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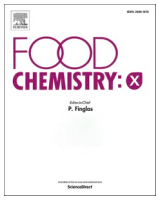

Volatile metabolomics analysis reveals the flavor response of different parts of celery to ultraviolet radiation

Zhengnan Yan [a,*,1], Zhixin Li [a,1], Haokai Wang [a], Haijie Dou [b], Jinxiu Song [c], Fang Ji [d], Yanjie Yang [a], Duo Lin [a,*]

[a] College of Horticulture, Qingdao Agricultural University, Qingdao 266109, China
[b] College of Intelligent Science and Engineering, Beijing University of Agriculture, Beijing 102206, China
[c] College of Agricultural Engineering, Jiangsu University, Zhenjiang 212013, China
[d] Key Laboratory of Agricultural Engineering in Structure and Environment of MARA, College of Water Resources & Civil Engineering, China Agricultural University, Beijing 100083, China

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ABSTRACT

Volatile metabolomics was used to analyze volatile organic compounds in celery (*Apium graveolens* L. cv. Dayehuang) leaves and petioles under ultraviolet (UV) radiation. Results indicated that celery encompassed 328 terpenes, 299 esters, 178 heterocyclic compounds, and 166 ketones. The additional UV radiation altered ester and heterocyclic compound in celery leaves and changed terpenoids, aldehyde, and ester in celery petiole. The content of volatile organic compounds in leaves and petiole of celery under UV radiation was significantly higher than that grown without UV radiation. The content of 40 compounds with green, floral, woody, sweet, citrus, and fruity aromas have significantly altered in celery petioles. In addition, 24 compounds were significantly altered in celery leaves, including woody and sweet. Our study provides a valuable insight into the influences of UV radiation on different parts of celery flavor, and offers a possible way to alter the flavor quality of celery.

1. Introduction

Celery (*Apium graveolens* L.), a member of the *Apiaceae* family, is the indigenous to the Mediterranean and the Middle East area, and has been extensively cultivated worldwide. It is renowned for its unique nutrients and health-related phytochemicals. In addition to being beneficial to human health, the secondary metabolites produced by celery can also enhance its own antioxidant capacity (Turner et al., 2021a).

Plant secondary metabolites are compounds produced from plant primary metabolic pathways that during the physiological processes of plants, including growth, development, and resilience (Çakmakçı et al., 2015; Gulcin et al., 2019; Gulcin et al., 2020). More than 200,000 secondary metabolites of plants have been detected and identified, which are classified into three categories: phenolics, terpenoids, and alkaloids (Zhan et al., 2022). Terpenoids are the family of compounds most relevant to plant physiology and metabolism among these three categories of compounds, which are generally thought to be produced by the methylerythritol phosphate or mevalonate pathway and are the essential components of many plants (Lanier et al., 2023). Plant odor is mainly driven by volatile organic compounds (VOCs) produced by the terpenoid biosynthesis pathway (Zhang et al., 2021). This phenomenon holds crucial implications for celery production, as celery serves as a vital raw material for cosmetics and spices. Studies have shown that a series of compounds, including alcohols, aldehydes, monoterpenes, hemiterpenes, and phthalides, are responsible for the alterations in celery flavor (Li, Li, Zhou, et al., 2022). However, the mechanism of the effects of these compounds on celery flavor is unclear, therefore, it is vital to elucidating how secondary metabolites regulate celery flavor formation.

Previous studies have shown that significant differences of VOCs were observed in different parts of the plants (Ma et al., 2022). For instance, the contents of monoterpenoids and sesquiterpenoids were different in the roots, leaves, and fruits of cucumber (Wei et al., 2016). Compared with tea leaves, tea stems have more pyrazine compounds, which gives tea stems their unique aroma (Liu et al., 2024). The VOCs in celery have delineated that the edible portions of celery predominantly consist of leaves and petioles, and the essential oil constituents of these edible segments are primarily composed of sesquiterpenes, alcohols, and

* Corresponding authors.
E-mail addresses: yanzn@qau.edu.cn (Z. Yan), 200201112@qau.edu.cn (D. Lin).
[1] These authors contributed equally to this work.

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fatty acids, however, there are differences in the composition of VOCs in the celery petioles and leaves (Chen et al., 2024). The reason of the difference can be attributed to the synthesis of VOCs by metabolic pathways within the plant (Gil et al., 2012). The variation of VOCs reflects the diversity of physiological activities within different parts of plant, and also illustrates the complexity of its chemical composition. The commercial value of celery primarily lies in the aroma of its leaves, however, the main edible part is the petiole of the celery (Wang, An, et al., 2023; Wang, Cheng, et al., 2023). Therefore, it is of great significance to figure out the main flavor substances in different parts of plants for the formation of celery quality.

A variety of abiotic factors affect the synthesis of VOCs in plants including temperature, relative humidity, and soil composition. These factors significantly influence the synthesis of primary and secondary metabolites, ultimately leading to variations in volatile compounds (Turner et al., 2021a). As one of the important environmental factors, light profoundly affects the synthesis of volatile compounds in plants (Zhang et al., 2021). Concurrently, plants perceive spectral changes through photoreceptors, so as to respond under different light environmental conditions, and make corresponding morphological and physiological metabolic reaction. The spectrum has been utilized to modulate specific metabolic processes in plants, enabling crops to produce products that are more beneficial to human health and more nutritious. In particular, the light spectrum influences the biosynthesis of terpenoids by up-regulating or down-regulating various enzymes in the biosynthesis pathway. Ultraviolet radiation (UV; 100–400 nm) is a substantial component of solar radiation, which is typically classified as UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (100–280 nm) (Verdaguer et al., 2017). Only UV-A and UV-B reach the Earth's biosphere due to the ozone and oxygen, and the UV-A radiation accounts for 95 % of the solar UV radiation that reaches the Earth's surface (Verdaguer et al., 2017). Previous studies have indicated that the vegetable quality was affected by the changes of season, which was partially due to the change of light quality (Teng et al., 2023). Eu surface ultraviolet data show that the UV radiation intensity varies with the seasons, and the surface UV radiation intensity is significantly lower in winter and spring than in summer (https://www.temis.nl/uvradiation/UVindex.php). In addition, UV radiation can enhance the content of flavor precursors such as sugars and organic acids in crops (Liu et al., 2015). Studies have shown that UV radiation can induce the increase of phenylalaninammonialyase (PAL) activity (Son et al., 2012), and the enzyme activities of PAL and leukocyteantigen relatedprotein (LAR) in black tea can be significantly increased after red-light withering (Li et al., 2021). These substances undergo transformation during the later stages of crop development, resulting in the formation of a greater array of flavor compounds and thereby enhancing the intensity of the crop's taste (Li, Li, Zhou, et al., 2022). For example, under low UV radiation intensity, the enzymatic activity of terpenoid synthase within the foliage of grapes was significantly increased, surpassing that observed in both the absence of UV radiation and at elevated light intensity of UV radiation, resulting in an increase in terpene content (Gil et al., 2012). In addition, cannabis plants produced more terpenes (β-caryophyllene, β-myrcene and α-humulene) and cannabinoids under higher intensity of UV radiation (Giupponi et al., 2020). Research has predominantly focused on the effects of various genotypes and post-harvest processing on the flavor of celery, while the influences of light environments, particularly UV radiation, the flavor metabolism of celery has been less explored.

Our investigation aimed to delineate the alterations in VOCs across different parts of celery exposed to supplemental UV radiation by gas chromatography–mass spectrometry (GC–MS), which offers novel insights into the changes in flavor components of celery in response to additional UV radiation, thereby offering guidelines for altering the flavor quality of the celery, and providing novel insights for enhancing crop quality and aligning with consumer preferences.

