

Soluble solids content-based fruit maturity affects postharvest fruit quality by mediating metabolic alterations in cold-stored ‘Autumn Sense’ hardy kiwifruit

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ABSTRACT

This study evaluated the impact of soluble solids content (SSC)-based maturity on fruit quality and non-targeted metabolite profiles of cold-stored ‘Autumn Sense’ hardy kiwifruit. Noticeable alteration of glycolysis, the tricarboxylic acid cycle, and the amino acid and fatty acid pathways were observed during vine maturation of fruit. The branched-chain and aromatic amino acids were enriched at early harvest (5.7 % SSC), whereas pyruvate metabolism and unsaturated fatty acid biosynthesis were upregulated at late harvest (7.9 % SSC) during cold storage. These metabolic shifts were related to either incomplete ripening in early-harvested fruit or enhanced physiological disorders in late-harvested fruit. Our findings provide the first evidence that SSC-based harvest maturity mediates postharvest hardy kiwifruit quality through specific metabolic pathways. This study suggested that fruit with approximately 7 % SSC exhibited the most balanced metabolic profile and postharvest quality, suggesting this range as a preliminary optimal harvest maturity stage for ‘Autumn Sense’ hardy kiwifruit.

1. Introduction

The popularity of kiwifruit (*Actinidia* spp.), including green, golden, and red varieties, has increased due to its significant health-beneficial effects and activities (Bursal & Gülçin, 2011; Chang & Liu, 2009; Collins, Horská, Hotten, Riddoch, & Collins, 2001; Hwang et al., 2017; Prior et al., 2007). Among various *Actinidia* spp., hardy kiwifruit [*Actinidia arguta* (Sieb. & Zucc.) Planch. ex Miq.] has garnered attention for its morphological characteristics, such as its smooth, thin, edible skin and small fruit size (Fisk, McDaniel, Strik, & Zhao, 2006; Park, Kim, Kim, Han, & Lee, 2022). Despite its convenience for distribution and consumption, the edible peel of hardy kiwifruit is prone to shriveling and bruising, which can reduce fruit quality during storage or distribution (Lim et al., 2016; Park et al., 2024). Several practical approaches have been actively applied to maintain the postharvest performance of kiwifruit to alleviate the incidence of quality deterioration during cold storage and improve shelf life. These include pre-storage cooling, storage temperature, and ethylene exposure (Choi, Baek, Cheol, Jeong, & Tilahun, 2022; Gwanpua, Zhao, Jabbar, Bronlund, & East, 2022; Lim,

Lee, & Lee, 2017; Manning et al., 2016; Sfakiotakis, Chlioumis, & Gerasopoulos, 2005). Postharvest ethylene treatment has been shown to reduce fruit decay rates and ensure sufficient ripening in cold-stored hardy kiwifruit (Oh, Kim, & Kim, 2014), thereby retaining fruit quality after cold storage (Cha, Kumarihami, Kim, Kwack, & Kim, 2019). Additionally, fruit maturity at harvest can be employed as another strategy to mitigate quality deterioration during cold storage (Choi et al., 2019; Manning et al., 2016). However, there is limited research on the effect of fruit maturity on the physiological and biochemical responses of hardy kiwifruit quality attributes during cold storage.

Hardy kiwifruit is typically harvested in a mature but firm state, after which it softens and develops other quality attributes until it reaches an edible stage for consumers (Fisk, McDaniel, et al., 2006). However, accurately determining the harvest maturity of green-coloured hardy kiwifruit has proven challenging. Typically, various methods are used to determine the harvest maturity of several fruits in commercial orchards, including soluble solids content (SSC) (Burdon, Pidakala, Martin, Billing, & Boldingh, 2016), starch pattern index (SPI) (Brookfield, Murphy, Harker, & MacRae, 1997), dry matter content (DMC) (Burdon

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et al., 2004), fruit colour (López Camelo & Gómez, 2004), fruit size, and SSC to titratable acidity (TA) ratio (Rivera, Kerckhoffs, Sofkova-Bobcheva, Hutchins, & East, 2022). Since the peel colour of hardy kiwifruit does not change during vine maturation, fruit colour cannot be considered a relevant indicator for maturity. Furthermore, a previous study demonstrated that the SPI test is unsuitable as a proxy for harvest maturity indicators in hardy kiwifruit (Fisk, Zhao, & Strik, 2006). Rather, for hardy kiwifruit, using the SSC values at harvest is considered important for determining harvest maturity. Several previous studies evaluated the effects of SSC-based maturity on fruit quality after ethylene treatment, ambient storage, cold storage, or controlled atmosphere (CA) storage (Fisk, McDaniel, Strik and Zhao, 2006; Han, Park, Kim, Kim, & Lee, 2019; Latocha, Krupa, Jankowski, & Radzanowska, 2014; Park et al., 2022). Harvest indexes ranging from 6.2 % SSC to 7–9 % SSC have been employed for kiwifruit, depending on its usage, and a 6.2 % SSC has been suggested to be at the initiation of the conversion process from starch to sugar and/or import of soluble carbohydrates (Burdon et al., 2016; Walsh, McGlone, & Han, 2020). However, hardy kiwifruit harvested at 6 % SSC fails to achieve adequate sugar levels, even after ripening (Han et al., 2019). This indicates that a 6 % SSC might be inadequate for the ideal harvest maturity of hardy kiwifruit. Thus, it is highly recommended to harvest the fruit when SSC is above 8 % rather than 6 % (Fisk, McDaniel, et al., 2006; Han et al., 2019). However, a 1 % difference in SSC value at harvest leads to distinctive fruit sweetness and sourness in ripened hardy kiwifruit (Park et al., 2022). Therefore, as fruit quality greatly depends on fruit maturity, optimal harvest maturity should be evaluated using more detailed criteria than previous studies to predict precise final fruit quality.

After harvest, the levels of starch, a major carbohydrate, markedly decrease in cold-stored kiwifruit along with a reduction in flesh firmness. Meanwhile, the levels of neutral soluble carbohydrates and SSC gradually increase (Arpaia, Labavitch, Greve, & Kader, 1987; MacRae, Lallu, Searle, & Bowen, 1989; Park, 2009; Wang et al., 2021; Wegrzyn & MacRae, 1995). The reduction in starch levels is highly associated with the high activity of α -amylase in cold-stored kiwifruit (Wegrzyn and MacRae, 1995), contributing to increased levels of reducing sugars during cold storage (Park, 2009). Its content decreases as starch is converted into major soluble carbohydrates, including glucose, fructose, and sucrose. In contrast, the levels of these soluble carbohydrates increase in both ambient-stored and cold-stored kiwifruit (*A. chinensis* 'Jinyan') (Mao et al., 2023; Xiong, Sun, Tian, Xu, & Jiang, 2023). Furthermore, the levels of major organic acids, such as citric, quinic, and malic acids, slowly decline after harvest (MacRae et al., 1989) and during cold storage in kiwifruit (Amodio, Colelli, Hasey, & Kader, 2007; Barboni, Cannac, & Chiaramonti, 2010). The levels of saturated fatty acids (SFA), such as palmitic and stearic acids, slowly decline, while those of unsaturated fatty acids (UFA), such as oleic and linoleic acids, gradually increase in cold-stored 'Hayward' kiwifruit, leading an increased UFA/SFA ratio (Antunes & Sfakiotakis, 2008). In contrast, the responses of individual fatty acids and the UFA/SFA ratio decrease in cold-stored 'Hongyang' kiwifruit (Yang, Wang, & Rao, 2016).

Advanced state-of-the-art analytical technologies, including gas chromatography–mass spectrometry (GC–MS) and liquid chromatography–mass spectrometry (LC–MS), have been exponentially developed and applied to understand the biochemical mechanisms of various fruits after harvest and during cold storage. A GC–MS/LC–MS-based untargeted metabolomics approach has been used to elucidate fruit ripening-related biochemical mechanisms and their integrated metabolomics profiling in kiwifruit (Lim et al., 2017), mangosteen (Mamat, Azizan, Baharum, Noor, & Aizat, 2020), and avocados (Pedreschi et al., 2014). Furthermore, several studies tried to identify unknown metabolites or biomarkers that may be associated with physiological disorders in various fruits. These include superficial scald in cold-stored 'Granny Smith' apples (Leisso, Buchanan, Lee, Mattheis, & Rudell, 2013; Rudell, Mattheis, & Hertog, 2009), soggy breakdown in cold-stored 'Honeycrisp' apples (Leisso et al., 2015; Leisso et al., 2016),

and firm flesh browning in CA-stored 'Empire' apples (Lee, Leisso, Rudell, & Watkins, 2022; Lee, Rudell, Davies, & Watkins, 2012), which were analysed using GC–MS and LC–MS technologies. Nevertheless, none of the untargeted metabolomics studies focused on determining the optimal harvest maturity to store 'Autumn Sense' hardy kiwifruit at low storage temperature. Previous studies have described postharvest quality changes or ethylene responses; however, the underlying metabolic alterations related to SSC-based maturity remain to be fully elucidated.

Therefore, in this study, we tested the hypothesis that the SSC-based fruit maturity at harvest could directly affect overall fruit quality by mediating metabolic alterations during cold storage. By integrating physiological measurements with untargeted GC–MS/MS-based metabolomics, this study provides a comprehensive understanding of how harvest maturity influences the biochemical processes responsible for fruit ripening and the incidence of physiological disorders in cold-stored 'Autumn Sense' hardy kiwifruit. The findings will contribute to establishing a more precise SSC-based harvest maturity index for commercial production and quality management of hardy kiwifruit, thereby improving storability and reducing postharvest losses.

