaviour referred to as suppressed climacteric metabolism, in which ripening related metabolic activity is temporarily inhibited under low temperature storage but resumes upon transfer to ambient conditions (Karagiannis, 2024). This phenomenon has been reported in stone fruits such as *Prunus domestica* 'Friar' plum, where cold storage suppresses respiratory and ethylene-associated processes that are subsequently reactivated during shelf life (Xu et al., 2023). A comparable pattern was observed in the two mango cultivars examined in the present study, in which key physiological and biochemical changes were minimal during cold storage but became pronounced following removal from low temperature. These similarities suggest that mango fruit may exhibit a suppressed climacteric like response under specific cold storage regimes, highlighting a reversible modulation of ripening metabolism rather than permanent cold-induced injury. Such behaviour underscores the importance of considering suppressed climacteric responses when interpreting postharvest physiological changes in tropical fruits subjected to cold storage.

Currently, the main method of quantifying mango ripeness and quality is through TSS. Previously, O'Brien et al. (2024) found that using the sum of mango individual sugars (i.e. the sum of the glucose, sucrose, and fructose content) outperformed TSS in predicting ripening and quality indices. As TSS is an optical density measurement, it includes all soluble solids, including non-sugars such as proteins and amino acids (Kusumiyati et al., 2020). In line with previous studies, we found a strong positive correlation between TSS and sugar content in control fruit (Munawar et al., 2013; Maraphum et al., 2022; Nordey et al., 2017; Pornprasit and Natwichai, 2013), reflecting the dominant contribution of sugars to TSS during normal ripening. By contrast, this relationship was absent in cold-stored fruit, likely due to metabolic disruptions caused by low temperature. Cold storage slows sugar metabolism but promotes the accumulation of other soluble compounds such as organic