2. Materials & methods

2.1. Plant materials and treatment design

Celery (*Apium graveolens* L. cv. Dayehuang) seedlings with five true leaves were selected uniformly and transplanted into 1.1 L plastic pots (diameter, 13.5 cm; depth, 11 cm) filled with mixed peat, vermiculite, and perlite (3:1:1, *v/v/v*) in a plant factory with artificial lighting (PFAL). In this experiment, the light intensity and photoperiod provided by white plus red LEDs (WR, Zhongshan Aier Lighting Technology Co., Ltd., Zhongshan City, China) are 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 12 h d^{-1} (CK), respectively, based on previous studies (Chu et al., 2023; Qin et al., 2024), the additional of UV-A (light intensity was 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Xiamen Lumigro Technology Co., Ltd., Xiamen City, China) were added in the WR LEDs, which was marked as UV treatment. The air temperature was maintained at 25 ± 1 °C/18 ± 1 °C (light/dark), and the relative humidity was maintained at 60–70 % in the PFAL during experimental period (from 25 March to 25 April 2024).

2.2. Sample preparation and extraction

The preparation and extraction of the leaves (L) and petiole (P) samples were completed by Wuhan Metville Biotechnology Co., Ltd. The leaves and petioles of celery in different treatments were frozen at −80 °C to facilitate further analysis. The sample was ground into a powder with liquid nitrogen, then the powder was placed into headspace vial (500 mg), the internal saturated solution was a NaCl standard solution. Headspace solid phase microextraction (HS-SPME) was used for automatic sample extraction. The extraction methods refer to previous studies (Wang, An, et al., 2023; Wang, Cheng, et al., 2023).

2.3. Gas chromatography-mass spectrometry conditions

After sample extraction, VOCs were analyzed in a gas chromatograph (Model 8890, Agilent) at 250 °C for 5 min. VOCs were qualitatively and quantitatively identified using Agilent gas chromatographs and mass spectrometers (8890-7000D, Agilent) equipped with a capillary column (30 m × 0.25 mm × 0.25 μm, DB-5MS, Agilent). Helium at a flow rate of 1.2 mL/min was used as the carrier gas at. The temperature of the injector remains constant (250 °C). The oven temperature was programmed from 40 °C (3.5 min), and the increase method in temperature was based on previous studies (Wang, An, et al., 2023; Wang, Cheng, et al., 2023). The mass spectra were recorded in the electron impact (EI) ionization mode at 70 eV. The ion source, quaternary mass detector and mass spectrum interface temperature were set at 230 °C, 150 °C and 280 °C, respectively. The mass spectrometer used ion detection (SIM) mode to identify the samples qualitatively and quantitatively. The substance species is determined based on the retention time and standard reference in an independent database established using data from various species, literature references, partial standards, and retention indices (Yuan et al., 2022).

2.4. Screening of differential accumulated metabolites

To analyze the difference of volatile compounds in celery leaves and petioles of two groups, the standard for significant differential metabolites were a VIP value of ≥1, and a $|\log_2$ Fold change$| \geq 1$ (Wang, An, et al., 2023; Wang, Cheng, et al., 2023; Yuan et al., 2022). The VIP values were obtained from the results of Orthogonal Projection to Latent Structures-Discriminant Analysis (OPLS-DA), which also provided the score and permutation plots of the compounds in the sample. The data were logarithmically transformed ($\log_2$) and mean centered before OPLS-DA. Then the MetaboAnalystR package OPLSR. Anal function in R software was used for analysis. To further analyze the classification of celery after CK and supplementary UV radiation, OPLS-DA analysis was performed. OPLS-DA optimized the orthogonal signal correction (OSC)

and PLS-DA methods, decomposed the X matrix information into two types of information related to Y and independent of Y, and removed the irrelevant differences to screen the differential metabolites (Yuan et al., 2022).

2.5. Calculation of rOAV

The rOAV of volatile compounds in the sample was calculated to assess their contribution to the overall flavor. rOAV was calculated with equation: rOAV=Ci/Ti, where Ci and Ti represent the relative concentration and odor threshold in the water of the compounds.

2.6. Statistical analysis

The analysis of PCA, HCA, Venn diagram, volcano plot, Flavor wheel, K-means clustering analysis, and Sankey diagrams were using the Metware Cloud, a platform for data analysis (https://cloud.metware.cn). The identified metabolites were annoted using the KEGG compound database (https://www.kegg.jp/kegg/compound/), the annotated metabolites were mapped to metabolic pathways in the KEGG pathway database (https://www.kegg.jp/kegg/pathway.html).

3. Results

3.1. Volatile metabolites in celery after supplementing UV radiation

A total of 1640 volatile components of 15 classes of celery were identified, including 328 terpenes, 299 esters, 178 heterocyclic compounds, 166 ketones, 135 alcohols, 103 aldehydes, 79 phenols, 79 acids, 77 hydrocarbons, 59 aromatics, 39 ethers, 25 nitrogen compounds, 13 halogenated hydrocarbons, and 8 sulfur compounds (Fig. 1a). Among the metabolites, terpenes accounted for 20 % of the total metabolites identified, followed by esters (18.23 %) and heterocyclic compounds (10.85 %). The biological replicates of each treatment exhibited no significant discrepancies; however, principal component analysis (PCA) revealed a substantial discrepancy between the CK and UV samples, which were accordingly segregated into four distinct groups based on their intersample distances (Fig. 1b). Through hierarchical clustering

