



## Review

## A matter of smell: The complex regulation of aroma production in melon

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## ABSTRACT

Melon fruit flavor is one of the most valuable traits for consumers. Aroma, formed by volatile organic compounds (VOCs), is a major component of flavor but has been neglected in breeding programs because of its complex regulation. Although the genetic regulation of VOCs biosynthesis is not fully understood, several advances have been recently achieved. VOCs originate from the degradation of fatty acids, aminoacids and terpenes, and the role of newly described enzymes, transcription factors and putative regulators is here discussed. Furthermore, ethylene plays a key role in fruit aroma production in melon, triggering the conversion of green-flavored aldehydes into fruity-flavored esters. A current challenge is to understand the ethylene-independent regulation of VOCs formation. Environmental conditions and human processing can also shape the melon volatile profile, and future research should focus on studying the effect of climate change in aroma formation.

## 1. Introduction

Melons are highly appreciated fruits mainly grown in Mediterranean and tropical latitudes. Melon production has been growing since the end of last century, China currently being the first producer, with almost half of the world melon production, and Spain being the leader in exports (FAO, 2022). One of the most valuable traits in melon is flavor, which is a combination of aroma and taste. Different elite varieties have been bred in order to match farmers' preferences, focusing on resistance, yield, sugar content and shelf-life. However, breeding for aroma has not been a priority until recently. In China, the most popular melon is the 'Hami' melon, that is usually sweet and aromatic (Moshonas et al., 1993). Nonetheless, both aromatic and non-aromatic melons are consumed in China (Yang et al., 2007). In Western Europe the most popular melons are cantaloupes from the 'Charentais' type, often called 'muskmelons', which are highly aromatic (Pitrat, 2017) (Fig. 1). 'Galia' melons, which are also quite aromatic, are popular in Eastern Europe. Less aromatic 'Charentais' type melons are preferred in the United States. On the other hand, in the Iberian Peninsula non-aromatic but very sweet melons are preferred such as 'Piel de Sapo', 'Branco' and 'Canary'. These *inodorus* varieties are included under the 'honeydew' name. Although every region has its preferred cultivars, consumers' preferences are in constant change. Nowadays, market demands small melons with longer shelf life, maintaining sweetness and aroma. The

current natural variability can be used to breed new varieties matching these new preferences, but knowledge of the genetic regulation of aroma production is essential for breeding programs.

## 2. Aroma in melon

Aroma is formed by the emission of volatile organic compounds (VOCs). More than 500 different VOCs have been already detected in melon using different techniques, one single variety being able to produce more than 100 compounds (Buttery et al., 1982; Chaparro-Torres et al., 2016; Esteras et al., 2018; Esteras et al., 2020; Galpaz et al., 2018; Hasbullah et al., 2019; Kemp et al., 1971; Lignou et al., 2013; Majithia et al., 2021; Mayobre et al., 2024; Pang et al., 2012; Perry et al., 2009; Shao et al., 2022; Wyllie et al., 1994; Wyllie & Leach, 1990; Yabumoto & Jennings, 1977). VOCs can be classified according to their main chemical group (Gonda et al., 2016). Fruits mainly produce esters, aldehydes, alcohols and terpenoids. Other minor groups are furans, ketones, lactones and aromatic compounds containing a benzene ring. Each VOC has a specific aroma; however, some generalizations can be done. Esters are typically described as fruity and sweet, whereas aldehydes usually give fresh, green notes (Schwab et al., 2008). Melon fruit aroma can vary depending on the accession. Two wide studies on flesh and rind aroma by Esteras et al. (Esteras et al., 2018; Esteras et al., 2020) classified melon accessions in two clusters and several sub-clusters according to

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their aroma profile. The main division was between aromatic and non-aromatic genotypes. Aromatic genotypes such as *cantalupensis*, *reticulatus* and *dudaim* were rich in esters, mainly in ethyl esters, and presented the highest internal variation. Within this cluster, differences between groups were found in the accumulation of acetates, ethyl esters, sulfur compounds, apocarotenoids, sesquiterpenes (in rind) and lactones. The non-aromatic cluster, including melons from the *inodorus*, *flexuosus*, *acidulus* and *momordica* groups, accumulated less esters and was rich in fatty acid-derived aldehydes and alcohols. In addition, the volatile profile of this group was less diverse than the one in aromatic melons.

Volatile measurements are generally carried out using Gas-Chromatography and Mass-Spectrometry (GC-MS), but they can differ in the way samples are processed and injected (Allwood et al., 2014; Metrani et al., 2022; Shi et al., 2020; Verzera et al., 2011). The most extended method nowadays is Solid-Phase Micro Extraction (SPME), consisting in the exposure of a fiber to the headspace of a vial containing the sample. Other possible approaches to measure volatiles are electronic noses and olfactometry (Chaparro-Torres et al., 2016; Lignou et al., 2013). The aromatic power of volatiles is usually studied by calculating the odor activity value (OAV) or by aroma extract dilution analysis (AEDA) (Hayata et al., 2003; Pang et al., 2012, 2019; Perry et al., 2009). The key compounds and potent odorants that have been described to play a major role in melon aroma are shown in Fig. 2 (Farcuh et al., 2020; Hayata et al., 2003; Pang et al., 2012; Peng et al., 2024; Wyllie et al., 1995).

Melon and cucumber-like flavors are predominantly associated to C9 aldehydes and alcohols such as 2,6-nonadienal-(E,Z), 2-nonenal-(E) or 3,6-nonadienol-(Z,Z). Tropical, sweet and fruity aromas mainly come from esters such as ethyl 2-methylbutanoate, methyl 2-methylpropanoate, ethyl butanoate, hexyl acetate, ethyl hexanoate or 2-methylbutyl acetate. Floral aromas are usually given by terpenes like  $\beta$ -ionone,  $\beta$ -damascenone and geranylacetone, whereas eucalyptol recalls minty notes. Moreover, unpleasant aromas can also be produced in melon, such as sulfides (sulfurous), 1-octen-3-ol (mushroom-like), and acetaldehyde (ethereal). As an example, 'Védrantais' and 'Queen Anne's pocket melon' accessions contain big quantities of ethyl hexanoate and ethyl 2-methylbutanoate, respectively, both fruity notes (Table 1). On the other hand, 'Piel de Sapo' contains more aldehydes such as hexanal,

