



Comparative responses of fruit quality attributes, mineral nutrients, and targeted metabolites in fruit of early- to mid-season apple cultivars at harvest

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Abstract

New apple cultivars develop to satisfy the market demand and extend the apple consumption. However, the comparisons of seasonal and cultivar-dependent studies remain limited. This study investigated the overall fruit quality attributes, mineral nutrients, and targeted metabolites of nine apple cultivars harvested from late July to mid-September. Significant variations in fruit attributes, such as fruit fresh weight, firmness, soluble solids content (SSC), titratable acidity (TA), peel hue angle value, and starch pattern index were observed with harvest season. Early-season cultivars, such as ‘Summer King’, exhibited higher TA, malic acid, and amino acids, while mid-season cultivars like ‘Arisoo’ and ‘Picnic’ had higher levels of volatile organic compounds (VOCs). Metabolomic profiling revealed that early-season apples, which were less mature, contained higher levels of organic acids and phenolic compounds, while mid-season apples had greater VOC accumulation. Seasonal apples, which can provide early-season apples, may exhibit different maturation and ripening processes compared to mid-season cultivars. The results indicated that targeted metabolites, fruit quality attributes, and mineral nutrients could respond differently to the fruit harvest season from early to mid-season cultivars at harvest.

Keywords Amino acids · Organic acids · Phenolic compounds · Soluble carbohydrates · Targeted metabolomics · Volatile organic compounds

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1 Introduction

Agronomic, morphological, and fruit quality traits vary extensively among 80 apple accessions (Reig et al. 2015). Fruit quality attributes, such as starch pattern index (SPI), fruit fresh weight, peel color variables, flesh firmness, soluble solids content (SSC), titratable acidity (TA), and internal ethylene concentration (IEC) are highly diverse among several commercial apple cultivars (Yoo et al. 2023). Flesh firmness, and respiration and ethylene production rates are highly distinctive among cultivars at harvest; however, flesh firmness is inversely related to respiration and ethylene production rates during shelf life, regardless of the cultivar (Zhang et al. 2024). Furthermore, IEC, firmness, SSC, and TA are differentially affected by fruit maturity and apple cultivar at harvest (Yoo et al. 2016). Traits, such as fruit fresh weight, flesh firmness, SSC, and starch degradation pattern are distinctive even among ‘Fuji’ apple strains (Fallahi et

al. 2014; Iglesias et al. 2012). The responses of peel color variables in terms of lightness, chroma, and hue angle show heavy diversity, depending on the cultivar (Jing et al. 2020; Piagentini and Pirovani 2017) and even among ‘Fuji’ apple strains (Fallahi et al. 2014; Iglesias et al. 2012). In contrast, K and B levels are dominant and highest in the ‘Gala’ and ‘Jonagold’ apple cultivars, respectively, compared with that of other macro- and micro-elements (Johnson 2000). Among the macro mineral nutrients (Na, K, Mg, and Ca), K and Mg levels vary widely not only among peel and cortex tissues but also among ancient and commercial apple cultivars; however, Na and Ca levels do not differ significantly (Preti and Tarola 2021). K and Fe levels are predominantly the highest among all macro- and micro-element nutrients, respectively, in numerous apple cultivars (Kumar et al. 2018).

Soluble carbohydrates play an essential role in determining fruit quality and sweetness at harvest. Among the soluble carbohydrates, fructose is ranked as the major soluble carbohydrate, which is similar in a wide range of cultivars, irrespective of peel pigmentation (Kumar et al. 2018; Wu et al. 2007) and fruit maturity (Rouchaud et al. 1985). Sorbitol exhibits the lowest concentration among the major soluble carbohydrates, irrespective of the cultivar (Rouchaud et al. 1985; Yamada et al. 1994). Additionally, apples contain minor soluble carbohydrates, such as galactose, and their levels fluctuate highly based on cultivar, canopy position (Feng et al. 2014), and fruit development stage (Zhang et al. 2010b). Among organic acids, malic acid plays a primary role in apple fruit acidity (Berüter 2004). Other organic acids in flesh tissue include citric, succinic, and maleic acids (Feng et al. 2014; Zhang et al. 2010b). Among amino acids, at least 18 have been detected in apple fruit extract (Gomis et al. 1990; Wu et al. 2007). Amino acid levels in apples are influenced by cultivar (Wu et al. 2007), canopy position, apple fruit tissue (Feng et al. 2014), and fruit development stage (Zhang et al. 2010b). Similarly, the levels and profiles of fatty acids differ widely among apple cultivars (Overton et al. 1988; Wu et al. 2007).

The profiles and compositions of phenolic compounds differ highly between apple populations and cultivars (Kumar et al. 2018; Song et al. 2023; Verdu et al. 2014). Phenolic compounds are more highly localized in apple peel tissue than in apple flesh (Assumpção et al. 2018; Raudone et al. 2017). The concentration of individual phenolic compounds directly contributes to the total antioxidant capacity (Lee et al. 2003). Thus, total antioxidant activity significantly higher in the fruit peel than in flesh tissues (Eberhardt et al., 2000). Volatile organic compounds (VOCs) are biochemically essential for apple flavour and aroma (Dixon and Hewett 2000). The factors that significantly impact

VOC profiles and composition are apple cultivar (Iglesias et al. 2012; Rizzolo et al. 2006) and fruit maturity stage (Mehinagic et al. 2006). Nonetheless, the overall association between fruit physiological quality attributes, mineral nutrients, and targeted metabolites in early- to mid-season apple cultivars is not fully understood. Thus, we hypothesized that fruit quality attributes, mineral nutrients, and targeted metabolites would be differed in coordinated patterns between early- and mid-season apple cultivars in relation to harvest season. Therefore, this study provides an integrated comparison of these traits at harvest to clarify cultivar-specific physiological and metabolic characteristics.

2 Materials and methods

2.1 Plant materials

Nine commercial apple cultivars used in this study were released from the Apple Research Center, National Institute of Horticultural and Herbal Science, RDA. They were cultivated in conventional apple orchards in Gunwi, Mungyeong, and Gimcheon, Republic of Korea. Fruits were harvested during the optimal harvest season for each apple cultivar. However, detailed information on cultivation management was not fully available (Table S1). ‘Summer Prince’ and ‘Summer King’ were harvested on 24 and 26 July from Gunwi, respectively. ‘Green Ball’ was obtained on 27 August, and the ‘RubyS’ and ‘Arisoo’ were harvested on 3 September. ‘Hwangok’ and ‘Hongro’ were harvested on 7 September, and ‘Picnic’ was harvested on 13 September at Mungyeong. ‘Honggeum’ was picked on 13 September at Gimcheon. Apple fruits without visible defects were selected for this study, as shown in Fig. 1A.

2.2 Fruit physiological parameters

Fruit quality parameters were individually measured for all harvested cultivars (Kim et al., 2018). Fruit fresh weight was measured with an analytical balance and flesh firmness was assessed using a TAHDi-500 texture analyzer with an 11-mm diameter probe. The peel color of the equator part was measured three times using a chroma meter. SSC measurement was performed with a refractometer from expressed flesh juice. TA was quantified by titrating the juice with 0.1 N NaOH to an endpoint pH of 8.2 using phenolphthalein indicator, and values were converted to malic acid equivalents (Lwin and Lee 2022). Fruit ripeness was assessed using the Cornell starch-iodine index, as described by Blanpied and Silsby (1992).

