The aroma volatile repertoire in strawberry fruit: a review

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Abstract

Aroma significantly contributes to flavor, which directly affects the commercial quality of strawberries. The strawberry aroma is complex as many kinds of volatile compounds are found in strawberries. In this review, we describe the current knowledge of the constituents and of the biosynthesis of strawberry volatile compounds, and the effect of postharvest treatments on aroma profiles. The characteristic strawberry volatile compounds consist of furanones, such as 2,5-dimethyl-4-hydroxy-3(2H)-furanone and 4-methoxy-2,5-dimethyl-3(2H)-furanone; esters, including ethyl butanoate, ethyl hexanoate, methyl butanoate, and methyl hexanoate; sulfur compounds such as methanethiol, and terpenoids including linalool and nerolidol. As for postharvest treatment, the present review discusses the overview of aroma volatiles in response to temperature, atmosphere, and exogenous hormones, as well as other treatments including ozone, edible coating, and ultraviolet radiation. The future prospects for strawberry volatile biosynthesis and metabolism are also presented.

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Keywords: aroma; volatile; flavor; postharvest; strawberry

INTRODUCTION

Strawberry fruit (Fragaria × ananassa), a genus of the Rosaceae family, is the most commonly consumed berry fruit crop worldwide and is valued for its unique flavor and nutritional quality.1 The pursuit of high yields, large size, and long shelf life has affected the flavor of strawberries, causing a decline in sales; this indicates that customers commonly purchase the fruit because of its special flavor.2 The contribution of taste and mouthfeel to the fruit’s flavor has attracted the attention of consumers. Nevertheless, the volatile compounds are the main constituents responsible for the volatile quality that is a direct factor attracting customers, and they have high correlation with overall liking of strawberry, although it looks as if sweetness is more important (Fig. 1).3

Volatile compounds are significant components of strawberry flavor, and slight changes may significantly modify the taste, although such compounds only account for 0.001–0.01% of the fruit’s weight.4 Strawberry aroma represents a good example of a complex fruit aroma. To date, more than 360 volatile chemicals have been observed in fresh strawberries.5 These compounds include esters, alcohols, ketones, furans, terpenes, aldehydes, and sulfur compounds.6 Types and concentrations of volatiles contributing to strawberries vary according to their cultivar and maturity.7 However, esters still represent the most abundant volatile compounds in strawberries, with as many as 131 different types accounting for 25–90% of all strawberry volatiles.8 Esters are also the major source of fruity and floral odors in strawberries, and the content of esters may be the basis for classifying different volatile patterns.9,10 Although the furanones, sulfur compounds, terpenoids and some other compounds exhibit much lower quantities compared with esters, these compounds demonstrated significant effects on strawberry volatile.

Considering the important influence of volatile compounds on flavor, numerous studies have been conducted on aroma volatiles of strawberries. These studies mainly focused on the research advances regarding the profiles and biosynthesis of specific strawberry volatiles. The present review will depict the dynamic changes of volatile compounds in strawberries in response to exogenous abiotic stimuli.

CHARACTERISTIC VOLATILE COMPOUNDS IN STRAWBERRY

Not all volatile compounds observed in strawberries actually affect the strawberry volatiles. The odor activity value (OAV) (ratio of concentration to its sensory threshold)11 has usually been utilized to distinguish these compounds. Only when the OAV value is higher than 1 is the compound regarded as possessing the characteristics of a volatile compound to a significant extent. The
higher OAV values of volatile compounds in strawberries indicate their more pivotal role in aroma. Some compounds (such as ketones and long-chain acids) feature lower sensory thresholds, even at higher concentrations. In contrast, certain low-content volatiles contribute significantly to the characteristic volatiles of strawberry. Esters, furanones, terpenes, and sulfur compounds are among the substances that account for the characteristics of strawberry volatiles. The esters include ethyl butanoate, ethyl hexanoate, methyl butanoate, and methyl hexanoate; the main furanones were 2,5-dimethyl-4-hydroxy-3(2H)-furanone (DMHF) and 4-methoxy-2,5-dimethyl-3(2H)-furanone (DMMF), and the major sulfur compounds and terpenes are methanethiol, linalool, and nerolidol.