2. Materials and methods

2.1. Plant material and storage conditions

Fruits of the hardy kiwifruit 'Autumn Sense' cultivar were cultivated at a commercial orchard (37° 27' 7" N, 127° 53' 18" E) in Wonju, Gangwon-do, Republic of Korea. The fruits were harvested on September 3, 13, and 23, 2021, corresponding to 100, 110, and 120 days after full bloom. The firmness of fruits at each harvest was 33.7 ± 0.4 , 25.4 ± 2.4 , and 24.6 ± 0.7 N and SSC values were 5.7 ± 0.1 , 6.9 ± 0.6 , and 7.9 ± 0.2 %, respectively. Following the harvest, fruit without defects were chosen at random to ensure they were of the same size. These selected fruits were then stored at 3 °C with a relative humidity of 95 % for up to 8 weeks.

2.2. Fruit quality attributes

The quality attributes of the fruit were evaluated at the time of harvest, after 2, 4, 6, and 8 weeks of cold storage, using four replicates ($n = 4$) with five fruits per replicate. Fruit weight loss (FWL) was determined by subtracting the weight of the fruit at harvest with its weight after a 2 h incubation at 22 °C following cold storage and expressing this difference as a percentage (Lwin, Leisso, & Lee, 2023). Flesh firmness of 20 fruits was determined using a rheometer (CR-3000EX-S, Sun Scientific Co., Tokyo, Japan) with a 5-mm flat probe, compressing each fruit by 5 mm depth at a rate of 10 mm s^{-1} . The maximum force results were expressed in Newtons (Park et al., 2022). Peel colour variables, including lightness (L^*), chroma (C^*), and hue angle (h°), were measured twice on the equatorial region of individual fruits using a chromameter (CR-300, Minolta Co., Tokyo, Japan) (Lee et al., 2022; Lwin et al., 2023). After cold storage, physiological disorders, including shriveling, peel browning, peel pitting, and decay, were evaluated using a subjective scoring system ranging from 0 to 5, with each score corresponding to the percentage of the affected area of the total fruit surface. The scoring system was defined as follows: 0 = 0 %, 1 = 1–10 %, 2 = 11–25 %, 3 = 26–50 %, 4 = 51–75 %, and 5 = 76–100 % (Byeon et al., 2023). Overall disorder symptoms were evaluated with three trained evaluators that independently conducted the assessments, and the mean of their scores was used in subsequent analyses. SSC and TA were measured using freshly extracted juice from a juicer (HY-UBF11B, Hurom Co., Gimhae, Korea). The SSC was quantified using a digital refractometer (PAL-1, Atago Co., Tokyo, Japan) and expressed as a percentage (%). The TA was measured using an automated titration system (EasyPlus Titrator, Mettler-Toledo, LLC, Columbus, OH, USA) by titrating 0.1 M NaOH until reaching a pH endpoint of 8.2. Results were

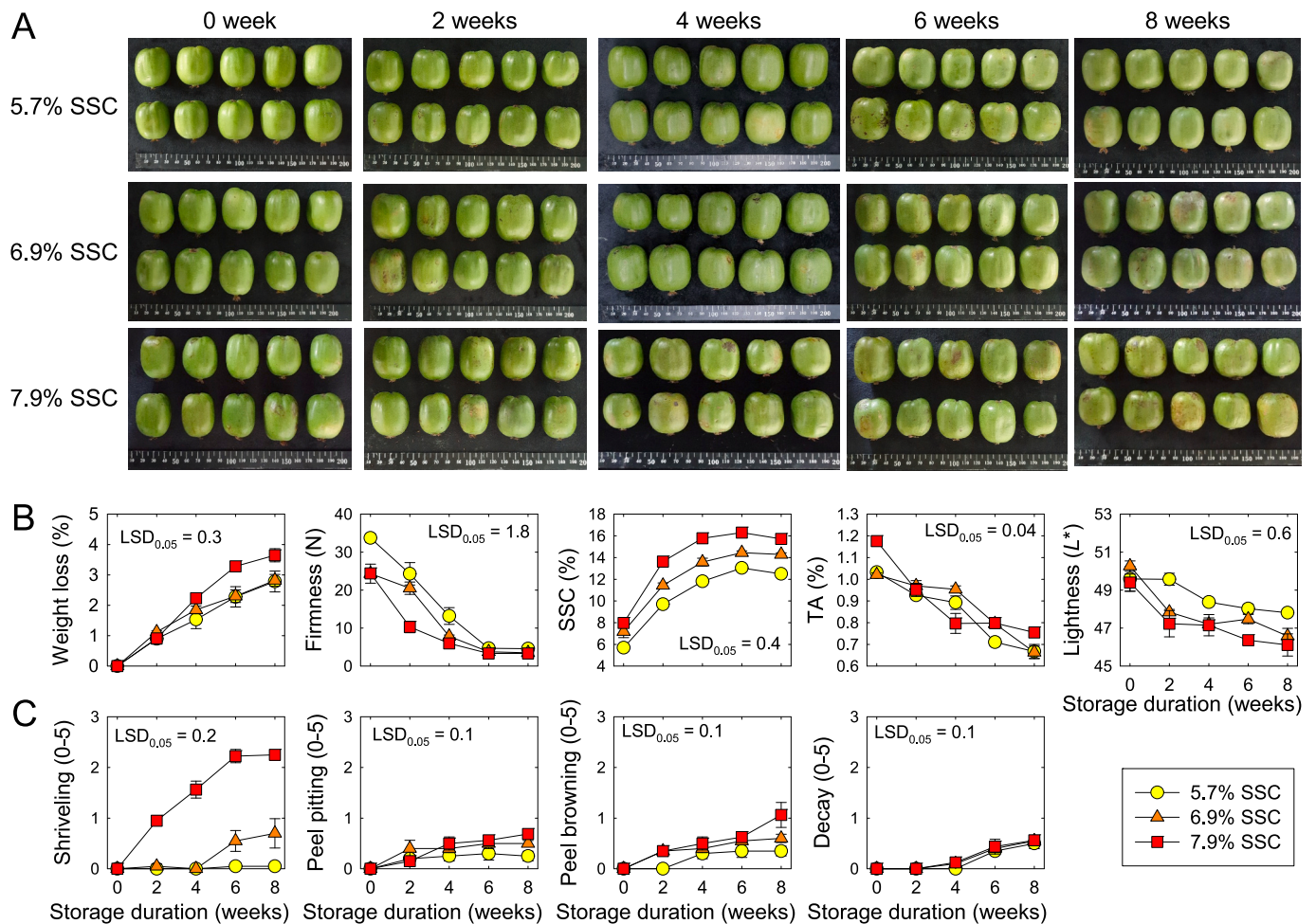


Fig. 1. Fruit visual appearances (A), weight loss, flesh firmness, soluble solids content (SSC), titratable acidity (TA), and peel lightness (B), and severity of physiological disorders (shriveling, peel pitting, peel browning, and decay) (C) in the fruit of ‘Autumn Sense’ hardy kiwifruit harvested at 5.7 %, 6.9 %, and 7.9 % SSC and stored at 3 °C for up to 8 weeks. Each data point represents the mean $\pm$ standard error (SE) of four replicates ($n = 4$), with five fruits per replicate. Statistical difference was determined using the least significant difference (LSD) test at $p = 0.05$.

expressed as a percentage based on anhydrous citric acid, which is the primary organic acid found in hardy kiwifruit (Lwin & Lee, 2022).

2.3. Chlorophyll and carotenoid contents

Two hundred milligrams of ground lyophilised samples were combined with 20 mL of 80 % acetone. The mixture was stirred in the dark at 22 °C for 2 h. Subsequently, the mixture was centrifuged at 1212 $\times g$ for 20 min. The supernatant was filtered through Whatman filter paper (No. 51, Merck KGaA, Darmstadt, Germany), and the absorbance of the extracted samples was measured at 662, 645, and 470 nm using a microplate spectrophotometer (Epoch 2, BioTek, Winooski, VT, USA). The concentrations of chlorophyll *a*, chlorophyll *b*, total chlorophylls, and total carotenoids were quantified using the equations in Arnon (1949) with minor modifications (Latt, Lwin, Seo, & Lee, 2023; Lwin, Lee, & Lee, 2022). The equations are as follows:

$$\text{Chlorophyll } a \text{ (Ch } a) = 11.24A_{662} - 2.04A_{645}.$$

$$\text{Chlorophyll } b \text{ (Ch } b) = 20.13A_{645} - 4.19A_{662}.$$

$$\text{Total chlorophylls} = 7.05A_{662} + 18.09A_{645}.$$

$$\text{Total carotenoids} = (1000A_{470} - 1.90\text{Ch } a - 63.14\text{Ch } b)/214.$$

The results were expressed in mg kg^{-1} on a dry weight basis.