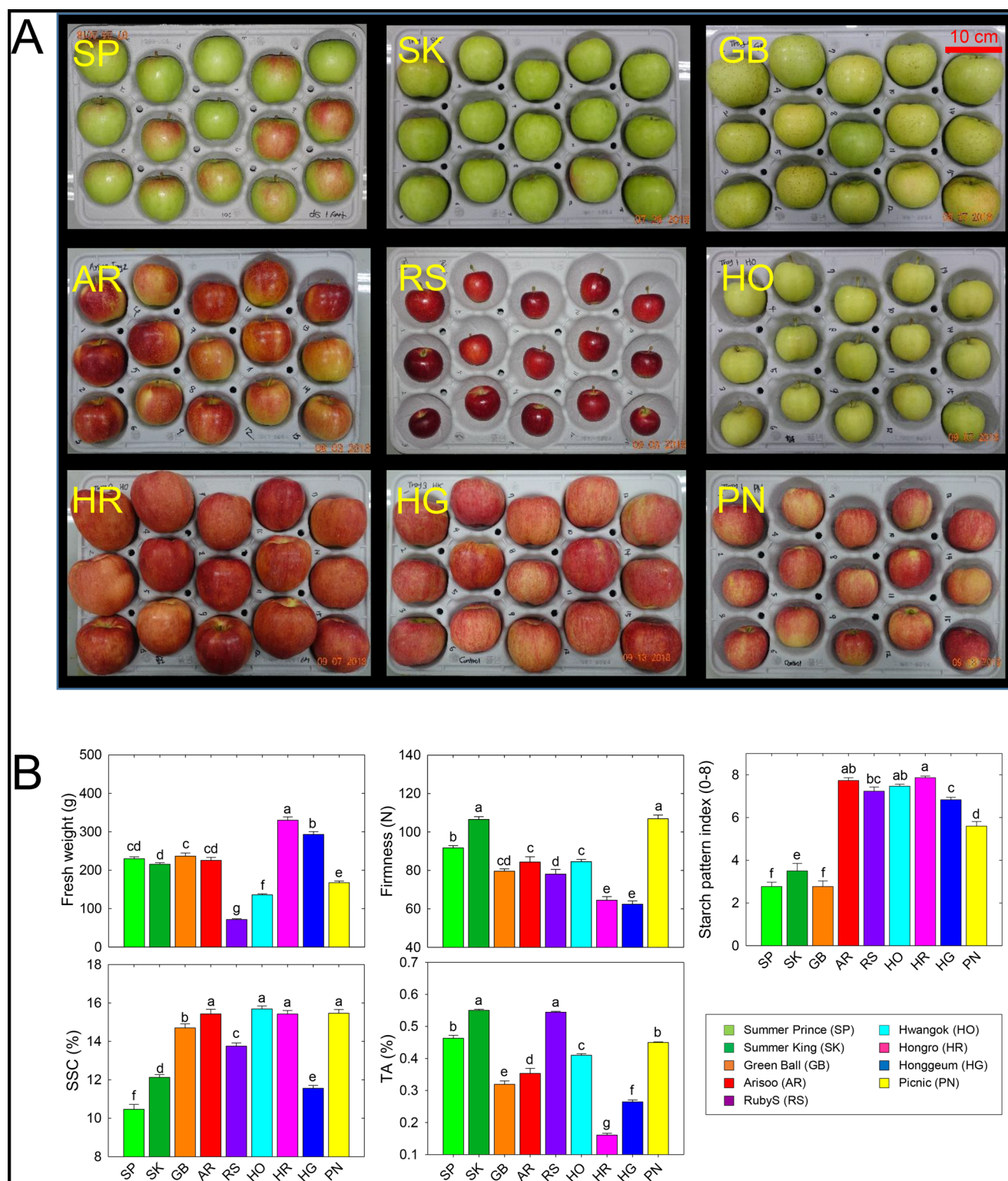


Fig. 1 The fruit appearance (**A**) and fruit quality characteristics (**B**) of nine apple cultivars at harvest. 490 mm (wide) × 330 mm (long) trays were used. First photograph on the upper left shows ‘Summer Prince’ (SP), ‘Summer King’ (SK), ‘Green Ball’ (GB), ‘Arisoo’ (AR), ‘RubyS’ (RS), ‘Hwangok’ (HO), ‘Hongro’ (HR), ‘Honggeum’ (HG), and ‘Picnic’ (PN) cultivars (**A**). Fruit fresh weight, flesh firmness, starch pat-

tern index (SPI), soluble solids content (SSC), and titratable acidity (TA) were expressed as the mean of 15 fruits as replicates ($n=15$) ± standard error (SE). Different letters on each bar indicate significant difference among nine apple cultivars based on least significant difference (LSD) test at $p<0.05$

2.3 Soluble carbohydrates, organic acids, and amino acids

Apple flesh tissue was analysed for soluble carbohydrates, organic acids, and amino acids using an adapted protocol from previous studies (Byeon and Lee 2020). For each cultivar, three biological replicates were analysed, each consisting of homogenized tissue from five fruits. Soluble carbohydrates were quantified by injecting 10 μ L of extract into an HPLC system with a refractive index detector and Sugar-Pak column. Organic acids were measured using HPLC with UV and refractive index detectors. Amino acids were analyzed by mixing 1 μ L of extract with borate buffer, *O*-phthalaldehyde, fluorenylmethyloxycarbonyl, and deionized water. A 0.5 μ L aliquot was injected into an HPLC with UV and fluorescence detectors, and a C18 column (Lwin et al. 2023a, b).

2.4 Phenolic compounds

The lyophilized powder (0.3 g) was homogenized with 3 mL of 80% methanol for 1 min, vortexed for 1 min, sonicated for 20 min on ice and later centrifuged at 4 °C for 10 min. Then, the supernatant was filtered using a syringe PVDF membrane filter.

Total phenolic content was determined using a modified Folin–Ciocalteu method (Singleton et al. 1999). Total flavonoid content was quantified using a previously reported method with modifications (Jia et al. 1999). The total anthocyanin content was determined using the pH differential method (Zhang et al. 2010a). Determination of total antioxidant activity was assessed by DPPH radical scavenging capacity (Win et al. 2021a). The 3 mL DPPH solution was mixed with 200 μ L extract, incubated for 30 min at 22 °C, and absorbance was measured at 517 nm. For the ABTS assay (Re et al. 1999), 200 μ L extract was mixed with 3 mL ABTS reagent, incubated for 6 min, and absorbance read at 734 nm.

The contents of individual phenolic compounds were determined using a previously reported method with some modifications (Latt et al. 2024; Zhang et al. 2010a). A lyophilized sample (0.5 g) was ground and extracted with 5.0 mL of 70% methanol containing formic acid (2%) and vortexed. The qualitative analysis was performed using an HPLC instrument equipped with a DAD detector and column. Individual phenolic compounds were classified and quantified according to their retention times in comparison to authentic standards.

2.5 Mineral nutrient contents

Frozen fruit samples (0.1 g) were mixed with 4 mL nitric acid and incubated at room temperature in a glass beaker for 24 h. The sample was placed on a hot plate at 200 °C, and hydrogen peroxide (3 mL) was added when the mixture began to boil. The solution was diluted to 10 mL with 1 N HCl and 1,000 ppm lanthanum⁺ and centrifuged at 4,000 rpm for 10 min. Supernatants were analyzed by inductively coupled plasma (Byeon et al. 2025).

2.6 Volatile organic compounds

Frozen ground samples were added to sodium chloride and 5 μ L 1,2,3-trichloropropane (internal standard) in a 20 mL head space vial. After vortexing, the mixture was analyzed using headspace solid-phase microextraction (HS-SPME) held with gas chromatography-mass spectrometry (GC-MS). The GC-MS injector was set at 250 °C for 3 min for desorption. A fibre conditioning station was used at 270 °C for 40 min. The gas chromatography instrument was equipped with MS and a DB-WAX capillary column (60 m $\times$ 0.25 mm $\times$ 0.5 μ m). For separation and identification of VOCs, the flow rate of carrier gas (He) was set at 2 mL min⁻¹. Identification of VOCs was performed using the NIST 2.0 mass spectral library.

2.7 Statistical analyses

A completely randomised design was used to evaluate the effects of fruit harvest-season based apple cultivars on fruit quality attributes, mineral nutrients, and untargeted metabolites at harvest. All analyses of mineral nutrients and targeted metabolites were performed in triplicate ($n=3$) with five fruits per replicate. The results were expressed as mean $\pm$ standard error (SE). Data were processed to analysis of variance (ANOVA) to determine the effects of fruit harvest-season based apple cultivars and then the least significant difference (LSD) test (Ver. 9.3; SAS Institute Inc., Cary, NC, USA) was applied for verifying the significant differences of fruit quality attributes, mineral nutrients, and targeted metabolites to apple cultivars at harvest. MetaboAnalyst 6.0 was employed to perform cluster analysis, partial least squares discriminant analysis (PLS-DA) and generate corresponding loading plots. Additionally, MetaboAnalyst 6.0 supported correlation coefficient heatmap matrix to examine interrelationships among fruit quality metrics, mineral components, and targeted metabolites. A correlation coefficient network was generated using MetScape (v3.1.3) integrated with Cytoscape.