After exploring aroma compounds in strawberries, considerable attention has recently been given to the metabolism of volatiles, especially those involved in biomolecule metabolism and gene expression. Many attempts have been made to elucidate the molecular mechanism of volatile profiles. The metabolism of furanones, esters, terpenoids, and other volatiles will now be discussed (see Table 1).

### Table 1. The characteristic volatile and corresponding precursor compounds in strawberry fruits

<table>
<thead>
<tr>
<th>Volatile group</th>
<th>Characteristic compounds</th>
<th>Precursors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Furanones</td>
<td>DMHF and its derivative</td>
<td>Carbohydrate</td>
</tr>
<tr>
<td>Esters</td>
<td>Methyl butanoate, ethyl butanoate, ethyl hexanoate, methyl butanoate</td>
<td>Fatty acids or amino acids</td>
</tr>
<tr>
<td>Terpenoids</td>
<td>Linalool and nerolidol</td>
<td>Carbohydrate</td>
</tr>
<tr>
<td>Sulfur compounds</td>
<td>Methanethiol</td>
<td>Unknown</td>
</tr>
<tr>
<td>Benzenoids</td>
<td>Benzyl alcohol and benzyl acetate</td>
<td>Amino acids</td>
</tr>
</tbody>
</table>

### Furanones

Strawberries contain very low amounts of volatile furanones. However, compared to their threshold values, the furanones have a considerable influence on the profiles of the volatiles. 4-Methoxy-2,5-dimethyl-3(2H)-furanone represents the characteristic volatile furanone in strawberries; its threshold value is $4 \times 10^{-5}$ mg kg$^{-1}$ in water. It was first discovered in 1965 and was described as caramel-like, sweet, floral, and fruity, offering a strawberry-like odor. It exists in natural fruits in four forms, namely, DMHF-glucoside, DMMF (mesifuran), DMHF-malonyl-glucoside, and free aglycone. Of these, DMHF and DMMF are the characteristic volatile compounds in fresh strawberry.

Furanones correspond to a few natural volatile compounds derived from hexoses and pentoses without the breakdown of the carbon skeleton. In the 1990s, as a result of investigation into the four DMHF forms, glucoside was considered as the probable precursor of free aglycone, whereas DMHF-glucoside was deemed to be the stable form of DMHF. As that time, new in vitro methods were applied to study biosynthetic pathways, aiding speculation about the precursors and derivatives of DMHF. It was previously discovered that d-fructose derivatives, such as d-fructose-6-phosphate, d-fructose-1,6-bisphosphate, and 6-deoxy-d-fructose, were the possible precursors of furanones as they increased the DMHF concentrations and its resulting derivatives. Strawberry callus culture was used in many studies as precursor feeding as no endogenous furanone existed in fresh tissue. Subsequently, analysis by high-performance liquid chromatography (HPLC) and radio labeling proved that d-fructose-1,6-bisphosphate was possibly the closest precursor to DMHF, and d-fructose could be transformed into DMHF. As expected, DMHF was converted into DMMF, DMHF-glucoside, and DMHF-malonyl-glucoside during late stages of strawberry ripening and development. Based on investigation of furanone precursors, the putative pathway featured d-glucose or d-fructose metabolized to d-fructose-6-phosphate before conversion from the resulting compound into d-fructose-1,6-diphosphate. It was reported that d-fructose-1,6-diphosphate was then converted into 4-hydroxy-5-methyl-2-methylene-3(2H)-furanone (HMMF), which then converted into DMHF; DMHF was converted into DMMF or DMHF-glucoside and then transformed into DMHF-malonyl-glucoside in later stages of fruit development. Nevertheless, the biosynthetic pathway of DMHF remained unclear, providing limited information regarding transformation of d-fructose-1,6-diphosphate into HMMF.