2.4. GC–MS/MS-based metabolomics analysis

We conducted fruit quality evaluation and sampling at harvest and at

2, 4, 6, and 8 weeks after cold storage. Based on the results of alteration of quality attributes, fruit samples at harvest, after 4 and 8 weeks of cold storage, were selected for further analysis using GC–MS/MS. Sample extractions for GC–MS/MS analysis were prepared according to Yu, Song, Keum, and Lee (2023) with slight modifications. Freeze-dried hardy kiwifruit was ground in a mortar and pestle, passed through a 60-mesh sieve, and 10 mg from each sample was used for extraction. The weighed samples were shaken with 750 μL of methanol solution containing 1 mg mL^{-1} of ribitol (Merck Korea, An affiliate of Merck KGaA, Darmstadt, Germany) and glycolic acid (Merck Korea, an affiliate of Merck KGaA, Darmstadt, Germany) as internal standards. After centrifugation, the supernatant was collected and evaporated using an SPD2010 speed vacuum concentrator (Thermo Fisher Scientific, Asheville, NC, USA). The dried residue was reacted with 50 μL of methoxyamine reagent (20 mg mL^{-1} methoxyamine-hydrochloride in pyridine) at 37 °C for 90 min. Then 50 μL of *N*-methyl-*N*-(trimethylsilyl) trifluoroacetamide (MSTFA) reagent (MSTFA + 1 % trimethylchlorosilane) was added and reacted at 37 °C for 30 min.

Derivatised samples were analysed using a GC–MS/MS system (GC–MS-TQ8050, Shimadzu Co., Kyoto, Japan) with multiple reaction monitoring (MRM) to detect metabolites. A 1.0 μL sample aliquot was injected into a BPX-5 column (30 m $\times$ 0.25 mm i.d.; 0.25 μm film thickness; Trajan Scientific and Medical, Victoria, Australia) in split mode (30:1). The GC–MS/MS settings were optimised for optimal performance, including an injector temperature of 250 °C and ion source

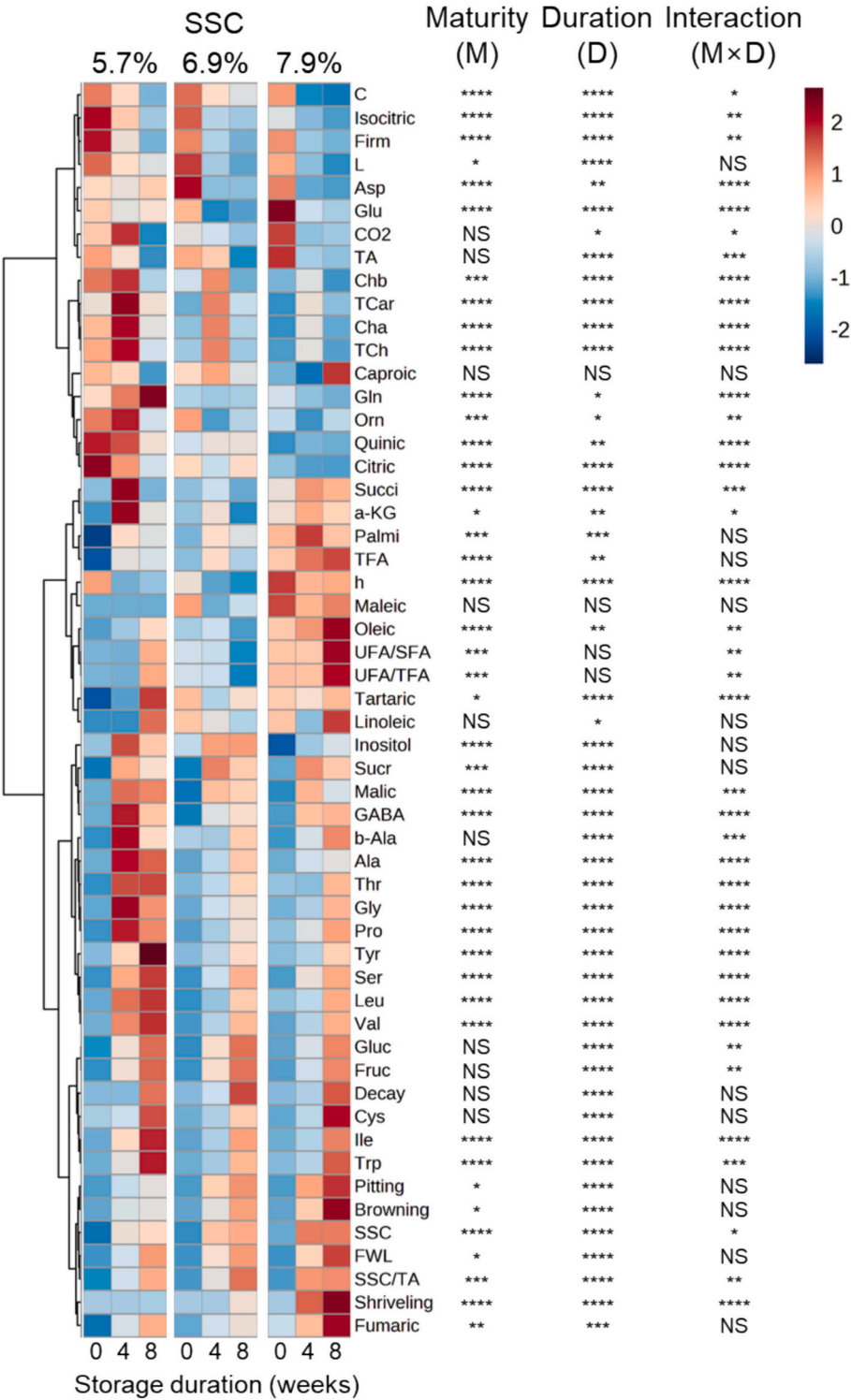


Fig. 2. Normalised heatmap matrix with a hierarchical cluster analysis of fruit physiological quality attributes, severity of physiological disorders, and major metabolites in the fruit of ‘Autumn Sense’ hardy kiwifruit harvested at 5.7 %, 6.9 %, and 7.9 % soluble solids content (SSC) and stored at 3 °C for up to 8 weeks. ANOVA results are shown for fruit maturity and storage duration as the main factors. NS, *, **, ***, or **** indicate not significant or significant at $p < 0.05$, 0.01, 0.001, or 0.0001, respectively.

and transfer line temperatures of 230 °C and 280 °C, respectively. The oven temperature was initially set to 60 °C for 2 min, then increased to 320 °C at a rate of 10 °C min⁻¹ and held for 15 min. Helium was the carrier gas at a flow rate of 1 mL min⁻¹, and argon was the collision gas. Electron ionisation energy was 70 eV. Data were processed using GC–MS solution software (version 4.53, Shimadzu Co., Kyoto, Japan). Peak

reconfirmation was conducted manually, and the relative area of each metabolite was determined by comparing the peak areas with those of ribitol and glycolic acid as internal standards (Yu et al., 2023).

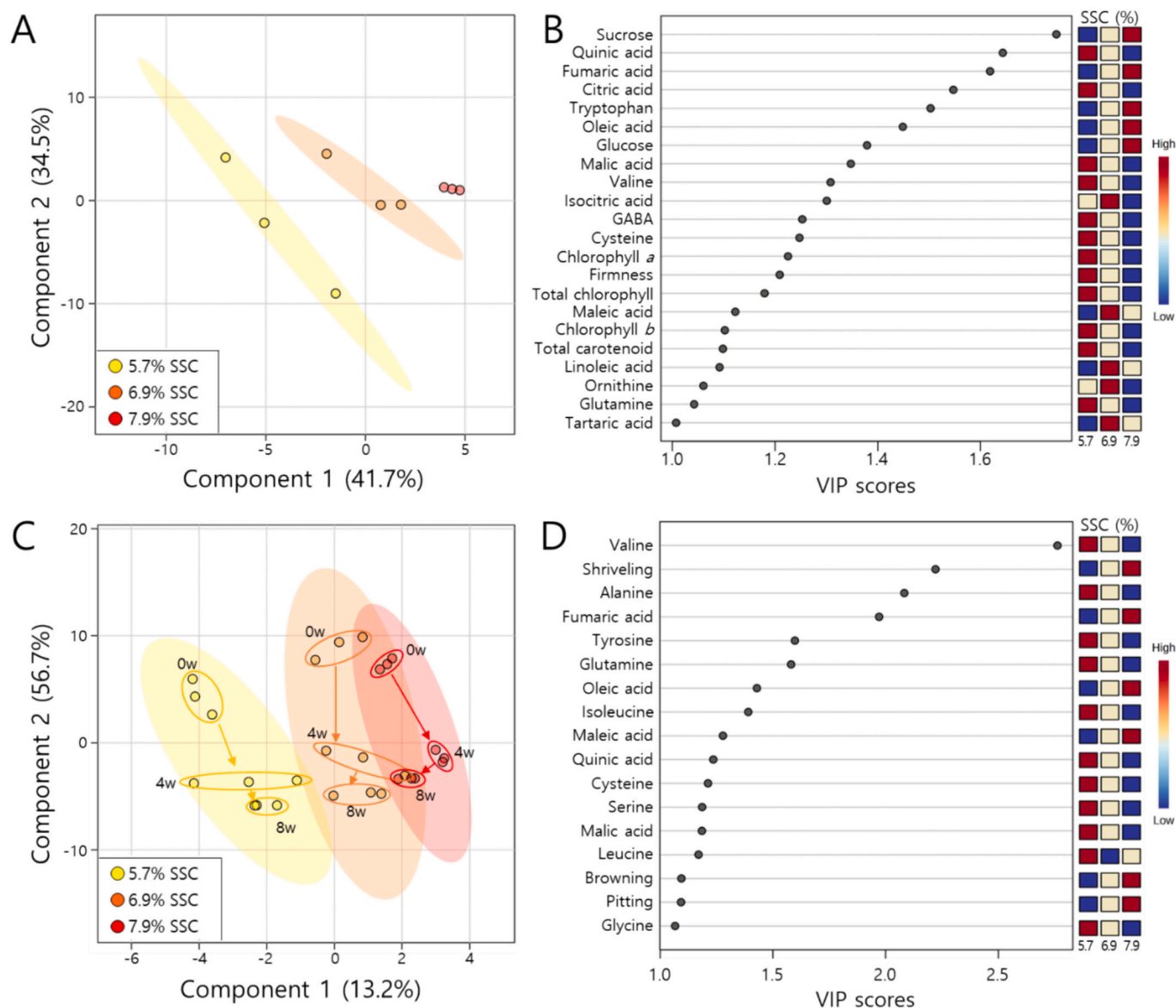


Fig. 3. Partial least squares-discriminant analysis (PLS-DA) scores plot (A and C) and variable importance in projection (VIP) scores plot (B and D) of fruit physiological attributes and major metabolites in the fruit of 'Autumn Sense' hardy kiwifruit harvested at 5.7 %, 6.9 %, and 7.9 % soluble solids content (SSC). The overall variables at harvest (A and B) and during 8 weeks of cold storage (C and D) were shown, respectively.

