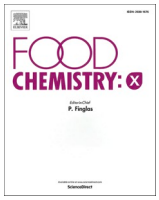
Food Chemistry: X 23 (2024) 101698

Contents lists available at ScienceDirect

Food Chemistry: X

journal homepage: www.sciencedirect.com/journal/food-chemistry-x



Metabolic basis for superior antioxidant capacity of red-fleshed peaches

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ARTICLE INFO

Chemical compounds studied in this article:
Chlorogenic acid (PubChem CID: 1794427)
Cryptochlorogenic acid (PubChem CID: 9798666)
Cyanidin-3-*O*-glucoside (PubChem CID: 441667)
Gallic acid (PubChem CID: 370)
Proanthocyanidin B2 (PubChem CID: 130556)
Rutin (PubChem CID: 5280805)

Keywords:
Red-fleshed peach
Phenolic compounds
Antioxidant activity
Anthocyanins
Phenolic acids

ABSTRACT

Peach fruit is an important natural source of phenolic compounds that are well-known to have health benefits, but their metabolic basis remain elusive. Here, we report on phenolic compounds accumulation and antioxidant activity of ripe fruits in peach. A considerable variation in phenolic compounds content was observed among peach germplasm, with significantly higher levels detected in red-fleshed peaches compared to non-red-fleshed peaches. Antioxidant activity of crude extracts from ripe fruits showed significant differences among peach germplasm, with red-fleshed peaches having the strongest antioxidant activity. Intriguingly, it was observed that total phenolics instead of anthocyanins were strongly associated with antioxidant activity. Phenolic compounds content and antioxidant activity showed dynamic changes throughout fruit development, and these were much higher in the peel than in the flesh. Metabolomic analysis unveiled a coordinated accumulation of anthocyanins as well as key components of flavonoids and phenolic acids, which endows red-fleshed peaches with superior antioxidant activity.

1. Introduction

Phenolic compounds, a diverse group of secondary metabolites, are widely distributed throughout plant kingdom with immense structures and functions. In fruit, phenolic compounds play a pivotal role in countering various biotic and abiotic stresses such as photoprotection and pathogens defense (Ortiz & Sansinenea, 2023; Šamec et al., 2021). Additionally, phenolic compounds are always stored at strategically crucial locations to facilitate pollination and seed dispersal. Besides the well-known physiological functions, phenolic compounds contribute to the overall fruit quality in terms of coloration, flavor, and nutritional value (Ogah et al., 2014).

In general, phenolic compounds are subdivided into several classes, mainly including phenolic acids, flavonoids and tannins (Vogt, 2010). Phenolic acids containing phenolic rings and organic carboxylic acid groups have been demonstrated to exhibit a degree of astringency (Huang & Xu, 2021; Sova & Saso, 2020). Ferulic acid and gallic acid are the predominant phenolic acids identified in banana (Singh et al., 2016; Tsamo et al., 2015). Comparatively, flavonoids, the most abundant category in subphenolic classes, are categorized into different subgroups, including flavones, flavanols, flavanones, flavonols, isoflavones and anthocyanins, with each displaying distinct chemical structures and biological activities (Shen et al., 2022; Winkel-Shirley, 2001). Flavones and flavanones are rich in *Citrus* fruits, with naringin, hesperidin and naringenin being the dominant components (Zhao, Wang, et al., 2020; Zou et al., 2016). As a subgroup of flavonoids, anthocyanins are

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https://doi.org/10.1016/j.fochx.2024.101698
Received 2 May 2024; Received in revised form 21 July 2024; Accepted 23 July 2024
Available online 31 July 2024

responsible for endowing fruit with diverse coloration. Anthocyanins, the glycosylated forms of anthocyanidin, have the C6-C3-C6 carbon structure. The concentration and type of anthocyanins play a pivotal role in fruit coloration (Jaakola, 2013). Anthocyanins are structurally diverse due to the degree and position of hydroxylation and/or methoxylation. The types of anthocyanins vary with fruit species, with cyanidin-3-O-glucoside and peonidin-3-O-glucoside being major components among various fruits (Sun et al., 2023). In Chinese cherry fruit, 26 structurally unique anthocyanins are identified, which contribute to the variation in fruit coloration (Liu et al., 2024). Proanthocyanidins, commonly referred to as condensed tannins, are intricate phenolic compounds with substantial molecular weights widely distributed in fruit (Saigo et al., 2020). The physicochemical and biological property of proanthocyanidins is significantly influenced by the degree of polymerization (Mannino et al., 2021). An appropriate quantity of proanthocyanidins in fruit can elevate the flavor, whereas excessive proanthocyanidins content tend to impart an unpleasant astringency by binding to salivary proteins (Wu et al., 2022).

It is worthy to note that phenolic compounds have drawn considerable attention due to the potential bioactivity. Numerous studies have revealed that phenolic compounds contribute to human health by serving as dietary antioxidants (Olas, 2018; Swallah et al., 2020). Moderate intake of phenolic compounds has positive health benefits such as antidiabetic, anti-inflammatory and cardiovascular protection (Huang et al., 2010; Maleki et al., 2019). The content of total phenolics is found to be related to the antioxidant capacity in *Citrus* species and pomegranate (Fang et al., 2022; Singh et al., 2018). Further investigations have revealed correlations between levels of total phenolics and scavenging activity in lingonberry (Bujor et al., 2018). In kiwifruit, epicatechin is recognized as a primary phenolic component responsible for antioxidant activity (Jiao et al., 2018). The qualitative and quantitative composition of phenolic compounds in fruit are determined by genetic factors and environmental conditions (Shen et al., 2023; Singh et al., 2010). Maintaining optimal level of phenolic compounds is essential for striking a balance between fruit quality and nutritional benefits.

Peach [*Prunus persica* (L.) Batsch] originated in China, where it is considered as an emblem of longevity and immortality. Currently, peach draws particular attention worldwide due to its nutritional properties (Bento et al., 2020; Chen et al., 2023), and red-fleshed peach stands out for the excellent antioxidant activity (Cosme et al., 2022). Previous studies have revealed that red-fleshed peach is abundant in anthocyanins in comparison to white-fleshed and yellow-fleshed peach, which is associated to its exceptional nutritional quality and economic value (Zhou et al., 2015). Furthermore, peach fruit is considered as an important natural source of phenolic compounds with considerable variations among varieties (Ding et al., 2020; Zhang, Su, et al., 2023). Although differences in anthocyanins accumulation have been widely reported, quantitative studies on phenolic compounds in peach fruit with diverse coloration remain limited. Little information is available on the diversity in the composition and concentration of phenolic compounds and antioxidant activity in peach.

This study was undertaken to investigation variations in phenolic compounds content and antioxidant activity among peach germplasm. We characterized the composition and concentration of phenolic compounds, and identified differences in phenolic compounds between red-fleshed and non-fleshed peaches. Our results will be helpful for developing varieties that are rich in bioactive components in peach breeding programs.

