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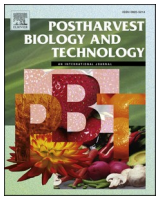

Molecular and metabolic response of 'Piccolo' cherry tomato to Graduated Controlled Atmosphere

Natalia Falagán *, Roberta Tosetti, Ewan Gage, Leon A. Terry

Plant Science Laboratory, Cranfield University, Bedfordshire MK43 0AL, UK

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ABSTRACT

Controlled atmosphere (CA) is used to extend the postharvest life of climacteric fruit by suppressing respiration and delaying ethylene mediated ripening. However, sudden exposure to low oxygen conditions can induce hypoxic stress, triggering metabolic and hormonal disruptions that negatively impact fruit quality. This study aimed to understand the mechanisms underlying ethylene sensitivity under low oxygen conditions through the application of a novel approach to CA, called Graduated Controlled Atmosphere (GCA), in 'Piccolo' cherry tomato. Compared to standard CA, GCA treatment resulted in greater suppression of respiration and improved firmness retention, indicating reduced physiological stress and slower cell wall degradation. Gene expression analysis revealed downregulation of *NCED1*, *ACS*, and *ACO* genes under GCA, indicating delayed ethylene-associated transcriptional activity. These hormonal adjustments were also reflected in lower abscisic acid (ABA) concentrations, implying a more stable ripening trajectory. Besides hormonal modulation, GCA-treated fruit exhibited alterations in primary metabolism. Sucrose accumulation and changes in malate levels under GCA conditions suggest a shift in energy metabolism, consistent with improved hypoxia tolerance. However, a notable trade-off was observed in reduced lycopene accumulation, potentially due to lower oxidative signalling and shared precursors between carotenoid and ABA biosynthesis. These findings demonstrate that GCA promotes a more controlled physiological and molecular response to hypoxic storage by reducing stress-associated metabolic and hormonal activity. GCA, as an advanced postharvest strategy, enhances texture retention and may reduce quality losses during storage. This work provides new mechanistic insights into hypoxia adaptation in fruit and supports the use of gradual atmosphere modification to optimise CA protocols.

1. Introduction

The plant hormone ethylene regulates key processes in climacteric fruit development, including changes in fruit colour, firmness, flavour, and aroma after harvest. Controlled atmosphere (CA) storage is widely used to extend shelf life by reducing fruit sensitivity to ethylene under low oxygen (O_2) conditions (Saltveit, 2016) and by suppressing ethylene production through inhibition of 1-aminoacyclopropane 1-carboxylate synthase (*ACS*), a key enzyme in ethylene biosynthesis, under elevated carbon dioxide (CO_2; Goldberg et al., 2017).

Tomatoes (*Solanum lycopersicum* L.) are climacteric and susceptible to chilling injury (Maharaj et al., 1999), which limits cold storage to 10 – 12 °C for 3 – 7 days. However, mature fruit can be stored for over a month under CA conditions with 3–5 kPa O_2 and 0–3 kPa CO_2 (Kader, 2002; Majidi et al., 2014). Despite these benefits, the sudden change from normal air atmosphere to a CA environment can trigger fruit stress responses, negatively impacting quality. For example, under hypoxic conditions, declines in the cellular adenylate energy state trigger widespread physiological disruptions and activate adaptive metabolic pathways to minimise the risk of internal anoxia (Eerdekens et al., 2025). These adaptations include activation of alternative respiratory pathways to minimise the risk of internal anoxia (Fatima et al., 2025). When severe anoxic stress occurs, further damage may develop upon re-exposure to air after storage, accelerating quality loss (Wood et al., 2022). Cherry tomato fruit can exhibit clear phenotypic responses to stress, including reduced fruit size and weight, delayed or uneven ripening, and altered colour intensity due to disruptions in carotenoid accumulation. Also, Fruit can also show changes in sugar–acid balance, accumulation of antioxidant compounds and shifts in texture and ripening rate, reflecting metabolic reprogramming to maintain cellular homeostasis (Durán-Soria et al., 2020).

Hypoxic stress under CA may also disrupt abscisic acid (ABA)

* Corresponding author.
E-mail address: natalia.falagan@cranfield.ac.uk (N. Falagán).

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signalling, with adaptative responses often associated with reductions in ABA levels (González-Guzmán et al., 2021). ABA interacts with ethylene during ripening to regulate processes such as cell wall degradation and the metabolism of volatiles and pigments (Kou et al., 2021). Thus, the rapid onset of CA conditions can cause physiological perturbations that affect fruit quality maintenance. However, knowledge gaps remain regarding how fruit perceive and physiologically respond to CA, limiting the optimisation of storage strategies. As an alternative to conventional CA treatment, we hypothesise that a graduated CA (GCA) approach can minimise risks of adverse physiological reactions as the fruit can progressively adapt to the new storage environment (Falagán et al., 2020). This study aims to investigate the physiological and molecular responses of cherry tomato fruit to CA and GCA storage, providing deeper insight into postharvest CA management and enhancing the application of CA and modified atmosphere packaging (MAP) to improve the quality of fresh produce.

2. Material and methods

2.1. Plant material

Ripe cherry tomatoes on vine (*S. lycopersicum* cv. Piccolo) grown commercially in Kent (A Pearson Growers Ltd. Canterbury, UK) were harvested across two consecutive seasons (21 April for Experiment 1 [year 1] and 17 June for Experiment 2 [year 2]). Trusses were c. 15 cm in length and pruned to 9 fruit per truss. Samples were transported directly to Cranfield University, UK, immediately after harvest within 3 h at 10 ºC. For both experiments, tomatoes were then graded for uniform red colour and absence of physical damage and transferred to the storage rooms at 10 ºC and 90–95 relative humidity (RH%).

2.2. Experimental set up

GCA treatments were applied as described in Falagán et al. (2020). For both experiments, forty-eight 12 L air-tight polypropylene boxes (L&L Nordic OÜ, Estonia) were used to store 2.5 kg of sound fruit each. They were kept in a cold room at 10 ºC and 90–95 RH%. Four treatments were considered: i) control, flushed with regular atmosphere gas concentrations (20.9 kPa O_2 and 0.03 kPa CO_2); ii) standard CA (3 kPa O_2 and 3 kPa CO_2); iii) graduated CA 3 (GCA3) flushed to reach the standard CA partial pressures in 3 days; and iv) GCA7 gradually flushed to reach the traditional CA conditions in 7 days (Fig. 1). For each CA condition, boxes were connected to an ICA6000 (International Controlled Atmosphere Ltd., Paddock Wood, Kent, UK) via PVC tubes. For each treatment, an extra empty box was used as a baseline to avoid cross contamination and allow respirometry calculations.

Sampling was carried out in triplicate on storage days 0, 7, 14, 21, and 28 during the first season for physical parameters and during the second season for biochemical parameters, tomatoes were sampled for transcriptomics analysis every 6 h during the first week of storage to better investigate the impact of each treatment on tomato physiology. The selection of the first week of storage for detailed analysis was based on the results obtained during the first season.

For each season, whole fruit (pericarp and seeds) were collected from each treatment/replicate at each sampling point. Ten fruit were halved before snap freezing in liquid nitrogen prior to storage at −80 °C. For biochemical analysis, snap-frozen fruit were freeze dried in darkness at −52 °C (Scanvac, Lynge, Denmark) before powdering and storage at −40 °C and −80° C. Results are reported as dry weight (DW).

2.3. Experiment 1

2.3.1. Physical quality

2.3.1.1. Respiration rate. Real-time respiration rate was recorded continuously and in situ (10 °C) using a Sable Respirometry System (model 1.3.8 Pro, Sable Systems International, Nevada, USA) as described in Alamar et al. (2017) with slight modifications. Air from each box passed through a CA-10 (Firmware version 1.05) and a FC-10 (Firmware version 3.0), which record CO_2 and O_2 pressures (kPa), respectively. For each treatment, an empty box was used as a baseline. These baseline boxes were sampled for 2 min between each replicate and for 6 min between each treatment to avoid cross-contamination. Baseline values were subtracted from sample values to obtain an accurate respiration rate expressed in mg CO_2 kg^{-1} s^{-1}. O_2 concentration was not measured directly; however, given the fixed headspace volume and the low permeability of the storage system, decreases in O_2 are stoichiometrically coupled to CO_2 accumulation under these conditions. Therefore, the recorded CO_2 values allow reliable inference of O_2 dynamics.