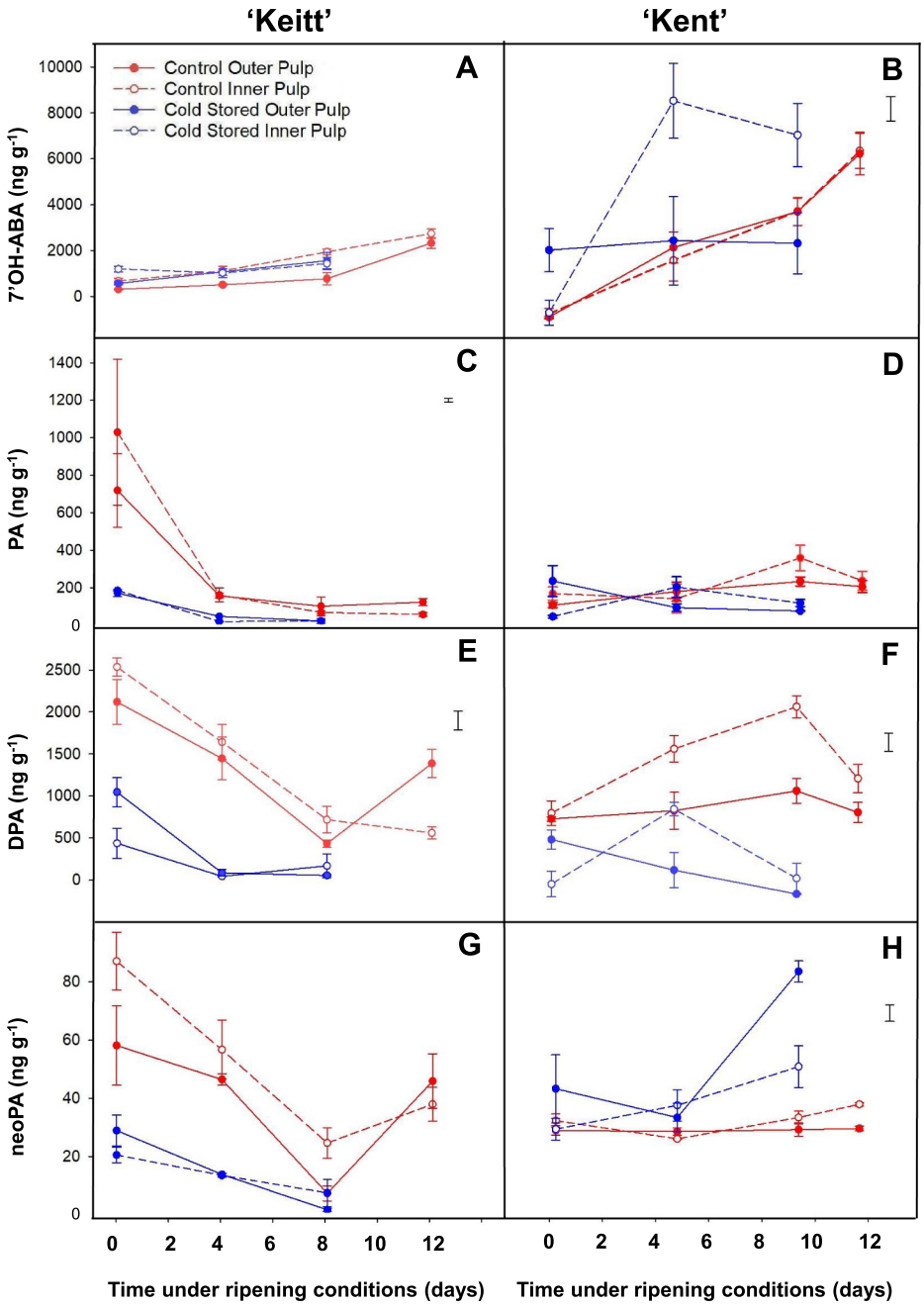

Fig. 7. Normalised gene expression patterns for the ethylene synthesis enzymes 1-aminocyclopropane-1-carboxylate synthase (ACS) 1 and 2, and ACC oxidase (ACO) in 'Keitt' mango pulp. All genes were normalised against Glyceraldehyde-3-phosphate dehydrogenase expression. Standalone Least Significant Difference ($LSD_{0.05}$) bars are shown for the interaction between pulp position and time. Error bars represent standard error, n = 3, with 10 fruit per replicate.

acids, amino acids, and stress-related proteins (Kusumiyati et al., 2020; Beckles, 2012), which also contribute to TSS. Additionally, chilling induced membrane damage may alter solute compartmentalisation, further decupling TSS from sugar levels (Harker et al., 2002; Hale et al., 2005; Beckles, 2012). Given the lack of correlation between TSS and the sugar content of the cold-stored mango fruit found in this study, TSS becomes a less reliable indicator of sweetness under cold storage conditions. Since TSS is widely used as a quality benchmark in non-tropical markets (Blasco et al., 2016; Cortés et al., 2017; O'Brien et al., 2024; OHF, personal communication), this reliance may contribute to misclassification, leading to unnecessary postharvest losses and potentially reducing the overall quality of fruit available to consumers. This finding highlights the need for alternative assessment criteria, for example, quality indices that integrate firmness, colour, and sweetness values (Blasco et al., 2016; Cortés et al., 2017; O'Brien et al., 2024).

5. Conclusions

Cold storage more than doubled the postharvest life of mango fruit by slowing the rate of firmness loss. This benefit allows time for long-distance transport, through which mango is primarily supplied to non-tropical markets. However, cold storage led to differences in colour and sugar profiles during ripening, which will affect consumer experience. The lack of correlation between sugar content and TSS in cold-stored fruit demonstrates that the postharvest management strategies developed for control fruit cannot be directly applied under cold storage conditions. A deeper understanding of the biochemical disruptions caused by chilling is therefore essential to reduce unnecessary losses in