2. Materials and methods

2.1. Sample preparation

A total of 110 peach germplasm were utilized (Table S1), consisting of 67 white-fleshed, 36 yellow-fleshed and 7 red-fleshed accessions. All peach accessions are maintained in the orchard located at Northwest Agriculture and Forestry University (Yangling, Shanxi) and Hubei Academy of Agricultural Sciences (Wuhan, Hubei). Flesh of all accessions were separated at the ripening stage. In addition, peel from three accessions, red-fleshed ('4–86-2'), yellow-fleshed ('Huangjinmi3, HJM3') and white-fleshed ('Baifeng, BF') peach, were separated at the mature stage. Flesh of two red-fleshed peach accessions, 'Heitao (HT)' and 'Heiyoutao (HYT)', were collected at five stages of development, including 30 days after full bloom (DAFB) (S1, the first exponential growth), 42 DAFB (S2, pit hardening), 60 DAFB (S3, the second exponential growth), 90 DAFB (S4, commercial maturity), and 120 DAFB (S5, fully ripe).

2.2. Extraction and measurement of phenolic compounds

The peel or flesh samples were ground into powder and 1 g of each sample was incubated with 3 mL extraction solution (1% formic acid in methanol) using ultrasound for 30 min. The supernatants were separated after centrifugation and residues were re-extracted two times more. All obtained extracts were pooled and kept at 4 °C until use. The contents of phenolic compounds were detected as follows.

The content of total phenolics was determined as described previously (Jiao et al., 2018). Briefly, 500 μL appropriately diluted crude extract or standard, 4 mL H_2O and proper Folin-Ciocalteu's phenol reagent were thoroughly mixed for 3 min. Subsequently, 1 mL saturated Na_2CO_3 was supplemented for neutralization. After incubated at 30 °C for 120 min, absorbance was recorded at 760 nm. Total phenolics content was calculated as milligrams of gallic acid equivalent (GAE) per gram of fresh weight (mg GAE/g FW).

The concentration of flavonoids was measured by the colorimetric assay (Zhao, Dong, et al., 2020). Reaction mixture containing appropriate dilutions of crude extract (500 μL), H_2O (1.9 mL), 95% ethanol (1 mL) and 5% $NaNO_2$ (300 μL) was incubated for 6 min. Then the mixture was supplemented with 10% Al $(NO_3)_3$ (300 μL) and kept for 6 min before the addition of 4% NaOH (2 mL). After left in dark at 24 °C for 10 min, absorbance was recorded at 510 nm. Flavonoids content was calculated as milligrams of rutin equivalent (RE) per gram of fresh weight (mg RE/g FW).

Quantitative analysis of flavonols content was performed with the colorimetric protocol method of aluminum chloride (Amoussa et al., 2015). Reaction mixture contained 500 μL extract solution and 500 μL 20% $AlCl_3$. Absorbance was read at 425 nm. Rutin was employed as calibration standard for flavonols quantification.

The proanthocyanidins content was quantified colorimetrically (Wang et al., 2011). Crude extract (500 μL) was supplemented with 3 mL 4% vanillin, followed by 1.5 mL concentrated HCl. Following incubation at 24 °C for 15 min, absorbance was recorded at 500 nm. Proanthocyanidins content was calculated as milligrams of proanthocyanidin B2 equivalent (PB2E) per gram of fresh weight (mg PB2E/g FW).

Anthocyanins content was determined as described previously (Niu et al., 2010). Crude extract (250 μL) was added to 1 mL of either solution A (0.4 M KCl) or solution B (0.4 M citric acid). Absorbance was read at 510 nm and 700 nm respectively.

2.3. Analysis of antioxidant activity by DPPH, ABTS and FRAP assays

The DPPH (2, 2-diphenyl-1-picrylhydrazyl) radical scavenging assay was conducted by following the protocol in a previous report, but with minor modifications (Pang et al., 2017; Zhang, Li, et al., 2023). Appropriately diluted crude extract or standard (180 μL) was added to 20 μL DPPH solution (25 μg/mL). Following incubation at 24 °C in the dark for 60 min, absorbance was recorded at 515 nm. DPPH values was calculated as milligrams of vitamin C equivalent (VcE) per 100 g of fresh weight (mg VcE/100 g FW).

The ABTS (2,2-azino-bis-(3-ehylbenzothiazoline-6-sulphonic acid) diammonium salt) free radical scavenging activity was measured by

previously reported method (Kim et al., 2018). Appropriately diluted crude extract (20 μL) and the ABTS reaction solution (180 μL) were mixed thoroughly and incubated for 6 min at 24 °C to obtain stable absorption values. Subsequently, absorbance was read at 734 nm, with vitamin C employed as the standard.

Ferric reducing antioxidant power (FRAP) assay was conducted as described previously (Ge et al., 2021). Appropriately diluted crude extract (20 μL) was added to 180 μL FRAP reagent solution. After left at 37 °C for 10 min in dark, absorbance at 593 nm was recorded. FRAP assay of crude extract was calculated based on the standard curve of vitamin C.

Based on the three methods described above, an overall antioxidant potency composite (APC) index was utilized to evaluate antioxidant activity of peach fruit as follows: APC = [(DPPH $_{sample}$/DPPH$_{max}$ + ABTS$_{sample}$/ABTS$_{max}$ + FRAP$_{sample}$/FRAP$_{max}$)/3] × 100% (Chen et al., 2021).

2.4. Quantification of phenolic compounds

A quantitative analysis of phenolic compounds was conducted using solvent A (0.1% formic acid) and solvent B (acetonitrile with 0.1% formic acid) (Yu et al., 2023). The flowrate was set as 0.35 mL/min at