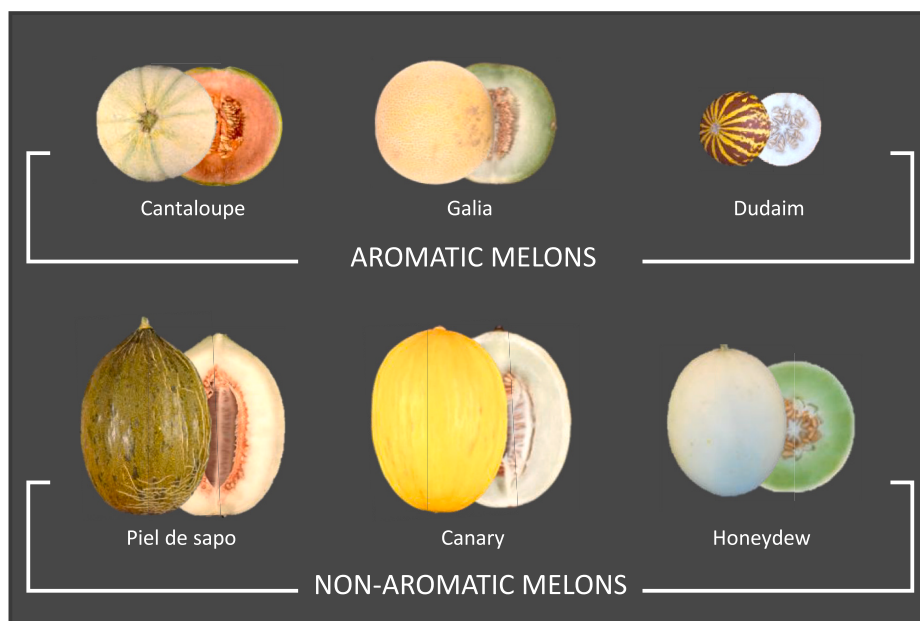
with leafy, grassy flavor. 'Songwan Charmi', an *agrestis* melon, has a great abundance of the unpleasant aroma 1-octen-3-ol (mushroom-like). A more extensive bibliographic review on the abundance of key aromas in 116 melon accessions can be seen on Supplementary Table S1.

VOCs biosynthesis pathways have been studied in economically important plant species such as petunia and tomato, finding some differences that suggest independent evolution of the pathways (Gonda et al., 2016). In melon, a study on more than 1000 melon accessions revealed that aroma in general is linked to two regions on chromosome 8, in addition to some significant SNPs on chromosomes 1, 5, 10 and 12 (Zhao et al., 2019). The region with the highest LOD, on chromosome 8, matches the ethylene QTL *ETHQV8.1*, suggesting a relationship between the evolution of aroma and ripening (Pereira et al., 2020). A few genes have been described in melon VOCs synthesis pathways, but knowledge is still limited. For instance, transformation from aldehydes to alcohols and esters has been well characterized, but many upstream enzymes remain unknown. Several volatile Quantitative Trait Loci (QTLs) have been identified in melon recombinant and introgression line populations (Galpaz et al., 2018; Mayobre et al., 2021; Mayobre et al., 2024; Perpiñá et al., 2021). These studies showed that single QTLs usually control the synthesis of several VOCs, suggesting a central regulation by transcription factors. Furthermore, several metabolic enzymes have been demonstrated to transform more than one substrate (Gonda et al., 2010).

Generally, VOCs can be originated from three different biosynthetic pathways involving fatty acids, aminoacids, and terpenoids.

### 2.1. The fatty acid pathway

Fatty acids can generate different straight-chain volatiles depending on the initial carbon chain (Schwab et al., 2008). Linoleic and linolenic acids undergo two degradation steps to form C6 and C9 aldehydes (Fig. 3). First, 9- or 13- lipoxygenases (LOX) generate hydroperoxides. Hydroperoxide lyases (HPL) then transform these intermediates into the final aldehydes. A total of 18 different LOXs have been described in the melon genome (C. Zhang et al., 2014). For instance, *CmLOX18* (*MELO3C024348*) was described to be a 13-LOX capable of transforming both linoleic and linolenic acid into C6 volatiles (C. Zhang et al., 2017). HPLs have been less studied in melon. Only one melon HPL (*MELO3C018413*) was described by Tijet et al. (2001) having both 9-



**Fig. 1.** Examples of aromatic and non-aromatic varieties of melon. Aromatic melons are 'Védrantais' cantaloupe (group *cantalupensis-charentais*), 'Galia' (group *cantalupensis-reticulatus*) and 'Queen Anne's pocket melon' (group *dudaim*; adapted from Pitrat, 2017); non-aromatic melons are 'Piel de Sapo' (group *inodorus*), 'Canary' (group *inodorus*) and 'Tam Dew' honeydew (group *inodorus*; adapted from Pitrat, 2017).