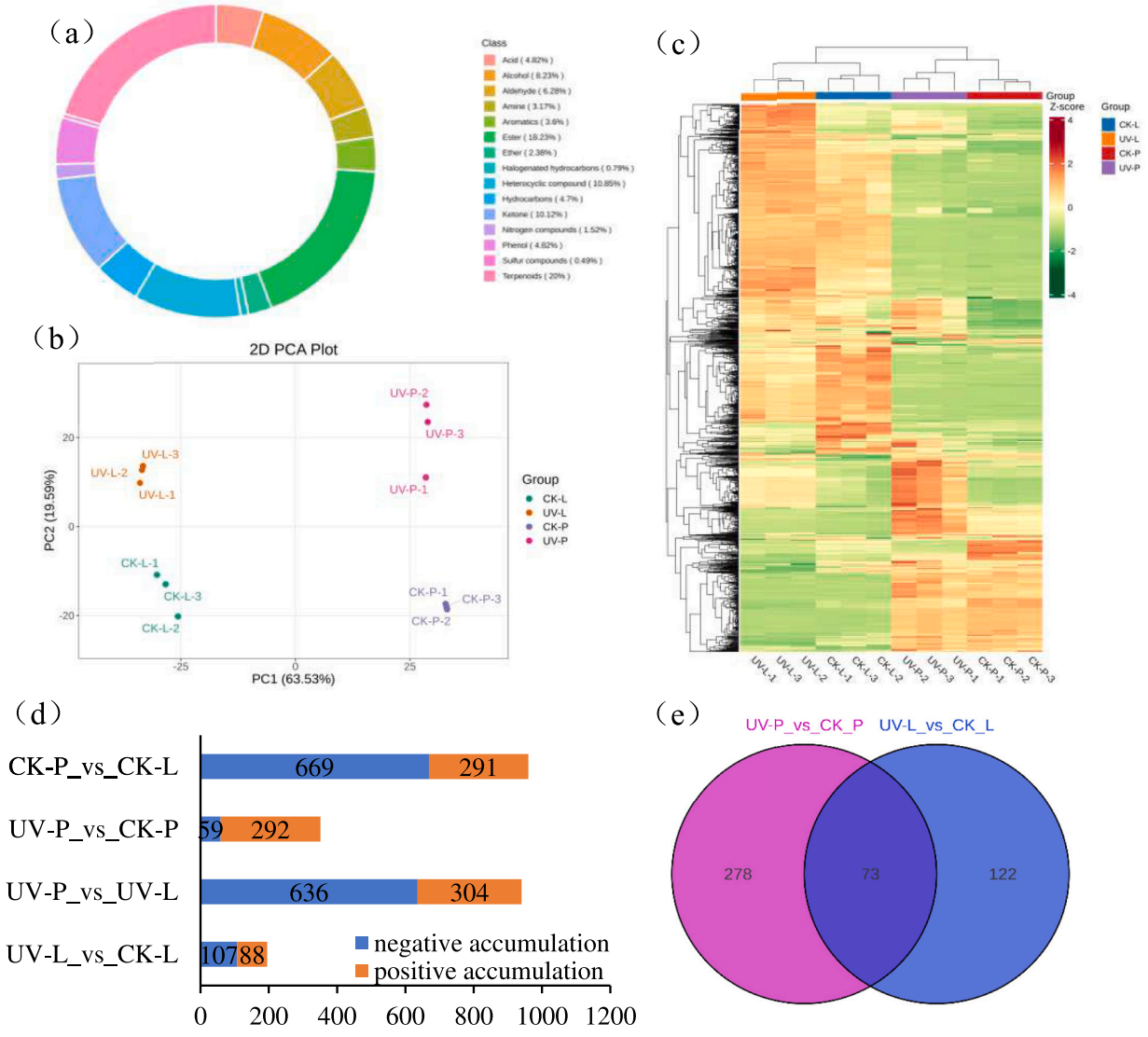

Fig. 1. Volatile metabolite analysis. (a) Classification and composition of identified metabolites. (b) Principal component analysis (PCA) of samples based on identified metabolites. (c) Hierarchical cluster analysis of volatile metabolites in different parts of celery after exposure to ultraviolet radiation. (d)Numbers of DAMs identified by pairwise comparisons. (e) Venn diagram of DAMs identified in leaves and petioles after exposure to ultraviolet radiation, UV-P and UV-L represent the samples of celery petioles and leaves exposed to ultraviolet radiation, respectively. CK-P and CK-L represent the samples of celery petioles and leaves not exposed to ultraviolet radiation, respectively.

analysis, the results displayed in the heat map are similar to the PCA results (Fig. 1c).

The additional of UV radiation induced the production of a total of 195 differential metabolites (88 upregulated and 107 downregulated) in celery leaves, 351 different metabolites (292 upregulated and 59 downregulated) were induced in the celery petiole (Fig. 1d). The volatile metabolites in celery leaves and petioles were analyzed, the results showed that 73 different metabolites were co-regulated in celery leaves and petioles (Fig. 1e).

3.2. Multivariate statistical analysis of differential accumulate metabolites

The volatile components in celery changed significantly after supplementing with UV radiation. In celery leaves, the volatile components were separated from CK treatment after supplementary UV radiation (Fig. 2a). In celery petiole, the volatile components were separated from CK treatment after UV radiation was added (Fig. 2b). The OPLS-DA model is verified by substitution test to confirm that the model is not overfitting, it shows that the model has good explanatory and predictive ability, and the further analysis can be carried out (Fig. 2c-d).

The leaves and petioles of celery treated with CK and supplemented with UV radiation were compared, 85 and 264 metabolites were upregulated (VIP > 1, $P < 0.05$, $|\mathrm{Log_2FC}| > 1.0$), respectively, 102 and 58 metabolites of were downregulated (VIP > 1, $P < 0.05$, $|\mathrm{Log_2FC}| > 1.0$), respectively (Fig. 2e-f).

After supplementary UV radiation, the differential accumulation metabolites of celery in its leaves and petioles were mainly reflected in 9 trends as shown in Fig. 3. Among them, sub class 1, 3, 5 contains metabolites that the content of leaves and petioles increased after UV

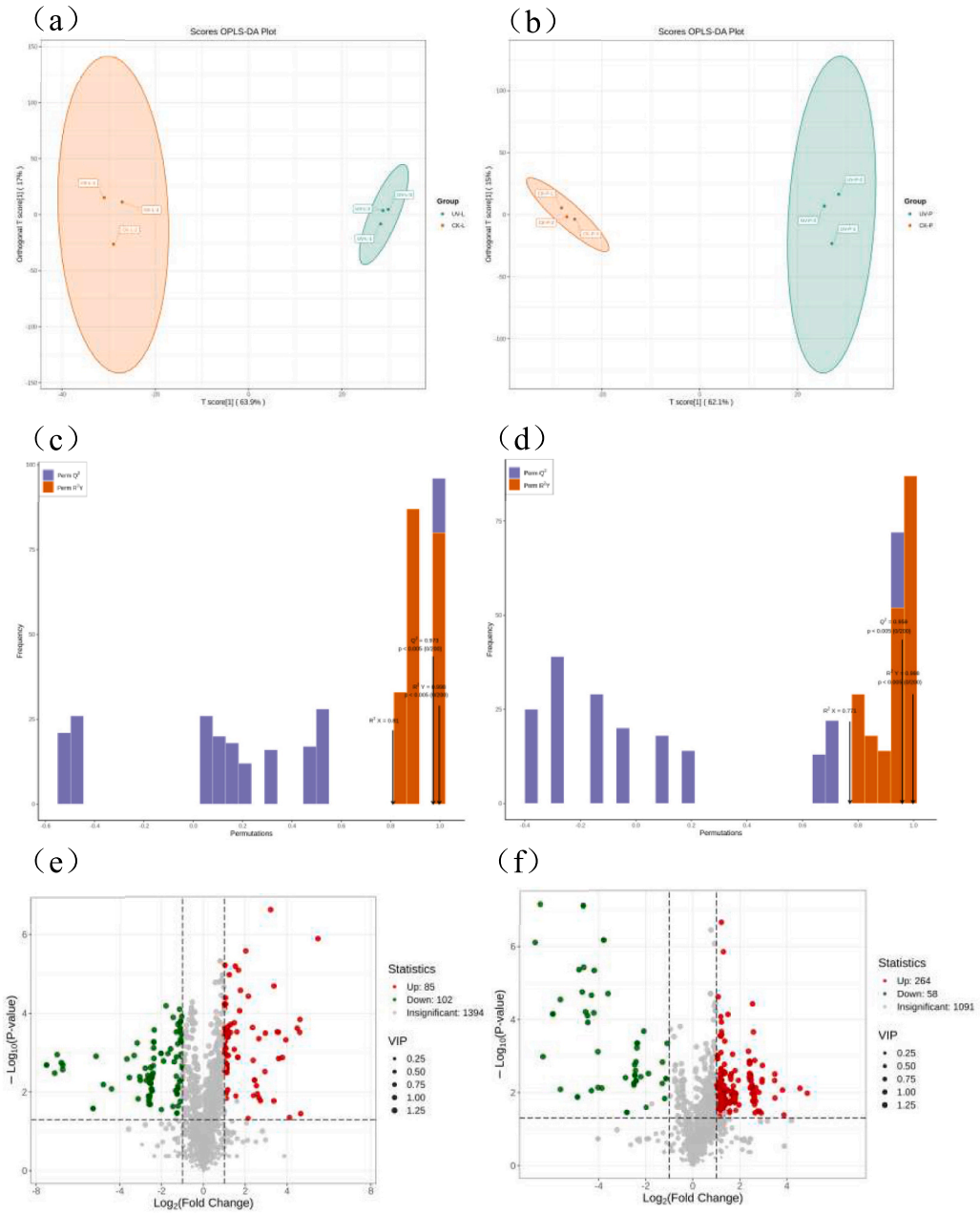

Fig. 2. Screening and classification of DAMs in celery after exposure to ultraviolet radiation. (a-b) OPLS-DA score plot of DAMs between UV-L and CK-L, UV-P and CK-P, respectively. (c-d) Permutations test results, with Q^2 at 0.973, 0.959 and R^2Y at 0.998, 0.998, respectively. (e-f) Volcano plot of volatile metabolites between UV-L vs CK-L, UV-P vs CK-P, respectively.