2.3.1.2. Firmness. Textural changes were examined for phenotypic indicators of stress as disruption of cellular energy balance and membrane integrity can accelerate softening under low oxygen conditions. A non-destructive compression test was performed on five fruit per replicate using a uniaxial texture analyser (model 5542, Instron, Norwood, USA) equipped with a 38 mm diameter flat steel disc and a calibrated 500 N load cell. Tomatoes were compressed by 2 mm, equatorially, at a rate of

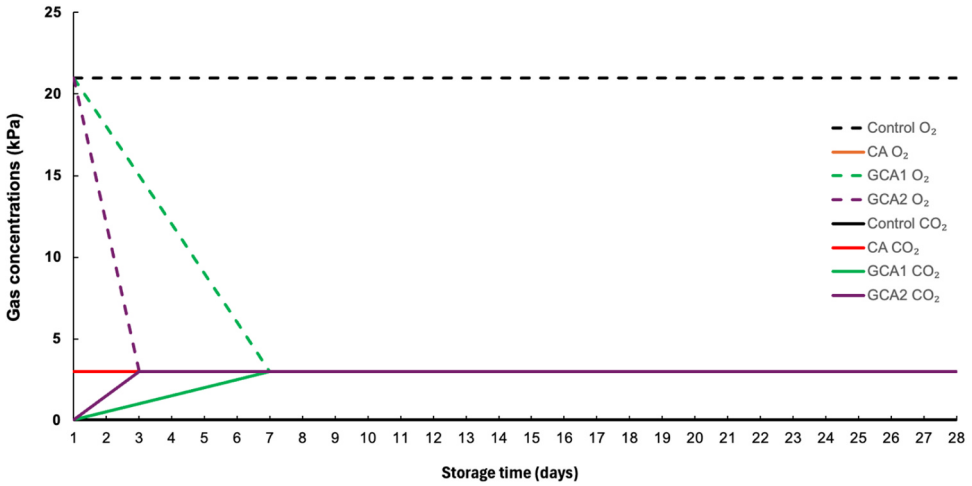


Fig. 1. Gas concentration [carbon dioxide (CO_2) and oxygen (O_2); kPa] supply throughout 28 days of storage at 10 °C and 90–95 % relative humidity; air (control); standard CA (3 kPa CO_2 + 3 kPa O_2); graduated CA 7 (GCA7; 7 days to achieve standard CA values); and GCA3 (3 days to achieve standard CA values).

1.2 mm s^{-1} according to Chope et al. (2006) with modifications. The peak force necessary to achieve the target distance was recorded. Firmness was expressed as Newton (N).

2.3.1.3. Decay incidence. Advancement of microbial decay was used as an indicator of low oxygen stress as hypoxic conditions can increase vulnerability to pathogenic activity. Fruit presenting fungal development, leakage, or collapse were considered as decayed. Decay was assessed on fifty cherry tomatoes per replicate and results were expressed as percentages based on Amoah et al. (2016). Decay severity was evaluated using a scale, where 1 = 0 %, 2 = 1–25 %, 3 = 26–50 %, 4 = 51–75 %, and 5 = 76–100 % of the decayed fruit. Fruit were counted and a percentage was attributed to each level of the scale.

2.3.1.4. Weight loss. Weight loss was used as an indicator of stress physiology. Weight was recorded weekly using a digital balance (Precisa Ltd., Bucks., UK) with 0.1 g accuracy. Weight loss was expressed as the percentage of loss compared to the initial weight (Amoah et al., 2016).

2.3.1.5. Chemical composition. The juice of five cherry tomato per replicate was extracted using a commercial blender (Moulinex, Berkshire, United Kingdom). pH was recorded using a pH-meter (model 3540, Jenway, Staffordshire, United Kingdom). Total soluble solids were determined using a digital refractometer (model PR-32α, Atago Ltd., Tokyo, Japan). Tritatable acidity was determined by titrating a solution of 5 mL of juice diluted in 45 mL of distilled water to pH 8.4 using 0.1 N NaOH and an automatic titrator (Mettler Toledo Ltd., Leicestershire, UK), according to Falagán et al. (2018) with slight modifications. Results were expressed as g citric acid L^{-1} (Falagán et al., 2020).

2.3.2. Biochemical analysis

2.3.2.1. Lycopene. Freeze-dried tomato powder (200 ± 0.5 mg) was extracted following the low volume hexane extraction method (LVHEM) established by Fish et al. (2002). Then, the samples were homogenised with 5 mL of 0.05 % (w/v) butylated hydroxytoluene (BHT) in acetone, 5 mL of 95 % USP grade ethanol, and 10 mL of hexane. Samples were extracted for 15 min on ice. After, 3 mL of deionized water was added to each vial and vortexed for an additional 5 min on ice. Finally, the vials were allowed to reach room temperature for 5 min to complete separation. The extract was measured in a 1 cm path length quartz cuvette at 503 nm blanked with hexane in a Camspec M501 UV/vis spectrophotometer (Camspec Ltd., Cambs., UK) according to Davis et al. (2003).

2.3.2.2. Organic acids. For each replicate, following Crespo et al. (2010) with modifications, freeze-dried cherry tomato powder (50 mg) was mixed with 3 mL of 3 % aqueous metaphosphoric acid, placed in an ice bath for 10 min, and vortexed for 30 s every 5 min. The mixture was then centrifuged (Haraeus Labofuge 400 R, Thermo Fisher Sientific, Leics, UK) at 8000 *g* at 4 °C during 10 min and passed through a 0.2 µm filter. An HPLC (Agilent Technologies 1200 series, Berks., UK) equipped with a diode array detector (DAD Agilent Technologies 1200 Series, G1315B) set at 210 nm was used to quantify ascorbic and citric acids (Sigma Aldrich, Kent, UK). Separation was performed on Prevail organic acid column of 250 mm× 4.6 mm, 5 µm particle size (Hichrom, Berks UK; Part no. 88645). Mobile phase was 25 mM KH_2PO_4 in water, adjusted to pH 2.5 using meta-phosphoric acid. Organics acids were eluted at 0.02 mL s^{-1} flow rate, at 35 °C.

2.3.3. Experiment 2

2.3.3.1. Individual sugars. For each replicate, following Downes and Terry (2010) with modifications, freeze-dried tomato powder (150 ± 0.5 mg) was mixed with 3 mL of HPLC grade methanol:water (62.5:37.5, v/v) solution, and placed in a low speed shaking water bath at 55 ºC for 15 min. Then, the samples were passed through a 0.2 µm filter. An HPLC (Agilent Technologies 1200 series, Berks., UK) with an evaporative light scattering detector (ELSD, Agilent Technologies 1200 Series, G1362A) was used to quantify sugar extracts (20 µL). Separation was performed on a Prevail Carbohydrate ES column of 250 mm× 4.6 mm diameter, 5 µm particle size (Alltech, UK; Part no. 35101) with a Prevail Carbohydrate ES guard cartridge of 7.5 mm × 4.6 mm diameter (Alltech; Part no. 96435). Mobile phase was composed of solvent A (water) and B (acetonitrile). Elution was performed at 0.02 mL s^{-1} flow rate, at 30 °C, as follow: 80 % B at 0 min, 50 % at 15 min, 50 % at 18 min and 80 % at 20 min. Sugars were quantified using the external standards: glucose, fructose and sucrose (Sigma-Aldrich Co., UK).