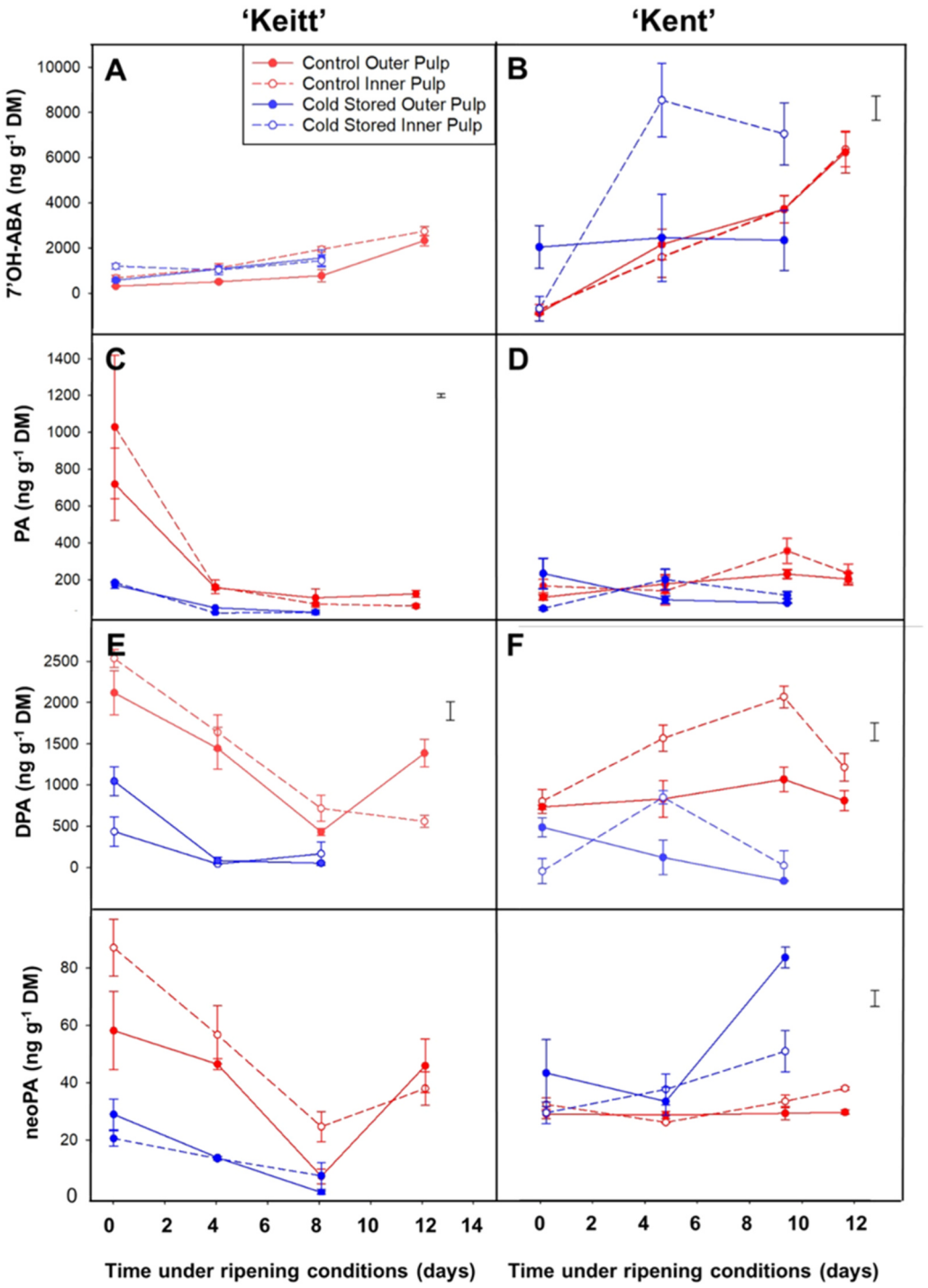

Fig. 8. Abscisic catabolites in control and cold stored mango fruit through ripening. Catabolites included are 7'OH-ABA, phaseic acid (PA), dihydro-PA (DPA), and neoPA. Least Standalone Significant Difference bars at $p < 0.05$ ($LSD_{0.05}$) are shown for the interaction between the factors pulp position and treatment, where relevant. Error bars represent standard error, n = 3. Each replicate contained ten ('Keitt') or eight ('Kent') fruit.

the food chain. Our findings indicate that ABA likely plays a central role in these differences, as ABA accumulated in the control fruit but declined in the cold-stored fruit during ripening, driven by shifts in its synthesis, sequestration, and catabolism.

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CRediT authorship contribution statement

Leon A. Terry: Writing – review & editing, Funding acquisition, Conceptualization. **Sofia Kourmpetli:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Natalia Falagán:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Ciara O'Brien:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M. Carmen Alamar:** Writing – review & editing, Supervision, Resources, Project

administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare no competing financial interests or personal relationships that could have influenced the work reported in this study.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.postharvbio.2026.114291.

Data availability

Data supporting this study are openly available from CORD at: https://doi.org/10.57996/cran.ceres-2796

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Cold storage extends mango postharvest life by modulating abscisic acid levels and sugar composition

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