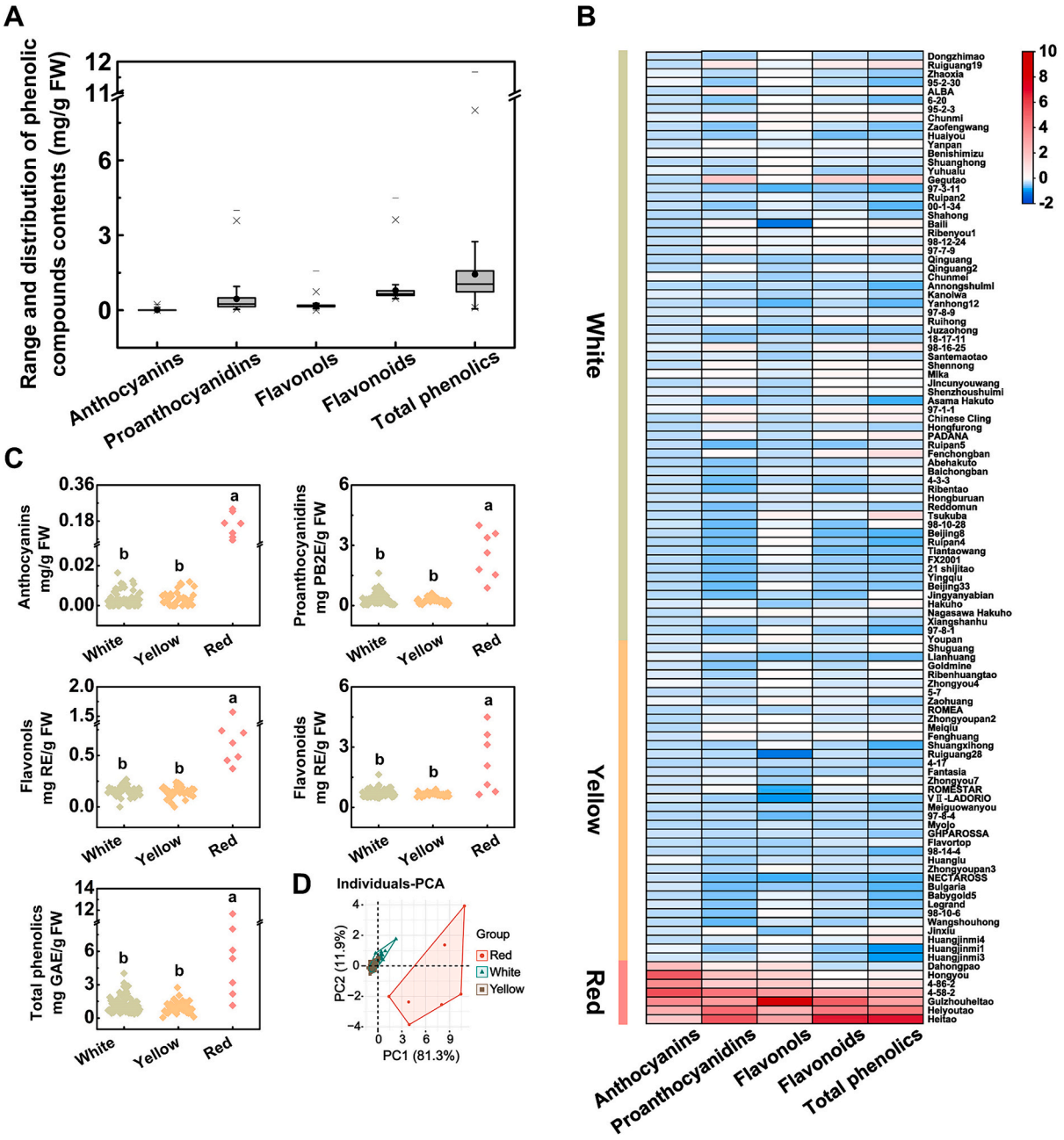

Fig. 1. Characters of phenolic compounds contents in mature fruits of 110 peach accessions. (A) Boxplot displaying anthocyanins, proanthocyanidins, flavonols, flavonoids, and total phenolics contents in texted peach accessions. The horizontal line in the interior of the box indicated the median. (B) Heatmap and clustering of phenolic compounds contents in peach with diverse coloration. White, white-fleshed peach; yellow, yellow-fleshed peach; red, red-fleshed peach. (C) Range and distribution of phenolic compounds contents in peach based on flesh coloration. Different letters above the columns represented significant differences at $p < 0.05$ level. (D) Principal component analysis (PCA) of phenolic compounds contents. Green, yellow and red dots represented white-fleshed, yellow-fleshed and red-fleshed peach, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

40 °C. The variable importance in projection (VIP) ≥ 1 and absolute Log_2 (foldchange) ≥ 1 were used to distinguish differentially accumulated metabolites (DAMs) for group discrimination.

2.5. Statistical analysis

All data were presented as means +/− SDs. An analysis of significant differences ($p < 0.05$) was conducted by Student's *t*-test with a one-way ANOVA (SPSS, IBM Corporation, USA). The cluster heatmap was analyzed and visualized by TBtools (version 2.025, China).

3. Results and discussion

3.1. Variations of phenolic compounds in ripe fruits among peach germplasm

The contents of phenolic compounds, including total phenolics and flavonoids, were measured in the flesh of ripe fruits of 110 peach accessions. Total phenolics content ranged from 0.053 to 11.67 mg gallic acid equivalent (GAE)/g FW, with an average of 1.43 mg GAE/g FW, while flavonoids content ranged from 0.46 to 4.50 mg rutin equivalent (RE)/g FW, with an average of 0.79 mg RE/g FW (Fig. 1A). Subsequently, the contents of three main subclasses of flavonoids, anthocyanins, proanthocyanidins and flavonols, were further measured. The average concentrations of anthocyanins, proanthocyanidins and flavonols were 0.013 mg/g FW, 0.45 mg proanthocyanidin B2 equivalent (PB2E)/g FW, and 0.19 mg RE/g FW, with ranges of 0–0.24 mg/g FW, 0.033–4.00 mg PB2E/g FW, and 0–1.57 mg RE/g FW, respectively. These results suggested that there were significant variations in phenolic compounds contents in ripe fruits of the peach germplasm used in this study.

We investigated the relationship between phenolic compound accumulation and fruit characteristics, including fruit shape, flesh texture, skin texture, flavor and coloration (Table S1). Contents of all analyzed phenolic compounds showed no associations with fruit shape, flesh texture, skin texture and the flesh coloration around the stone (Figs. S1-S4). This finding confirms those previously reported by Tomás-Barberán et al. (2001). Intriguingly, the average contents of phenolic compounds in freestone peaches were significantly higher than in clingstone peaches (Fig. S5). Sour-tasting peaches had significantly higher levels of all tested phenolic compounds compared to sour-sweet-tasting, sweet-tasting and strong-sweet-tasting peaches (Fig. S6). This finding was likely due to pleiotropic effects of flavonoid regulators such as MYB transcription factors on organic acid accumulation (Hu et al., 2016).

There were significance differences detected in accumulation of phenolic compounds among red-fleshed, white-fleshed, and yellow-fleshed peaches (Fig. 1B and C). The average content of anthocyanins in red-fleshed peaches (0.16 mg/g FW) was 49.82-fold and 43.29-fold higher than that in white-fleshed (0.0032 mg/g FW) and yellow-fleshed (0.0037 mg/g FW) peaches, respectively; thus, demonstrating notable differences in red-fleshed versus non-red-fleshed peaches. Likewise, the proanthocyanidins and flavonols also accumulated at higher contents in red-fleshed peaches than those in non-red-fleshed peaches. Accordingly, the average content of flavonoids in red-fleshed peaches was 3.20-fold and 3.50-fold higher than that in white-fleshed and yellow-fleshed peaches, respectively. In addition, the average content of total phenolics in red-fleshed peaches was 4.28-fold and 5.37-fold higher than that in the white-fleshed and yellow-fleshed peach, respectively. Furthermore, a principal component analysis (PCA) revealed distinct separation between red-fleshed and non-red-fleshed peaches (Fig. 1D). All the above findings demonstrated that accumulation of all analyzed phenolic compounds were significantly higher in red-fleshed peaches than in non-red-fleshed peaches, which were in agreement with the results of Zhang, Su, et al. (2023).