2.3.3.2. Plant growth regulators. Freeze-dried powdered cherry tomato material (5.0 ± 0.1 mg) was weighed and extracted with 500 µL of an ice-cold HPLC grade methanol:water:formic acid (60:35:5 v/v) after Alamar et al. (2020) with modifications. The labelled form of [$^2H_4$]-abscisic acid (-)-5,8'8'8'- (d4-ABA) was added to the mixture as an internal standard. Endogenous ABA was quantified according to Morris et al. (2019) with slight modifications, using a LC/MS-MS instrument with an Agilent 1200 series HPLC system (Agilent, Berks., UK) coupled to a Q-Trap 6500 mass spectrometer (AB Sciex, Framingham, USA). The extracts were analysed injecting 20 µL onto a Phenomenex 3 µm C18 Luna 100 × 2 mm with guard column at 40 ºC. The mobile phases were: (A) 2 % acetonitrile in 2 mM ammonium formate, and (B) 95 % acetonitrile in water with 0.1 % formic acid, using an increasing gradient of B (2 % for 4 min, 16 % at 20 min and 34.5 % at 25 min) at a flow rate of 3.3 µL s^{-1}.

2.3.3.3. RNA isolation and next generation sequencing. RNA from samples collected during the first week in Experiment 2 were extracted from circa 25 ± 1.5 mg freeze dried material (whole cherry tomato) with the Qiagen RNeasy Plant Mini Kit (Qiagen, Germany) and treated with column DNaseI (Qiagen) following the manufacturer's instructions. RNA quantity and integrity were evaluated with a Genova Nanodrop (Jenway, UK) and with gel electrophoresis respectively. Between 3 and 5 µg of good quality total RNA were shipped in dry ice to Novogene (Beijing, China) for the RNAseq service (including library preparation), and relative bioinformatics analysis. Libraries were prepared using NEBNext® Ultra™ RNA Library Prep Kit for Illumina® (USA) following manufacturer's recommendations and the sequencing was performed on an Illumina Hiseq platform (125 bp/150 bp paired end reads). Raw data (raw reads) of fastq format were processed through a Novogene-built perl scripts. Trimmed reads were mapped against the tomato reference 'ITAG2.3_cdna' (http://solgenomics.net/) using Bowtie v2.2.3 and TopHat v2.0.12. HTSeq v0.6.1 was used to count the reads numbers mapped to each gene and generate the FPKM values. Details of bioinformatic analysis are given in Supplementary Information 1. Genes belonging to pathways of interest (ethylene, sugars, ABA) were selected and extracted. The impact of the storage strategy on their expression was evaluated and reported as FPKM values.

2.4. Statistics

2.4.1. Statistical analysis of physical and biochemical parameters

Statistical analyses were carried out using GenStat for Windows, Version 14 (VSN International Ltd., Herts., UK). Analysis of variance (ANOVA) was used to identify significant differences ($p < 0.05$) between the main factors and their interactions. The assumptions of ANOVA (normality, homogeneity of variances, and independence) were evaluated prior to analysis and were met. Least Significant Differences (LSD) bars are displayed on all graphs.

2.4.2. Statistical analysis of transcriptomic data

To evaluate the statistical differences in gene expression levels, the ANOVA was performed on relative expression values (fpkm) with Statistica software v12. The analysis of Differential Expressed (DE) genes (BH adjusted p-value < 0.05) was performed by Novogene with the DESeq R package (1.18.0), while GOseq R package was used for the GO enrichment analysis.

3. Results

3.1. Physiological response to Graduated Controlled Atmosphere

Tomatoes subjected to GCA showed a delayed respiration rate peak with respect to CA and thereafter reached a lower steady state respiration rate, compared to control and CA fruit (Fig. 2).

The three CA strategies halved the weight loss of 'Piccolo' tomatoes from day 0 when compared to control, especially GCA3 up to day 21 (Fig. 3A). Firmness values displayed a sharp decline in all treatments during the first week of storage, while in the following weeks only control fruit exhibited a significant loss of firmness (Fig. 3B). Decay incidence was almost non-existent in samples subjected to GCA7 and GCA3 (below 3 % after 28 d). Control tomatoes were highly affected by *Penicillium* and *Rhizopus spp.* growth (Fig. 3C and D). Regarding taste parameters, no significant differences were found in total soluble solids, titratable acidity and pH among treatments across the experiments (data not shown).

3.2. Biochemical and molecular responses linked to Graduated Controlled Atmosphere

The contents of glucose and fructose remained stable throughout the experiment in all cases. However, sucrose concentration gradually increased during storage in tomatoes subjected to either of the CA strategies, reaching levels three times higher than the initial values, while control fruit maintained consistent sucrose levels (Fig. 4).

The expression profiles of the two sucrose synthase genes (SuSy3, Solyc07g042550, and SuSy4, Solyc09g098590) showed opposite responses to the CA treatments, with SuSy4 being downregulated. In contrast, the expression of SuSy3 was strongly upregulated following the CA treatments, with treated fruit exhibiting a 2- to 4-fold higher transcript abundance than untreated fruit. The increase in SuSy3 expression was proportional to the severity of the CA treatment, with the greatest upregulation observed under CA, and a reduced response under GCA (Fig. 5).

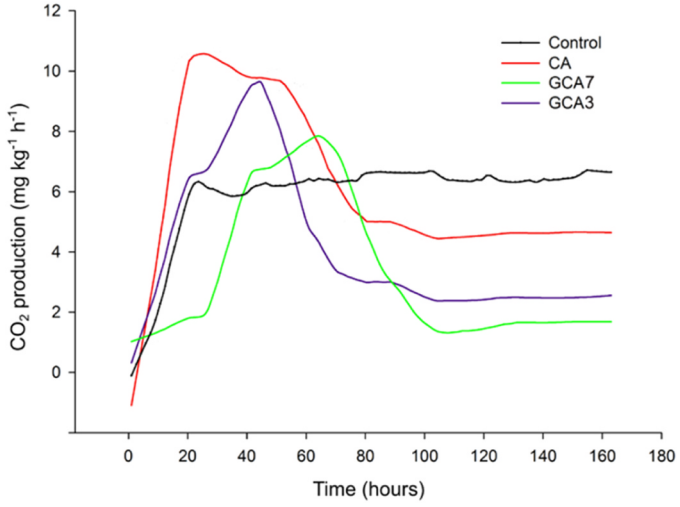


Fig. 2. Real-time respiration rate [carbon dioxide (CO_2) production expressed as mg kg^{-1} h^{-1}] of 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 28 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Lines represent smooth fit curves.

Lycopene content increased with storage under air increasing by 115 % by 28 d (Fig. 6). This rise was reduced by CA treatment, with reduced lycopene accumulation with less severe onset of CA conditions. Lycopene increased 59 % under CA compared with 35 % and 15 % under GCA7 and GCA3, respectively.

No significant differences according to time, treatment, or their interaction were observed for succinic, citric, ascorbic, glutamic, shikimic, and quinic acids (data not shown). However, malic acid concentration exhibited a significant response to treatment. Specifically, malate levels showed a marked reduction under CA conditions by 7 d compared with the control (Fig. 7). The GCA3 treatment also resulted in a decrease in malate concentration, albeit delayed until 14 d, while GCA3 maintained malate levels comparable to the control until 21 d. This decline in malate concentration correlates with changes in fruit firmness and aligns with transcriptomic data highlighting differential expression of genes related to malate metabolism and cell wall modification under CA treatments. Regarding tartaric acid, all three CA storage regimes induced an increase in its concentration over time, in contrast to control tomatoes which maintained stable tartaric acid levels (Fig. 7).

CA treatment gave an initial spike in ABA accumulation for 24 h, followed by a rapid decline, which was maintained for the remainder of the experiment compared with the relative stability in control fruit (Fig. 8). GCA treatment prevented the initial ABA spike and promoted a rapid reduction in ABA accumulation. From day 14 onward, ABA content in both GCA treatments did not differ significantly from the CA treatment and was approximately tenfold lower than that of the control.