3 Results

3.1 Fruit quality attributes among cultivars at harvest

The fruit appearance of nine commercial apple cultivars used in this study, in terms of fruit size and peel pigmentation at harvest was shown in Fig. 1A. Fruit fresh weight was highest in the ‘Hongro’ but lowest in the ‘RubyS’. Flesh firmness was highest in ‘Summer King’ and ‘Picnic’ cultivars, but lowest in the ‘Honggeum’. Starch pattern index (SPI) for starch degradation rate was highest in the ‘Hongro’ but lowest in ‘Summer Prince’ and ‘Green Ball’ cultivars. Soluble solids content (SSC) was highest in the ‘Hwangok’ but lowest in the ‘Summer Prince’. Titratable acidity (TA) was greatest in the ‘Summer King’ but lowest in the ‘Hongro’ (Fig. 1B).

3.2 Normalized heatmap matrix for overall responses to apple cultivars

The normalized heatmap matrix system, with a hierarchical cluster analysis, was applied to evaluate the overall response of fruit quality attributes, mineral nutrients, and targeted metabolites (Fig. 2). The results showed two major clusters with the ‘Hwangok’, ‘Summer Prince’, and ‘Summer King’ cultivars clustered into one major cluster and the other cultivars clustered into another. ‘Hongro’ was the least clustered with the other cultivars within the other major cluster. Nonetheless, the ‘Hongro’, ‘Honggeum’, ‘RubyS’, and ‘Picnic’ cultivars were closely clustered; the ‘Arisoo’ and ‘Green Ball’ were tightly clustered; and the ‘RubyS’ and ‘Picnic’ were clustered the closest (Fig. 2).

3.3 Partial least squares-discriminant analysis (PLS-DA) and variable importance in projection (VIP) scores

The partial least squares-discriminant analysis (PLS-DA) model (Fig. 3) showed that latent variables 1 and 2 accounted for 37.5% and 17.8% of the total variance on the X- and Y-axes, respectively. ‘Summer King’ was closely associated with the ‘Summer Prince’, but the ‘Summer King’ was tightly associated with itself, but less so in the ‘Summer Prince’. The ‘Honggeum’, ‘Hongro’, ‘RubyS’, and ‘Picnic’ cultivars were closely associated. Additionally, the ‘Arisoo’, ‘Green Ball’, and ‘Hwangok’ were closely linked (Fig. 3A). Based on the normalized heatmap and PLS-DA scores from nine cultivars, ‘Summer King’, ‘Arisoo’, and ‘Picnic’ showed minimal internal variation, resulting in clear separation in the scores plot (Fig. 3B). In this plot, latent variables 1 and 2 accounted for 41.0% and

35.1% of variance, respectively. To determine the important predictor variables, the variable importance in projection (VIP) scores plot approach was applied (Fig. 3C). Important variables derived from all the predictor variables were screened from ≥ 1 VIP scores. 49 variables had $\text{VIP} \geq 1$, regardless of cultivar. Among these variables, the ‘Arisoo’ showed higher levels of hyperin, SPI, amyl acetate, hexanal, quercetin, 1-butanol, quercitrin, 2-methyl-1-butyl acetate, 2-methyl-1-butanol, butyl 2-methylbutyrate, caffeic acid, isoleucine, aspartic acid, and Mg. Meanwhile, the ‘Summer King’ indicated higher levels of TA, malic acid, *p*-coumaric acid, cortex h° , glutamic acid, methionine, alanine, ferulic acid, rutin, lysine, citric acid, asparagine, tyrosine, peel C^* , glutamine, arginine, fumaric acid, histidine, threonine, core h° , proline, phenylalanine, serine, total anthocyanin, valine, and peel h° . However, the ‘Picnic’ had higher levels of the variables such as SSC, firmness, sucrose, sorbitol, glucose, 1-hexyl acetate, benzothiazole, pentanoic acid, and core C^* (Fig. 3C).

3.4 Comparative responses of individual variables to apple cultivars

Based on the results of the VIP scores, in which the individual variables were higher than 1 VIP scores, TA, malic acid, *p*-coumaric acid, cortex h° , glutamic acid, methionine, alanine, ferulic acid, rutin, lysine, citric acid, asparagine, tyrosine, peel C^* , glutamine, arginine, fumaric acid, histidine, threonine, core h° , proline, phenylalanine, serine, total anthocyanins, valine, and peel h° were higher in the ‘Summer King’ than in ‘Arisoo’ and ‘Picnic’ (Fig. 4A). Hyperin, SPI, amyl acetate, hexanal, quercetin, 1-butanol, quercitrin, 2-methyl-1-butyl acetate, 2-methyl-1-butanol, butyl 2-methylbutyrate, caffeic acid, isoleucine, aspartic acid, and Mg were highest in the ‘Arisoo’, compared with that of the ‘Summer King’ and ‘Picnic’ (Fig. 4B). Additionally, SSC, flesh firmness, sucrose, sorbitol, glucose, 1-hexyl acetate, benzothiazole, pentanoic acid, and core C^* were highest in the ‘Picnic’, compared with that of the ‘Summer King’ and ‘Arisoo’ (Fig. 4C).

3.5 Metabolic pathway analysis between ‘Summer King’ and ‘Arisoo’

Metabolic pathway analysis of three apple cultivars was conducted using the *Arabidopsis thaliana* KEGG database (Figs. S10, S11, and 6). Based on VIP scores (Fig. 3C) and related results (Fig. 4A and B), the comparison between ‘Summer King’ and ‘Arisoo’ was prioritized. A total of 46 metabolic pathways were matched with the detected metabolites. Among the upregulated metabolic pathways in the ‘Summer King’, compared with those in the ‘Arisoo’,