3.2. Evaluation of antioxidant activity in ripe fruits among peach germplasm

A total of three common assays, including DPPH, ABTS, and FRAP were used to estimate activities of crude extracts from mature fruits. Pearson correlation coefficients showed strong correlations among the DPPH, ABTS and FRAP values ($r > 0.95$, $P < 0.01$), indicating the reliable assessment of antioxidant activity. Overall, significant differences in antioxidant activities were observed among peach fruits of different colorations (Fig. 2A and B). Previous studies have revealed that the antioxidant activities in fruits vary widely depending on the cultivars, with red-fleshed fruits being antioxidant-rich sources due to their substantial amounts of bioactive components (Gonçalves et al., 2024). Consistent with the findings in kiwifruit and apple (Li et al., 2020; Liu et al., 2019), among all analyzed accessions, red-fleshed peaches had highest levels of antioxidant activities ranging from 48.63 to 239.69 mg VcE/100 g FW for DPPH, 65.78–197.59 mg VcE/100 g FW for ABTS and 25.87–252.41 mg VcE/100 g FW for FRAP, respectively. On average, the DPPH, ABTS and FRAP values in red-fleshed peaches were 6.15–8.84, 4.63–6.39 and 6.05–8.65 folds higher than those in white-fleshed and yellow-fleshed peaches (Fig. 2B).

Antioxidant potency composite (APC) index showed great variations ranging from 1.37% to 100% in all tested accessions (Fig. S7A). Red-fleshed peach 'Heitao' ('HT') displayed the strongest antioxidant activity, followed by 'Heiyoutao' ('HYT'), and the weakest antioxidant activity was detected in white-fleshed peach '98–10-28' (Fig. S7B). 'Gegutao' ('GGT') and 'Huangjinmi4' ('HJM4') showed high antioxidant activity in white-fleshed and yellow-fleshed accessions, respectively (Fig. S7B). The average APC indexes in red-fleshed, white-fleshed and yellow-fleshed accessions were 60.45%, 11.06% and 7.84%, respectively. These results suggested that antioxidant activity of crude extracts from ripe fruits displayed a considerable variation among peach germplasm, with red-fleshed peaches exhibiting the strongest antioxidant activity.

3.3. Phenolic compounds played a crucial role in the antioxidant activity of peach fruit

Linear-regression analysis was conducted to assess the correlation between phenolic compounds content and antioxidant activity. The contents of flavonoids, proanthocyanidins and total phenolics were strongly correlated with the DPPH, ABTS and FRAP values ($R^2 > 0.8$, $P < 0.01$). The strongest linear correlation was observed for proanthocyanidins with antioxidant activities ($R^2 = 0.88–0.94$, $P < 0.01$), followed by total phenolics ($R^2 = 0.83–0.90$, $P < 0.01$) and flavonoids ($R^2 = 0.81–0.90$, $P < 0.01$) (Fig. 2C). However, flavonols showed a low linear correlation with antioxidant activities ($R^2 = 0.53$, $P < 0.01$, Fig. S8A). The lowest linear correlation was found for anthocyanins with antioxidant activities ($R^2 = 0.42–0.43$, $P < 0.01$, Fig. S8A) although anthocyanins have been well recognized as the naturally occurring antioxidants in fruit (Bendokas et al., 2020), which could be attributed to a smaller proportion of red-fleshed group compared to non-red-fleshed group among these detected accessions.

Pearson correlation coefficients were also calculated to clarify the relationship between phenolic compounds content and antioxidant activity (Fig. S8B—C). The highest correlation coefficients were detected between the content of total phenolics, flavonoids, proanthocyanidins and antioxidant activities ($r \geq 0.9$, $P < 0.01$). Whereas, the relatively lower correlation coefficients were found for anthocyanins ($r = 0.65–0.66$, $P < 0.01$), flavonols ($r = 0.72–0.73$, $P < 0.01$), with antioxidant activities. Taken together, these above results suggested that antioxidant activity of peach fruit was more closely related to proanthocyanidins, flavonoids and total phenolics than to anthocyanins and flavonols. It was concluded that multiple phenolic compounds, rather than a single class of component, might act a determinant role in the overall antioxidant activity of peach fruit.