Expression of genes associated with ABA metabolism were differentially affected by CA conditions (Fig. 9). ABA biosynthesis was generally downgraded with CA treatment, particularly *Psy1/Psy2* (Solyc03g031860.2/Solyc02g081330.2), and of *NCED* (Solyc07g056570.1/Solyc08g016720.1), which showed the greatest downregulation. Promoted oxidation of abscisic aldehyde to ABA was seen in later CA treatment through upregulation of *AO3/AAO* (Solyc11g071600.1/Solyc11g071620.1) on day 3 and day 7, although this coincided with substantial upregulation of ABA breakdown through promotion of abscisic acid 8' hydroxylase (Solyc10g083790.1). The onset of gene expression changes was earlier and of greater magnitude in CA treated fruit compared with GCA. For example, *NCED1* expression showed large scale reductions on day 2 in CA treated fruit, whilst down regulation was not demonstrated in GCA treated fruit until day 2 (GCA3) and d7 (GCA7; Fig. 10).

With respect to genes related to ethylene biosynthesis, 1-aminocyclopropane-1-carboxylic synthase genes *ACS4* (Solyc05g050010) and *ACS6* (Solyc08g008100) exhibited opposite responses to GCA conditions. *ACS4* was markedly downregulated by CA conditions (regardless of the O_2 levels), while *ACS6* expression was induced by CAs. In control fruit *ACS4* decline was not as marked and *ACS6* expression was kept at steady levels (Fig. 11). The expression of *ACO1* (Solyc07g049530) was strongly downregulated by the application of GCA conditions. 1-aminocyclopropane-1-carboxylic oxidase expression (*ACO1*) showed a transient upregulation during the first two days of storage in the treatments with $O_2 > 10$ %, while below 10 % (O_2) *ACO1* expression was downregulated (Fig. 11).

4. Discussion

4.1. GCA induces enhanced metabolic adaptation to hypoxia stress

The transition from ambient air into refrigerated CA storage with low O_2 availability in a matter of hours limits the time for adaptive responses to chilling and hypoxia. This abrupt shift can impair the ability of fruit to maintain quality. Under CA conditions, hypoxic stress reduces the

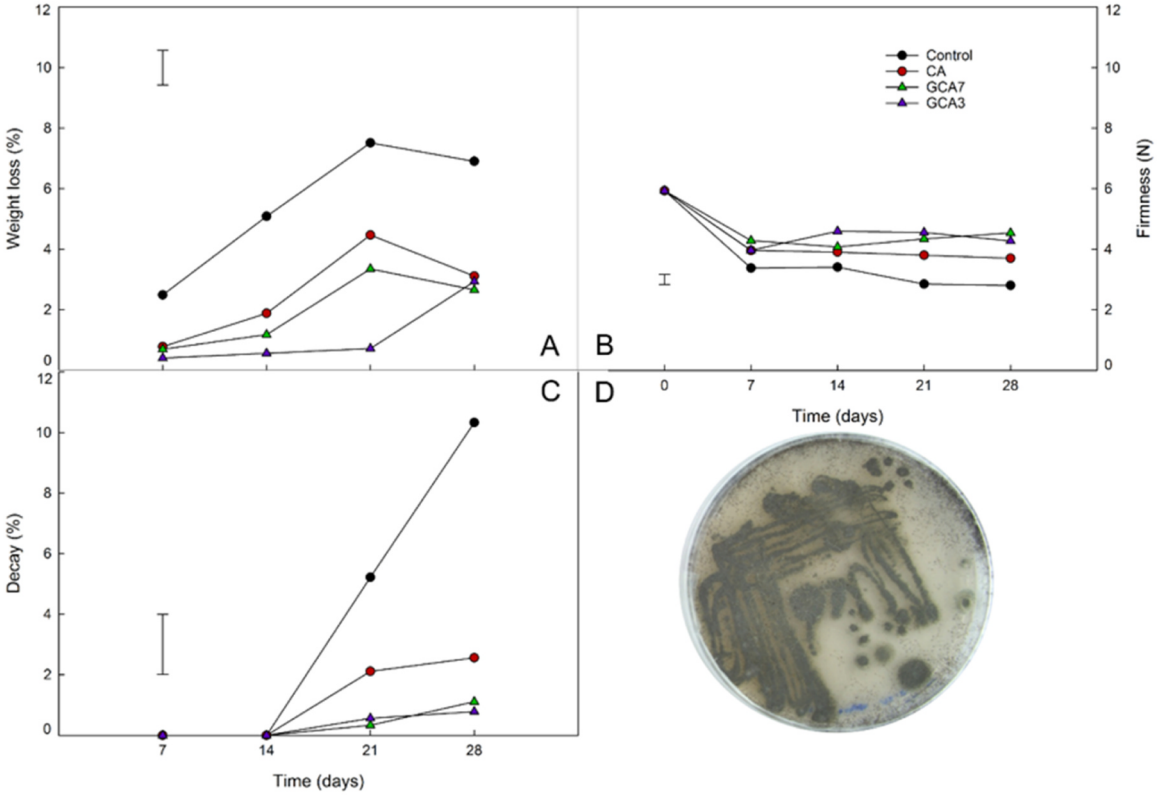


Fig. 3. Weight loss (A; %), firmness (B; Newton; N), and decay (C; %) of 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 28 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Data represent means of ten replicates (n = 10 ± SE) for firmness, and 80 replicates (n = 80 ± SE) for weight loss and decay. $LSD_{0.05}$ bar for the interaction treatment * time point is shown. The graph includes a Petri plate with positive results for *Penicillium spp.* and *Rhizopus spp.* found in decayed samples (D).

adenylate energy charge of cells by limiting aerobic mitochondrial respiration, thereby promoting reliance on alternative respiratory pathways such as glycolysis (Blokhina et al., 2003). Simultaneously, non-essential metabolic processes are downregulated to reduce energy consumption (Geigenberger, 2003). For example, tomato fruit stored under CA conditions exhibited reduced activity of pigment biosynthesis and cell wall degrading enzymes (Sozzi et al., 1999). In addition to providing insights into metabolic processes, the monitored quality attributes also constitute phenotypic indicators of mild hypoxia stress. Low O_2 conditions reduce the cellular energy charge and compromise membrane integrity, which in turn promote texture softening and susceptibility to opportunistic pathogens (Mustafa et al., 2025). Therefore, the greater retention of firmness and reduced decay under GCA treatments not only reflects delayed senescence, but also demonstrates improved tolerance to hypoxia compared with the abrupt transition imposed by conventional CA.

Our results show that GCA conditions enhance metabolic adaptation to hypoxic stress, particularly under the GCA7 regime compared to the sudden onset of standard CA. This is evidenced by the progressively lower respiration rate achieved under GCA3 and GCA7, indicating more effective suppression of metabolic activity and/or improved energy efficiency.

Hypoxic conditions can weaken the TCA cycle, resulting in the accumulation of certain intermediates (Mustroph et al., 2014). In our study, the decline in malate levels observed in CA and GCA3 treated fruit suggests TCA cycle disruption; however, this effect was mitigated in GCA7 fruit, which maintained malate concentrations similar to the Control. Under hypoxia, malate can be consumed as an alternative respiratory substrate and contributes to cytosolic pH stabilisation (Mandal et al., 2022). Thus, the accelerated malate decline under CA and GCA3 may reflect adaptive metabolic adjustments rather than solely loss of TCA intermediates.

Further evidence of improved metabolic adjustment under GCA7 is seen in the progressive increase in sucrose content and the reduced expression of *SuSy3* compared to CA treatment. Under hypoxia, sucrose metabolism often shifts from invertase to sucrose synthase (*SuSy*)-mediated pathways (Geigenberger et al., 2003), with increased *SuSy3* expression and altered sucrose profiles indicating metabolic adjustment (Zhu et al., 2013). The reduced *SuSy3* expression in GCA7 fruit, along with the sustained sucrose levels, suggests reduced hypoxic stress due to improved metabolic adaptation. Beyond serving as a metabolic reserve, sucrose acts as a signalling molecule regulating stress tolerance and senescence-associated gene expression. Thus, sucrose accumulation under CA and GCA may also contribute to improved hypoxia adaptation through signalling mechanisms in addition to energy conservation.