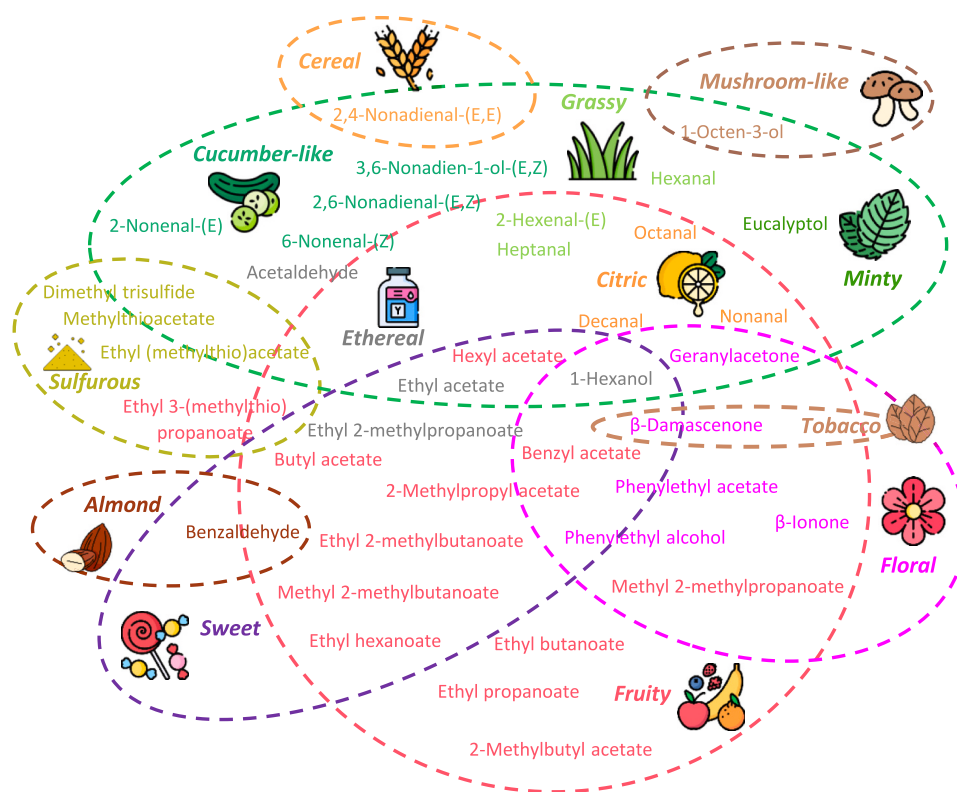


Fig. 2. Melon key volatiles and potent odorants, and their main aromatic descriptors.

HPL and 13-HPL activities (Grechkin et al., 2006). The products of this pathway include melon key volatiles such as 3,6-nonadienal-(Z,Z), 3-nonenal-(Z), 3-hexenal-(Z) and hexanal, which are commonly referred as green leaf volatiles (GLVs). GLVs have a fresh flavor and are mainly produced by plants during the quick response to herbivore-induced damage, so they have both aromatic and ecological importance (Arimura et al., 2009). These compounds can be later transformed into alcohols and esters by alcohol dehydrogenases (ADH) and alcohol acyltransferases (AAT), respectively (Schwab et al., 2008). Moreover, a 3Z-2E enoyl-CoA isomerase (ECI) has been postulated as the missing step between 3-hexenal-(Z) and 2-hexenal-(E) (Mayobre et al., 2024; Nagashima et al., 2021). In cucumber, a cupin was demonstrated to be responsible for this reaction, also active for the synthesis of the key volatile 2,6-nonadienal-(E,Z) (Spyropoulou et al., 2017). It is yet unclear whether an ECI or a cupin perform this reaction in melon.

Recently, a GWAS study in watermelon highlighted an omega-3 fatty acid desaturase (*Cla97C03G051490*) as putatively responsible for the linoleic acid transformation into linolenic acid, affecting the accumulation of 2-pentylfuran, hexanal and 2-octenal-(E) (Gong et al., 2023). In addition, an enoyl reductase (*Cla97C02G049790*) was found to link volatile formation in cucurbits to fatty acid metabolism. The homologous genes in melon for the watermelon candidates, *MELO3C020541* and *MELO3C014644*, could have a similar function and should be further studied. For instance, *MELO3C020541* can be found within the genetic interval of a 2-pentylfuran QTL recently described (Mayobre et al., 2021).

## 2.2. The aminoacid pathway

Aminoacids are the main source of branched-chain and aromatic volatiles (Fig. 4). Different aminoacids such as methionine, leucine, valine, isoleucine, tyrosine and phenylalanine have been described to be the first substrate for several VOCs synthesis. In melon, the first step is a deamination, which is catalyzed by an aminotransferase (Gonda et al., 2016). *CmBCAT1* (*MELO3C010776*) and *CmArAT1* (*MELO3C025613*)

have been reported to transform branched-chain and aromatic aminoacids, respectively, into  $\alpha$ -keto acids (Gonda et al., 2010). According to the knowledge in tomato and petunia, the next step should be a decarboxylation (Kaminaga et al., 2010; Tieman et al., 2006). A  $\alpha$ -keto acid decarboxylase (*CmPDC1*, *MELO3C009145*) was recently described in melon. It was reported to produce acetaldehyde, propanal and pentanal, but no significant activity in aminoacid-derived molecules was observed (Wang et al., 2019). Currently no other aminoacid decarboxylases have been identified and tested in melon.

A second degradation pathway was found for some aminoacids. Methionine, apart from being transformed by an aminotransferase, has also been reported to generate methanethiol,  $\alpha$ -keto butyrate and ammonia by the action of a methionine gamma-lyase (*CmMGL*, *MELO3C013774*), suggesting a connection with the isoleucine metabolism (Gonda et al., 2013). In addition, a second pathway for phenylalanine transformation linked to the phenylpropanoid pathway is believed to occur in melon. Gonda et al. (2018) identified two enzymes, *CmCNL* (*MELO3C025110*) and *CmBAMT* (*MELO3C003803*), responsible for cinnamoyl-CoA and methyl benzoate synthesis, respectively. Other enzymes have been hypothesized to play a role in phenylalanine-derived volatiles production. For instance, several cinnamoyl-CoA reductases (*CmCCR*) have been found in melon (Gonda et al., 2018; Niyakan et al., 2023). The expression of some cinnamyl alcohol dehydrogenases (*CmCAD*) has been found in fruit and respond to ethylene administration (Jin et al., 2014; Niyakan et al., 2023). In the same way, an aldehyde oxidase (*CmAao*) is believed to be the step between benzaldehyde and benzoic acid, however, no genes have yet been validated (Mayobre et al., 2021). There is still very few knowledge about how phenylalanine-derived volatiles such as benzaldehyde are formed. These volatiles are also related with the lignin pathway and the fungal defense (Lin et al., 2019; Liu et al., 2020). Therefore, it is of great interest to continue studying this pathway over the next years.