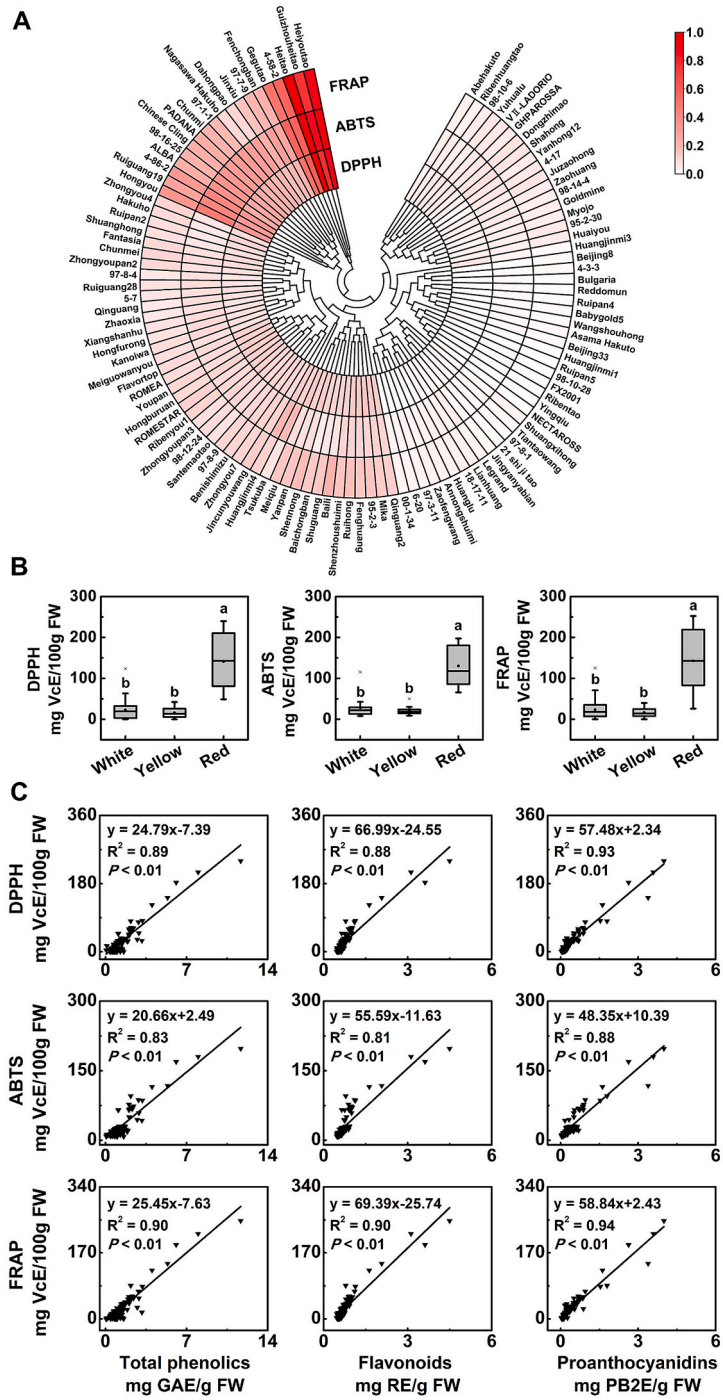

Fig. 2. Comparison analysis of antioxidant activity in mature fruits of 110 peach accessions. (A) The antioxidant activity in peach determined by DPPH, ABTS and FRAP assays. DPPH, DPPH radical scavenging activity; ABTS, ABTS free radical scavenging activity; FRAP, Ferric reducing antioxidant power assay. (B) Range and distribution of antioxidant activity in peach based on flesh coloration. Different letters above the columns represented significant differences at $p < 0.05$ level. White, white-fleshed peach; yellow, yellow-fleshed peach; red, red-fleshed peach. (C) The linear-regression analysis between the content of total phenolics, flavonoids or proanthocyanidins and antioxidant activity in texted peach accessions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Differences in phenolic compounds accumulation between the peel and flesh of peach

The difference in phenolic compounds accumulation between the peel and flesh was explored using three different accessions, including the white-fleshed ('Baifeng, BF'), yellow-fleshed ('Huangjinmi3, HJM3') and red-fleshed ('4–86-2') peach (Fig. 3A). Overall, the contents of total phenolics, flavonoids, flavonols, proanthocyanins and anthocyanins in the peel were significantly higher than those in corresponding flesh extracts, with the increases of 1.89–4.86, 1.65–6.53 and 2.37–33.95 folds in '4–86-2', 'BF' and 'HJM3', respectively (Fig. 3B). In addition, antioxidant activities of both flesh and peel extracts were measured. Consistently, the APC index of the peel extracts from all three tested accessions were 1.60–9.78 times higher than those of the flesh extracts. Similar results were found in previous studies on fruits such as apple, pear, pitahaya and kiwi (Kaeswurm et al., 2022; Michailidis et al., 2021;

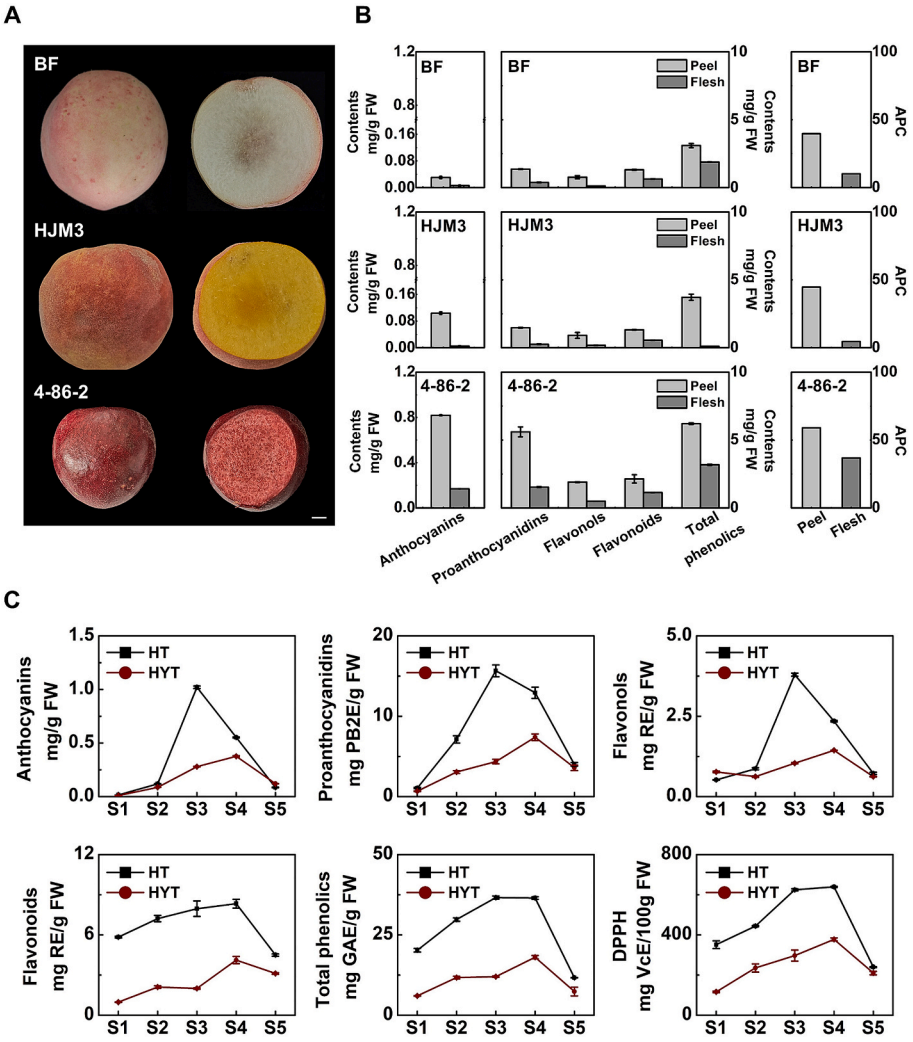

Fig. 3. Analysis of phenolic compounds levels in different tissues and developmental stages of peach. (A) Photograph of mature fruits of three peach accessions with diverse coloration ('Baifeng, BF'; 'Huangjinmi3, HJM3' and '4–82-2'). Scale bar indicated 1 cm. (B) The phenolic compounds contents and antioxidant potency composite (APC) index in peel and flesh in mature fruits of these three peach accessions ('BF', HJM3' and '4–82-2'). (C) Dynamic changes in phenolic compounds contents in red-fleshed peach ('Heitao, HT'; 'Heiyoutao, HYT') during fruit development. Each bar indicated the mean ± SD of three biological replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Tang et al., 2021; Zhang et al., 2021). Phenolic compounds in fruit extracts have been discovered to exhibit strong antioxidant activity and antimicrobial property (Peng et al., 2019). Phenolic compounds are not homogenously distributed in fruits, and their physiological importance can be reflected by the spatial distribution and concentration within different tissues (Zhou et al., 2023). The peel is a natural protective layer for the inner nutritious flesh against insect and pathogenic damage. The abundance of phenolic compounds in the peach peel could be due to their pivotal role in protecting fruit from various abiotic and biotic stresses. According to these findings, apart from the flesh, peach peel as an excellent fruit by-product, can be served as the valuable and potential nature source of phenolic antioxidants.