Although *SuSy4* expression was uniformly downregulated under CA treatment, this isoform is predominantly localised to phloem companion cells in *Arabidopsis* (Yao et al., 2020), possibly indicating that its reduced expression reflects decreased sucrose translocation rather than a direct metabolic adjustment, as is the case for *SuSy3*.

Active starch degradation has been reported under chilling induced conditions respiratory stress (Albornoz et al., 2019). The enhanced maintenance of sucrose in GCA7 treated fruit likely demonstrates better conservation of carbohydrate reserves, facilitated by reduced respiration. This also correlates with the observed reduction in weight loss under GCA7 treatment.

These findings suggest that a gradual onset of CA conditions via GCA enables an adaptative metabolic response, facilitating energy conservation through downregulation of respiration and improved resource use. Lower respiration rates under hypoxia have been associated with

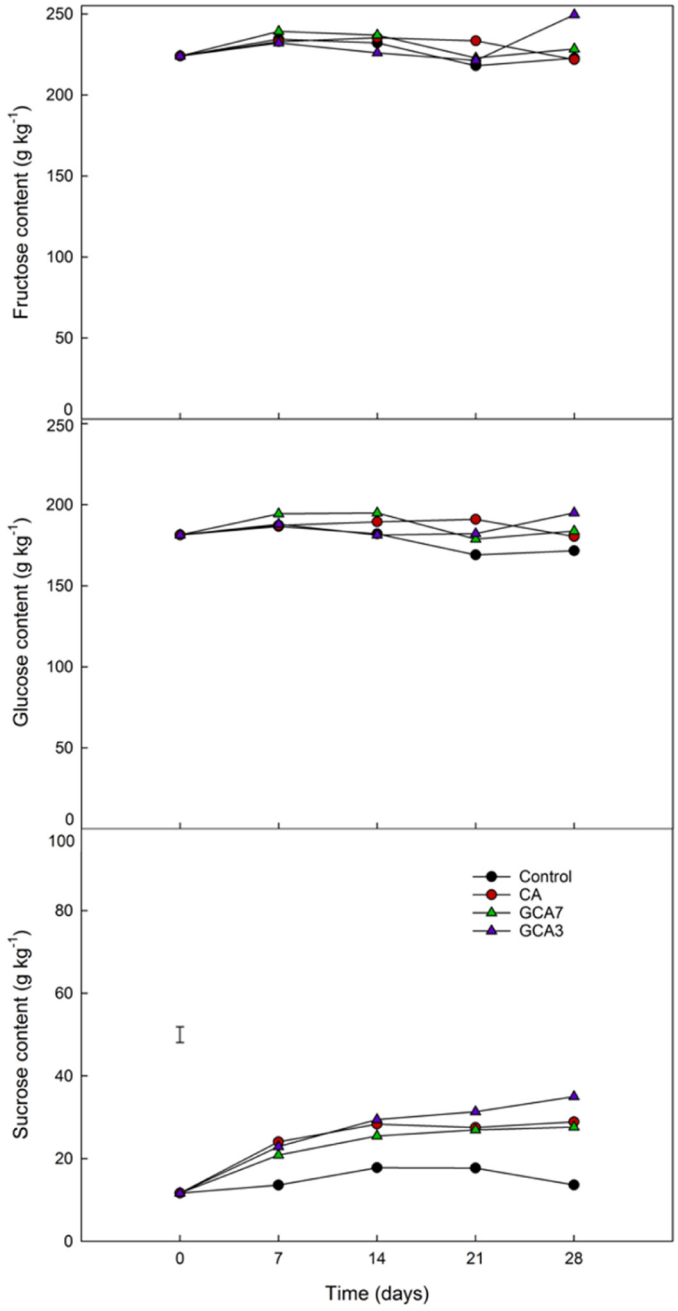


Fig. 4. Fructose, glucose, and sucrose content (g kg^{-1} dry weight) of 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 28 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Data represent means of three replicates (n = 3 ± SE). $LSD_{0.05}$ bar for treatment and time point is shown regarding sucrose results.

enhanced stress tolerance due to minimised metabolic demand. The improved hypoxia tolerance observed under GCA further suggests that fruit experience reduced stress compared to sudden CA transitions.

The observed decline in malate under CA treatments coincided with changes in fruit firmness, consistent with its role in cell wall metabolism. Malate contributes to cell wall structure and participates in pathways associated with cell wall remodelling, and the early reduction in malate under CA may reflect enhanced cell wall modification leading to softening. Conversely, the stability of malate levels in GCA3 until 21 d suggests that this treatment may help maintain cell wall integrity,

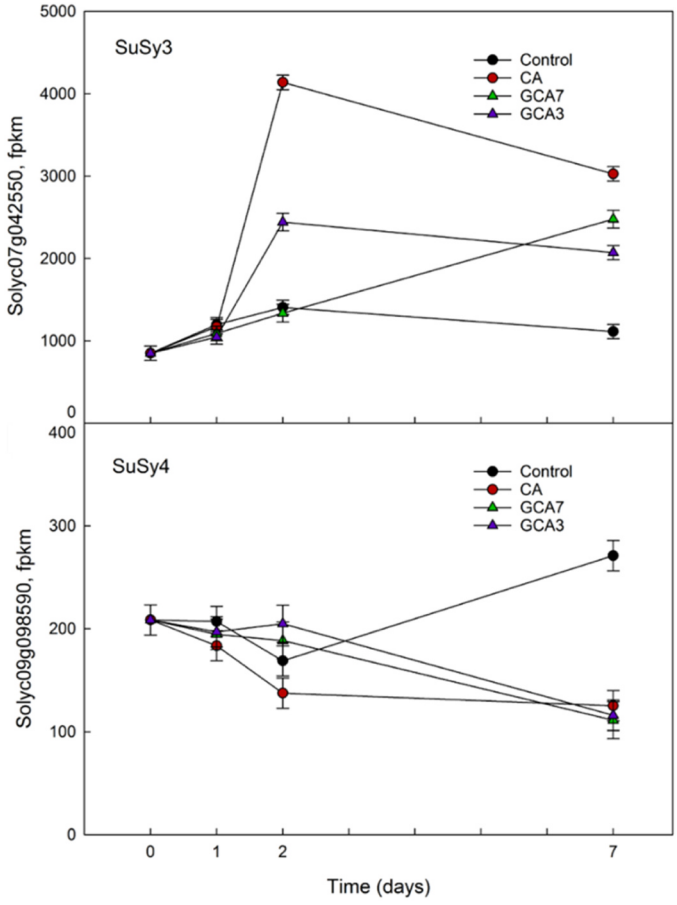


Fig. 5. Relative expression (fpkm) values of *SuSy3* (top) and *SuSy4* (bottom) in 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 7 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Data represent means of three replicates (n = 3 ± SE).

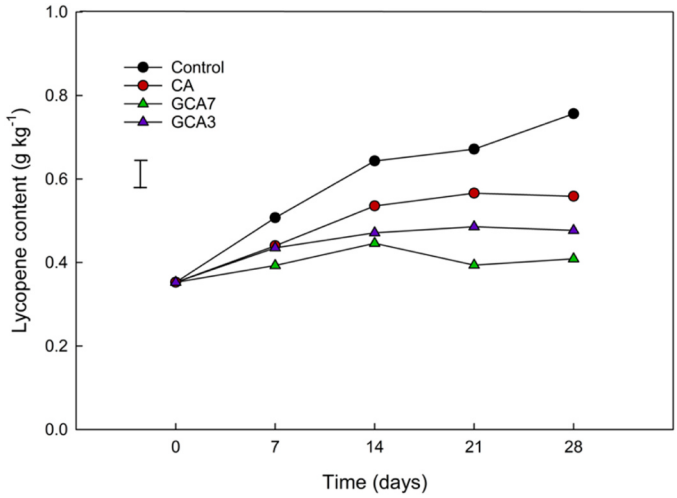


Fig. 6. Lycopene content (g kg^{-1} dry weight) of 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 28 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Data represent means of three replicates (n = 3 ± SE). $LSD_{0.05}$ bar for treatment and time point is shown.