**Table 1**  
Key melon volatiles, aromatic descriptors, and abundances in four different melon accessions.

Class	Compound	Aromatic descriptor <sup>a</sup>	VOCs abundance <sup>b</sup>				
			Védantais <sup>c</sup> ( <i>cantalupensis-charentais</i> )	Songwan Charmi <sup>d</sup> PI 161375 ( <i>agrestis</i> )	Queen Anne's pocket melon <sup>e</sup> PI 273438 ( <i>dudaim</i> )	Piel de Sapo <sup>c</sup> T111 ( <i>inodorus</i> )	
Alcohols	1-Hexanol	Ethereal, fruity, sweet, flower, green	12054.05	380.41	24954.33	57.78	
	1-Octen-3-ol	Mushroom, earthy, green	391.38	13682.74	824.00	410.28	
	3,6-Nonadien-1-ol-(E,Z)	Green, cucumber, grassy	0.00	nd	nd	1.06	
	Phenylethyl alcohol	Floral, lilac, rose, honey, spice	1062.10	0.00	nd	19.64	
Aldehydes	2,4-Nonadienal-(E,E)	Cereal, wet wool, watermelon, fatty	4.74	0.00	752.00	0.71	
	2,6-Nonadienal-(E,Z)	Fresh, green, melon, cucumber	800.76	1240.20	nd	344.32	
	2-Hexenal-(E)	Leafy, apple, vegetable, fatty, plum	17.52	23.47	3335.00	66.82	
	2-Nonenal-(E)	Melon, cucumber, waxy, green, fatty	775.33	770.89	19582.33	217.97	
	6-Nonenal-(Z)	Melon, cucumber, waxy, green	209.46	464.92	nd	181.04	
	Acetaldehyde	Ethereal, whiskey, pungent, fruity	nd	nd	nd	nd	
	Benzaldehyde	Almond, burnt sugar, cherry, sweet	1357.91	160.51	226101.67	75.02	
	Decanal	Citrus, orange peel, soap, floral, sweet	140.69	26.14	8611.33	98.52	
	Heptanal	Citrus, herbal, fresh, fatty, green	749.17	150.56	25845.67	167.25	
	Hexanal	Leafy, grass, fresh, fruity, fatty	2231.04	0.00	41306.33	577.50	
	Nonanal	Lime, orange peel, green, fatty, fresh	639.55	449.24	nd	461.44	
	Octanal	Lemon, orange peel, soap, fatty, green	11239.87	98.34	28567.67	175.76	
	Esters	2-Methylbutyl acetate	Apple, banana, pear, peanut	4495.84	6902.95	364444.00	21.57
		2-Methylpropyl acetate	Apple, tropical, banana, sweet, floral	6788.76	7122.77	754687.67	81.98
Benzyl acetate		Apple, apricot, plum, floral, sweet	nd	nd	nd	nd	
Butyl acetate		Apple, banana, pear, ethereal, glue	6371.48	4278.16	180639.00	3.14	
Ethyl (methylthio)acetate		Sulfurous, onion, radish, green, fruity	7257.74	0.00	693031.00	93.80	
Ethyl 2-methylbutanoate		Apple, sweet, plum, sharp	24524.21	1682.71	856788.67	73.98	
Ethyl 2-methylpropanoate		Ethereal, strawberry, sweet, alcoholic	3737.35	833.63	62538.00	35.18	
Ethyl 3-(methylthio)propanoate		Fruity, sulfurous, pineapple, tomato	2235.94	172.97	143022.00	1.99	
Ethyl acetate		Ethereal, pineapple, sweet, green	20070.46	9862.15	497667.33	586.33	
Ethyl butanoate		Apple, pineapple, banana, cognac	33560.81	3462.36	501371.00	71.27	
Ethyl hexanoate		Pineapple, apple peel, sweet, banana	69020.92	3005.16	312189.33	25.17	
Ethyl propanoate		Pineapple, grape, strawberry, rum	4023.13	673.87	104494.33	84.26	
Hexyl acetate		Apple, banana, sweet, green, herbal	13468.86	13219.06	344093.67	14.58	
Methyl 2-methylbutanoate		Apple, strawberry, sweet	4884.26	17.39	30063.33	3.94	
Methyl 2-methylpropanoate		Apple, pineapple, floral	33.17	0.00	3332.33	0.00	
Methylthioacetate		Sulfurous, garlic, cheese, cabbage	nd	nd	46911.00	nd	
Phenylethyl acetate	Floral, rose, honey	687.78	803.51	736218.33	0.83		
Sulfides	Dimethyl trisulfide	Sulfurous, onion, cabbage	7.26	29.52	nd	44.53	
Terpenoids	Eucalyptol	Mint, herbal, eucalyptus, pepper	3719.89	0.00	86360.00	11.43	
	Geranylacetone	Floral, magnolia, rose, fruity, leafy, fresh	7408.77	nd	2496.67	0.33	
	$\beta$ -Damascenone	Floral, rose, apple, tobacco, honey	nd	nd	53117.33	nd	
	$\beta$ -Ionone	Floral, violet, orange, jam, raspberry	1028.05	93.41	17703.33	0.00	

nd = not detected.

<sup>a</sup> FlavorDB (Garg et al., 2018).

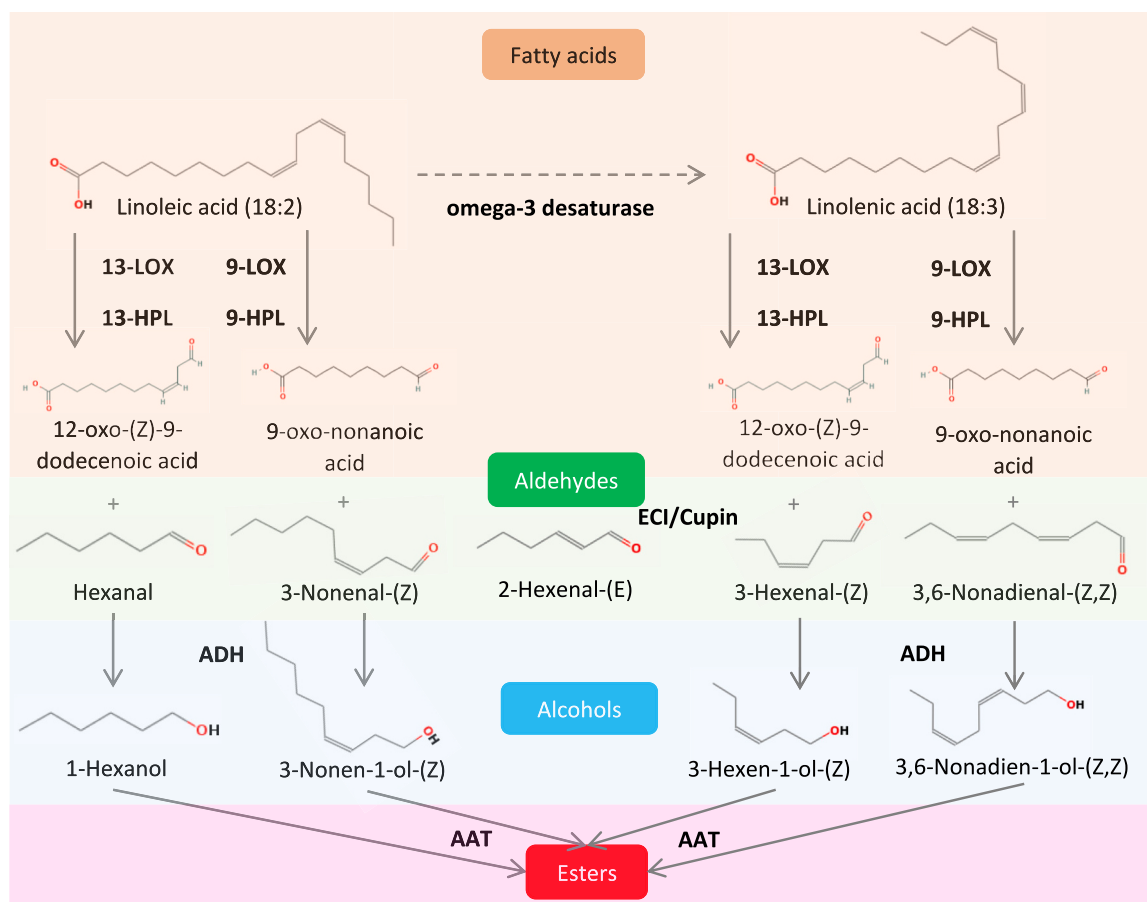
<sup>b</sup> Obtained by SPME-GCMS. Color gradient from low quantities (in light grey) to high quantities (in dark grey).