3.5. Dynamic changes in phenolic compounds of peach during fruit development

Since the red-fleshed peaches showed the highest concentrations of phenolic compounds and the strongest antioxidant activities, two red-fleshed peach accessions, 'HT' and 'HYT', were selected to investigate accumulation patterns of phenolic compounds during fruit development. The contents of anthocyanins, proanthocyanidins, flavonols, flavonoids and total phenolics in 'HT' and 'HYT' at S1 were all extremely low (Fig. 3C). The accumulation of all tested phenolic compounds showed an increasing trend in the early stages and reached a peak at S3 or S4, then decreased dramatically at S5. Anthocyanins content in 'HT' and 'HYT' at S3 were 66.98 and 28.91 times higher than those at S1, respectively, with a final increase by 5.55 and 12.50 times higher at S5 relative to S1. Proanthocyanidins content reached a peak at S3 and S4 in 'HT' and 'HYT', respectively, with 14.81-fold and 11.05-fold higher than that at S1. Likewise, total phenolics content reached a peak at S3 and S4 in 'HT' and 'HYT', respectively, with 1.81-fold and 3.01-fold higher than that at S1. Additionally, the DPPH values in 'HT' and 'HYT' exhibited an increasing trend in the early stages and reached a peak at S4, then decreased dramatically at S5 (Fig. 3C). Overall, the dynamic changes in patterns of antioxidant activities throughout fruit development were similar to those of phenolic compounds contents. These findings further demonstrated the critical importance of these of phenolic compounds in antioxidant activities of peach fruit. Dynamic changes in antioxidant activities during fruit development presented different trends among species and cultivars. During fruit development, the antioxidant activity showed a continuous increase followed by a decrease in jujube and dragon (Elídio et al., 2022; Yan et al., 2022), whereas it gradually declined in plum, orange and apple (Hou et al., 2021; Wojdyło & Oszmiański, 2020; Zhang et al., 2022). However, changes in antioxidant

activities were consistent with the accumulation of phenolic compounds in these fruits, which were in accord with our findings.

3.6. Metabolic basis for the superior antioxidant activity of red-fleshed peach

To explore phenolic compounds responsible for antioxidant activity of peach, three accessions with different antioxidant activities, 'HT' (red-fleshed), 'GGT' (white-fleshed) and 'HJM4' (yellow-fleshed), were

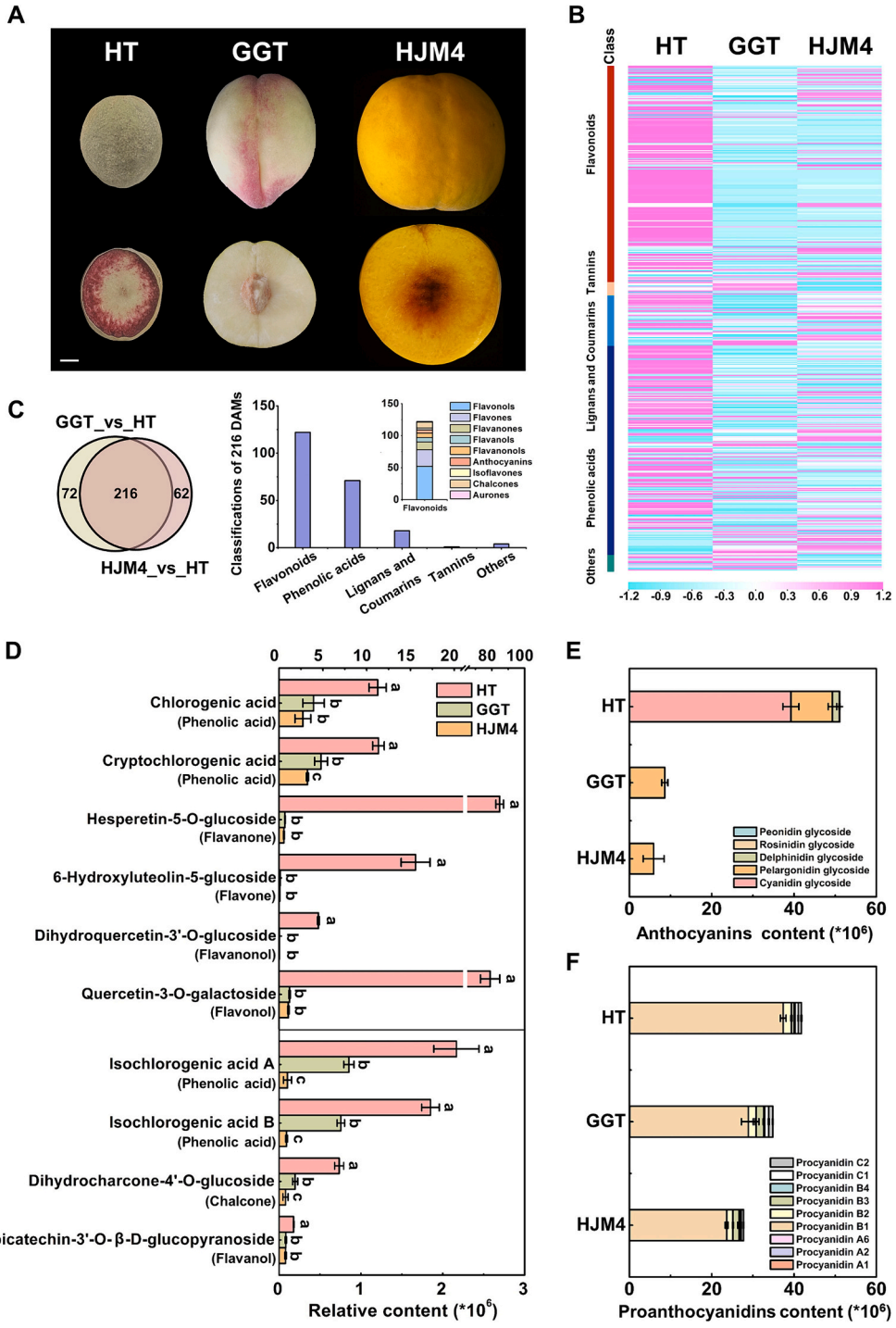

Fig. 4. Overview analysis of phenolic metabolites in peach with diverse coloration. (A) Fruit phenotypes of the three representative accessions, including red-fleshed ('Heitao, HT'), white-fleshed ('Gegutao, GGT') and yellow-fleshed ('Huangjinmi4, HJM4') peach. Scale bar indicated 1 cm. (B) Heatmap visualization of individual phenolic compound among different groups. (C) Venn diagram and classifications of 216 DAMs identified in the 'GGT' vs 'HT' and 'HJM4' vs 'HT' comparisons. (D) The relative contents of differentially abundant and representative phenolic acids and flavonoids in peach. Different letters above the columns represented significant differences at $p < 0.05$ level. (E) The concentration and distribution of anthocyanins in peach. (F) The concentration and distribution of proanthocyanidins in peach. Each bar indicated the mean ± SD of three biological replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