2.5. Statistical analyses

A completely randomised design was used to evaluate the effects of fruit harvest maturity on fruit quality attributes, physiological disorders, and untargeted metabolites during cold storage. The experiment was conducted with four replicates ($n = 4$) and five fruits per replicate, and the results were expressed as mean $\pm$ standard error (SE). Data were subjected to analysis of variance (ANOVA) to determine the effects of fruit maturity based on SSC-based maturity, storage duration, and their interactions with fruit metabolites (SAS version 9.3, SAS Institute Inc., Cary, NC, USA). The least significant difference (LSD) test was applied to verify significant differences among fruit maturities and storage duration on the fruit quality attributes, physiological disorders, and metabolites of hardy kiwifruit at $p < 0.05$. In addition, Student's t -test was applied to determine the fruit maturity effect on the major metabolites during cold storage at each removal time point at $p < 0.05$.

The data set was normalised by median and adjusted by auto-scaling for statistical analysis, including hierarchical clustering heatmap, partial least squares-discriminant analysis (PLS-DA), volcano plot, and

correlation coefficient test using MetaboAnalyst 5.0 (<https://www.metaboanalyst.ca/>) (Latt et al., 2023; Lwin et al., 2023). Hierarchical clustering heatmaps were generated based on the Euclidean distance measure and Ward's clustering algorithm, and the distance measure in the correlation coefficient heatmap was calculated using Pearson correlation coefficients (r). The correlation coefficient-based network of physiological fruit quality variables and metabolites was displayed using the MetScape (Version 3.1.3) plugin in Cytoscape (Version 3.9.1) (Lwin, Han, et al., 2023). Pathway analysis based on the KEGG database was conducted using the MetaboAnalyst 5.0 program. The reliability of the metabolomics model was validated using the leave-one-out cross-validation (LOOCV) and 1000 permutation test ($p = 0.039$) in MetaboAnalyst 6.0, confirming that the model was not overfitted and the classification was statistically valid.

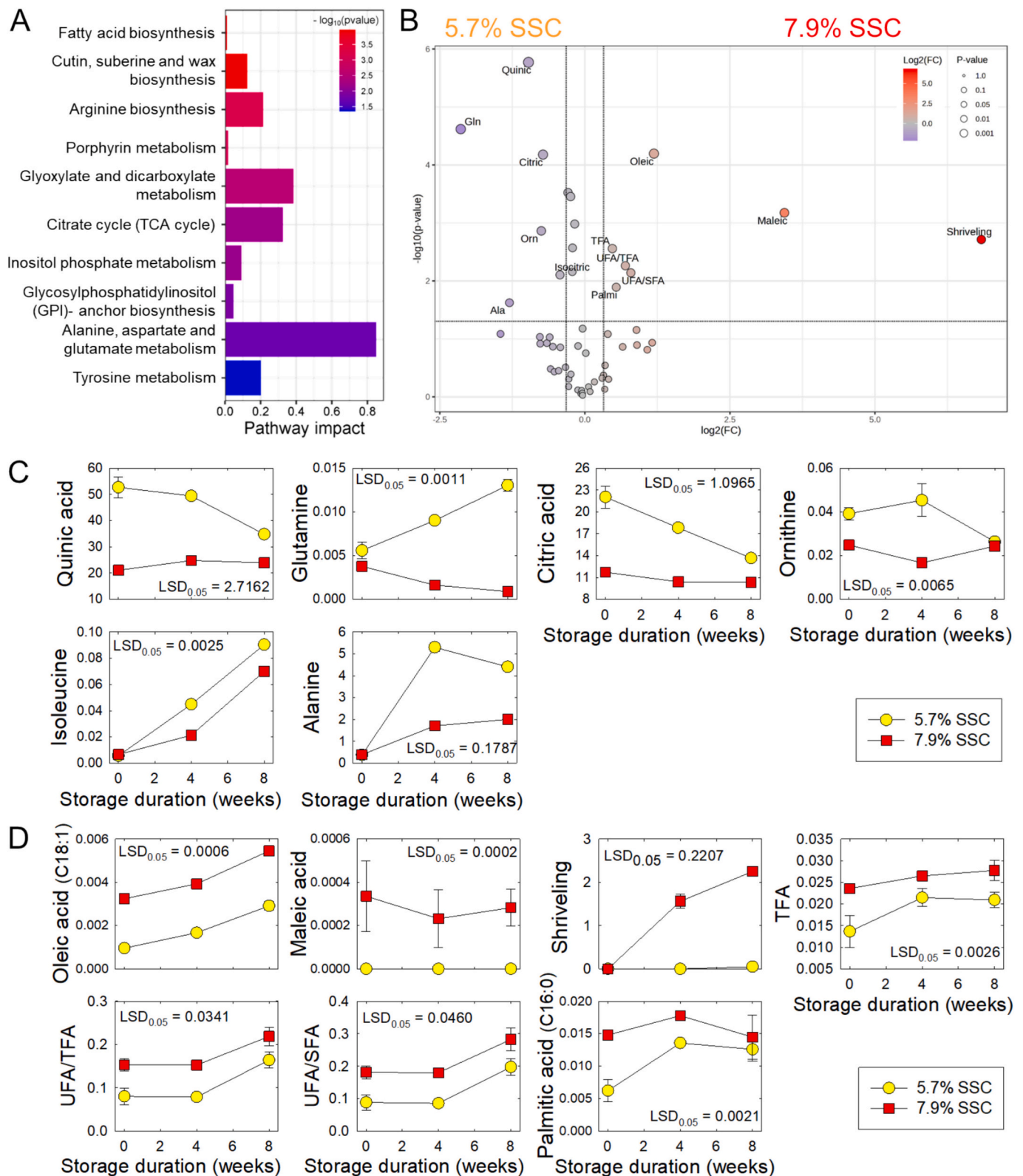


Fig. 4. Key KEGG pathway analysis (A) and Volcano plot (B) of differentially expressed major metabolites in the fruit of 'Autumn Sense' hardy kiwifruit harvested at 5.7 % soluble solids content (SSC), compared to 7.9 % SSC and stored at 3 °C for up to 8 weeks of cold storage. The X-axis of pathway analysis indicates each pathway impact score of each pathway, from purple to red, representing $-\log_{10}(\text{p-value})$. The X-axis and the Y-axis in the volcano plot indicate $\log_2$ fold changes (FC) between the two harvest maturity groups and $-\log_{10} \text{p-values}$ of all variations, respectively. The horizontal dotted line indicates a p -value cut-off of 0.05, and vertical dotted lines indicate FC values of 1.25. Upregulated variables at 5.7 % SSC are shown at left side of volcano plot, providing with individual results of corresponding single variables in (C), while upregulated variables at 7.9 % SSC are shown at right side of volcano plot, providing with individual results of corresponding single variables in (D). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Fruit appearance and major fruit quality responses during cold storage

The fruit visual appearances of 'Autumn Sense' hardy kiwifruit harvested at 5.7 ± 0.1 %, 6.9 ± 0.6 %, and 7.9 ± 0.2 % SSC and then stored at 3 °C for up to 8 weeks were shown in Fig. 1A. Physiological disorders, such as fruit shriveling, peel pitting, and peel browning were more severely detected at 7.9 % SSC than at 5.7 % and 6.9 % SSC harvest fruit after storage. Fruit quality attributes, including weight loss, fruit firmness, SSC, and lightness, were shown in Fig. 1B. Weight loss and SSC indicated higher in 7.9 % SSC than in other SSC levels during the whole storage period, while firmness was higher than other maturities. Peel lightness was relatively maintained at 5.7 % SSC, compared to 6.9 % and 7.9 % SSC.

3.2. Primary metabolites and normalised heatmap responses of all the variables

Based on the analysis of primary metabolites conducted through GC–MS/MS indicated the differential metabolic alterations during cold storage, depending on SSC-based fruit maturity. Of detected metabolites, a total of 34 metabolites, including 4 soluble carbohydrates, 9 organic acids, 17 amino acids, and 4 fatty acids, were identified in the fruit of 'Autumn Sense' hardy kiwifruit during cold storage (Supplementary Table S1).