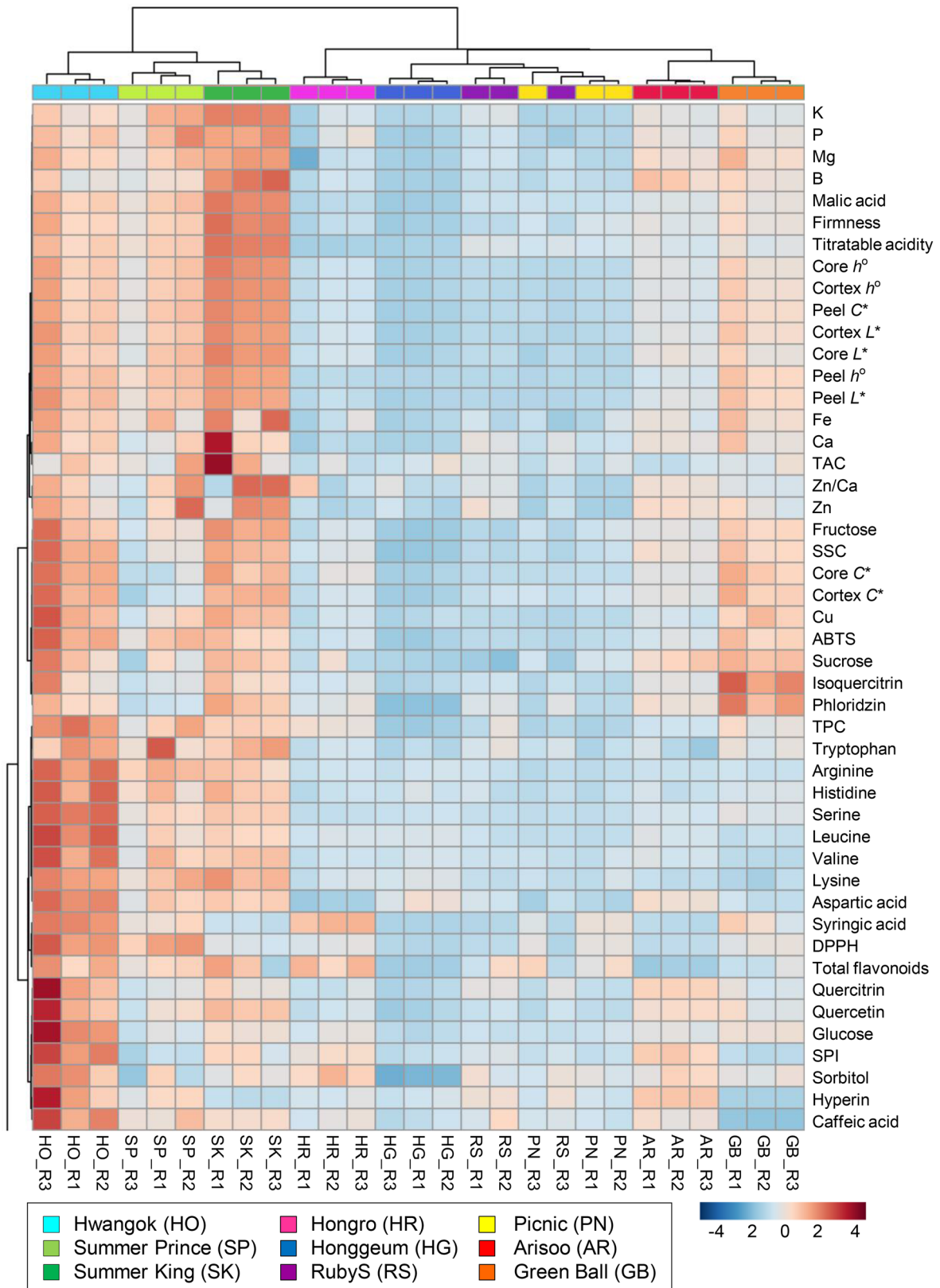


Fig. 2 Normalized heatmap matrix with a hierarchical cluster analysis of fruit physiological quality attributes, soluble carbohydrates, organic acids, amino acids, phenolic compounds, volatile organic compounds

(VOCs), and mineral nutrients in nine apple cultivars at harvest. Each cell indicates the results of five fruits per replicate (R)

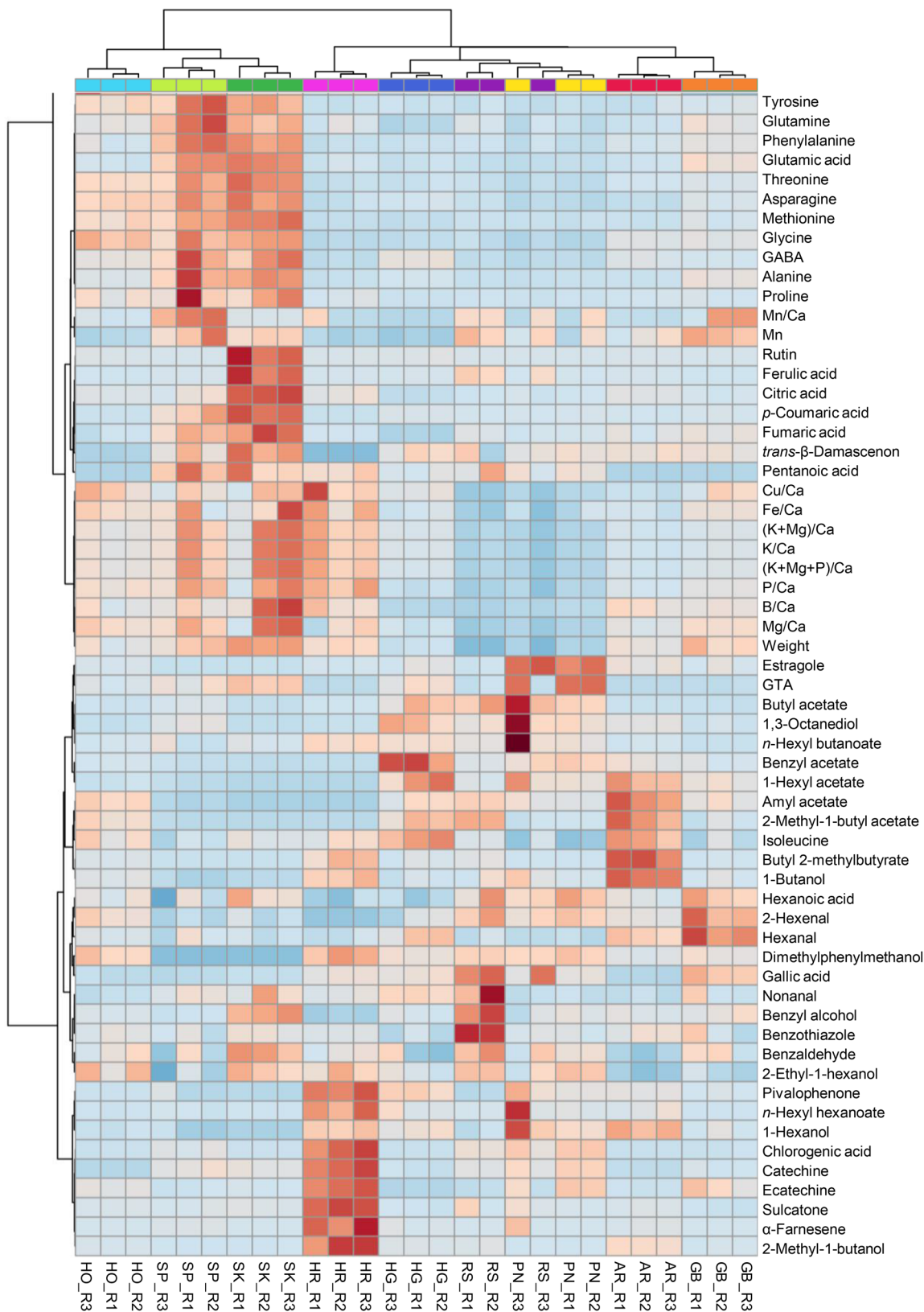


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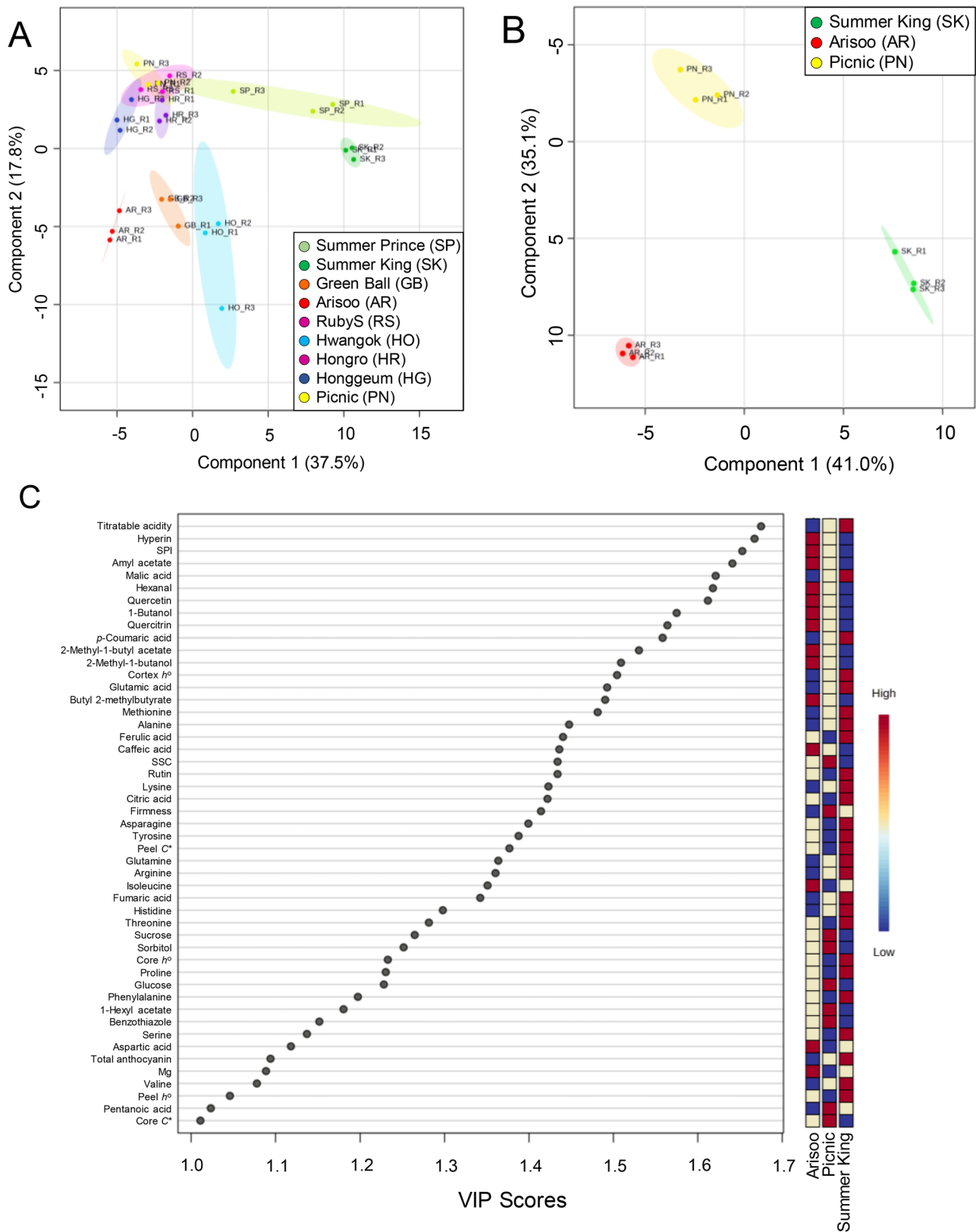