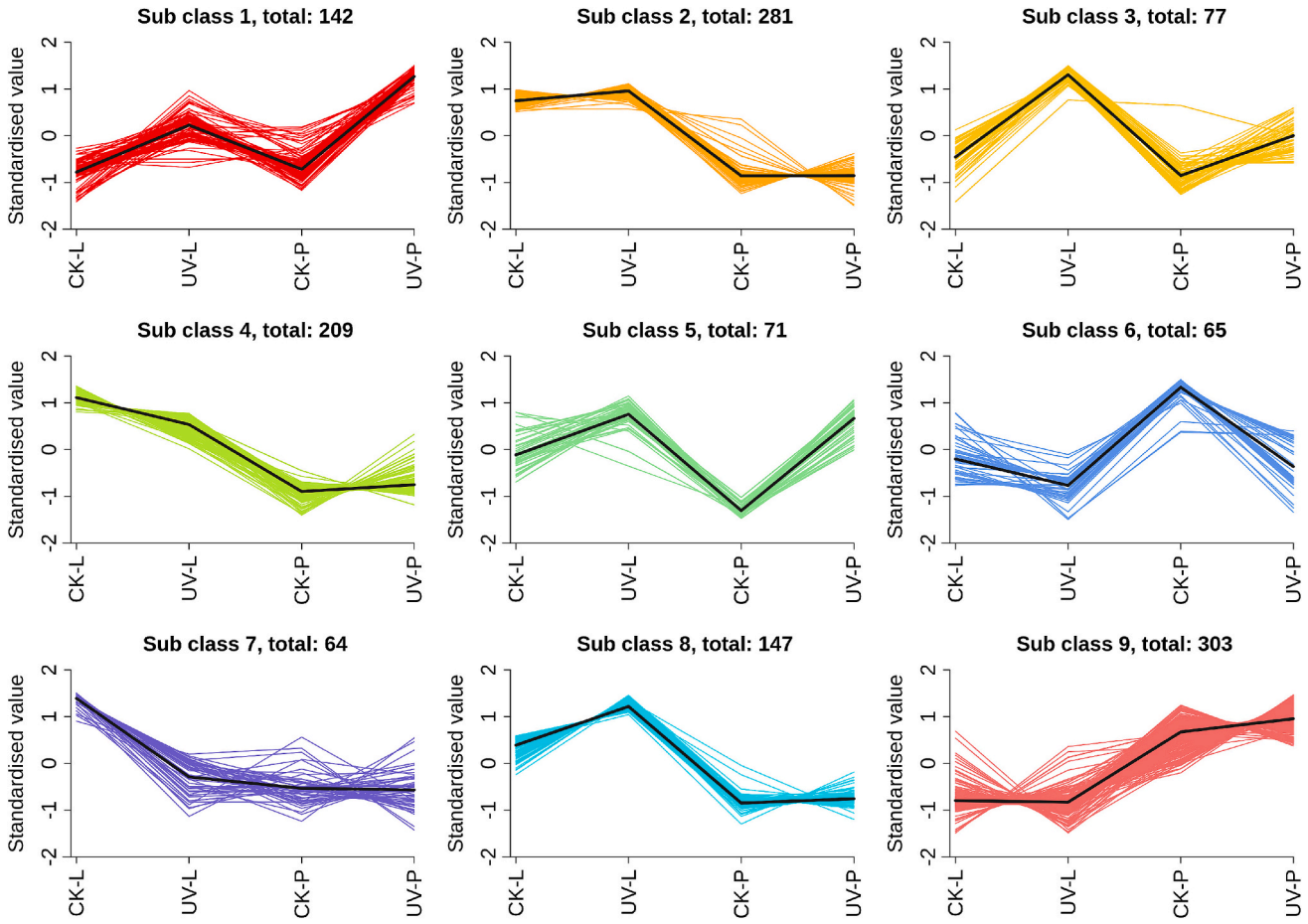

Fig. 3. K-means clustering analysis of differentially accumulated metabolites of different parts of celery after ultraviolet treatment. The y-axis shows the standardized amount of each metabolite, and the x-axis shows the different samples.

irradiation. The sub class 2, 8 contains metabolites that the content of leaves increased after UV radiation supplementation, while sub class 4 and 7 contains opposites ones, but there was no significant change in petiole. In subclass 6, supplementary ultraviolet radiation reduced the content of metabolites in both leaves and petioles, while in subclass 9, the content of metabolites in petioles increased, however, no significant difference in the content of metabolites were observed in leaves.

3.3. KEGG enrichment analysis of differential accumulate metabolites

KEGG database was used to annotate and enrich the differential metabolites between supplementary UV radiation treatment and CK treatment. The results showed that differential accumulate metabolites in celery leaves were significantly enriched in the biosynthesis of sesquiterpene and triterpene compounds and in the biosynthesis of phenylpropane (Fig. 4a). The differential metabolites in celery petioles were significantly enriched in the biosynthesis of sesquiterpene and triterpene compounds and in the biosynthesis of secondary metabolites (Fig. 4b). Therefore, supplementing UV radiation significantly affected the biosynthesis of terpene compounds in celery leaves and petioles, which had significant effects on the overall flavor of celery.

3.4. rOAV analysis and odor correlation analysis

The differential metabolites which contributed directly to celery flavor were obtained (Table 1; Table S1). The results showed that after supplementary UV radiation, the odors directly contributed by different metabolites in celery leaves were mainly embodied in woody, sweet, green, fruity, fatty, floral, waxy, herbal, dry and pine (Fig. 5a), the odors directly contributed by different metabolites in celery petioles were mainly embodied in green, floral, woody, citrus, sweet, fruity, fatty, waxy, orris, herbal (Fig. 5b). To better understand the relationship between odors and volatile components, Sankey diagrams were used to visualize them. Supplementing UV radiation could inhibit herbal and pine odors in celery leaves, the effects on woody, sweet, green, fruity, fatty, floral, waxy and dry scents were both promoted and inhibited (Fig. 5c). Supplementary UV radiation can promote citrus, fruity, fatty, waxy, orris and herbal odor in celery petioles, while scents such as green, floral, woody and sweet can both promote and inhibit, most are facilitating (Fig. 5d).

3.5. Differential accumulate metabolites on the celery flavor

The differential accumulation of metabolites plays a major role in the flavor of celery leaves following additional UV radiation exposure (Fig. 6a). The differential metabolites most associated with flavor were concentrated on seven compounds, Ester, Heterocyclic compound, Alcohol, Terpenoids, Aldehyde and Ketone had 3, 3, 2, 2, 1 and 1 substances upregulated, respectively, while the Terpenoids, Ester, Alcohol, Aldehyde, Ketone and Phenol had 6, 2, 1, 1, 1, and 1 substance downregulated, respectively (Fig. 6b). The differential accumulated metabolites that play a major role in petiole of celery flavor after supplementary UV radiation as shown in Fig. 6c. The differential metabolites in petiole of celery most associated with flavor were concentrated on nine compounds, terpenoids, aldehyde, ester, ether, heterocyclic compound, ketone, sulfur compounds, alcohol and phenol had 14, 6, 6, 2, 2, 2, 2, 1, and 1 substance upregulated, respectively, while the aldehyde, ester, ketone and terpenoids had 1, 1, 1 and 1 substances downregulated,