As more studies on biomolecular aspects in strawberries were performed, some of the enzymes involved in the pathways were reported. It was stated that quinine oxidoreductase catalyzed the transformation of HMMF to DMHF, O-methyltransferase participating in the DMHF methylation, glucosyl transferase, and malonyl transferase converting DMHF into DMHF-glucoside and then into DMHF-malonyl-glucoside, respectively. Some genes encoding the enzymes involved were identified, i.e. *Fragaria x ananassa* quinine oxidoreductase gene (FaQR) and *Fragaria x ananassa* O-methyltransferase gene (FaOMT). A study of FaQR showed that FaQR cDNA consisted of 969bp, and FaQR protein featured 322 amino acids with a calculated molecular mass of 34.3 kDa. The monomer expressed in *Escherichia coli* can catalyze the formation of DMHF. Specific transcripts of FaOMT accumulated in ripening strawberries were only observed in fruits instead of in other tissues, strawberry flowers, leaves, and roots. Substrates of FaOMT protein exhibited a common structural feature: a diphenoquinone structure, as shown in DMHF and its diphenolic tautomer. It was also supposed that FaOMT significantly influenced the biosynthesis of vanillin and participated in the lignifications of achenes and vascular bundles in fruits. According to recent research on FaOMT, a homolog of FaOMT was partly responsible for the natural variation of DMHF.

![Figure 1](image-url). The correlation between sensorial qualities and overall liking of strawberry (regressed against coefficient of determination).
in DMMF content, and the 30 bp homolog could be a significant tool in regulating gene expression during strawberry ripening.  

Esters

Esters are the characteristic volatile compounds that define the strawberry volatiles.  

Different cultivars contained different kinds and different quantities of ester compounds. The most important odorants of *F. x ananassa* are methyl butanoate, ethyl butanoate, ethyl hexanoate, and 2-methylbutanoate; whereas the butyl formate, octyl acetate, decyl acetate, benzyl acetate, carvyl acetate, decyl butanoate, methyl nicotinate, methyl anthranilate, and methyl N-formylanthranilate were only found in *F. x versa*.  

In the biosynthesis of strawberry volatiles, the last important step is the esterification of alcohols with an acyl moiety of acyl-CoA by catalysis of different alcohol acyl-transferases (AATs).  

The fatty acids and amino acids are the precursors of alcohols and acyl-CoAs in fruits.  

On the one hand, the fatty acids, and linoleic and linolenic acids in general, turn into volatile aldehydes, such as hexanal and (3Z)-hexenal through the oxidative degradation of lipoxygenase (LOX) or hydroperoxide lyase (HPL).  

Then which convert to the alcohols by alcohol dehydrogenases (ADHs).  

The \( \beta \)-oxidation of fatty acids results in the formation of \( C_2 \) units (acyt-COA).  

On the other hand, the catabolism of amino acids by amino transferases forms \( \alpha \)-keto acids, and then \( \alpha \)-keto acids become the substrates for \( \alpha \)-keto acid decarboxylase or \( \alpha \)-keto dehydrogenase, converting into the volatile aldehydes or acetyl CoA. Afterwards, the aldehydes and acetyl-CoA are converted into the esters by the actions of ADH and AAT.  

Recently, considerable attention has been focused on the enzymes and genes involved in the fruit ester biosynthesis. Existing studies indicate that both ADH and AAT play a vital role in ester biosynthetic pathways, which result from their activity and expression in ripe fruits. Alcohol dehydrogenases contributed to survival from hypoxia, the production of cinnamyl alcohols for lignification of cell walls, and protection from chilling, as well as the biogenesis of flavor and fragrance volatiles in advanced plant tissues.  