Fig. 3 Partial least squares-discriminant analysis (PLS-DA) scores plot (A) among nine apple cultivars at harvest; partial least squares-discriminant analysis (PLS-DA) scores plot (B) and variable importance

in projection (VIP) scores plot (C) only among three apple cultivars at harvest. The selected individual variables based on the results of a VIP score higher than 1.0 were only present

pyruvate metabolism, TCA cycle, and glyoxylate and dicarboxylate metabolism mapped with two, three, and six metabolites, respectively. Arginine and proline metabolism; alanine, aspartate, and glutamate metabolism; tyrosine metabolism; arginine metabolism; glycine, serine, and threonine metabolism; and phenylalanine metabolism were mapped with four, six, two, five, five, and one metabolite, respectively. Isoquinoline alkaloid biosynthesis, glutathione metabolism, and butanoate metabolism were mapped as one, two, and two metabolites, respectively. However, for the ‘Arisoo’ compared with that of the ‘Summer King’, flavone and flavonol biosynthesis and starch and sucrose metabolism mapped with three and four metabolites, respectively (Fig. 5).

3.6 Comparative responses of amino acids, phenylpropanoid, and volatile organic compounds metabolic pathways

Based on the results of all the targeted metabolites, we focused on the comparative metabolic responses of the amino acid, phenylpropanoid, and VOC biosynthesis pathways among the three (‘Summer King’, ‘Arisoo’, and ‘Picnic’) cultivars (Fig. 6). Based on the VIP scores (Fig. 3C), important metabolites were identified in the amino acid, phenylpropanoid, and VOC biosynthesis pathways. Among amino acid pathways, serine, alanine, valine, asparagine, threonine, methionine, lysine, phenylalanine, tyrosine, proline, glutamic acid, glutamine, arginine, and histidine levels were highest for the ‘Summer King’. Isoleucine and aspartic acid levels were highest in the ‘Arisoo’ (Fig. 6A). For the phenylpropanoid metabolic pathway, *p*-coumaric acid, ferulic acid, and rutin levels were highest in the ‘Summer King’. However, caffeic acid, quercetin, and quercitrin levels were highest in the ‘Arisoo’ (Fig. 6B). Among VOC metabolic pathways, the relative ratios of hexanal, 2-methyl-1-butanol, 1-butanol, amyl acetate, 2-methyl-1-butylacetate, and butyl 2-methylbutyrate were highest in the ‘Arisoo’. However, the relative ratios of benzothiazole and pentanoic acid were highest in the ‘Picnic’ (Fig. 6C).

4 Discussion

Apple fruit quality attributes varied among cultivars and across the harvest season (Figs. 2 and S1). Fruit peel pigmentation and fruit size also differed among cultivars, as shown in Fig. 1A and B due to the variation among apple cultivars. In addition, some fruit quality traits appeared to show seasonal trends between July and mid-September. Among the fruit quality attributes, a decrease in flesh firmness was highly correlated with the lateness of the fruit

harvest season and strongly associated with an increase in SSC and decrease in TA (Fig. 1B) with some exceptions. Flesh firmness gradually declined with advances in harvest time across all cultivars (Yoo et al. 2016; Zhang et al. 2019). However, flesh firmness and IEC were correlated inversely with advance in harvest season (Watkins et al. 2000). Nonetheless, the harvest time-dependent response of flesh firmness remains inconsistent with the harvest time in harvest-season based cultivars (Chai et al. 2020; Feng et al. 2014). Additionally, a generally negative relationship exists between SSC and TA in harvest-season based apple cultivars, and the relationship between SSC and TA across apple cultivars does not consistently respond to harvest (Drogoudi et al. 2008). These results suggest that fruit physiological attributes such as flesh firmness, SSC, and TA exhibit cultivar dependent seasonal patterns at harvest rather than uniform responses to harvest season alone.

The levels of SSC and major soluble carbohydrates such as sucrose, sorbitol, and glucose were highest in the mid-season cultivar ‘Picnic’ compared with those in early-season cultivars (Figs. 1B and 4C). However, SPI was not the greatest in the ‘Picnic’ (Fig. 1B) despite the high responses of SSC and soluble carbohydrates. This result may reflect the unique fruit characteristics of the ‘Picnic’ apple cultivar, which are medium-sized and have higher flesh firmness compared to the other mid-season cultivars (Kwon et al. 2015; Win et al. 2021b). Among the major soluble carbohydrates, sorbitol was correlated more strongly with perceived sweetness than with a single soluble carbohydrate or total sugar content (Aprea et al. 2017). Thus, soluble carbohydrates and SSC were not upregulated in either cultivar or did not match in any potential metabolic pathway analysis (Fig. 5). The individual soluble carbohydrate levels per fruit increased sharply with the advance in fruit development and ripening; however, starch levels reduced inversely (Zhang et al. 2010b). It could be explained that the accumulation of single soluble carbohydrates indicates the starch hydrolysis process and that soluble carbohydrate levels gradually increase with advance in fruit development and ripening, highly influenced by fruit harvest-season based cultivars. Therefore, the negative relationship between the decrease in starch and the increase in soluble carbohydrate levels reflects cultivar-dependent developmental and ripening patterns at harvest, rather than a uniform response driven solely by harvest season.