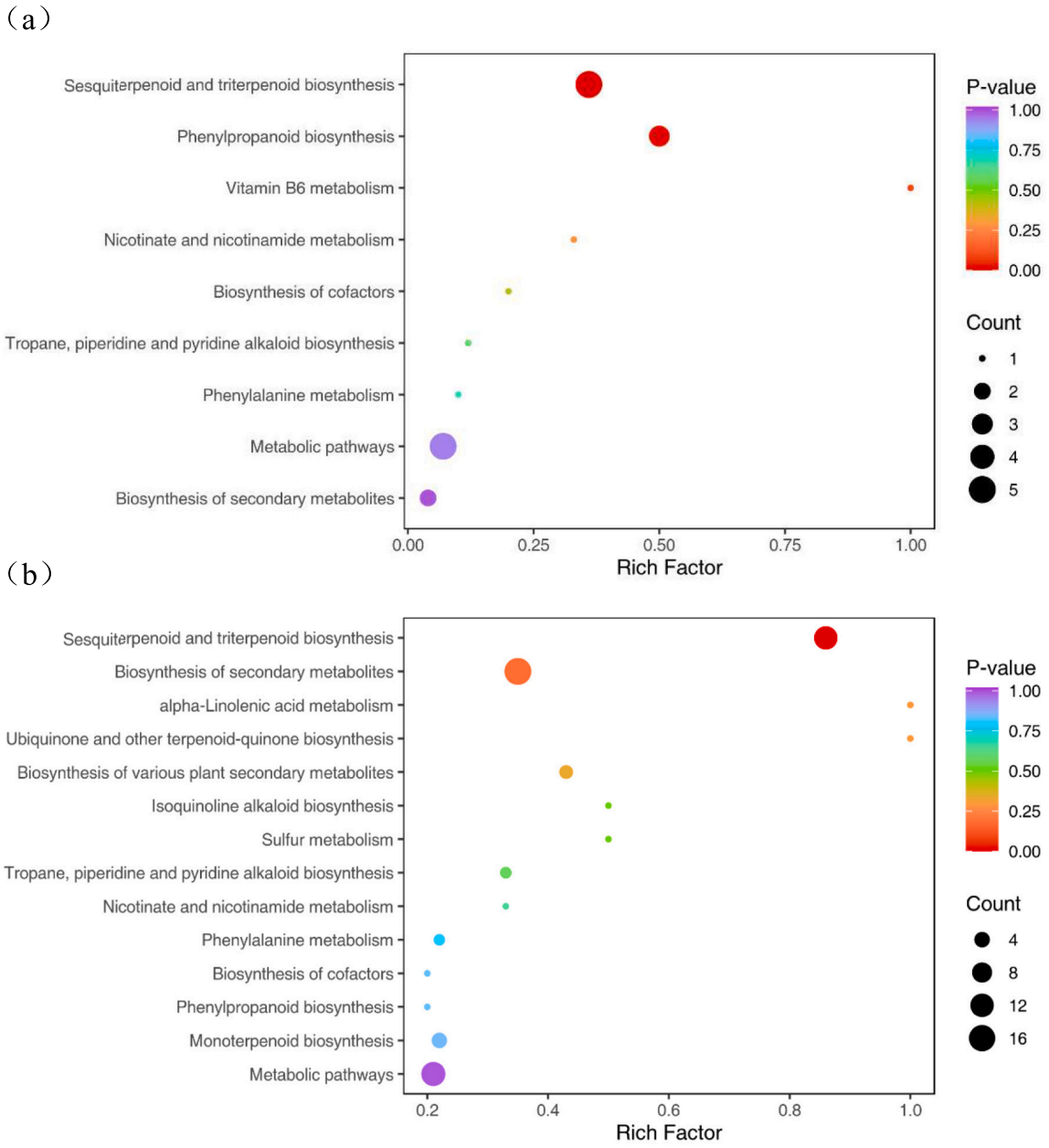

Fig. 4. Kyoto Encyclopaedia of Genes and Genomes (KEGG) enrichment analysis of differentially accumulated metabolites (DAMs) and in-depth analysis of key metabolites. (a) KEGG enrichment analysis for DAMs in UV-L and CK-L. (b) KEGG enrichment analysis for DAMs in UV-P and CK-P.

respectively (Fig. 6d; Table 2).

4. Discussion

There has been an ongoing exploration into the fields of plant photosynthesis, growth dynamics, quality development, and secondary metabolism, with a particular focus on the effects of varying light conditions. Additionally, research concerning the metabolic responses and impacts of UV radiation on diverse crop species has experienced continuous expansion. Concurrently, integrated analytical methodologies that combine metabolomics and transcriptomics have been increasingly utilized to provide a comprehensive understanding of these biological processes. Our results exhibited the identification of 1640 volatile organic compounds within celery leaves and petioles, with terpenes comprising roughly 20 % of the overall compounds detected. This result aligns with previous research, indicating that terpenes are the predominant volatile constituents in celery (Li, Li, Zhou, et al., 2022; Sun et al., 2023). The outcomes of both principal component and cluster analyses indicate that different parts of celery also have different VOCs responses after receiving UV radiation (Fig. 1b, Fig. 1c). Indeed, the distinct segments of the celery significantly contribute to the composition and quantity of its volatile constituents, corroborating findings from a prior study (Lykomitros et al., 2016). In addition, the previous studies have also suggested that the biosynthesis of volatile compounds in celery may also be related to the color formation pathway (Li, Li, Tan, et al., 2022).

Our results indicated that celery leaves significantly contribute to the production of volatile substances within the plant, similar results were elicited by Li et al. (2018), our results also exhibited that celery petioles exposure to UV radiation generate a greater array of distinct volatile metabolites by the further research (Fig. 1c). Studies have indicated that *TPS* genes constitute a gene family instrumental in modulating the

Table 1
Top 30 volatile aroma-active compounds in celery.