<sup>c</sup> Data from Mayobre et al. (2024) in ng/g fresh tissue.

<sup>d</sup> Data from Santo Domingo et al. (2022) in ng/g fresh tissue.

<sup>e</sup> Data from Esteras et al. (2018) as a ratio to a sample mix.





**Fig. 3.** Biosynthetic pathway of fatty acid-derived VOCs in melon. Dashed lines represent hypothesized steps of the pathway. LOX = lipoxygenase, HPL = hydroperoxide lyase, ECI = enoyl-CoA isomerase, ADH = alcohol dehydrogenase, AAT = alcohol acyltransferase.

### 2.3. The terpenoid pathway

Terpenoids are the most diverse group of volatiles. They are formed from isoprenoid units synthesized in the acetate/mevalonate or the pyruvate/glyceraldehyde-3-phosphate pathways (Croteau et al., 2000) (Fig. 5). The diversity within terpenoids comes from the multiple modifications their chain can suffer. Terpenoids can be divided according to the number of carbons in the molecule, being constructed from multiple five-carbon isoprene units (IPP). The most relevant are monoterpenes (IPP x2, C10), sesquiterpenes (IPP x3, C15), diterpenes (IPP x4, C20), triterpenes (IPP x6, C30) and tetraterpenes (IPP x8, C40). Short terpenes are generally associated to responses to herbivore-induced damage, although they are synthesized later than GLVs (Arimura et al., 2009). In melon, a few terpene synthases (TPS) have been identified. *CmTpsDul* (MELO3C016595) and *CmTpsNY* (MELO3C016588) were discovered in two different melon varieties. *CmTpsDul* catalyzed the conversion of farnesyl diphosphate (FPP) into  $\alpha$ -farnesene, while *CmTpsNY* was able to synthesize several sesquiterpenes including  $\gamma$ - and  $\delta$ -cadinene (Portnoy et al., 2008).

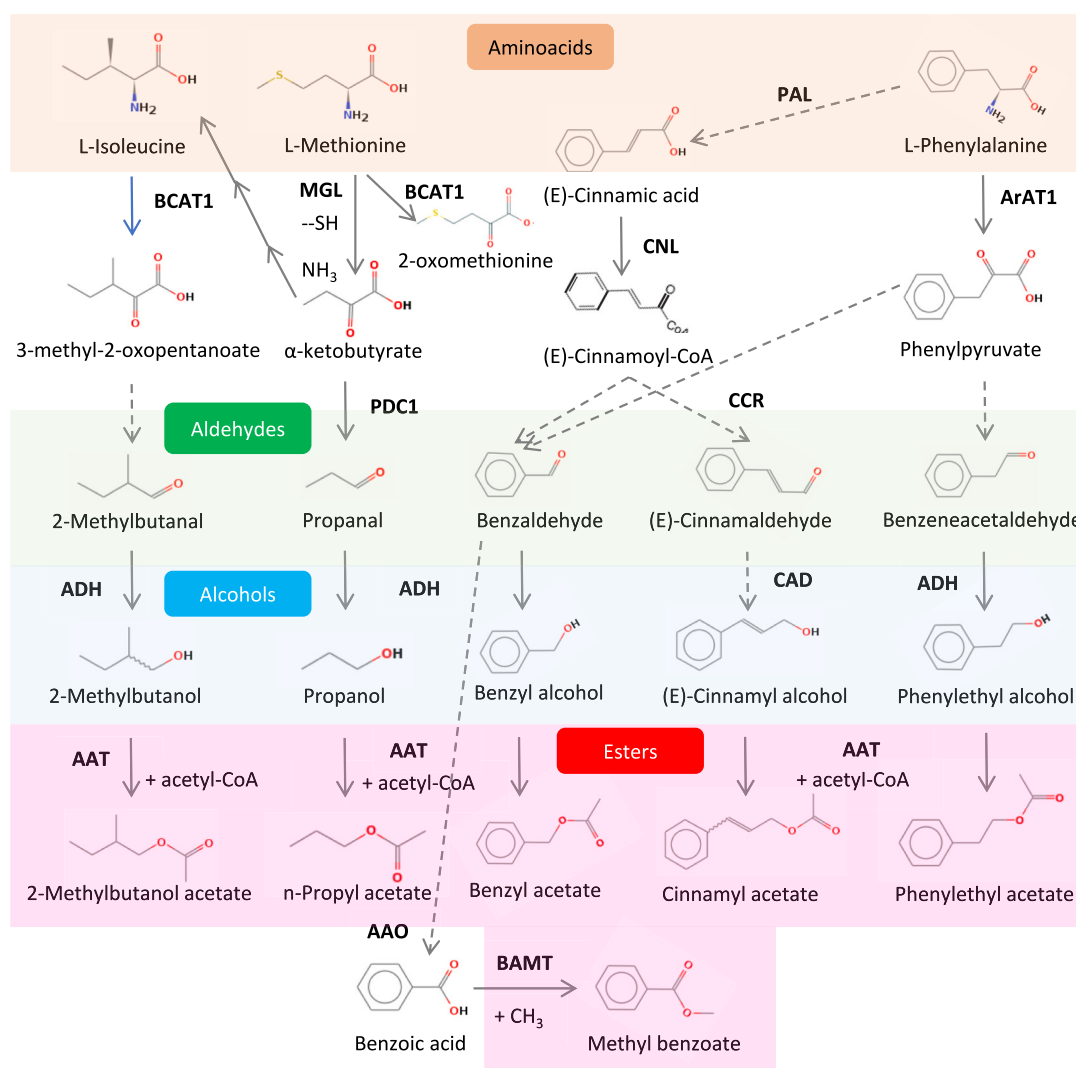
Within tetraterpenes, carotenoids are an important origin of volatiles in fruits and are also linked to benefits to human health (Bohn et al., 2021). Carotenoid synthesis has been widely studied in tomato. The first carotenoid, phytoene, is synthesized by a phytoene synthase (PSY) (Zhu et al., 2022). Afterwards, phytoene is transformed by a phytoene desaturase (PDS), a  $\zeta$ -carotene isomerase (ZISO), a  $\zeta$ -carotene dehydrogenase (ZDS) and a carotene isomerase (CRTISO), forming the red pigment lycopene. Then, lycopene cyclases can generate different forms of carotene, that end up transformed into xanthophylls. Several of these carotenoids can be cleaved to form volatile molecules called