Both nicotinamide dinucleotide phosphate (NADP)-dependent and nicotinamide adenine dinucleotide (NAD)-dependent ADHs in strawberry were reported to possess wide substrate specificities, including alcohols and aldehydes. Nicotinamide adenine dinucleotide-dependent ADHs activities are mainly against short-chained alcohols, whereas NADP-dependent ADHs activities are mainly against aromatic and terpene alcohols. The ADH activity increased progressively and differentially between receptacle and achene tissues during strawberry ripening.  

A previous study revealed that the molecular weight of ADH was 24.6 kDa and the optimum pH was 6 for ADH activity in strawberry callus cultures.  

The appropriate substrates of ADH included 1-propanol (Michaelis constant (Km) = 3.54 mmol L\(^{-1}\)) and ethanol (Km = 6.66 mmol L\(^{-1}\)).  

The characteristics of ADH in strawberry achenes differed depending on callus culture. The optimum substrates for achene ADH were ethanol (Km = 5.950 mmol L\(^{-1}\)) and methanol (Km = 12.610 mmol L\(^{-1}\)).  

The ADH gene was the first protein-encoding gene completely sequenced in strawberries.  

This gene and its intron-containing sequence were commonly applied in ongoing phylogenetic studies on *Fragaria* species.  

Until now, limited information about the relationship between ADH transcript expression and volatile performance has been reported in strawberries. The rate-limiting and the last step in biosynthesis of volatile esters is the reaction catalyzed by AAT, which depended on substrate availability and AAT specificity.  

Several AAT enzyme isozymes and their corresponding genes were widely studied in strawberries with high commercial interest recently because of the critical role of AAT in ester biosynthesis. It was reported that the structure of AAT proteins featured several motifs analogous to BAHD, derived from the abbreviations of the names (BEAT, AHCT, HCBT, and DAT) of the first four enzymes identified and characterized in this family of acyltransferases.  

Among these compounds, the HXXXD motif and the DFGWG sequence were characteristic motifs that were located separately in the middle of the protein sequence and close to the carboxylic end. Both of the sequences exhibited a decisive effect on the AAT and its isomers. The DFGWG sequence maintained the conformational integrity of AAT enzyme structure whereas the HXXXD motif was out of action without the histidine residue.  

As expected, the AAT expression level was positively correlated with the total ester content as strawberries ripened and developed, which further confirmed the involvement of AATs in ester production. Several AAT genes were extracted from *F. ananassa* (SAAT, and AAT2), wild strawberry *F. vesca* (VAAT), and *F. chiloensis* (FcAAT1) in studies to prove this theory. The maximum transcript levels of AATs were observed in red-ripe fruits, and their expression was parallel with ester production. Nevertheless, different AATs acted on different substrates. Strawberry alcohol acyl-transferase preferred the medium-chain aliphatic alcohols in combination with different acyl-CoAs, whereas FaAAT2 exhibited higher activities with short straight-chain alcohol and aromatic alcohols, such as cinnamyl alcohol.  

Wild strawberry alcohol acyl-transferases and SAAT were shown in phylogenetic analysis as closely related, and VAAT acted on short-chain alcohol substrates.  

The discrepancy in AATs and the corresponding substrates resulted in different ester categories and contents among *F. vesca* and Tudnew, Carisma, Camarosa, Sweet Charlie, and Eris in *F. ananassa*.  

Differcult cultivars and changes in volatile esters in strawberries can thus be identified through the analysis of the transcript expression of AATs.  

Terpenoids

Among terpenoid compounds, volatile monoterpene (C\(_{10}\)) and sesquiterpenes (C\(_{15}\)) were identified in most soft fruits.  

In cultivated ripe strawberry, linalool, and nerolidol were detected as volatile terpenoids, whereas \( \alpha \)-pinene, \( \beta \)-myrcene, \( \alpha \)-terpineol, \( \beta \)-phellandrene, and myrtanyl acetate, were identified in wild strawberries.  