compounds	Class I	Formula	CAS	Odor	Threshold	rOAV			
						CK-L	UV-L	CK-P	UV-P
2-Methoxy-3,5-dimethylpyrazine	Heterocyclic compound	$C_7H_{10}N_2O$	92508-08-2	bread, mousy	0.0000004	12383665.97 ±1187975.79	13267005.67 ±515720.07	11808916.53 ±560209.24	13733803.16 ±798975.26
2,6-Nonadienal, (E,Z)-	Aldehyde	$C_9H_{14}O$	557-48-2	cucumber, green	0.00001	1480990.15 ±43953.7	2304465.42 ±205345.87	253357.99 ±10916.67	256790.45 ±7737.65
3-Buten-2-one, 4-(2,6,6-trimethyl-1-cyclohexen-1-yl)-	Terpenoids	$C_{13}H_{20}O$	14901-07-6	floral, woody, sweet, fruity, berry, tropical, beeswax	0.000007	639546.84 ±14579.54	401564.67 ±38283.74	217521.78 ±25584.54	179688.83 ±26453.09
2,4-Undecadienal	Aldehyde	$C_{11}H_{18}O$	13162-46-4	green, buttery, spicy, baked, fruity, fatty, aldehydic, chicken	0.00001	400239.43 ±47496.25	736282.6 ±32907.13	447425.12 ±33470.37	1028307.93 ±105200.4
2(5H)-Furanone, 5-ethyl-3-hydroxy-4-methyl-	Ketone	$C_7H_{10}O_3$	698-10-2	sweet, fruity, caramel, maple, fenugreek, brown, sugar, nutty, chicory, praline, butterscotch	0.000002	204729.69 ±52237.27	113414.37 ±2159.52	465353.99 ±22704.71	464343.24 ±14787.99
3-Cyclohexene-1-methanethiol, . alpha.,.alpha.,4-trimethyl-	Alcohol	$C_{10}H_{18}S$	71159-90-5	sulfury, aromatic, grapefruit, naphthyl, resinous, woody	2E-08	135884.74 ±156588.46	796362.73 ±74543.08	51265.38 ±2208.92	280372.94 ±14998.11
Pyrazine, 2,3-diethyl-5-methyl-	Heterocyclic compound	$C_9H_{14}N_2$	18138-04-0	musty, nut skin, earthy, roasted, hazelnut, toasted, potato, dusty,	0.000031	133622.58 ±14936.39	323063.37 ±21306.92	80430.4 ±12854.91	150963.48 ±19621.13
3-Mercapto-3-methylbutyl formate (ester)	Ester	$C_6H_{12}O_2S$	50746-10-6	foliage, vegetable sulfury, catty, caramel, onion, roasted coffee, roasted meat, tropical	0.000002	107422.27 ±5676.62	206145.43 ±5968.73	58914.77 ±2821.86	138757.7 ±4783.1
2-Nonenal, (E)-	Aldehyde	$C_9H_{16}O$	18829-56-6	fatty, green, cucumber, aldehydic, citrus	0.00008	58811.46 ±4183.83	90183.3 ±3819.87	94.47±4.07	516.56 ±27.33
Butanoic acid, 3-methyl-, 2-phenylethyl ester	Ester	$C_{13}H_{18}O_2$	140-26-1	floral, fruity, sweet, rose, peach, apricot	0.00001	48167.26 ±5765.2	69733.18 ±1847.38	28377.21 ±5233.81	52746.15 ±17681.04
Pyrazine, 2-methoxy-3-(1-methylethyl)-	Heterocyclic compound	$C_8H_{12}N_2O$	25773-40-4	beany, pea, earthy, chocolate, nutty	0.000002	47928.32 ±3022.74	46786.06 ±6497.55	6884.95 ±1093.72	3562.45 ±339.14
2-Nonenal	Aldehyde	$C_9H_{16}O$	2463-53-8	fatty, green, waxy, cucumber, melon	0.0001	47049.17 ±3347.06	72146.64 ±3055.9	75.57±3.26	413.24 ±21.87
2-Furanmethanethiol, 5-methyl-	Alcohol	C_6H_8OS	59303-05-8	sulfury, roasted, coffee	0.00005	36420.93 ±5254.57	51954.52 ±2464.8	8372.96 ±565.33	12293.79 ±831.98
2,6-Nonadienal, (E,E)-	Aldehyde	$C_9H_{14}O$	17587-33-6	fresh, citrus, green, cucumber, melon	0.0005	29619.8 ±879.07	46089.31 ±4106.92	5067.16 ±218.33	5135.81 ±154.75
trans-.beta.-Ionone	Terpenoids	$C_{13}H_{20}O$	79-77-6	dry, powdery, floral, woody, orris	0.0002	22384.14 ±510.28	14054.76 ±1339.93	7613.26 ±895.46	6289.11 ±925.86
Benzenemethanethiol	Alcohol	C_7H_8S	100-53-8	sharp, alliaceous, onion, sulfury, garlic, horseradish, minty, coffee	0.0000035	12749.6 ±305.63	7752.54 ±666.8	1361.53 ±58.67	1379.97 ±41.58
Dodecanenitrile	Nitrogen compounds	$C_{12}H_{23}N$	2437-25-4	citrus, orange, peel, metallic, spicy	0.00009	10347.18 ±1307.62	14174.87 ±522.12	10704.93 ±584.84	14904.21 ±1691
1-Hexen-3-one	Ketone	$C_6H_{10}O$	1629-60-3	cooked, vegetable, metallic	0.00002	8656.14 ±302.44	8286.01 ±620.18	730.6±31.48	740.49 ±22.31
Germacrene D	Terpenoids	$C_{15}H_{24}$	23986-74-5	woody, spice	0.0012	6917.06 ±633.74	9837.2 ±244.17	6533.67 ±835.7	10815.51 ±1211.83
Cyclohexanone, 2,2,6-trimethyl-	Ketone	$C_9H_{16}O$	2408-37-9	pungent, thujone, labdanum, honey, cistus	0.0001	5983.24 ±223.63	6463.03 ±332.9	5810.26 ±222.12	6619.03 ±127.94
Limonene	Terpenoids	$C_{10}H_{16}$	138-86-3	citrus, herbal, terpene, camphor	0.01	5740.42 ±387.34	12495.82 ±448.48	5296.24 ±299.13	10944.84 ±731.12
2-Hexenal, (E)-	Aldehyde	$C_6H_{10}O$	6728-26-3	green, grassy	0.0031	5050.28 ±371.34	4250.37 ±339.5	325.01±14	329.41±9.93
Acetic acid, cyclohexyl ester	Ester	$C_8H_{14}O_2$	622-45-7	fruity, sweet, musty, ethereal	0.0016	4861.54 ±180.94	5215.67 ±258.7	5140.87 ±262.76	5718.65 ±208.69
2,4-Undecadienal, (E,E)-	Aldehyde	$C_{11}H_{18}O$	30361-29-6	oily, caramel, spicy, citrus, buttery, baked	0.001	4002.39 ±474.96	7362.83 ±329.07	4474.25 ±334.7	10283.08 ±1052
(Z,Z)-3,6-Nonadienal	Aldehyde	$C_9H_{14}O$	21944-83-2	fatty, soapy, cucumber	0.00005	3492.93 ±175.1	5683.96 ±808.93	191.37±8.25	1033.2 ±49.63

(*continued on next page*)

Table 1 (*continued*)

compounds	Class I	Formula	CAS	Odor	Threshold	rOAV			
						CK-L	UV-L	CK-P	UV-P
Pyrazine, 2-methoxy-3-(1-methylpropyl)-	Heterocyclic compound	$C_9H_{14}N_2O$	24168-70-5	musty, green, pea, galbanum, bell pepper, pepper	0.000002	2787.78 ±65.32	1969.25 ±151.91	6666.2 ±999.61	4846.87 ±119.16
Pyridine, 2-propyl-	Heterocyclic compound	$C_8H_{11}N$	622-39-9	green, fatty, roasted, tobacco, nutty	0.011	2563.05 ±377.2	3639.89 ±166.78	607.07±41.5	901.84 ±65.68
Acetylpyrazine	Heterocyclic compound	$C_6H_6N_2O$	22047-25-2	popcorn, nutty, corn, chip, bread, crust, chocolate, hazelnut, coffee	0.01	2268.78 ±275.89	3790.41 ±120.24	1920.74 ±104.42	3165.58 ±547.28
Naphthalene, 2-methyl-	Aromatics	$C_{11}H_{10}$	91-57-6	sweet, floral, woody	0.004	1786.58 ±106.06	2180.15 ±78.9	101.55±8.48	156±7.46
.beta.-Phellandrene	Terpenoids	$C_{10}H_{16}$	555-10-2	terpenic, herbal	0.036	1779.34 ±210.39	2704.95 ±92.02	1315.56 ±72.83	2242.37 ±502.82

Note: The aromatic active compounds were screened according to rOAV>1 and arranged according to rOAV value.

variety and composition of terpenoids within horticultural plants, the expression levels of the transcriptional pathway genes associated with these *TPS* genes exhibit variability in different sections of the leaves and petioles (Huang et al., 2021), the relative gene expression level in the leaves of most horticultural plants such as celery was significantly higher than that in the petioles. However, the expression levels of kiwi fruit (*Actinidia deliciosa*) sesquiterpene synthetase, farnesene (*AdAFS1*) and germacrene synthases (*AdGDS1*) in flowers were significantly higher than those in leaves, indicating that there were differences in gene expression among different plants (Nagegowda, 2010). Concurrently, the celery petioles exhibited a greater quantity of differential volatile metabolites compared to the leaves following UV radiation, suggesting a pronounced impact of UV radiation on the petioles. Furthermore, the application of supplementary UV radiation concurrently modulated 73 volatile compounds across celery leaves and petioles, indicating a conserved metabolic trajectory among distinct segments of the same crop plant (Wong & Matus, 2017). Therefore, UV radiation can promote the synthesis of terpenoids by promoting the transcription level of *TPS* genes in plants, however, the parts that exert effects vary depending on the species of plants.

In order to further analyze the differential metabolites between different groups, a suitable OPLS-DA model was established, which has a high R^2Y value and Q^2 value, and can effectively classify the samples. Secondly, the OPLS-DA model can also highlight the relevant characteristics of different parts of celery and whether they receive ultraviolet radiation. In the process of analysis, VIP value is an effective method to classify differential metabolites, and it is usually used to explain the contribution of variables to the model. When VIP $>$ 1, variables are considered to have a greater impact on the model. Utilizing the OPLS-DA model, complete separation of the sample groups was achieved, with no observed crossover. Concurrently, 670 compounds exceeding a Variable Importance in Projection (VIP) score of 1 were identified from the leaf samples, while the petioles yielded 776 substances with a VIP $>$ 1, highlighting their distinct chemical profiles. Based on the criteria of VIP greater than 1, screening metabolites exhibiting fold-changes exceeding 2 in magnitude to identify significant differences. The study has shown that UV radiation can promote the increase of volatile compounds in celery, which is consistent with the trend of UV radiation can promote the increase of UV-absorbing compounds (Sun et al., 2024), however, the content of volatile compounds in celery may change under different processing conditions, the species of these compounds do not change accordingly.