apocarotenoids (Lewinsohn et al., 2005). In melon, DnaJ cysteine-rich domain-containing protein *CmOr* (MELO3C005449) was proven to enable the accumulation of carotenoids (Tzuri et al., 2015), and the *CmOr-like* gene is hypothesized to complement *CmOr* mutations (Chayut et al., 2017). Recent studies in oriental melons also demonstrated that transcription factors *CmWRKY49* (MELO3C012130) and *CmNAC34* can bind to phytoene synthase (*CmPSY1*, MELO3C025102) and lycopene  $\beta$ -cyclase (*CmLCYB*, MELO3C020744) promoters, respectively, inducing  $\beta$ -carotene accumulation (Duan et al., 2022; Zhao et al., 2022). In addition, a *CmCRTISO* (MELO3C009571) mutant was described to modify carotenoid and apocarotenoid production (Galpaz et al., 2013). Regarding volatile production, only one carotenoid cleavage dioxygenase (*CmCCD1*, MELO3C023555) has been validated in melon, although it can use several different substrates. *CmCCD1* was able to cleave phytoene, lycopene,  $\beta$ -carotene and  $\delta$ -carotene into volatile geranylacetone, pseudoionone,  $\beta$ -ionone and  $\alpha$ -ionone, respectively (Ibdah et al., 2006).

Knowledge about the terpenoid pathway in melon is growing in the last decades, but there is still a plethora of genes to discover and study. Moreover, modulation of terpenoid volatiles could be tackled by the mutation of known genes. The importance of this pathway, linking fruit color, aroma and human health, makes it a very interesting topic to study in the following years.

### 2.4. From aldehydes to esters

The conversion of aldehydes to esters is made in two steps, alcohols being the intermediate phase. The first reaction is catalyzed by alcohol dehydrogenases (ADHs) (Figs. 3 and 4). Twelve ADHs have been



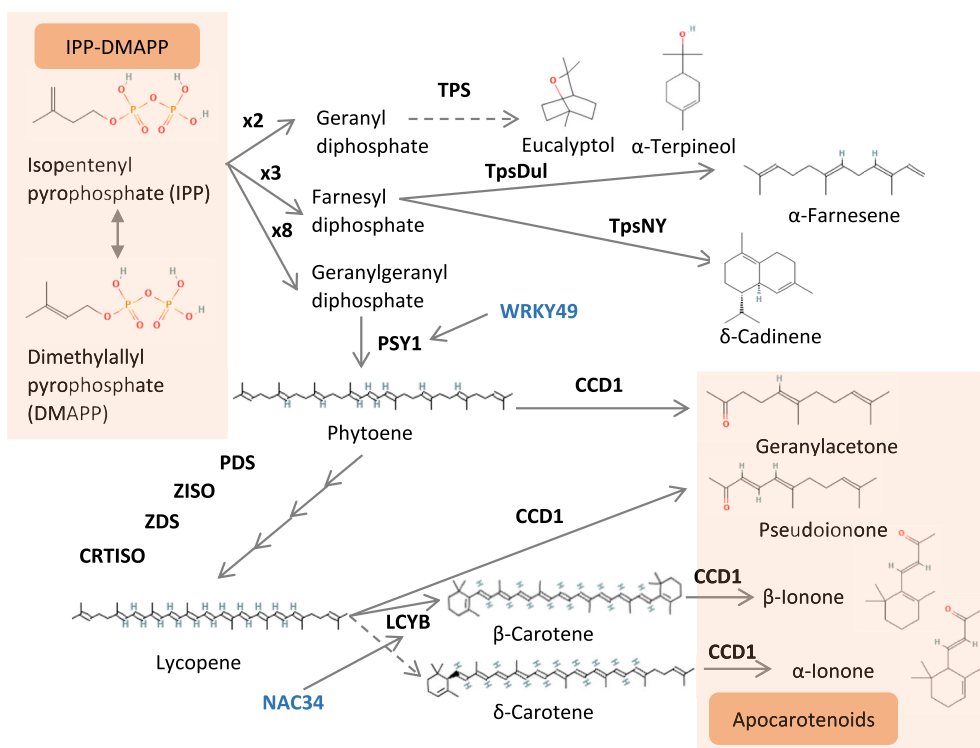
**Fig. 4.** Biosynthetic pathway of aminoacid-derived VOCs in melon. Dashed lines represent hypothesized steps of the pathway. BCAT = branched-chain aminoacid aminotransferase, MGL = methionine gamma lyase, -SH = methanethiol, PDC = pyruvate decarboxylase, ADH = alcohol dehydrogenase, AAT = alcohol acyltransferase, PAL = phenylalanine ammonia-lyase, CNL = cinnamoyl-CoA synthase, ArAT1 = aromatic aminoacid aminotransferase, CCR = cinnamoyl-CoA reductase, CAD = cinnamyl alcohol dehydrogenase, AAO = aldehyde oxidase, BMT = benzoic acid methyl transferase.