Although TA showed wide variation across apple cultivars at harvest, it was highest in the early-season cultivars, namely, ‘Summer Prince’ and ‘Summer King’ than in the other cultivars (Fig. 1B). Additionally, malic acid level was higher in the ‘Summer King’ than in the ‘Arisoo’ and ‘Picnic’ (Fig. 4). This was associated with a greater enhancement of the TCA cycle, pyruvate metabolism, and glyoxylate and

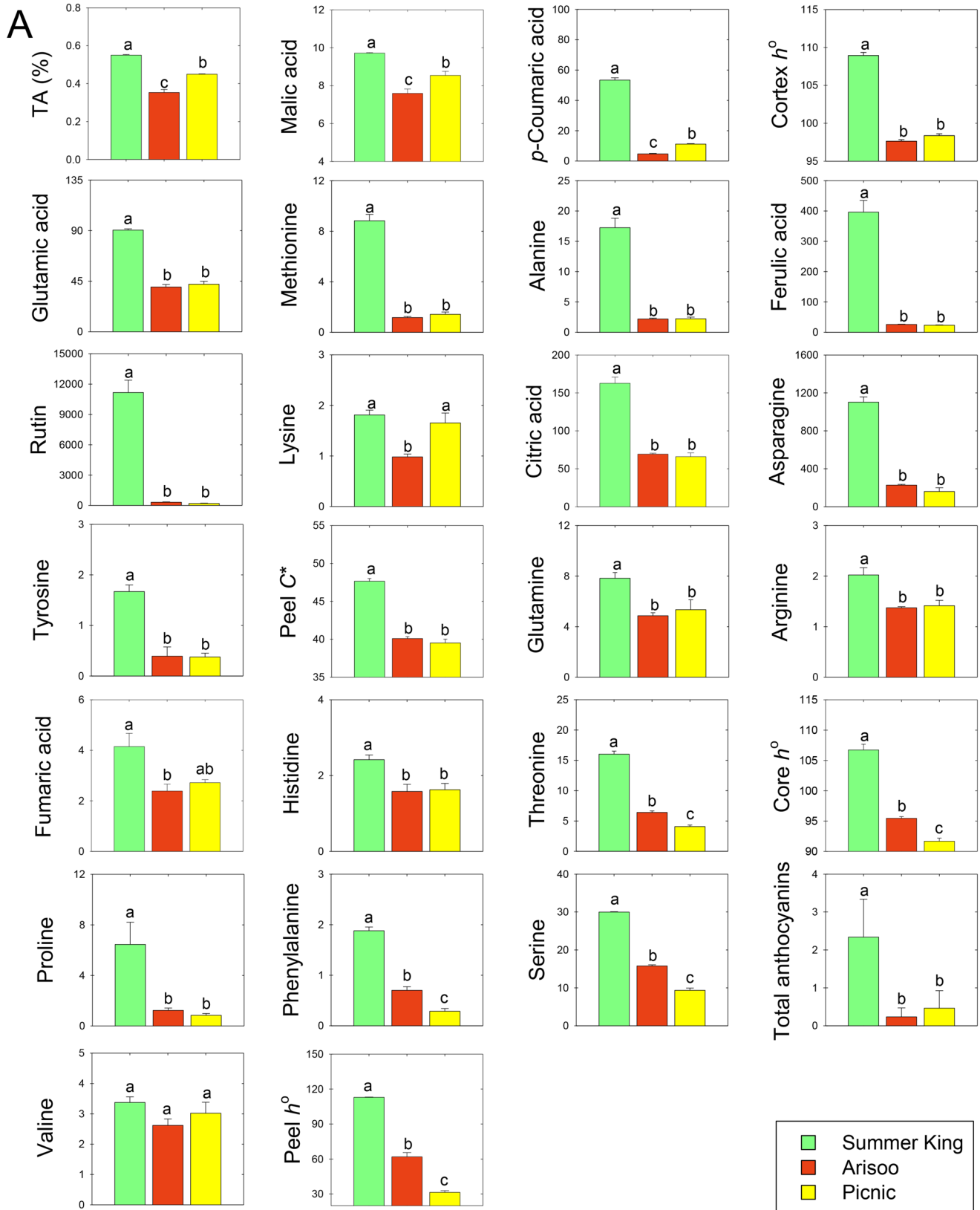


Fig. 4 The responses of selected individual variables based on higher than 1.0 VIP score as well as higher values in ‘Summer King’ cultivar (A), ‘Arisoo’ cultivar (B), and ‘Picnic’ cultivar (C) only present, respectively. The units of organic acids, amino acids, and phenolic compounds are represented in g kg^{-1} FW, mg kg^{-1} FW, and mg kg^{-1} DW, respectively. The results of volatile organic compounds (VOCs) are expressed as relative response ratio. Each data point was the mean ($n=3$) $\pm$ standard error (SE) with five fruits per replicate. Different letters on each bar indicate significant differences among three apple cultivars based on least significant difference (LSD) test at $p<0.05$

dicarboxylate metabolism in the ‘Summer King’ than in ‘Arisoo’, as evidenced by the results of the metabolic pathway analysis (Fig. 5). Similarly, malic acid level was higher in the ‘Summer King’ than in both newly released and conventional apple cultivars at harvest. It was mentioned that, among total organic acids, the TA level was highest in the ‘Summer King’ (Kim et al. 2019). This may imply that higher malic acid and TA levels could be attributed to the fact that early season apple cultivars may be relatively less mature or ripe compared with late-harvest apple cultivars, thereby potentially delaying the downregulation of the TCA cycle, pyruvate metabolism, and glyoxylate and dicarboxylate metabolism. With advances in fruit development and ripening, organic acid levels have gradually declined, although individual organic acids respond differently in different cultivars (Sadar et al. 2016; Xu et al. 2020). Most differentially expressed genes (DEGs) that are associated with the TCA cycle are highly upregulated as fruit development and ripening process (Xu et al. 2020). Therefore, these results suggest that early-season cultivars may be relatively less mature. This implies that organic acid-related metabolisms, including the TCA cycle, pyruvate metabolism, and glyoxylate and dicarboxylate metabolism, remains at a relevant level to retain major organic acids such as malic acid, which helps maintain a higher TA level at harvest compared to mid-season cultivars.

Several amino acids were more highly accumulated in the ‘Summer King’ cultivar compared to the others (Fig. 4). Consequently, several amino acid metabolism pathways, including those for arginine and proline; alanine, aspartate, and glutamate; tyrosine; glycine, serine, and threonine; arginine; and phenylalanine metabolisms matched and were more upregulated in the ‘Summer King’ than in ‘Arisoo’ (Figs. 5 and 6A). The levels of most amino acids continued to increase with fruit development and ripening; however, the levels of some of the amino acids, such as glutamic acid, arginine, alanine, phenylalanine, and methionine, suddenly declined at the end of fruit development and ripening stage in the flesh tissues of the ‘Honeycrisp’ cultivar (Zhang et al. 2010b). Additionally, advances in fruit maturation and ripening are correlated with a gradual increase in levels of certain amino acids, including aspartic acid, histidine, methionine, isoleucine, lysine, threonine, and tyrosine in the

‘Jonamac’ apple peel tissues (Li et al. 2013). However, most amino acid levels gradually declined during the pre-climacteric period of ripening. In contrast, the ‘Jonagold’ cultivar had a slower increase in histidine, isoleucine, leucine, methionine, phenylalanine, tryptophan, and valine concentration during the post-climacteric stage of fruit ripening after harvest (Sugimoto et al. 2011). Thus, aromatic and branched-chain amino acid levels fluctuated highly during fruit maturation and ripening (Gonda et al. 2010; Tieman et al. 2006). Additionally, the levels of most amino acids were significantly higher in the early-season cultivar than in the other cultivars. This phenomenon could be attributed to the higher levels of precursors or intermediate metabolic compounds made available from the TCA cycle, pyruvate metabolism, and glyoxylate and dicarboxylate metabolism in the ‘Summer King’ (Fig. 5). Thus, increased activity of glycolysis- and TCA cycle-based energy metabolism results in a greater availability of substrates to generate or elevate the levels of numerous amino acids. Furthermore, the differential responses of amino acids among apple cultivars may be associated with their harvest seasons. For example, the early-season ‘Summer King’ cultivar showed higher levels of numerous amino acids than the other mid-season cultivars. These results suggest that fruit maturity could differ at harvest between early- and mid-season cultivars.