selected to perform metabolomic analysis (Fig. 4A). A total of 495 phenolic metabolites were identified in ripe fruits of the three tested accessions, with 467, 407 and 437 in 'HT', 'GGT' and 'HJM4', respectively. Among these 495 phenolic compounds, 211 (42.63%), 205 (41.41%), 50 (10.10%) and 13 (2.63%) were flavonoids, phenolic acids, lignans and coumarins, tannins, respectively, while the remaining 16 (3.23%) belonged to others (Fig. S9). PCA of the phenolic metabolites revealed that biological replicates of each accession were clustered closely to each other, suggesting the highly reproducible results of metabolomic analysis. Meanwhile, it indicated that the three accessions were clearly separated from each other (Fig. S10A). Correlation analysis revealed that metabolomic profiles of 'GGT' and 'HJM4' were more similar to each other than to that of 'HT' (Fig. S10B). Moreover, the cluster heatmap showed that the composition and concentration of phenolic compounds were obviously different in the tested accessions (Fig. 4B). The majority of phenolic compounds (61.42%) were highly accumulated in 'HT', whereas only a small number of metabolites (15.15% and 23.43%) were prominently accumulated in 'GGT' and 'HJM4' respectively.

The comparisons of 'GGT' or 'HJM4' versus 'HT' were conducted to identify the critical metabolites associated with the red-fleshed trait. Based on the criteria of VIP value $\geq$1 and an absolute Log_2 (foldchange) $\geq$ 1, 216 common differentially accumulated metabolites (DAMs) were found in the 'GGT' vs 'HT' and 'HJM4' vs 'HT' comparisons (Fig. 4C, Table S2). The 216 DAMs consisted of 122 flavonoids (i.e., 9 chalcones, 12 flavanones, 1 aurones, 3 isoflavones, 26 flavones, 7 flavanols, 7 flavanonols, 52 flavonols, and 5 anthocyanins), 71 phenolic acids, 18 lignans and coumarins, 1 tannin and 4 others (Fig. 4C). These findings suggested that in additional to the difference in anthocyanins content, there was a significant difference in the composition and concentration of multiple phenolic acids and flavonoids between red-fleshed and non-red-fleshed peaches.

Correlation analysis was further conducted to investigate the relationship between the content of 216 DAMs and antioxidant activity in these three tested accessions. As a result, 43 DAMs were found to be positively correlated with antioxidant activity (Table S3), suggesting their crucial role in determining the superior antioxidant property of red-fleshed peaches. The 43 DAMs mainly contained 11 (25.58%) phenolic acids and 24 (55.81%) flavonoids. Among the 11 phenolic acid-related DAMs, four predominant hydroxycinnamic acids, i.e. chlorogenic acid, cryptochlorogenic acid, isochlorogenic acid A and B, exhibited significantly higher accumulation in red-fleshed peach compared to non-red-fleshed peaches. The levels of chlorogenic acid, cryptochlorogenic acid, isochlorogenic acid A and B in 'HT' were 2.86, 2.37, 2.54 and 2.45 folds higher than in 'GGT', while 4.14, 3.51, 21.12 and 20.46 folds higher than in 'HJM4', respectively (Fig. 4D). Notably, protocatechuic acid, an important hydroxybenzoic acid (Kumar & Goel, 2019), was not included in the 11 phenolic acid-related DAMs. However, protocatechuic acid exclusively accumulated in 'HT', but was undetectable in 'GGT' and 'HJM4' (Fig. 5). Phenolic acids play important roles in the nutrition and health-promotion values of *Citrus* and banana fruits due to their strong free radical scavenging properties (Singh et al., 2016; Zou et al., 2016). The above findings suggested that there were significant differences in the composition and concentration of phenolic acids among peach accessions with diverse coloration. The plentiful phenolic acids like chlorogenic acid and cryptochlorogenic acid might serve as contributors to strong antioxidant activity in red-fleshed peach.

The flavonoid-related DAMs consisted of 1 chalcone, 3 flavanones, 6 flavones, 1 flavanol, 4 flavanonols, 8 flavonols and 1 anthocyanin. The chalcone, i.e. dihydrochalcone-4'-*O*-glucoside accumulated 3.75 and 9.39 folds higher in 'HT' than in 'GGT' and 'HJM4', respectively (Fig. 4D). Hesperetin-5-*O*-glucoside was the predominant flavanone, with 127.67 and 156.31 times higher in 'HT' compared to 'GGT' and 'HJM4'. Likewise, the level of the representative flavone, 6-hydroxyluteolin-5-glucoside, was 138.15 and 208.99 folds higher in 'HT' than that in 'GGT' and 'HJM4'. Epicatechin-3'-*O*-β-D-glucopyranoside and