identified in melon and divided in short, medium and long-chain alcohol dehydrogenases according to their phylogeny (Jin et al., 2016). However, the activity of these enzymes has only been tested for *CmADH1* (MELO3C023685) and *CmADH2* (MELO3C014897), slightly differing on their catalytic activity (Manríquez et al., 2006). For instance, branched or aromatic aldehydes were exclusively transformed by *CmADH1*, whereas both enzymes were active for straight-chain compounds. Alcohols can be esterified with an acyl-CoA molecule by the action of alcohol acyltransferases (AATs). Four different AATs have been identified in a *Charentais* melon (El-Sharkawy et al., 2005). *CmAAT1* (MELO3C024771), *CmAAT3* (MELO3C024762) and *CmAAT4* (MELO3C017688) were reported to have different substrate preference. The three enzymes could esterify several compounds but AAT1 was the preferred enzyme for 2-hexen-1-ol acetate-(E), whereas phenylethyl alcohol was mainly transformed by AAT3, and cinnamyl alcohol by AAT4. This specificity was reported to depend on the solvent channel of the enzyme (Galaz et al., 2013). On the other hand, AAT2 (MELO3C024766) was reported to be inactive in this melon accession (El-Sharkawy et al., 2005). Nevertheless, other AATs can be found in the melon genome, with unknown activity (Castanera et al., 2020). Furthermore, the origin of the acyl-CoA molecules that bind with

alcohols is not yet known, some studies relating acyl-CoA abundance with the expression of primary metabolism enzymes from the  $\beta$ -oxidation of fatty acids, such as acyl-CoA oxidase (MELO3C005515), acetyl-CoA acetyltransferase (MELO3C024190) and 3-ketoacyl-CoA thiolase (MELO3C020466) (Shao et al., 2022).

## 2.5. Aroma and ripening

Several studies have highlighted the relationship between aroma production and ripening behavior. During melon fruit development, aldehydes and alcohols are produced in unripe stages, and esters appear along ripening (Defilippi et al., 2009; Nagashima et al., 2021; Oh et al., 2011). In general, esters are the main produced compounds in climacteric varieties, whereas aldehydes are predominant in non-climacteric melons (Esteras et al., 2018; Esteras et al., 2020; Mayobre et al., 2021; Obando-Ulloa et al., 2008). The link between esters, aldehydes and ripening is ethylene, as ADHs and AATs have been demonstrated to be induced by exogenous ethylene application (El-Sharkawy et al., 2005; Jin et al., 2016; Manríquez et al., 2006). An effect of ethylene in melon gene expression has also been suggested for *CmBCAT1* and *CmArAT1* (Li et al., 2016).



**Fig. 5.** Biosynthetic pathway of terpenoid-derived VOCs in melon. Dashed lines represent hypothesized steps of the pathway, transcription factors are in blue. TPS = terpene synthase (Dul = ‘Dulce’, NY = ‘Noy Yizre’el’), PSY = phytoene synthase, CCD = carotenoid cleavage dioxygenase, PDS = phytoene desaturase, ZISO = ζ-carotene isomerase, ZDS = ζ-carotene dehydrogenase, CRTISO = carotene isomerase, LCYB = lycopene β-cyclase. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The effect of ethylene on melon aroma has also been studied using recombinant and introgression lines (Dos-Santos et al., 2023; Mayobre et al., 2024; Pereira et al., 2020; Perpiñá et al., 2017; Santo Domingo et al., 2022). Mapping populations obtained by crossing non-climacteric ‘Piel de Sapo’ melons with climacteric ‘Védrantais’ melons revealed that many aroma QTLs overlapped with ripening-related QTLs (Mayobre et al., 2021; Mayobre et al., 2024). For instance, the two regions linked to aroma on chromosome 8 described by Zhao et al. (2019) were later related to ripening. The first, around 3,809,200 bp, matches ripening and aroma QTLs in introgression line VED8.1 (Mayobre et al., 2024). The second, around 9,633,973 bp and matching *ETHQV8.1* has been recently characterized, demonstrating that *CmERF024* (*MELO3C024520*), an ethylene-responsive transcription factor, is the causal gene (Pereira et al., 2020; Santo Domingo et al., 2024). *CmERF024* seems to be involved in chromatin configuration changes during the ripening process. Another region linking aroma and ripening is *ETHQV6.3*, encoded by *CmNAC-NOR* (*MELO3C016540*) (Ríos et al., 2017). The edited melon line containing a knock-out of this gene is unable to ripe nor produce esters, confirming the role of ethylene in ester formation (Liu et al., 2022). Moreover, on chromosome 10, Perpiñá et al. (2017) described a ripening QTL affecting only the aroma of the rind. A NAC/NAM transcription factor (*MELO3C012390*) was proposed as candidate gene, but more studies are needed to confirm this association. Finally, pyramiding of three ethylene QTLs (*ETHB3.5*, *ETHQV6.3* and *ETHQV8.1*) in a non-climacteric melon background demonstrated that esters can be produced just by activating ethylene production (Santo Domingo et al., 2022). The regulation of aroma in melon is similar to other climacteric fruits such as apple, papaya, banana, peach and tomato, where ethylene can affect AATs expression through MYB or NAC transcription factors (Balbontín et al., 2010; Cao et al., 2021; Defilippi et al., 2005; Li et al., 2014; Wei et al., 2023).

The tight relationship between aroma and ripening makes it difficult to separate their regulation, the main goal in melon breeding being to

improve aroma in extended shelf-life varieties (Pujol & Garcia-Mas, 2023). Nevertheless, in contrast to tomato (Li et al., 2020), carotenoids have been proven to be synthesized in the absence of ethylene in melon, representing an interesting point for the study of ethylene-independent volatile production (Pech et al., 2008).