Several phenolic compounds, including *p*-coumaric acid, ferulic acid, rutin, and total anthocyanins, were highest in the ‘Summer King’ than in the others (Fig. 4A); however, the quercetin, quercitrin, and caffeic acid levels were highest in the ‘Arisoo’ (Fig. 4B). In addition, several individual phenolic compounds were more upregulated in the ‘Summer King’ than in the ‘Arisoo’. This could be attributed to the upregulation of phenylalanine metabolism in the ‘Summer King’, as evidenced by the results of the metabolic pathway analysis (Figs. 5 and 6A and B). The phenolic compound profiles and contents are highly diverse across apple cultivars during fruit development and the ripening period (Kondo et al. 2002; Renard et al. 2007; Wojdyło et al. 2008), geographic region (McGhie et al. 2005), and production systems (Hecke et al. 2006; Veberic et al. 2005). The concentrations of individual and total phenolic compounds decline with advances in fruit development and ripening, irrespective of the cultivars (Kondo et al. 2002; Renard et al. 2007; Zhang et al. 2010b). This study showed that no single cultivar exhibited consistent changes in individual or total phenolic compounds across a wide range of fruit ripening and maturity stages. However, early-season cultivars generally showed higher levels of phenolic compounds, and these compounds were further upregulated in mid-season cultivars. These results suggest that the upregulation of phenolic compounds could be a strong factor in fruit maturation and ripening. Additionally, flavone and flavonol

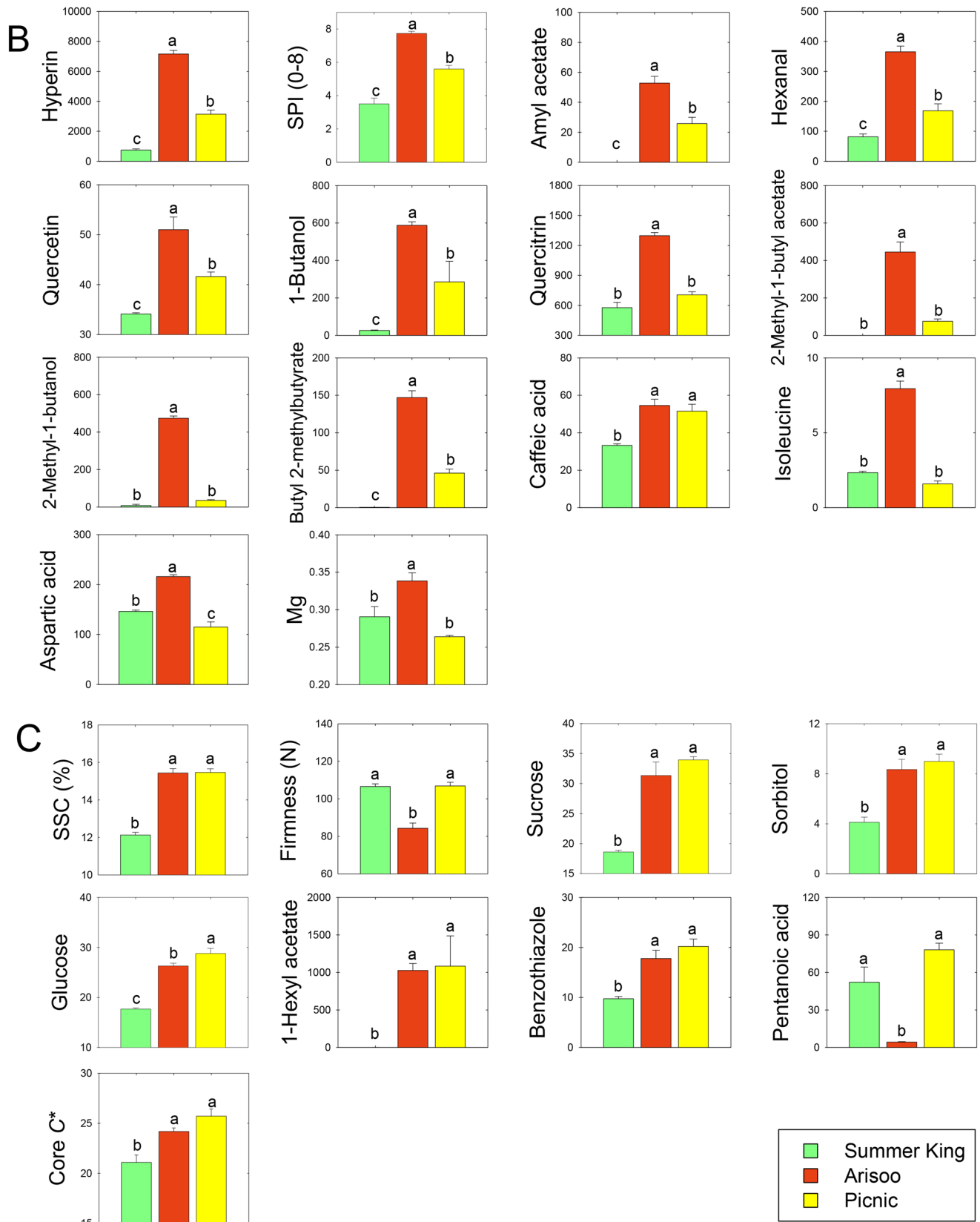
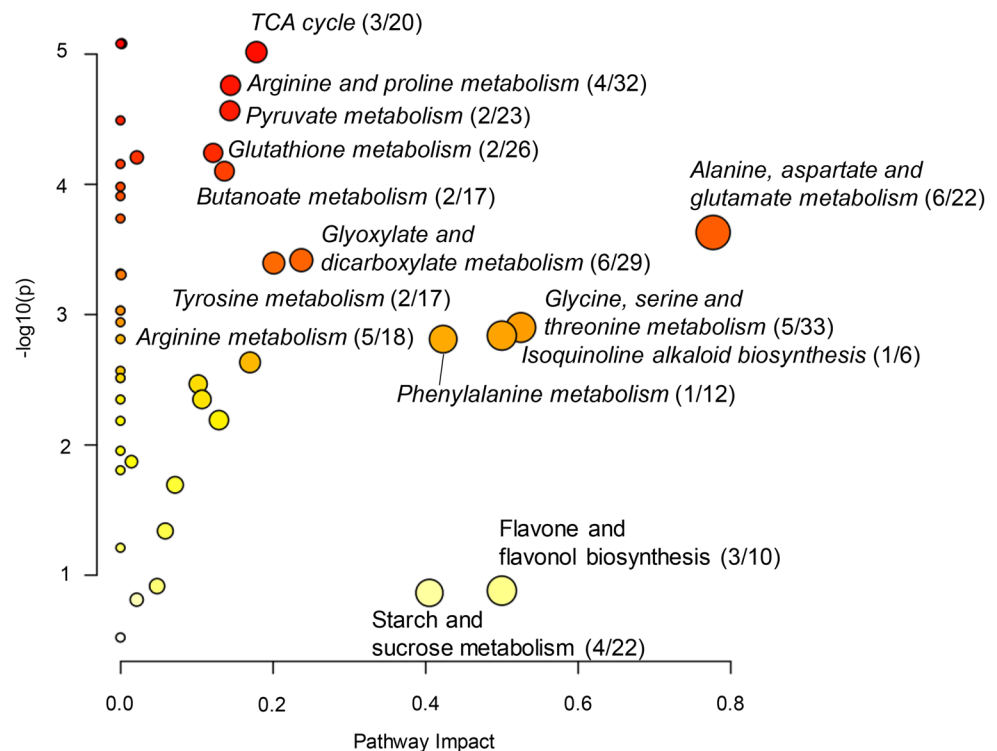


Fig. 4 (continued)