A normalised heatmap matrix system with a hierarchical cluster analysis was used to provide an overview of the physiological and untargeted metabolic responses of fruit to maturity in terms of SSC at harvest and during cold storage (Fig. 2). The information on the abbreviations of metabolites was listed in Supplementary Table S2. Additionally, the results of a two-way ANOVA were incorporated into the normalised heatmap matrix. As one of the main factors, fruit maturity (M), in terms of SSC at harvest, significantly affected numerous variables, including peel chroma (C^*), isocitric acid, firmness, peel lightness (L^*), aspartic acid, glutamic acid, chlorophyll *b*, total carotenoids, chlorophyll *a*, total chlorophyll, glutamine, ornithine, quinic acid, citric acid, succinic acid, α -ketoglutaric acid, palmitic acid, total fatty acids (TFA), peel hue angle (h°), oleic acid, UFA/SFA ratio, UFA/TFA ratio, tartaric acid, *myo*-inositol, sucrose, malic acid, GABA, alanine, threonine, glycine, proline, tyrosine, serine, leucine, valine, isoleucine, tryptophan, peel pitting, peel browning, SSC, FWL, SSC/TA ratio, shriveling, and fumaric acid, during cold storage. Similar to the fruit maturity factor, the storage duration (D) factor also significantly affected many variables, including fruit respiration, TA, linoleic acid, β -alanine, glucose, fructose, decay, and cysteine, but not the UFA/SFA and UFA/TFA ratios. The interaction effect of fruit maturity and storage duration on the response variables was less significant than the main effects (Fig. 2 and S1–S5). Individual responses of all variables were also provided in Fig. S1–S5, based on the category of the corresponding variables.

3.3. Partial least squares-discriminant analysis

A partial least squares-discriminant analysis (PLS-DA) modelling approach was adopted to evaluate the overall effect of fruit maturity on response variables during the increase in SSC at harvest and cold storage. Additionally, a variable importance in projection (VIP) scores plot derived from the PLS-DA modelling approach was used to assess the variables, with a VIP score > 1 classified as a distinctive indicator (Fig. 3). The PLS-DA scores plot represented the physiological and biochemical responses of hardy kiwifruit, which were varied by fruit maturity (SSC) at harvest. The total variance of components 1 and 2 was 41.7 % and 34.5 %, respectively. The plot showed a wider 95 % confidence region at 5.7 % SSC than at 7.9 % SSC (Fig. 3A), indicating that

fruit quality attributes were relatively less consistent at 5.7 % SSC compared to 7.9 % SSC at harvest. Sucrose, quinic, fumaric, and citric acids, tryptophan, oleic acid, glucose, malic acid, valine, isocitric acid, GABA, cysteine, chlorophyll *a*, and firmness, which have VIP scores greater than 1.2, were considered important variables distinguishing hardy kiwifruit maturity at harvest (Fig. 3B).

The PLS-DA scores plot of overall fruit quality and physiological and biochemical metabolic responses during cold storage was shown in Fig. 3C. The total variance of components 1 and 2 was 13.2 % and 56.7 %, respectively. The PLS-DA scores plot indicated that the response variables were separated by fruit maturity and storage duration (Fig. 3C). The VIP scores plot highlighted important variables distinguishing the three maturity stages during cold storage. Regarding physiological disorders, fruit shriveling, peel browning, and peel pitting were important for classifying the three maturity stages during cold storage. Moreover, major metabolites, including valine, alanine, fumaric acid, tyrosine, glutamine, oleic acid, isoleucine, maleic acid, quinic acid, cysteine, serine, malic acid, leucine, and glycine, were considered as the important variables distinguishing the three maturity stages in cold-stored fruit (Fig. 3D).

3.4. Pathway analysis of metabolic responses to fruit maturity

The results of metabolic pathway analysis using the KEGG pathway library highlighted the metabolic differences between fruit maturities of hardy kiwifruit during cold storage (Fig. 4A and S8). Pathway analysis was primarily conducted between 5.7 % SSC and 7.9 % SSC to evaluate the contrast effects of fruit maturity on metabolites changes (Fig. 4A). The results indicated that fatty acid biosynthesis, cutin, suberine and wax biosynthesis, and arginine biosynthesis were greatly affected and altered by SSC-based fruit maturity during cold storage.

In the 5.7 % SSC harvested fruit, the pathways of alanine, aspartate, and glutamate metabolism, glycine, serine and threonine metabolism, and isoquinoline alkaloid biosynthesis were significantly altered during cold storage. Additionally, the metabolism of starch and sucrose, glyoxylate and dicarboxylate metabolism, and the TCA cycle also changed significantly in cold-stored fruit after harvesting at 5.7 % SSC (Fig. S8A). On the other hand, the metabolism of glycine, serine, and threonine, isoquinoline alkaloid biosynthesis, and starch and sucrose metabolism were detected as significantly altered metabolic pathways in 7.9 % SSC fruit during cold storage (Fig. S8B).

3.5. Differential responses of response variables to fruit maturity during cold storage

A volcano plot was used to evaluate the differential responses of fruit physiological and metabolic parameters between 5.7 % SSC and 7.9 % SSC during cold storage (Fig. 4B). In the volcano plot, blue and red dots represent fold change values of 1.5 ($\log_2$ 1.5 indicates 0.58) and *p*-values of 0.05 cut-off ($-\log_{10}$ 0.05 indicates 1.30) between 5.7 % SSC and 7.9 % SSC during cold storage. At 5.7 % SSC, valine, glutamine, alanine, tyrosine, glycine, leucine, quinic acid, malic acid, isoleucine, and cysteine were upregulated during cold storage. Conversely, fumaric acid, shriveling, oleic acid, maleic acid, SSC/TA, peel browning, peel pitting, tartaric acid, linoleic acid, sucrose, UFA/SFA, UFA/TFA, and palmitic acid were upregulated at 7.9 % SSC during cold storage (Fig. 4B).

The results focused on the metabolic responses from 5.7 % SSC and 7.9 % SSC to confirm the metabolic alterations of individual metabolites in relation to fruit maturity during cold storage (Fig. 4C and D). Valine, leucine, isoleucine, glutamine, tyrosine, and cysteine continuously increased at 5.7 % SSC during cold storage, while quinic acid gradually declined. Additionally, malic acid, alanine, and glycine sharply increased during the first half of cold storage. Then, it remained unchanged or slightly decreased during the second half of cold storage (Fig. 4C). On the other hand, SSC/TA, sucrose, fumaric acid, tartaric

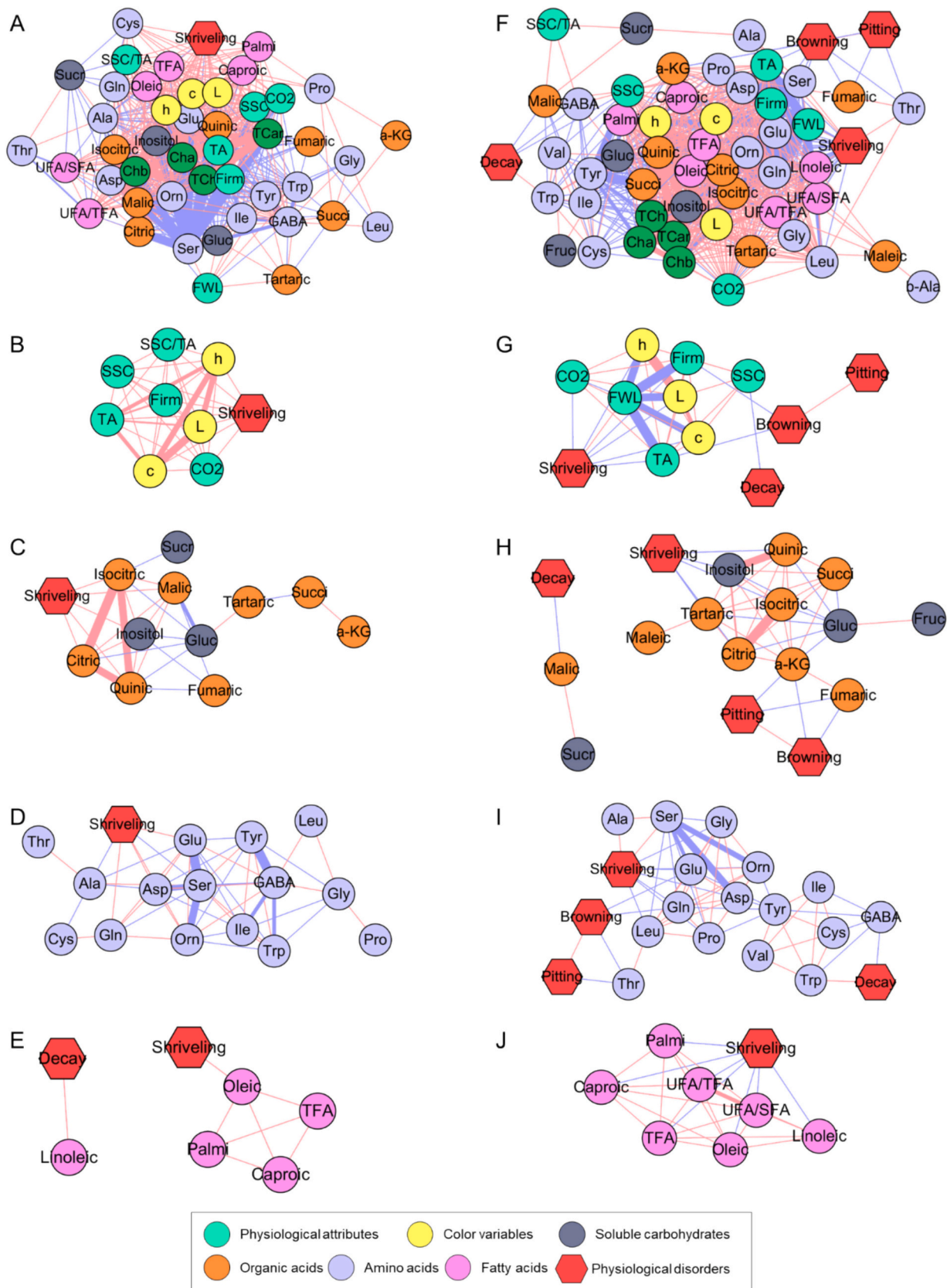


Fig. 5. Pearson correlation coefficient network ($r \geq |0.75|$) among overall variables (A and F), physiological disorders correlated with fruit quality attributes (B and G), soluble carbohydrates and organic acids (C and H), amino acids (D and I), and fatty acids (E and J) in the fruit of 'Autumn Sense' hardy kiwifruit harvested at 5.7 % SSC (A-E) and 7.9 % SSC (F-J) and then stored at 3 °C for up to 8 weeks. Red and blue lines indicate positive and negative correlations among variables, respectively. The thickness of the correlation coefficient network lines provides the significance of the correlation coefficient (r) among variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