K-means clustering analysis and KEGG pathway enrichment were employed to furnish metabolomic evidence elucidating the variances in flavor among distinct segments of celery supplementary ultraviolet irradiation. Our findings revealed that the impacts of UV radiation on the VOCs in celery varies by anatomical segment, however, the significantly enriched metabolic pathways remain consistent. Studies has shown that there were significant differences in the VOCs in the stems and leaves of large-leaf yellow tea, and the compounds in the tea stems were the key components of the characteristic flavor of large-leaf yellow tea (Liu et al., 2024). Metabolomic profiling, albeit unable to quantify the absolute concentration of individual metabolites, remains a powerful approach for discerning variations in VOCs within celery samples subjected to diverse treatments, as indicated by relative metabolite levels. Employing a cutoff of $|\text{Log}_2$ fold change$|$ greater than 1.0, we identified differential metabolites and characterized VOCs present in celery leaves and petioles subsequent to UV exposure. The Log_2 (fold change) values revealed that terpenoids and esters emerged as predominant metabolites in both celery petioles and leaves following UV irradiation, highlighting the significant role of UV radiation in celery's flavor formation. Previous studies have shown that UV-A promotes the synthesis of most terpenoids in lettuce derived from the shikimic acid pathway and the methylerythritol phosphate pathway (Zha et al., 2024), which has similar results to our study.

Although differential volatile metabolites in celery grown with UV radiation were detected, odor activity values were used for further understanding the changes in celery flavor after UV radiation. This metric serves as a quantitative indicator for assessing the impact of volatile organic compounds on biological perception, and underpins the efficiency of olfactory information transmission and reception within the environment. Specifically, the concept of odor activity value integrates the concentration of chemical molecules, sensory thresholds, and the efficiency of interactions between these molecules and biological receptors, thereby creating a comprehensive evaluation system. The establishment of this system has undoubtedly provided a scientific basis for understanding how organisms perceive their surroundings through olfaction and the functional role of odors within ecosystems. Consequently, the odor activity value plays a crucial role in elucidating the survival strategies of organisms, interspecies interactions, and environmental adaptability. Our results indicated that upon exposure to UV radiation, the aromatic profiles of celery leaves exhibited notable alterations, with pronounced changes in the woody and sweet notes. Similarly, the petioles demonstrated significant variations across a spectrum of odors, including green, floral, woody, sweet, citrus, and fruity nuances. The aroma of celery is often described as fresh, herbal, woody and citrusy, and the main contributors to these fragrance descriptions are terpenoids (Turner et al., 2021b). Among the difference accumulate metabolites, the leaves of celery exhibited pronounced woody and sweet notes, primarily attributed to terpenoids and esters. The petiole, on the other hand, carried diverse notes including green, floral, woody, and sweet, which are mainly composed of terpenes,

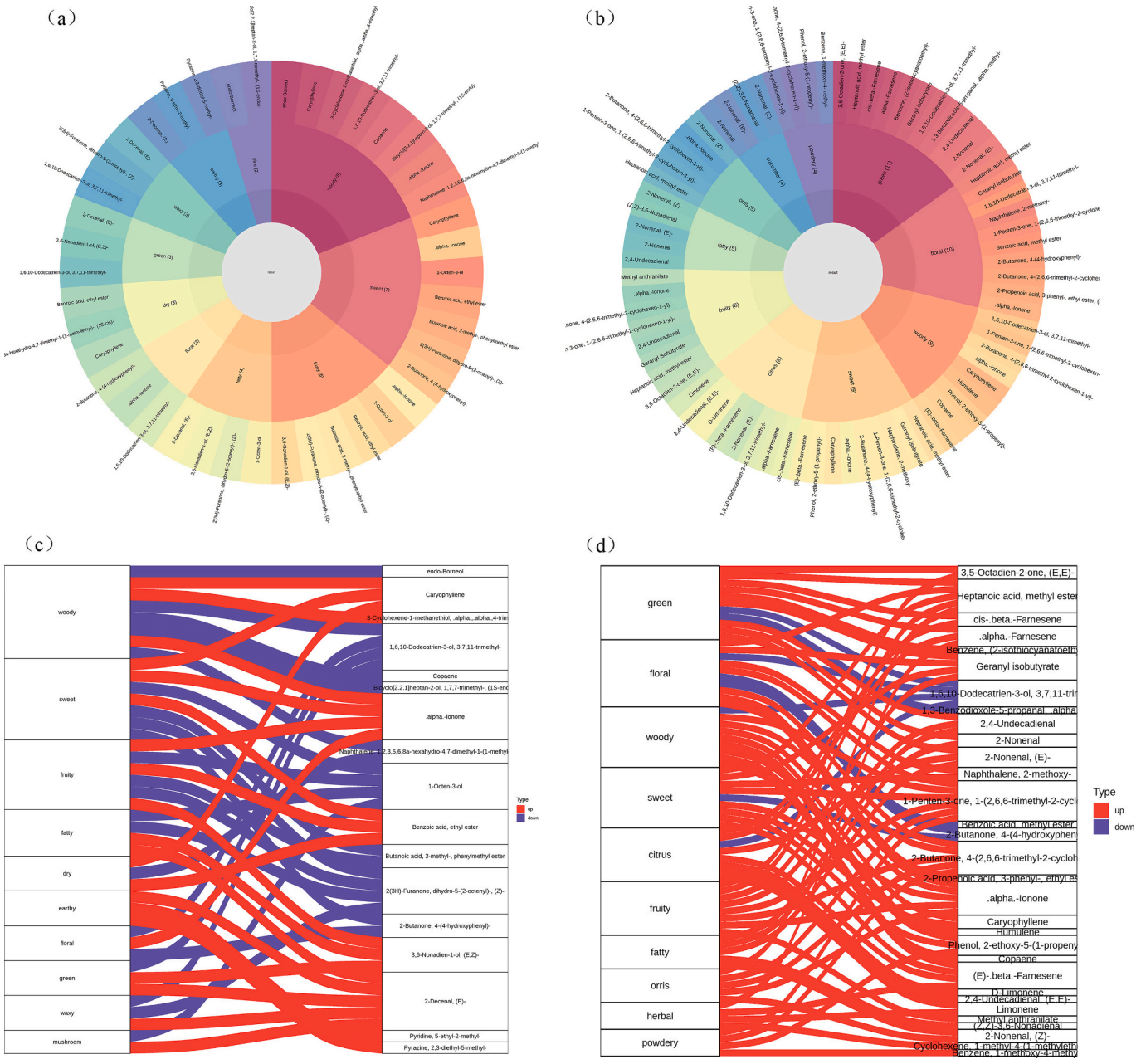

Fig. 5. Flavor omics analysis of volatile differential accumulated metabolites. (a) Flavor wheel of DAMs in group UV-L vs CK-L. (b) Flavor wheel of DAMs in group UV-P vs CK-P. (c) Sankey diagrams between aroma and differential volatile metabolites in group UV-L vs CK-L. (d) Sankey diagrams between aroma and differential volatile metabolites in group UV-P vs CK-P.

aldehydes, and esters. Previous studies indicates that ultraviolet radiation alters the concentration of grape's indigenous amino acids, which act as precursors to aroma compounds (Li et al., 2020). Consequently, variations in amino acid profiles lead to modifications in grape aroma. It has been suggested that enhancing ultraviolet exposure can augment the volatile compound aroma in crops (Zhu et al., 2022). Simultaneously, UV radiation significantly influences the transcriptional profile and metabolic processes in tea, particularly with respect to the synthesis of flavor metabolites critical to tea quality. Following exposure to 35 $\mu W \cdot cm^{-2}$ UV radiation for a duration of 0.5 h, there was a notable upsurge in the expression of genes associated with the terpene biosynthetic pathway, which was accompanied by a consequent elevation in the abundance of volatile terpenoids (Shamala et al., 2020).