It is interesting that three triterpenoids – euscaphic, tormentic, and myrianthic acids – were found as antennal phytoalexins in unripe Houkouwase fruit and were not characteristic volatiles.  

Recently, it was reported that, in Falandi strawberries, nine sesquiterpenoids and three triterpenoids were isolated as nonphenolic constituents for their antiobiotic, antitumor, and antioxidiant effects.  

According to previous studies performed on terpenes, terpenoids were biosynthesized through the mevalonate pathway (MVA pathway) or the 2-C-methyl-d-erythritol 4-phosphate pathway (MEP pathway); the former occurred in cytosol, and the latter transpired in plastids. The MVA pathway was not absolutely separated from the MEP pathway because of the exchange across plastidial membrane by unknown transporters, and the establishment of so-called ‘metabolic cross-talk’ (Fig. 2).  

The gene expression and action substrates of terpene synthase *F. ananassa* nerolidol synthase 1 (FaNES1), was revealed in different stages and fruit tissues of cultivated strawberries. In wild strawberries, *F. vesca* pinene synthase (FvPINS) was reported to be involved in a typical monoterpene biosynthesis, and FvPINS protein was proven effective in the biosynthesis of \( \alpha \)-pinene, \( \beta \)-phellandrene,
and \( \beta \)-myrcene from GPP.\(^5\) As reported, FvPINS converted GPP into \( \alpha \)-pinene, and the enzyme encoding cytochrome P450 gene (pinene hydroxylation) catalyzed the transformation from \( \alpha \)-pinene to myrtenol.\(^5\) In the research, FaNES1 and FvPINS gene expressions accounted for different dominant terpenes in cultivated and wild strawberries.\(^5\)

**Other volatile compounds**

### Sulfur compounds

Sulfur compounds influence volatiles, because of the low level of their odor thresholds.\(^6\) Sulfur compounds in strawberries were first reported in 1963.\(^6\) However, there are still difficulties in exploring trace contents and the biosynthesis of sulfur compounds in strawberries. To date, 19 sulfur compounds have been found in strawberries. Such compounds include 10 thioesters, eight alkyl sulfides, and an unknown component. The thioesters consist of methyl thioacetate, methyl thiobutyrate, methyl thiopropionate, ethyl thiobutanoate, methyl thiohexanoate, methyl (methylthio) acetate, ethyl (methylthio) acetate, methyl 2-(methylthio) butyrate, methyl 3-(methylthio) propionate,ethyl 3-(methylthio) propionate, and methyl thiooctanoate, and alkyl sulfides comprise hydrogen sulfide, methanethiol, dimethyl sulfide, dimethyl disulfide, dimethyl trisulfide, and sulfuryl oxide.\(^6\) Except for hydrogen sulfide and methanethiol contents remaining relatively consistent during ripening, most sulfur compounds increased as fruit ripened. It was also revealed that most sulfur compounds increased dramatically during the commercial ripening, full ripening, and over-ripening stages.\(^5\) Between the full ripening and the over-ripening stages, in particular, the concentration of total sulfur compounds doubled.\(^5\) Later studies on strawberry sulfur compounds showed that a puree process in the experimental pretreatment of strawberries affected the analysis of volatile sulfur compounds; except for methanethiol, the dimethyl disulfide and dimethyl trisulfide in the puree exhibited lower amounts while most sulfur compounds were similar to, or higher than, those in intact strawberries.\(^5\) Principal component analysis (PCA) of sulfur compounds among 12 strawberry cultivars showed differences in constituents and in the amounts of sulfur compounds in a cultivar dependent manner; for instance, ‘Strawberry Festival’ and ‘Florida Radiance’ possessed high thioester concentrations, whereas ‘Dover’, ‘Rosa Linda’, and ‘Florida Belle’ contained higher sulfide and lower thioester concentrations.\(^6\) Through the measurement of these sulfur compound OAVs, methanethiol was determined to be the predominantly active volatile sulfur compound.\(^6\)