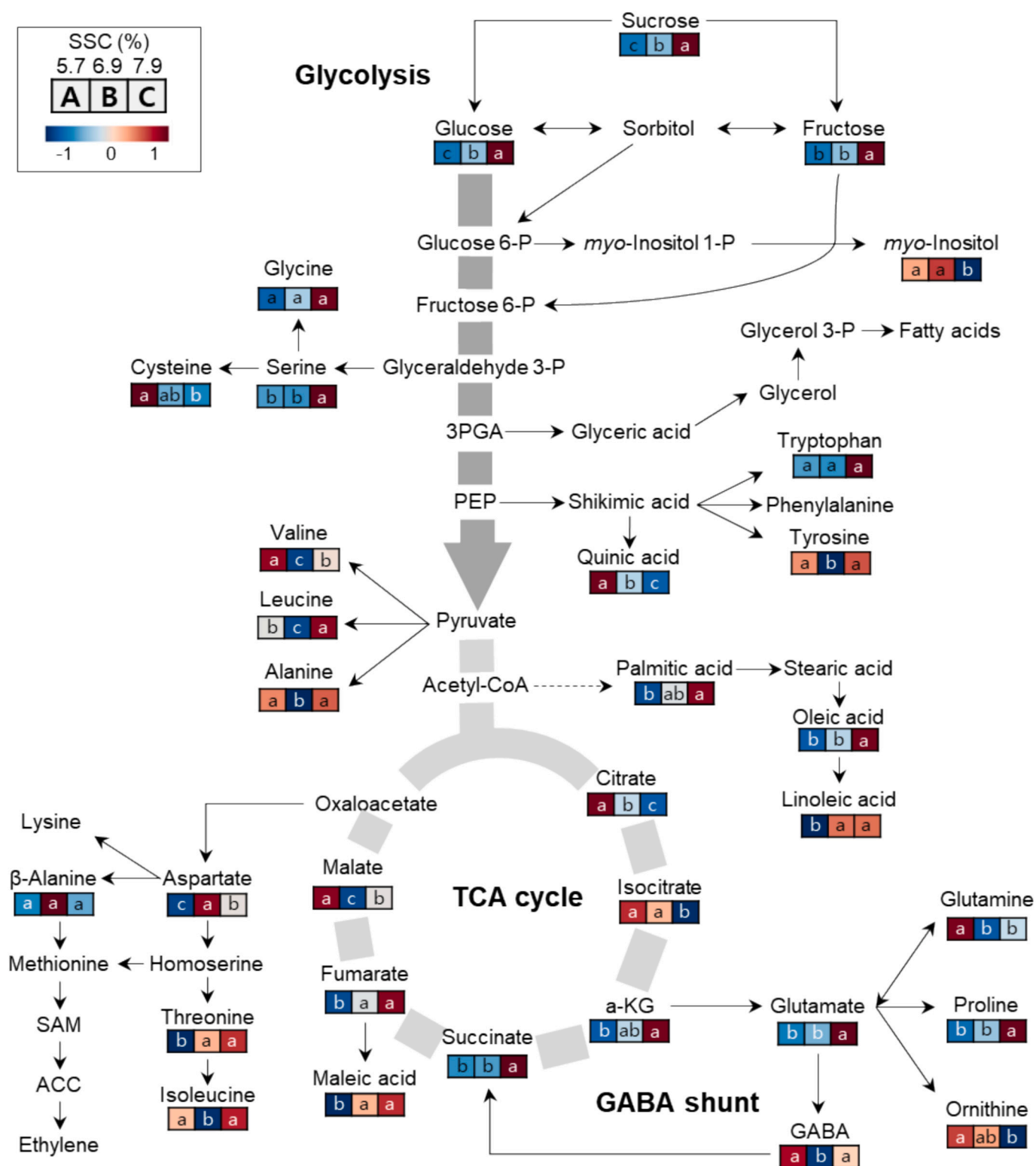
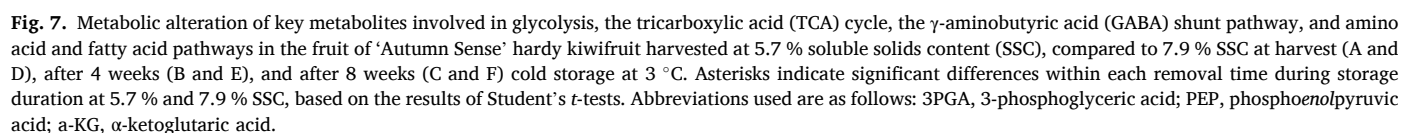


Fig. 6. Alteration of key metabolites involved in glycolysis, the tricarboxylic acid (TCA) cycle, the γ -aminobutyric acid (GABA) shunt pathway, and amino acid and fatty acid pathways in the fruit of 'Autumn Sense' hardy kiwifruit harvested at 5.7 % (A), 6.9 % (B), and 7.9 % (C) soluble solids content (SSC). Different lowercase letters within the array of boxes indicate the statistical difference among fruit maturities by Fisher's least significant difference (LSD) test at $p < 0.05$. Abbreviations used are as follows: 3PGA, 3-phosphoglyceric acid; PEP, phosphoenolpyruvic acid; a-KG, α -ketoglutaric acid.

acid, maleic acid, palmitic acid, oleic acid, linoleic acid, UFA/SFA, UFA/TFA, shriveling, peel browning, and peel pitting were higher at 7.9 % SSC, compared to 5.7 % SSC during cold storage. These parameters gradually increased mainly at 7.9 % SSC during cold storage (Fig. 4D).

3.6. Comparative responses of correlation coefficient network

Pearson correlation coefficient heatmap matrix system with a hierarchical cluster analysis was applied to evaluate the overall responses of all variables to fruit maturity during cold storage, along with the results



for each harvest maturity (Fig. S6). The results showed that the fruit quality, major metabolites, and physiological disorders were differentially responded to harvest fruit maturity during cold storage (Fig. S7). A Pearson correlation coefficient-based network system was generated using a cut-off value of $r \geq |0.75|$ to elucidate the detailed relationship among all variables at 5.7 % SSC and 7.9 % SSC fruit during cold storage (Fig. 5). At 5.7 % SSC fruit, serine negatively correlated with respiration rate, SSC, malic acid, ornithine, colour variables (lightness, chroma, and hue angle), firmness, chlorophyll-related components, *myo*-inositol, TA, quinic, citric, isocitric acids, aspartic acid, and glutamic acid while positively correlated with glucose. Additionally, GABA showed negative correlation with tyrosine, tryptophan, isoleucine, and glucose but positively correlated with malic, quinic acids, ornithine, and SSC during cold storage (Fig. 5A). On the other hand, at 7.9 % SSC fruit, FWL indicated obvious negative correlation with ornithine, firmness, aspartic acid, glutamic acid, TA, glutamine, isocitric acid, chroma, citric acid, lightness, and hue angle (Fig. 5F).

The incidence of physiological disorders is highly related to the alteration patterns of major metabolite levels at harvest and during storage. Therefore, a Pearson correlation coefficient network based on a cut-off value of $r \geq |0.75|$ was generated to compare the correlation between physiological disorders and all response variables in cold-stored hardy kiwifruit harvested at 5.7 % and 7.9 % SSC (Fig. 5B-E and 5F-J). Among the physiological disorders, only shriveling was positively correlated with lightness, chroma, hue angle, SSC, TA, firmness, respiration rate, and SSC/TA at 5.7 % SSC (Fig. 5B). Conversely, at 7.9 % SSC, shriveling was negatively correlated with respiration rate, hue angle, firmness, lightness, chroma, and TA. Furthermore, peel browning, which was positively correlated with peel pitting, showed negative correlation with firmness and TA, while decay was negatively correlated with SSC (Fig. 5G). Isocitric, malic, quinic, and citric acids and *myo*-inositol were positively correlated with shriveling at 5.7 % SSC but negatively correlated with shriveling at 7.9 % SSC. Additionally, peel pitting and peel browning were negatively correlated with α -KG and fumaric acid at 7.9 % SSC (Fig. 5C and H). Only shriveling was positively correlated with glutamine, aspartic acid, ornithine, and glutamic acid while it was negatively correlated with alanine and serine at 5.7 % SSC (Fig. 5D). However, at 7.9 % SSC, shriveling and peel browning negatively correlated with glutamic acid and glutamine (Fig. 5I). At 5.7 % SSC, decay positively correlated with linoleic acid and shriveling positively correlated with oleic acid, which indicated positive correlation with TFA, palmitic, and caproic acids (Fig. 5E). On the other hand, at 7.9 % SSC, shriveling negatively correlated with palmitic, caproic, oleic, linoleic acids, TFA, UFA/TFA, and UFA/SFA (Fig. 5J).