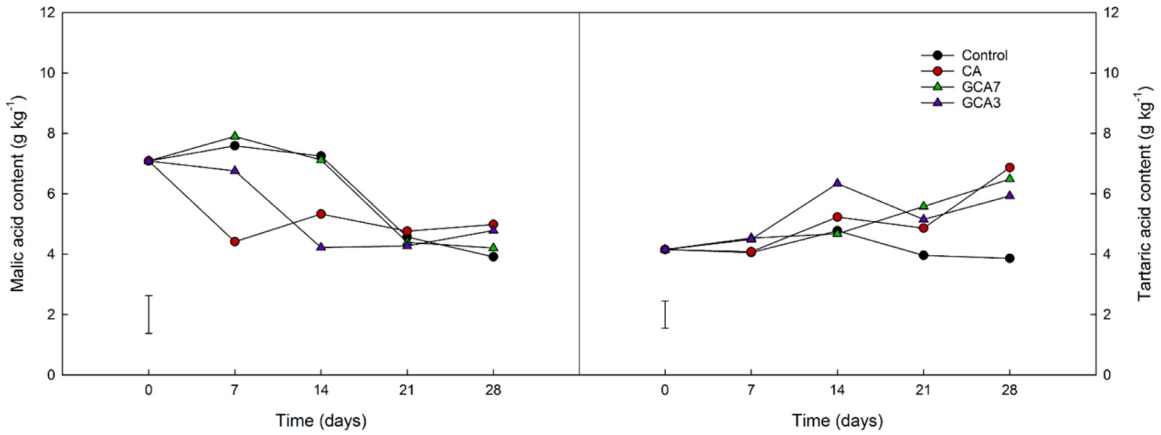


Fig. 7. Tartaric and malic acid contents (g kg^{-1} dry weight) of 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 28 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Data represent means of three replicates (n = 3 ± SE). $LSD_{0.05}$ bar for treatment and time point is shown.

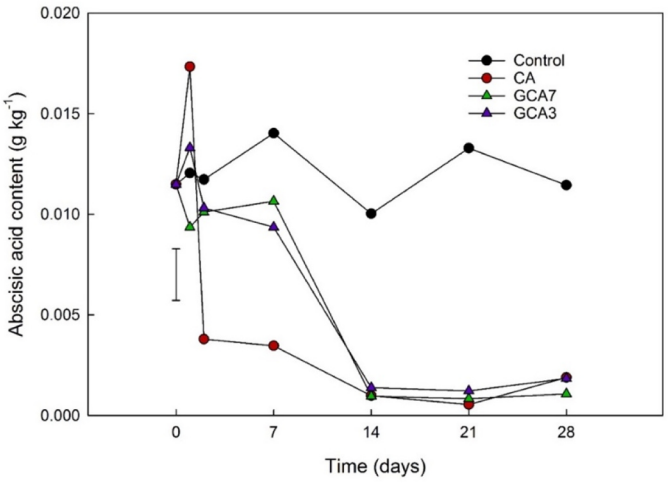


Fig. 8. Abscisic acid (g kg^{-1} dry weight) of 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 28 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Data represent means of three replicates (n = 3 ± SE). $LSD_{0.05}$ bar for treatment and time point is shown.

contributing to the preservation of firmness.

Interestingly, tartaric acid exhibited the opposite trend, increasing under all CA treatments while remaining stable in control fruits. Although tartaric acid metabolism is not well characterised in tomato, its accumulation may reflect shifts in organic acid flux related to redox balance or secondary metabolism under CA storage. The differential behaviour of malate and tartaric acid highlights potential interactions between primary and secondary metabolic pathways during storage and suggests that changes in organic acid metabolism may contribute to both structural and physiological adaptations under low oxygen conditions. These interpretations remain speculative but provide a basis for future investigations.

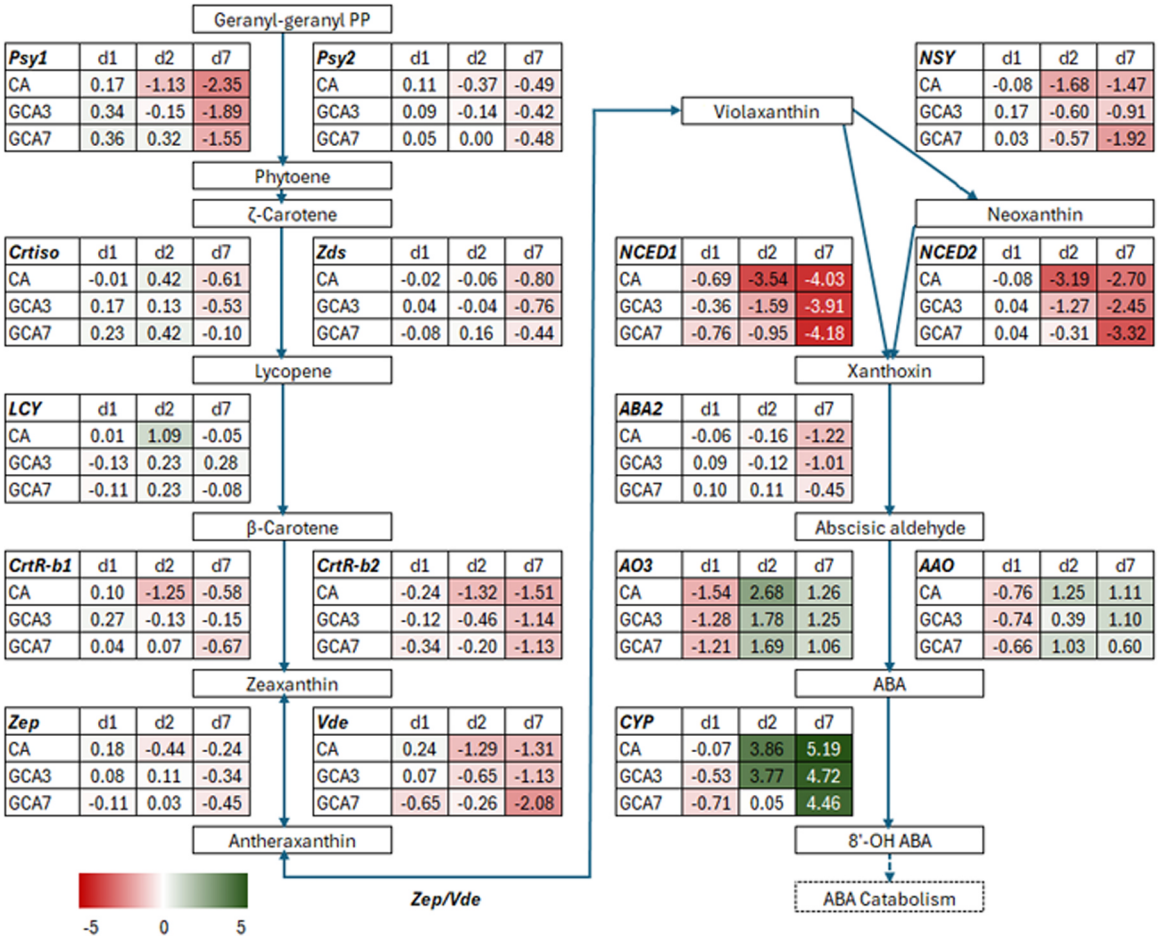
4.2. Hypoxia-induced ABA and ethylene pathway modulation under GCA treatment

The alleviation of hypoxic stress under GCA treatment is also evident in changes to hormonal regulation. Rapid declines in ABA typically occur at the onset of hypoxic stress, primarily due to reduced ABA biosynthesis via downregulation of *NCED* and increased ABA catabolism (González-Guzmán et al., 2021; Wang et al., 2021). Both instances are seen in the present study with widespread downregulation of ABA biosynthesis, and promotion of catabolic abscisic acid 8′-hydroxylase under CA. The onset of expression changes also correlated with the timing of CA application, such as the delayed reduction of *NCED* expression with GCA7 treatment. *NCED* encodes a key enzyme in the ABA biosynthesis pathway, catalysing carotenoid cleavage (Iqbal et al., 2017). Lowered ABA synthesis was also attributable to reductions in activity of the wider carotenoid biosynthesis pathway as demonstrated by down regulation of *Psy1/Psy2*, corresponding with the observed reduction in both lycopene and ABA accumulation with CA treatment. A key outcome of this study is the identification of a clear trade-off associated with GCA storage. While GCA treatment effectively extended shelf-life by maintaining firmness, reducing weight loss, and suppressing respiration, it was accompanied by a reduction in lycopene accumulation. This suggests that although GCA mitigates physiological stress and slows ripening, it may partially compromise certain aspects of nutritional quality. Such trade-offs are commonly observed in postharvest research, reflecting the balance between preserving structural integrity and maintaining the accumulation of bioactive compounds. Future optimization of GCA protocols should aim to identify conditions that maximize the benefits to fruit texture and shelf-life while minimising impacts on nutritional quality, providing an integrated approach to postharvest management.