### Volatile benzenoids

In ripe strawberries, volatile benzenoid concentrations were measured at trace levels compared with those characteristic volatile compounds like esters, terpenes and furanones. The volatile concentrations of benzyl alcohol and benzyl acetate decreased as the strawberries ripened and developed.\(^9\) These volatile benzenoids were known to be derived from the shikimate pathway via \( L \)-phenylalanine, and the first step of this pathway involves the deamination of \( L \)-phenylalanine to trans-cinnamic acid by phenylalanine ammonia-lyase (PAL).\(^6\) The reaction catalyzed by phospho-2-dehydro-3-deoxyheptonate aldolase (DAHPS) represented the rate-determining step in this pathway.\(^6\) Benzenoids were also formed via a CoA-dependent, \( \beta \)-oxidative pathway from \( L \)-phenylalanine and cinnamate. Coenzyme A ligase (CNL) was reported as a significant peroxisome that catalyzed the cinnamoyl-CoA formation in this pathway.\(^6\) Later, through the isolation and analysis of strawberry-volatiles-related genes, the \( F. \ ananassa \) cinnamate CNL (FaCNL) gene, \( F. \ ananassa \) DAHPS (FaDAHPS1 and FaDAHPS2) gene, and \( F. \ ananassa \) PAL (FaPAL1 and FaPAL2) gene were reported to be related to the biosynthesis of volatile benzenoids in strawberries.\(^6\)

As previous research provided limited information on volatile benzenoids in strawberries, further studies should identify the influence of volatile benzenoids on strawberries and biosynthetic mechanisms.

**EFFECTS OF POSTHARVEST FACTORS ON VOLATILES PERFORMANCE**

Considerable attention has been focused on the variations in the characteristic volatile compounds during postharvest storage. We
will thus discuss the influence of postharvest treatment on strawberry volatiles. The temperature, atmospheric gas, and exogenous postharvest treatment (spraying, coating or dipping) contribute to the maintenance of the fruit’s postharvest quality.

Temperature

Low temperature is widely known to decrease the respiratory rate and metabolic activity in fruits. Studies have been inconsistent regarding the influence of temperature on different volatile compounds. Except for 3-hexenyl acetate and ethyl butanoate, furanones and most volatile esters increased gradually with increasing temperature. As for the effect of temperature on volatile terpenes, a report revealed that the terpene content in ‘Akihime’ after 9 days of storage at low temperature declined less than that at room temperature, whereas another study found that in white ‘Sweet Charlie’ fruit, after storage at 15 and 25 °C separately, terpenes increased with elevation in temperature. The acid and alcohol content in strawberries after storage at low and room temperatures showed minimal changes with variation in temperature. Volatile benzenoids, including benzyl alcohol and benzyl acetate, were down-regulated by an increase in temperature.

Recently, further studies concentrated on the effects of molecular factors on strawberry volatiles. The quantity of FaQR declined remarkably at low temperature versus room temperature. The quantity of pyruvate decarboxylase isozyme 2 (PDC2) was also lower at low temperature. In a dark environment, the increase in temperature was accompanied by up-regulated expressions of FaQR and FaOMT but decreased transcriptions of FaAAT, FaNEN, and FaPAL1. The same research showed that total esters and terpenes increased with increased temperature, and the phenomena were probably caused by the interaction of light and temperature or some unknown pathway involved in the volatile biosynthetic compounds.

Atmosphere

The production of volatiles was affected by certain modified atmospheric conditions, which were usually applied to maintain fruit quality, such as controlled-atmosphere (CA) and modified-atmosphere packaging (MAP). Nevertheless, inadequate or extreme atmospheres could result in the fruit possessing an ‘off’ flavor.