3.7. Overall alteration in metabolites associated with key metabolisms during fruit maturation and cold storage

To verify the overall alteration in metabolites associated with key metabolic pathways, we focused on glycolysis, the tricarboxylic acid (TCA) cycle, the γ -aminobutyric acid (GABA) shunt pathway, and amino acid and fatty acid pathways in the fruit of 'Autumn Sense' hardy kiwifruit at harvest (Fig. 6) and during cold storage (Fig. 7). The metabolic alterations of targeted metabolites in hardy kiwifruit harvested at 5.7, 6.9, and 7.9 % SSC were shown in Fig. 6. The levels of soluble carbohydrates, including sucrose, glucose, fructose, and *myo*-inositol, which are intermediates of glycolysis, rapidly increased and were significantly higher at 7.9 % SSC as fruit maturity increased (Fig. 6C). Levels of the intermediates of the TCA cycle, such as quinic, citric, isocitric, and malic acids, gradually decreased, while those of α -ketoglutaric, succinic, fumaric, and maleic acids significantly increased during fruit maturation. Serine, leucine, tryptophan, threonine, glutamic acid, and proline levels were significantly higher at 7.9 % SSC than at the other fruit maturity stages. At the same time, those of cysteine, valine, glutamine, GABA, and ornithine were lower at 7.9 % SSC. The levels of major fatty acids, such as palmitic, oleic, and linoleic

acids, increased as SSC at harvest increased (Fig. 6A-C).

A comparison of two contrasting harvest maturities based on the results of SSC at harvest for up to 8 weeks of cold storage was shown in Fig. 7. The levels of quinic, citric, and isocitric acids at harvest were statistically higher at 5.7 % SSC than at 7.9 % SSC (Fig. 7A-C). Intermediates derived from the glycolysis pathway, such as serine, valine, leucine, alanine, and tyrosine, significantly accumulated at 5.7 % SSC during cold storage. Intermediates derived from the TCA cycle, such as threonine, isoleucine, β -alanine, GABA, glutamine, and proline, also more accumulated at 5.7 % SSC than at 7.9 % SSC during cold storage (Fig. 7A-C). In contrast, the levels of fatty acids, including palmitic, oleic, and linoleic acids, were higher at 7.9 % SSC than at 5.7 % SSC at harvest and during cold storage (Fig. 7D-F).

4. Discussion

Hardy kiwifruit could face considerable challenges after cold storage due to various quality deterioration factors (Latocha et al., 2014; Lim et al., 2016). To alleviate the development of deterioration factors, determining optimal fruit maturity has been considered one of the potential approaches to managing overall fruit quality and incidence of physiological disorders during cold storage in kiwifruit (Gwanpua, Jabbar, Zhao, Heyes, & East, 2018; Koutsofili, Gerasopoulos, & Vasilakakis, 2013; Maguire, Amos, & Kelly, 2005; Manning et al., 2016; Tilahun et al., 2020). In addition, several maturity biomarkers identified using multi-omics approaches could play a predictive role in controlling the storage risk of cold-stored kiwifruit (Favre et al., 2023). Nonetheless, no studies have been reported on the effect of fruit maturity on the development of, and associated with, fruit quality issues, such as inadequate ripening or physiological disorders, based on GC-MS/MS-based metabolic profiling in 'Autumn Sense' cold-stored hardy kiwifruit. Therefore, this study aimed to test the hypothesis that SSC-based fruit maturity would be highly relevant to controlling overall fruit quality and the risk of developing physiological disorders in cold-stored hardy kiwifruit.

On-vine ripened kiwifruit showed considerable differences in fruit quality attributes compared with off-vine ripened kiwifruit (Burdon, Pidakala, Martin, & Billing, 2017). Hardy kiwifruit also exhibited metabolic alterations during fruit maturation (Fig. 3B and 6). The increased respiration rate and SSC values from 5.7 % to 7.9 % indicated fruit maturation in the hardy kiwifruit (Fig. 3B and S2). Starch degradation occurs during fruit maturation, and soluble carbohydrates are directly imported into the fruit, depending on environmental conditions (Burdon et al., 2014). In the fruit of 'Mitsuko' hardy kiwifruit, starch degradation coincided with increased levels of glucose, fructose, sucrose, and *myo*-inositol (Kim, Beppu, & Kataoka, 2012). Organic acids, significant contributors to fruit flavour, accumulate at the early stages of fruit development (Jia et al., 2023; Mao et al., 2023). The contents of major organic acids, including quinic, citric, and malic acids, were highest in fruit harvested at 5.7 % SSC and decreased during fruit maturation (Fig. 6A-C). The accumulation of organic acids was highly related to the substrate supply for respiration during fruit development (Batista-Silva et al., 2018). The soluble carbohydrates, including sucrose and glucose, and intermediates of the tricarboxylic acid (TCA) cycle, such as citrate and fumarate were key contributors classifying the fruit maturity levels, suggesting enhanced energy metabolism and carbohydrate accumulation at a higher SSC (Fig. 3B). Although palmitic, oleic, and linoleic acid contents increased, the UFA/SFA ratio also increased during fruit maturation (Fig. 6 and S5). Palmitic, oleic, and linoleic acids are the major fatty acid components of the kiwifruit membrane (Huang et al., 2019). The increase in the UFA/SFA ratio during fruit development and cold storage is linked to membrane permeability in kiwifruit (Sfakiotakis et al., 2005; Xiong et al., 2020). Thus, these metabolic alterations during fruit maturation on the vine of hardy kiwifruit could play a crucial role in fruit quality and susceptibility to abiotic/biotic stresses during cold storage.

Indeed, the incidence and severity of fruit shriveling, peel pitting, and peel browning increased as storage duration and fruit maturity advanced (Fig. 2 and S2). Furthermore, these physiological disorders, with VIP scores higher than 1.0, were considered indicators to distinguish maturity stages (Fig. 3D). The hardy kiwifruit over-matured on the vine became highly susceptible to various physiological disorders during cold storage (Fig. 2 and 5C). When kiwifruit is damaged by cold stress, the levels of palmitic, stearic, and oleic acids increase during cold storage (Choi, Baek, Tilahun, & Jeong, 2022), which corresponds with our findings. The membrane lipid could be modified from a flexible liquid crystalline to a solid gel structure in response to chilling damage (Lyons, 1973). The levels of oleic and linolenic acids increased due to the adjustment of membrane fluidity in cold-stored tomatoes (Sossi, Valle, & Boggio, 2022). Putrescine treatment alleviated chilling injury symptoms in kiwifruit by inducing chilling tolerance as the unsaturation of membrane lipids increased (Yang et al., 2016). In our study, the increasing levels of UFA, such as oleic and linoleic acids, and the UFA/SFA ratio during cold storage might be a response to the cold storage temperature. However, the severity of physiological symptoms worsened (Fig. 4D).

Changes in soluble carbohydrate contents are a major event during kiwifruit growth, maturation, and postharvest ripening (Richardson, McAneney, & Dawson, 1997). Among soluble carbohydrates, sucrose had the highest VIP scores, which could indicate that it is one of the crucial variables for classifying SSC-based fruit maturity in hardy kiwifruit (Fig. 3B). These soluble carbohydrates showed similar trends in cold-stored kiwifruit and hardy kiwifruit, thereby contributing to enhancing SSC levels (Mitalo et al., 2019; Xiong et al., 2023). In contrast, many organic acids were differentially affected by fruit maturity and storage duration, while TA was only affected by storage duration during cold storage (Fig. 2 and S3). The levels of organic acids generally declined in cold-stored kiwifruit, regardless of the type of organic acids (Barboni et al., 2010; Taş, Berk, Kibar, & Gündoğdu, 2022). However, the contents of quinic and malic acids were retained or increased during cold storage (Amodio et al., 2007; Choi, Baek, Cheol, Jeong and Tilahun, 2022), consistent with our results. Malic acid showed more variation in response to a wide range of storage temperatures than citric acid, contributing to retaining higher TA levels at lower storage temperatures than at higher storage temperatures (Cha et al., 2019). Thus, as major organic acids, citric and quinic acids were relatively stable, but the levels of minor organic acids varied during cold storage, depending on fruit maturity.

Amino acids are crucial to the metabolic shift during kiwifruit development and ripening (Xiong et al., 2020). The levels of branched-chain amino acids, such as leucine, isoleucine, and valine (Kochevenko et al., 2012), and aromatic amino acids, such as tyrosine and tryptophan (Tzin & Galili, 2010), gradually increased during cold storage, regardless of the fruit maturity stage (Fig. 2 and S4). Fruit respiration declined at low storage temperatures during the storage period, potentially delaying ripening and suppressing the activation of volatile organic compounds (VOCs) metabolism. The lower activation of VOCs metabolism contributed to the accumulation of branched-chain and aromatic amino acids during cold storage (Brizzolara, Hertog, Tosetti, Nicolai, & Tonutti, 2018). Additionally, alanine, glycine, proline, and threonine were highly accumulated at 5.7 % SSC after four weeks of cold storage (Fig. S4). The accumulation of alanine, glycine, proline, and ornithine suggests a partial improvement in fruit tolerance under various biotic and abiotic stress conditions (Botondi, Russo, & Mencarilli, 2012). These results demonstrate that hardy kiwifruit harvested at 5.7 % SSC would be exposed to chilling stress-induced metabolic alterations as opposed to those harvested at 6.9 % SSC or 7.9 % SSC. That is, during cold storage, amino acids such as alanine and serine became strong discriminators, consistent with stress-related metabolic shifts related to shriveling and browning symptoms. Furthermore, aspartic acid, glutamine, and glutamic acid levels decreased during kiwifruit ripening (Choi, Baek, Cheol, et al., 2022; Tian et al., 2021). The reduction in glutamine level could be strongly associated with the

decrease in glutamic acid content, causing an increase in α -ketoglutaric acid level, thereby contributing to the incorporation of other amino acids, such as asparagine, methionine, lysine, threonine, GABA, proline, and arginine, using the enzymatic reactions of a wide range of multi-specific aminotransferases (Forde & Lea, 2007). Meanwhile, the conversion of aspartic acid to methionine, a precursor of ethylene, is necessary for ethylene biosynthesis in plants (Ainalidou et al., 2016). Interestingly, the levels of aspartic and glutamic acids decreased at 6.9 % SSC and 7.9 % SSC, whereas 5.7 % SSC-harvested fruit maintained or increased the levels of aspartic and glutamic acids during cold storage (Fig. 7 and S4). Based on the results from amino acid metabolism, 5.7 % SSC indicated differential ripening patterns during cold storage, compared with 6.9 % SSC or 7.9 % SSC.