Adaptability is essential for plant survival, as light fluctuations significantly impact growth and metabolic processes of plants, including formation of product quality and secondary metabolism. UV radiation is recognized as a stressor due to its shorter wavelengths, exerting coercion on plants. Studies have shown that UV-A radiation has a significant effect on the increase of gene transcription abundance in the terpene biosynthesis pathway (Zha et al., 2024). Concurrently, pigments such as anthocyanins are also regulated by ultraviolet radiation (Liu et al., 2015). Therefore, UV radiation impacts the physiological characteristics and bioactive components of different parts of crops in varying ways. These variations necessitate a detailed analysis of its role in the metabolic pathways of bioactive components, which could enhance the medicinal and nutritional benefits of crops in the future.

5. Conclusion

Celery exhibited more differential volatile metabolites after

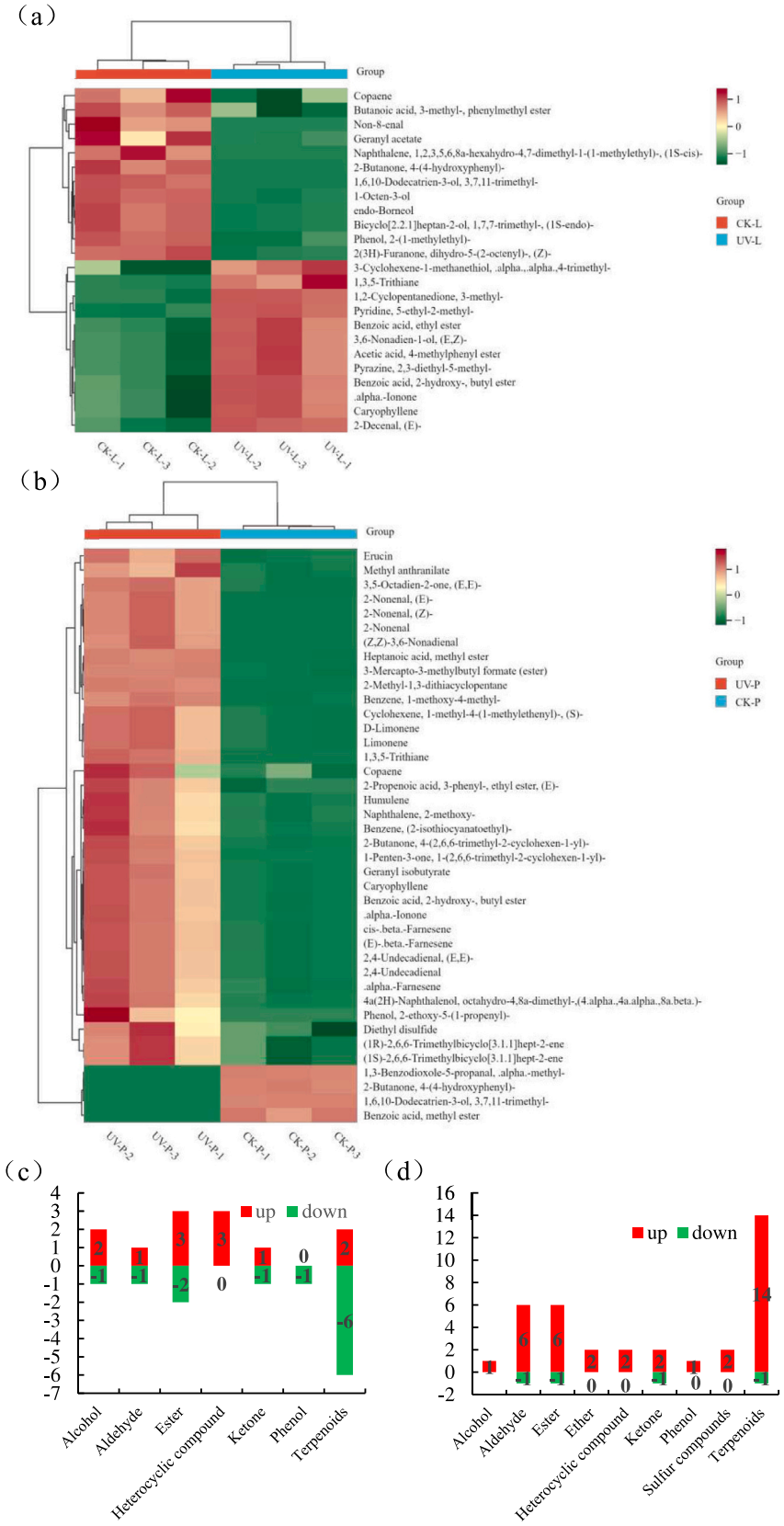

Fig. 6. DAMs in key flavor compounds. (a) Heat map comparing WR-L and UV-L. (b) Heat map comparing WR-P and UV-P. (c) Classification and quantity of DAMs in WR-L and UV-L. (d) Classification and quantity of DAMs in WR-P and UV-P. (Red indicates a relatively high metabolite abundance, and green indicates a relatively low abundance.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
The species and quantity of differentiated metabolites in each differentiated group.

Group name	Compounds classification	All sig diff	Type	sig diff
UV-P vs CK-P	Alcohol	1	up	1
	Aldehyde	7	up	6
			down	1
	Ester	7	up	6
			down	1
	Ether	2	up	2
	Heterocyclic compound	2	up	2
	Ketone	3	up	2
			down	1
	Phenol	1	up	1
	Sulfur compounds	2	up	2
	Terpenoids	15	up	14
			down	1
UV-L vs CK-L	Alcohol	3	up	2
			down	1
	Aldehyde	2	up	1
			down	1
	Ester	5	up	3
			down	2
	Heterocyclic compound	3	up	3
	Ketone	2	up	1
			down	1
	Phenol	1	down	1
	Terpenoids	8	up	2
			down	6

Note: The screening criteria for differential metabolites were VIP > 1, rOAV>1, $|Log_2FC| > 1$, $P < 0.05$.

supplementary UV radiation. A total of 1640 volatile metabolites were detected, 195 differential metabolites were detected in celery leaves and 351 differential metabolites were detected in celery petioles. Moreover, compounds such as 2-Methoxy-3,5-dimethylpyrazine, (E,Z)-2,6-Nonadienal, 4-(2,6,6-trimethyl-1-cyclohexen-1-yl)-3-Buten-2-one, 2,4-Undecadienal and 5-ethyl-3-hydroxy-4-methyl-2(5H)-Furanone with higher rOAVs were pivotal contributors to the aroma quality under different light irradiation treatments. Among them, 24 and 40 volatile metabolites in leaves and petiole of celery were deemed as the key differential metabolites under different UV radiation treatments. In addition, the biosynthesis of sesquiterpene and triterpene compounds was the main metabolic pathway of celery after exposure to UV radiation. The sweetness and woody aroma of celery leaves and petioles were regulated after receiving UV radiation, and the green, floral, citrus and fruit flavors of celery petioles were also different. Our investigation delineated the variations in volatile compounds and flavor disparities among distinct segments of celery subjected to ultraviolet radiation, offering significant insights for deeper exploration into the chemical attributes and utilization of celery.

Ethical approval

This article does not contain any studies with human participants or animals performed by any of the authors.

CRediT authorship contribution statement

Zhengnan Yan: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Zhixin Li:** Writing – original draft, Software, Methodology, Investigation, Data curation, Conceptualization. **Haokai Wang:** Methodology, Data curation. **Haijie Dou:** Supervision, Methodology, Conceptualization. **Jinxiu Song:** Supervision, Conceptualization. **Fang Ji:** Supervision, Conceptualization. **Yanjie Yang:** Supervision, Methodology, Funding acquisition, Conceptualization. **Duo Lin:** Writing – review & editing, Resources, Project administration, Methodology, 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.

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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.2025.102213.

Data availability

Data will be made available on request.

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