The degree of ABA suppression and *NCED1* downregulation correlated with the severity of CA onset, with the smallest change observed in GCA7. This result suggests that the gradual application of CA conditions under GCA7 mitigated hypoxic stress by allowing greater physiological adaptation.

ABA is also known to promote ethylene biosynthesis (Zhang et al., 2009). Therefore, the ABA reductions observed under CA and GCA may have contributed to the decreased expression of ethylene biosynthetic genes, as reflected by the downregulation of *ACS4* and *ACO1*. In addition, high CO_2 levels have been reported to suppress ethylene biosynthesis, including downregulation of *ACS4* under elevated CO_2 (Park et al., 2021), and are consistent with our observations. The concurrent reduction in *ACO1* expression may reflect a downstream bottleneck in ethylene synthesis, possibly contributing to the maintenance of fruit quality by limiting ethylene activity. The absence of significant differences in *ACS6* and *ACO1* expression among CA and GCA treatments by day 7 after full CA implementation implies that this inhibition may be more strongly influenced by CO_2 levels than by respiratory suppression.

Besides fruit development and ripening, ethylene also plays a role in hypoxic stress responses (Hartman et al., 2021; González-Guzmán et al., 2021). In *Arabidopsis*, *ACS* genes are upregulated under hypoxia, which



Symbol	ITAG Gene ID	KEGG ID	Gene
Psy1	Solyc03g031860.2	543988	phytoene synthase 1
Psy2	Solyc02g081330.2	543964	phytoene synthase 2
Crtiso	Solyc10g081650.1	101267857	prolycopene isomerase
Zds	Solyc01g097810.2	543629	zeta-carotene desaturase
LCY	Solyc10g079480.1	101267662	lycopene beta cyclase
CrtR-b1	Solyc06g036260.2	544133	beta-carotene hydroxylase
CrtR-b2	Solyc03g007960.2	544297	beta-carotene hydroxylase
Zep	Solyc02g090890.2	544162	zeaxanthin epoxidase

Symbol	ITAG Gene ID	KEGG ID	Gene
Vde	Solyc04g050930.2	543696	violaxanthin de-epoxidase
NSY	Solyc06g074240.1	543649	neoxanthin synthase
NCED1	Solyc07g056570.1	544163	9-cis-epoxycarotenoid dioxygenase
NCED2	Solyc08g016720.1	100316877	9-cis-epoxycarotenoid dioxygenase
ABA2	Solyc04g071940.2	101254297	xanthoxin dehydrogenase
AO3	Solyc11g071600.1	543652	abscisic-aldehyde oxidase
AAO	Solyc11g071620.1	543650	abscisic-aldehyde oxidase
CYP	Solyc10g083790.1	101249565	abscisic acid 8'-hydroxylase CYP707A1

Fig. 9. Expression of abscisic acid (ABA) metabolism genes in 'Piccolo' cherry tomato subject to controlled atmosphere (CA) applications throughout 28 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Expression values are log_2-transformed CA-treatment (CA, GCA3, GCA7) to control expression values ($n = 3$).

may explain the observed induction of *ACS6* in our study. However, GCA treatment delayed the onset of hypoxic stress, in agreement with other metabolic indicators discussed earlier.

Despite the upregulation of *ACS6*, its contribution to ethylene biosynthesis may be limited due to the concurrently reduced *ACO1* expression. Given that *ACO* activity is suggested to be the rate limiting step for ethylene production in post-climacteric tomato fruit (Houben and Van de Poel, 2019), the inhibition of *ACO1* may suppress overall ethylene output. *ACO1* expression declined under CA and GCA3, while slight increases were observed under GCA7. This may imply that alleviation of stress under GCA conditions permits partial recovery of ethylene biosynthesis capacity.

Our results demonstrate that CA and GCA treatments significantly affect the hormonal regulatory networks underlying ripening and senescence. While hypoxia-induced ABA suppression has been previously attributed to negative regulation by ethylene (Wang et al., 2021), our results suggest that ABA reduction can occur independently of ethylene signalling, similar to findings by Müller et al. (2021). This suggests that hypoxia responses in fruit may be modulated differently due to the central role that ethylene plays in ripening regulation. Further research is needed to clarify the interactions between these hormonal pathways and their contribution to hypoxia responses under CA storage (Boeckx et al., 2019).

It should also be noted that ethylene concentration was not monitored due to storage system constraints. Although this limitation does not affect the interpretation of our metabolic and hormonal findings, they should be considered when comparing this study to experiments that directly quantify internal ethylene production. The scope of this work was physiology-centred, with molecular markers included to support interpretation of stress responses rather than to provide exhaustive pathway or metabolomics analysis. Accordingly, transcriptomic data are used here to contextualise respiration, firmness and hormonal trends, not to map complete metabolic networks. Future studies incorporating real-time ethylene measurements during storage

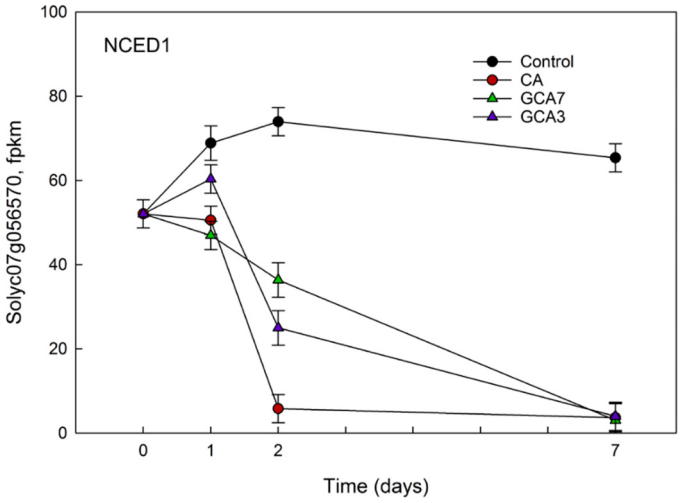


Fig. 10. Relative expression (fpkm) values of *NCED1* in 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 7 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Data represent means of three replicates (n = 3 ± SE).

will be essential to validate whether transcriptional changes translate to modified ethylene production and to further clarify the regulatory effects of gradual atmosphere establishment on ethylene metabolism.

4.3. Metabolic and hormonal modulation under GCA influences ripening and quality outcomes

In addition to coordinating responses to stress, both ABA and ethylene play key regulatory roles in ripening and fruit development (Kou et al., 2021). Therefore, the observed reduction in both hormone pathways under CA and GCA treatments may contribute to fruit quality preservation not only through metabolic suppression but also via regulatory control. This is reflected in the differential effects on GCA treatment on quality parameters.