The profiles and contents of fatty acids responded differentially to a wide range of storage temperatures during the kiwifruit storage period (Antunes & Sfakiotakis, 2008). Pathway analysis indicated that fatty acid biosynthesis, cutin, suberine, and wax biosynthesis, and linoleic acid metabolism were affected by fruit maturity during cold storage (Fig. 4A). Similar to our findings, fruit maturity differentially affected the levels of fatty acids in cold-stored avocado mesocarp, where fatty acid levels declined in immature fruits but increased in matured fruits (García-Rojas et al., 2016). In kiwifruit, oleic acid and UFA/SFA levels gradually increased at lower than higher storage temperatures (Antunes & Sfakiotakis, 2008) and long-term cold storage (Choi, Baek, Tilahun, & Jeong, 2022). This study showed similar results, including increased oleic acid and UFA/SFA levels during fruit maturation and cold storage, except in fruit harvested at 6.9 % SSC (Fig. 3B and S5). Therefore, the alteration of fatty acid profiles and levels could be induced during cold storage and differentially responded to fruit maturity.

Chlorophyll degradation is vital during plant leaf senescence and fruit ripening (Ren et al., 2007; Yang et al., 2009). In the present study, although the contents of chlorophyll-related components decreased during fruit maturation, they were maintained during cold storage at 5.7 % and 6.9 % SSC harvested fruit (Fig. 2 and S5). On the other hand, the 7.9 % SSC fruit had the lowest chlorophyll-related components during cold storage (Fig. S5). At the same time, the severity of peel browning and peel pitting was increased, resulting in a rapid decrease of peel lightness and chroma (Fig. S1 and S5). Concurring with our results, chilling damaged olives showed chlorophyll degradation, along with increased pulp browning index (Kuang et al., 2023). Upon comparing chlorophyll and carotenoid contents in stay-green to yellow-pears, these contents did not markedly change during ripening (Charoenchongsuk, Ikeda, Itai, Oikawa, & Murayama, 2015), similar to our findings. Chlorophyll degradation-related genes and enzymes are highly suppressed in fruits that undergo a “stay-green even when ripe” phenomenon (Charoenchongsuk et al., 2015).

Overall, our findings highlight the notable impact of SSC-based fruit maturity on fruit quality. The major metabolic alterations identified in this study are highly dependent on SSC-based fruit maturity, which may lead to fruit quality issues during cold storage. The hardy kiwifruit harvested at 5.7 % SSC showed an unusual ripening pattern, while 7.9 % SSC fruit had severe physiological disorders after cold storage. Under the conditions of this study at 3 °C storage with RH 95 %, fruit harvested at approximately 6.9 % SSC demonstrated the most balanced postharvest quality, suggesting this maturity level as a potentially optimal harvest maturity for ‘Autumn Sense’ hardy kiwifruit. However, as this study was conducted within a single production season with relatively wide sampling intervals, subtle fluctuations in metabolic and fruit quality attributes may not have been fully captured. Furthermore, environmental variables, such as air temperature, precipitation, relative humidity, fertilizer, and soil composition may influence SSC accumulation and postharvest metabolic responses. Therefore, future studies conducted across multiple seasons and growing orchards will be essential to validate the proposed harvest maturity levels for ‘Autumn Sense’ hardy kiwifruit from this study.

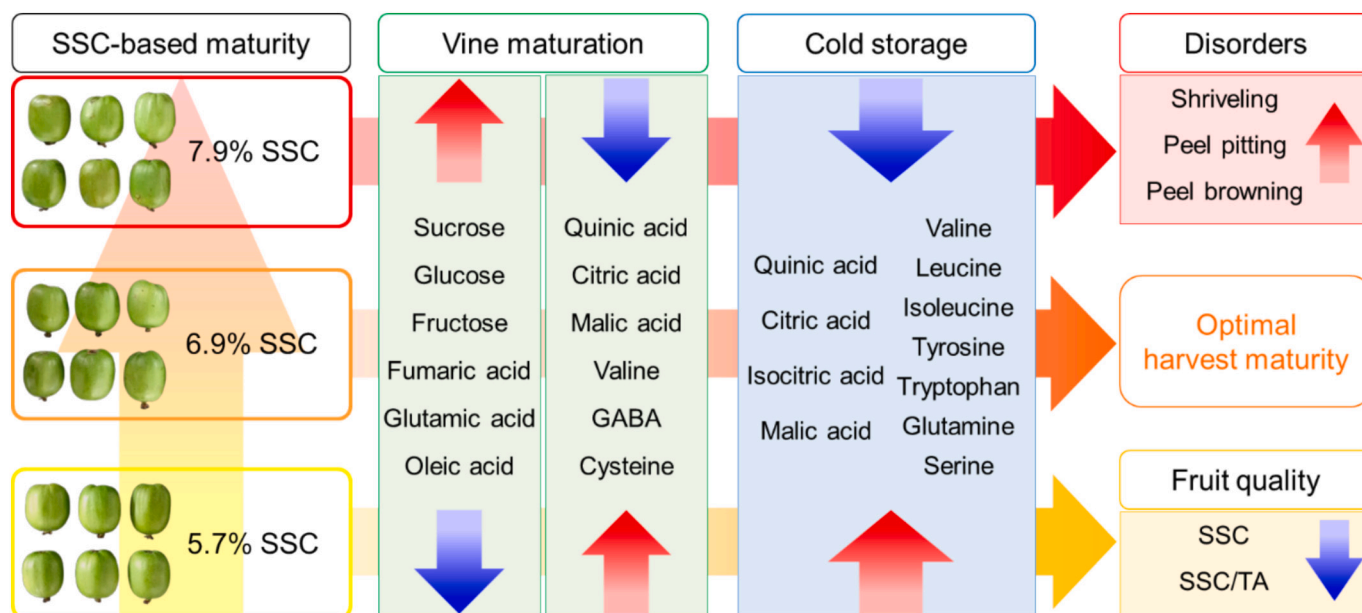


Fig. 8. Schematic illustrating the physiological and biochemical responses of fruit quality attributes and main metabolites in the fruit of 'Autumn Sense' hardy kiwifruit harvested at 5.7 %, 6.9 %, and 7.9 % soluble solids content (SSC) and stored at 3 °C for up to 8 weeks. Red and blue arrows indicate increase and decrease responses of each variable to the SSC-based fruit maturity during cold storage. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusion

Since significant alterations in metabolic patterns occur during fruit maturation, inappropriate harvest maturity of hardy kiwifruit may lead to inadequate ripening or a higher incidence of physiological disorders during cold storage. In 5.7 % SSC-harvested hardy kiwifruit, lower SSC and accumulated branched-chain, aromatic, and stress-related amino acids could result from insufficient or delayed fruit ripening during cold storage. Conversely, fruit harvested at 7.9 % SSC, the metabolic changes during fruit maturation could induce the rapid development of physiological disorders, such as fruit shriveling, peel browning, and peel pitting during cold storage. Under the specific environmental and experimental conditions of this study, the fruit harvested at approximately 6.9 % SSC exhibited a more balanced metabolic profile and better postharvest fruit quality, suggesting this range as a preliminary optimal harvest maturity for 'Autumn Sense' hardy kiwifruit (Fig. 8). Overall, the results suggest that even a 1 % difference in SSC at harvest could considerably influence both fruit quality attributes and major metabolic pathways of hardy kiwifruit during cold storage. Since these results are based on a single growing season, further validation across multiple environmental conditions, production years, and orchard variations is required to establish the broader applicability of the identified SSC threshold. Nevertheless, these results provide essential insights into the role of SSC-based harvest maturity in modulating the metabolic regulation of postharvest fruit quality in hardy kiwifruit during cold storage. Furthermore, we can establish a basis for improved harvest guidelines for commercial cultivation and production.

CRediT authorship contribution statement

Hyowon Park: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation. **Hyun Ji Eo:** Writing – review & editing, Validation, Investigation, Formal analysis, Data curation. **Chul-Woo Kim:** Writing – review & editing, Validation, Investigation, Formal analysis, Data curation. **Jane E. Stewart:** Writing – review & editing, Investigation, Conceptualization. **Uk Lee:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **Jinwook Lee:** Writing –

review & editing, Writing – original draft, Supervision, Project administration, Investigation, Data curation, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fochx.2025.103373>.

Data availability

Data will be made available on request.

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