## 2.6. Effect of the environment and grafting on aromas

Environmental conditions can affect the melon metabolic profile (Bernillon et al., 2013; Kyriacou et al., 2018; Niyakan et al., 2023; Perpiñá et al., 2021; Shao et al., 2022). Environmental changes include differences in temperature, sunlight, water or nutrient regime. For instance, Shao et al. (2022) detected an increase in ester production when ‘Nasmi’ melons were grown in Altay (China) in summer versus Turpan (China) in spring. Changes were associated to the different altitude, temperature and light conditions. They identified differentially expressed genes from the primary metabolism, *ADHs* and *AATs*. Niyakan et al. (2023) supported this study, describing changes in esters, terpenoids and lipid-derived VOCs depending on the location within the USA. They found changes in gene expression on the lipid, terpenoid, and aldehyde to ester pathways. DNA methylation and histone acetylation could be playing an important role on these expression changes and should be studied into deep. Volatile changes can be a way of plant adaptation and communication, influencing both plant-insect and plant-plant interactions (Schuman, 2023). For instance, GLVs and terpenoids have antimicrobial and antifungal properties, and methyl jasmonate and methyl salicylate are signaling molecules to other plants in response to biotic stress (Arimura et al., 2009; Lin et al., 2019; Schuman, 2023). Indeed, GLVs can be diffused at long distances, suggesting they play important roles in plant interactions with the environment.

Additionally, grafting has also proven to affect melon aroma. Flores-León et al. (2021) detected an increase in the overall VOCs production when grafting snake melons. Both Lecholocho et al. (2022) and

Verzera et al. (2014) detected an increase in esters and a reduction in alcohols and aldehydes when grafting both cantaloupes and honeydews into *Cucurbita* rootstocks. On the other hand, grafting negatively changed the volatile profile of ‘Qingxin Yangjiaocui’ melons, with many key volatiles being lost when pumpkin rootstocks were used (Guo et al., 2024). This effect was related to a reduction in the AATs and ADHs expression. It seems that the effects of grafting on melon fruit aroma are highly dependent on the genotypes, rootstocks, and the compatibility between species, so specific strategies should be used for each cultivar.

## 2.7. Effects of postharvest processing on melon aroma

After fruit harvest, melons can undergo different processing treatments depending on their destination or use. For human consumption, melons are usually stored in cold chambers at 4 °C, and after some days, fruits are taken to room temperature. The volatile content has been demonstrated to change during storage, although the effect depends on the season (Spadafora et al., 2019). While storage at room temperature generally increases volatile production, during chilling ester production is reduced by the downregulation of ADHs and AATs, losing fruity and sweet aromas and increasing the cucumber-like and grassy flavor (Peng et al., 2024; H. Zhang et al., 2023). However, after recovery at room temperature, the respiration rate, the ethylene production and the ester content increase again, enhancing fruity flavor (Farcuh et al., 2020). Another study with fresh-cut melons managed to maintain the acetate content at low temperature storage by using a high oxygen modified atmosphere during packaging (Amaro et al., 2012). High oxygen modified atmospheres have also been proven to help maintaining quality and aroma in broccoli (He et al., 2024). All these changes in aroma during postharvest might be regulated by DNA and histone methylation changes, as it was described in other plant species such as tea (Yang et al., 2021).

Another way melons are consumed is by obtaining the flesh juice, which must be treated to eliminate microorganisms and extend the shelf-life of the product. Juice treatments have been demonstrated to modify the volatile profile. High pressure can reduce the content of some fruity esters such as hexyl acetate, ethyl hexanoate and methyl 2-methylbutanoate, and increase the perception of fatty acid-derived aldehydes with cucumber-like flavor (Pei et al., 2020). On the other hand, heating treatments can enhance the sulfurous aromas, which are off odors (Pang et al., 2019). These effects could be related to a change in enzymatic activity, as it was reported in other species. For instance, in raspberry juice, high pressure and temperature treatments reduce LOX, HPL, ADH and AAT enzymatic activity, contributing to the loss of some key volatiles due to higher decomposition than synthesis rates (Zhang et al., 2024).

## 2.8. Current challenges and future prospects

The knowledge in VOCs regulation in melon has expanded in the last few years. In this review we have described key genes recently discovered, such as *CmPDC1*, *CmBAMT*, *CmLOX18*, *CmNAC34*, *CmWRKY49*, in addition to several hypothesized enzymatic activities on fatty acid degradation pathways (enoyl-CoA isomerase, omega-3 desaturase), creating a more complex and complete picture of VOCs biosynthesis. Moreover, the role of ripening, environmental factors and postharvest processing has been discussed, which represent challenges for melon aroma improvement often unconsidered. Nonetheless, further studies are needed to decipher the full biosynthetic pathways leading to volatiles, with special focus on the phenylalanine and the fatty acid pathways. Regulation by transcription factors is yet to be tackled. Besides, the role of epigenetic regulation on gene expression, i.e. DNA methylation and histone acetylation, should be considered in future studies.

One of the current challenges in breeding for aroma, as previously mentioned, is the ethylene-independent regulation. For instance, by focusing on enzymes and pathways not regulated by this plant hormone,

such as the terpenoid pathway or the primary metabolic pathways, enhancing of aroma could be obtained in non-climacteric accessions, whereas fruity aromas could be preserved when increasing the shelf-life of climacteric varieties.

The other challenge is climate change. As temperatures are rising in the summer and severe periods of drought are more common, this will definitely affect the quality of melon and its volatile profile. As an example, *CmLOX10* overexpression has been associated to JA-mediated drought tolerance (Xing et al., 2020). More studies in melon tolerance to these abiotic stresses should be performed in the near future, as drought stress has been demonstrated to affect several melon metabolic pathways (Ansari et al., 2019).

Finally, the ecological aspect of melon aroma has not been well studied. In tomato and cucumber, melon fly is known to be attracted by a blend of volatiles including some monoterpenes (Njuguna et al., 2018). Furthermore, some volatiles such as benzaldehyde and GLVs are known to act against fungi and herbivores, respectively (Arimura et al., 2009; Lin et al., 2019). There have been some studies in nectar volatiles, associating phenylpropanoids, benzenoids and terpenoids with attractive or repellent activities to insects and pollinators (Slavković & Bendahmane, 2023). Nevertheless, additional studies are needed on the effect of melon fruit volatiles on surrounding fauna, with possible implications on pest resistance or fruit production.

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## CRediT authorship contribution statement

**Carlos Mayobre:** Writing – original draft, Conceptualization. **Jordi Garcia-Mas:** Writing – review & editing, Funding acquisition, Conceptualization. **Marta Pujol:** Writing – review & editing, 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

No data was used for the research described in the article.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foodchem.2024.140640>.

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