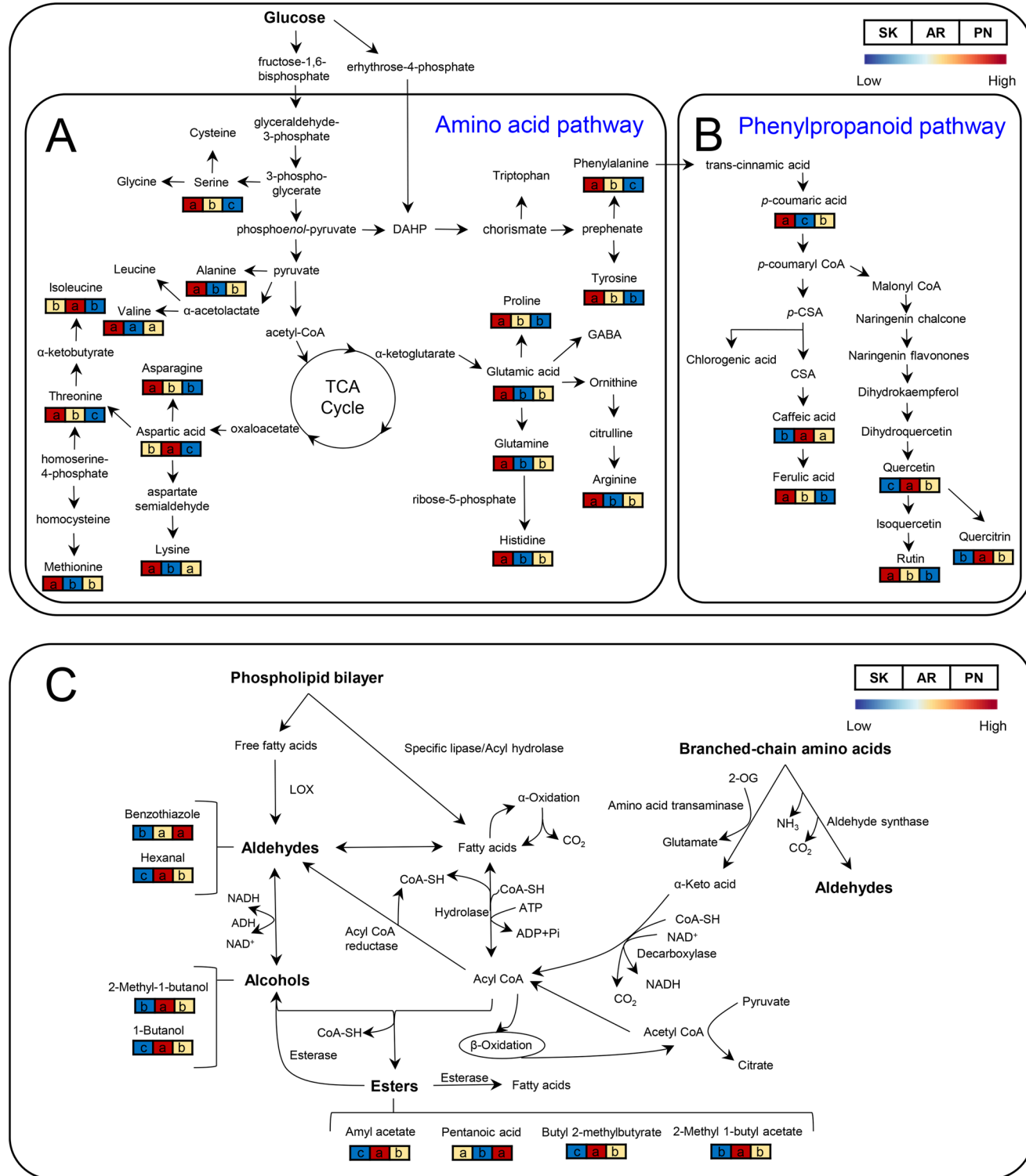
Fig. 5 Pathway analysis of annotated metabolites in the ‘Summer King’ and ‘Arisoo’ cultivars. The X-axis marks pathway impact, and the Y-axis represents statistical significance of pathway enrichment. Pathway annotation is based on the Kyoto Encyclopedia of Genes and Genomes (KEGG) metabolic pathway database in *Arabidopsis thaliana*. Redder circle colors indicate more significant changes in metabolites in the corresponding pathway. The size of the circle corresponds to the pathway impact score and is correlated with the centrality of the involved metabolites. The italic font and the number in parentheses indicate up-regulated pathways in the ‘Summer King’ cultivar and matching status of each metabolite in each pathway, respectively



biosynthesis metabolism was upregulated in the early-season apple cultivars according to the results of the metabolic pathway analysis (Fig. 5). Thus, the final metabolites of the phenylpropanoid pathway accumulated to higher levels in the early-season cultivar ‘Summer King’ compared with the other cultivars (Fig. 6B). These results suggest that elevated phenolic compounds are more closely associated with relatively lower fruit maturity and ripening at harvest in early-season cultivars than in mid-season cultivars.

In contrast, the mid-season cultivars, ‘Arisoo’ and ‘Picnic’ showed the highest levels of several VOCs than those observed in early-season cultivars (Fig. 4B and C). Most of the VOCs were primarily upregulated in the ‘Arisoo’ but responded negligibly in the ‘Summer King’ cultivar. Except for butanoate metabolism, no other VOC metabolism showed upregulation in the ‘Summer King’ (Fig. 5). In addition to increased VOC levels, isoleucine, which is a branched-chain amino acid, plays a pivotal role in VOC metabolism during fruit ripening (Gonda et al. 2010; Kochevenko et al. 2012). Therefore, more aldehydes, alcohols, and esters accumulated in the mid-season cultivars than in the early-season cultivars (Fig. 6C). Unlike amino acid responses, most VOCs accumulate as a result of aromatic and branched-chain amino acid metabolism during fruit maturity and ripening (Defilippi et al. 2005; Sugimoto et

al. 2021). Moreover, the distinctive responses of VOCs to apple cultivars suggest an association between fruit maturity and ripening, although they varied across apple cultivars from early- to mid-season cultivars, but not across a wide range of fruit maturities from a single cultivar. In contrast, the highest levels of the aromatic amino acids, tyrosine and phenylalanine were detected in the ‘Summer King’ compared to the mid-season cultivars (Fig. 4A). This implies that tyrosine and phenylalanine metabolisms were relatively more upregulated in the early-season cultivar, based on the metabolic pathway analysis (Fig. 5). Tyrosine and phenylalanine are aromatic amino acids that are essential for VOC metabolism during fruit maturity and ripening (Gonda et al. 2010; Tzin et al. 2013). Phenylalanine is accumulated highly after 1-methylcyclopropene (1-MCP) treatment in long-term controlled atmosphere (CA)-stored ‘Empire’ apples along with the accumulation of branched-chain amino acids, which suppressed VOC production (Lee et al. 2012). This suggests that, although the metabolite (or substrate) pool of aromatic amino acids was sufficiently high in fruits from early-season cultivars, they could not be used to produce any relevant VOCs because they would impede full maturity or ripening at harvest. Therefore, most VOC levels tended to be lower in the early-season cultivars than in the mid-season cultivars.



5 Conclusion

Of the nine apple cultivars harvested between late July and mid-September, flesh firmness and TA were higher in the early- than in mid-season cultivars, while SSC and SPI were lower. Hierarchical cluster analysis detected two major clusters: found with three cultivars, namely the ‘Summer King’, ‘Summer Prince’, and ‘Hwangok’ in the first cluster and the remaining six cultivars in the second major cluster. The normalized heatmap matrix indicated that all variables derived from fruit quality attributes, mineral nutrients, and targeted metabolites were clearly segregated depending on the cultivar. The PLS-DA scores plot indicated that the apple cultivars were clearly separated based on the harvest season. In conclusion, three cultivars showed the tight response to and the least degree of fluctuation in all variables among the nine cultivars. The VIP scores indicated that TA, malic acid, *p*-coumaric acid, cortex *h*^o, glutamic acid, methionine, alanine, ferulic acid, rutin, lysine, citric acid, asparagine, tyrosine, peel *C*^{*}, glutamine, arginine, fumaric acid, histidine, threonine, core *h*^o, proline, phenylalanine, serine, total anthocyanin, and peel *h*^o were highest in the ‘Summer King’ but hyperin, SPI, amyl acetate, hexanal, quercetin, 1-butanol, quercitrin, 2-methyl-1-butyl acetate, 2-methyl-1-butanol, butyl 2-methylbutyrate, caffeic acid, isoleucine, aspartic acid, and Mg were highest in the ‘Arisoo’. Furthermore, SSC, firmness, sucrose, sorbitol, glucose, 1-hexyl acetate, benzothiazole, pentanoic acid, and core *C*^{*} were highest in the ‘Picnic’. The different metabolic responses between the ‘Summer King’ and ‘Arisoo’ showed that the most amino acids, organic acids, and phenolic compounds were highly upregulated in the ‘Arisoo’. Overall, the results indicated that the differential responses of all variables in apples harvested from early- to mid-season cultivars may be strongly associated with fruit maturity and ripening.

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Data availability The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethical approval Not applicable.

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