Beyond reducing weight loss, GCA treatment was particularly beneficial in maintaining fruit firmness, with the highest firmness retention observed under the least severe CA imposition. The relationship between ABA concentration and textural degradation is noteworthy in this context. Reduced ABA accumulation has been linked with delayed softening; for instance, *NCED* deficient mutants exhibit improved firmness due to altered cell wall composition (Wang and Seymour, 2022). ABA responsive *ABA-Stress-Ripening* transcription factors are known to promote cell wall disassembly by upregulating carbohydrate hydrolases during ripening (Jia et al., 2016). However, despite the more rapid reduction in ABA levels under abrupt CA treatment, this did not translate into improved firmness. In contrast, GCA treatments, which showed more gradual ABA decline, exhibited greater firmness retention. This suggests that the observed effects on texture are likely independent on ABA mediated pathways and instead arise from the greater overall metabolic suppression achieved with GCA, which may reduce the activity of cell wall degrading enzymes. We acknowledge that direct evidence linking metabolic suppression to cell wall stability is lacking. Future studies should investigate the activity and gene expression of key cell wall–modifying enzymes, such as polygalacturonase and pectin methylesterase, to directly confirm the molecular mechanisms underlying slowed cell wall degradation under GCA.

While GCA improved texture retention, it negatively affected nutritional quality, particularly in terms of lycopene content. Lycopene accumulation was lower under GCA compared to both CA and control

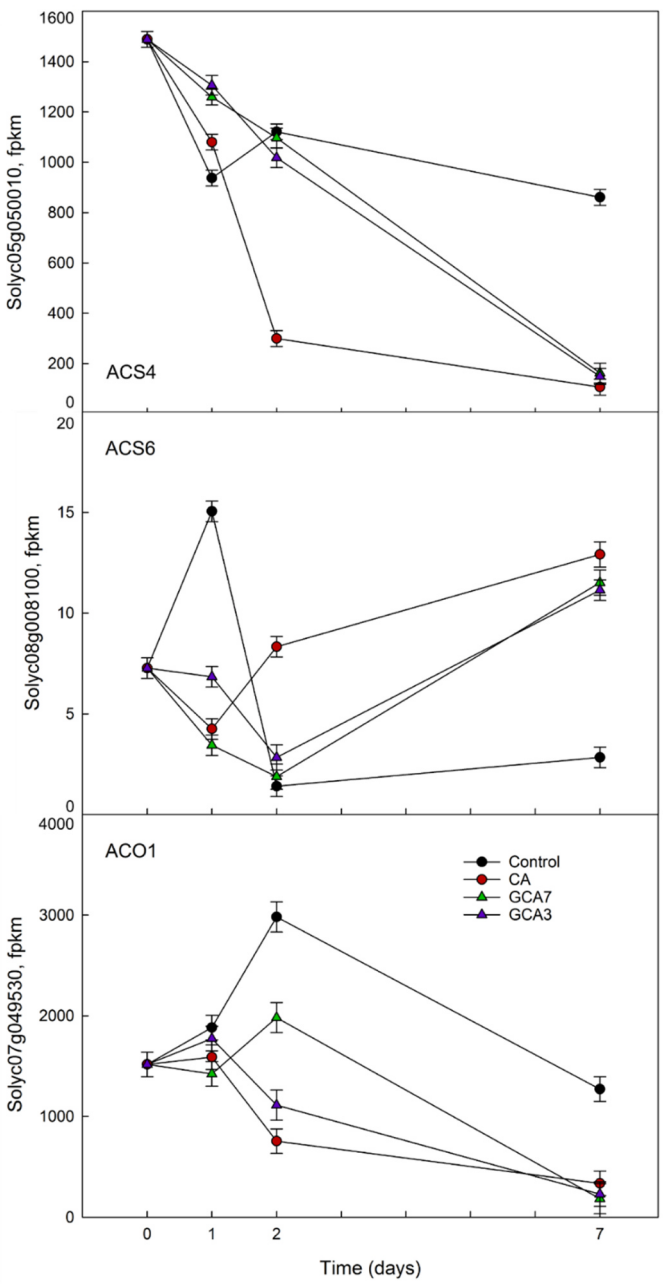


Fig. 11. Relative expression (fpkm) values of *ACS4* (top), *ACS6* (middle), and *ACO1* (bottom) in 'Piccolo' cherry tomato subjected to controlled atmosphere (CA) applications throughout 7 d of storage at 10 °C and 90 % relative humidity; air (control); traditional CA (3 kPa CO_2 + 3 kPa O_2); gradual CA 7 (GCA7; 7 d to achieve traditional CA values); and GCA3 (3 d to achieve traditional CA values). Data represent means of three replicates (n = 3 ± SE).

treatments. Previous studies have reported reduced lycopene biosynthesis under low O_2 concentrations during CA storage (Domínguez et al., 2016), and the current results indicate a similar trend, where lower respiration rates under GCA correspond with reduced lycopene accumulation. This may be a direct consequence of enhanced metabolic suppression under GCA, which could inhibit carotenoid biosynthesis during storage.

Alternatively, lycopene accumulation has also been associated with oxidative stress responses (Pan et al., 2009; Bravo et al., 2012), which may be alleviated under GCA treatment, leading to reduced biosynthesis. Disruption of the TCA cycle can stimulate mitochondrial ROS production (Decros et al., 2019), and CA conditions have been shown to

suppress ROS formation (Mditshwa et al., 2017). Therefore, the further reduction in respiration under GCA may enhance ROS homeostasis, thereby reducing stress-induced lycopene production. In addition, suppression of ethylene and ABA under CA and GCA may further limit lycopene biosynthesis, given the shared carotenoid precursors pathways between ABA and lycopene (Su et al., 2015; Kou et al., 2021).

Although GCA7 provided the greatest retention of marketable quality in 'Piccolo' tomato, further research is required to clarify the broader implications of GCA on fruit quality. Modified CA strategies can significantly alter volatile profiles (Brizzolara et al., 2017), and the increased metabolic suppression seen under GCA may be detrimental to flavour profile development of stored fruit. Furthermore, varietal differences in response to CA have been widely reported (Brizzolara et al., 2017), highlighting the need to validate these findings across other tomato cultivars, particularly those more susceptible to postharvest softening.

It is also important to note that this study focused on fully ripe fruit, in which postharvest quality decline is primarily driven by senescence rather than ripening. Since the development stage of the fruit influences its responsiveness to CA (Batu, 2003), GCA may elicit different effects in earlier harvest stages. For example, malate metabolism during climacteric ripening (Batista-Silva et al., 2018) could be affected, particularly in light of the GCA induced changes to TCA cycle activity observed in this study. Maturity stage plays a critical role in postharvest physiology and in the responsiveness of fruit to CA and GCA, and therefore the outcomes reported here primarily apply to late-ripened fruit. Earlier maturity stages differ in metabolic plasticity and hormonal regulation, and their response to gradual atmosphere establishment may not mirror the patterns observed in ripe fruit. Future investigations should therefore evaluate GCA performance across multiple ripening stages to determine its broader applicability.

5. Conclusions

Our results demonstrate that CA storage has a profound impact on both the physiological and regulatory responses of tomato fruit to hypoxic stress. Reduced oxygen availability suppresses respiration and metabolic activity, contributing to the conservation of fruit quality during storage. The use of a GCA, particularly over a seven-day period, enabled a more adaptive transition into hypoxia, resulting in lower respiration rates, improved energy management, and reduced indicators of stress compared to conventional controlled atmosphere. Overall, this study provides new insight into the metabolic and hormonal mechanisms underpinning hypoxia responses in fully ripe cherry tomato, demonstrating that the method of CA application plays a critical role in shaping postharvest physiology. These findings offer a strong foundation for refining CA protocols to optimise quality, and open new avenues for exploring hormone–stress interactions in fleshy fruit under low oxygen storage.

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CRediT authorship contribution statement

Natalia Falagán: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Roberta Tosetti:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ewan Gage:** Writing – review & editing, Formal analysis. **Leon A. Terry:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of Competing Interest

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

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.postharvbio.2025.114133.

Data availability

The underlying data can be accessed at https://doi.org/10.57996/cran.ceres-2808.

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Falagán, Natalia; Tosetti, Roberta; Gage, Ewan; Terry, Leon A.

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