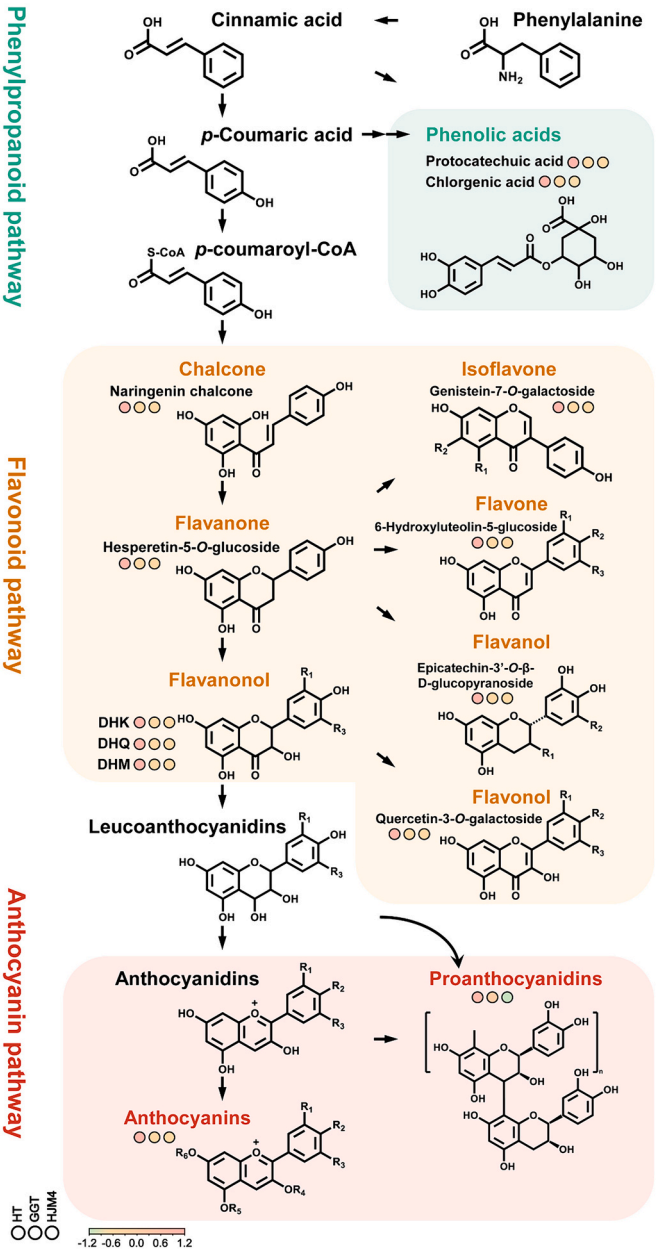

Fig. 5. The levels of characteristic metabolites in each category of phenolic compounds identified in peach with diverse coloration. The solid circle represented the contents of corresponding metabolites in peach accessions ('Heitao, HT'; 'Gegutao, GGT' and 'Huangjinmi4, HJM4'). DHK, dihydrokaempferol; DHQ, dihydroquercetin; DHM, dihydromyricetin.

dihydroquercetin-3'-*O*-glucoside, belonging to flavanol and flavanonol, exhibited the increases of 2.17–2.27 and 164.61–217.77 folds in 'HT' compared to 'GGT' and 'HJM4', respectively. The eight flavonols contained quercetin-3-*O*-galactoside, 6-hydroxykaempferol-7-*O*-glucoside, quercetin-3-*O*-glucoside, quercetin-7-*O*-glucoside, quercetin-4'-*O*-glucoside, isohyperoside, kaempferol-7-*O*-glucoside, quercetin-3-O-apiosyl(1 → 2)galactoside. All these flavonols accumulated abundantly in 'HT', and their average levels were over 80 times higher than those in 'GGT' and 'HJM4'. Moreover, naringenin chalcone, the initial metabolite for converting into a variety of flavonoids, showed significantly higher accumulation in red-fleshed peach compared to non-red-fleshed peaches (Fig. 5), ensuring the substantial substrate for subsequent accumulation of flavonoids in red-fleshed peach. Most of the mentioned flavonoids have been recognized as crucial bioactive compounds with a

wide range of pharmacological activity for promoting human health (Eberhardt et al., 2000; Lopez-Corona et al., 2022). The differential accumulation of bioactive flavonoids caused variations in the antioxidant activity of peach accessions with diverse coloration.

The anthocyanin-related DAM, cyanidin-3-*O*-glucoside, which was recognized as the dominant anthocyanin component, accounting for 76.79% of total anthocyanins in 'HT' (Fig. 4E). Cyanidin-3-*O*-glucoside showed a 321.04-fold and 580.71-fold increase in 'HT' compared to that in 'GGT' and 'HJM4', respectively. This finding was consistent with previous reports (Cheng et al., 2014; Zhou et al., 2015). Beside cyanidin glycoside, other 6 types of anthocyanins (1 pelargonidin, 3 delphinidins, 1 peonidin and 1 rosinidin) were also identified in these analyzed accessions (Fig. 4E). All detected anthocyanin components exhibited increased accumulation in red-fleshed peach compared to non-red-fleshed peaches, strongly associated with the level of the important precursor flavanonols (dihydrokaempferol, dihydroquercetin and dihydromyricetin) for anthocyanin biosynthesis (Fig. 5). Delphinidin glycosides were specifically enriched in 'HT' and rarely detected in 'GGT' and 'HJM4' (Fig. 4E). This was partially due to the exclusive accumulation of dihydromyricetin in 'HT', which acted as the substance for delphinidin glycosides (Fig. 5). In addition, although no proanthocyanidins was identified in these 43 DAMs, the level of the predominant proanthocyanidins component, procyanidin B1, which accounted for 82–89% of proanthocyanidins content, exhibited 1.29 and 1.58 folds higher in 'HT' than that in 'GGT' and 'HJM4', respectively (Fig. 4F). This was consistent with the above-mentioned positive correlation between proanthocyanidins content and antioxidant activity.

These above results indicated that the biosynthesis of anthocyanins was accompanied by an increased accumulation of phenolic acids and flavonoids in red-fleshed peach. We proposed a schematic diagram illustrating the metabolic pathways of the significantly increased phenolic acids and flavonoids in red-fleshed peach (Fig. 5). Phenolic acids are recognized as a key class of natural antioxidants (Lorenzo et al., 2021), and almost every group of flavonoids possesses antioxidant activity (Swallah et al., 2020). Thus, the reason for the superior antioxidant activity of red-fleshed peach is likely due to the coordinated accumulation of anthocyanins as well as phenolic acids and flavonoids, with the phenolic compounds being more important. Given that flavonoid biosynthesis pathway is broadly conserved in plants (Winkel-Shirley, 2001), it is reasonable to deduce that the health benefits of anthocyanin-pigmented fruits and vegetables are attributed to the coordinated accumulation of multiple phenolic compounds.

4. Conclusion

In the study, the concentration and composition of phenolic compounds in ripe fruits were qualitatively and quantitatively analyzed in a large-scale peach germplasm. A considerable variation in phenolic compound content was observed among peach germplasm. Crude extracts from ripe fruits of red-fleshed peaches had significant higher levels of antioxidant activity compared to those of non-red-fleshed peaches. Antioxidant activity was highly associated with phenolic compounds content. The accumulation of phenolic compounds varied throughout fruit development, and exhibited higher levels in the peel than in the flesh. Metabolomic analysis revealed 495 phenolic metabolites in peach fruits. A total of 43 differentially accumulated metabolites, most of which belonged to flavonoids and phenolic acids, were identified between red-fleshed and non-red fleshed peaches. The accumulation of multiple compounds of phenolic acids and flavonoids was enhanced coordinately by the increase of synthesis of anthocyanins in red-fleshed peaches, which is responsible for the superior antioxidant activity of red-fleshed peaches.

CRediT authorship contribution statement

Yun Zhao: Writing – original draft, Investigation, Data curation, Conceptualization. **Juanli Sun:** Data curation. **Yudi Liu:** Investigation. **Xian Zhang:** Investigation. **Yunpeng Cao:** Formal analysis. **Beibei Zheng:** Data curation. **Ruo-Xi Zhang:** Data curation. **Caiping Zhao:** Resources. **Xiaoyan Ai:** Resources. **Huaping He:** Resources. **Yuepeng Han:** Writing – review & editing, Visualization, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgements

This project was financially supported by the National Natural Science Foundation of China (U23A20206, 32202460 and 32272687), Hubei Hongshan Laboratory (2021hszd017), the China Agriculture Research System (CARS-30) and Sino-Africa Joint Research Center, CAS (SAJ202109).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fochx.2024.101698.

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