Modified atmosphere packaging was carried out to fill the package with a particular ‘atmosphere’ to prolong the shelf life of fresh fruits. It was reported that both total volatile compounds and the butanoate amount in strawberry under MAP conditions (11% CO2 + 1% O2 + 78% N2 or 100% CO2) were lower than control. However, in another study, the profile of the volatiles in Honeoye strawberries remained constant during storage in the 11–14% O2 and 9–12% CO2 packages, whereas a considerable increase was observed in ethyl acetate levels in ‘Korona’ fruits. The cultivar- and temperature-dependent ‘off’ odors were reported to result from CO2 treatment.

The atmosphere is adjusted to a particular range in CA packaging to maintain fruit quality and delay senescence. The ethanol and ethyl acetate content in wild strawberries stored at 15% CO2/6% O2 and 10% CO2/11% O2 increased 42 times and 12 times compared to their initial value, respectively; and the treatment contributed to the elucidation of the relationship between ‘off’ flavor development and high CO2 concentration. The acetaldehyde concentration increased as CO2 partial pressure decreased, and the acetaldehyde content in the untreated control was three times higher than that in CA storage. Furthermore, other research reported that the formation of volatile esters and volatile furanones was promoted and the decline in volatile acids, alcohol, and terpenes was delayed in 2% O2 and 12% CO2 CA storage.

The influence of atmosphere on the biosynthesis of volatiles varied. It was reported that, in strawberries, AAT activity was in response to exogenous high CO2, as methyl and ethyl acetate were the characteristic ester compounds. The abundance of quinone oxidoreductase dramatically decreased in CA, whereas PDC2 showed higher abundance in strawberries under CA. These results proved that the expressions of both quinone oxidoreductase and pyruvate decarboxylase which coincided with volatile performance were in response to CA condition.

Exogenous postharvest treatments

Exogenous spraying, coating, or dipping were widely used to prolong the shelf life of strawberries. Previous studies examined the effects of exogenous treatments on strawberry quality, but little information exists on the effects of exogenous treatments on strawberry volatiles. As expected, in the non-climacteric fruit, exogenous ethylene and 1-methylcyclopropene (1-MCP) showed minimal effect on strawberry volatiles. However, the application of exogenous cytokinin significantly reduced total volatile amounts, including esters and alcohols, and demonstrated that exogenous cytokinin may inhibit glycolysis, fatty acid metabolism, and the conversion from sugar to esters and alcohols in ‘Akihime’ strawberries. Strawberries treated with 0.1% hexanal showed a remarkable decline in LOX activity but a significant increase in phospholipase D (PLD) activity; these changes are related to the volatile biosynthesis during ripening. Strawberries treated with 0.5–1 mmol L−1 phenylethyl alcohol after 15-day storage still showed a similar volatile profile to fresh strawberries; however, no report was available on the quantities of specific compounds that might cause an ‘off’ flavor in strawberries.

Methyl jasmonate (MJ) is a natural hormonal compound that can reduce decay and maintain the quality of fruits and vegetables. Strawberries treated with MJ plus ethanol (MJ-ETOH) showed higher concentration of the major volatile compounds including methyl acetate, isoamyl acetate, ethyl hexanoate, butyl acetate, and hexyl acetate, than independent ethanol treatment and control. Another research also reported that MJ treatment increased the content of 1-octanol, 1-hexanol, linalool, furaneol, 2-heptanone, and ethyl hexanoate after five or seven-day storage, whereas MJ exhibited less effect on ethyl butanoate. There was evidence that 1-hexanol content declined after 7 days due to an increase in AAT in response to MJ treatment. Different enantiomers of MJ also affected the volatile profiles differently. Interestingly, the (+)-MJ inhibited the formation of ethyl 2-methyl butanoate and isoamyl acetate but promoted the formation of ethyl hexanoate and hexyl acetate, whereas (−)-MJ inhibited the formation of these four esters; however, the mixture of (+)/(−)-MJ exhibited lower activity than separate (+)-MJ or (−)-MJ. Polysaccharides, proteins, and lipids, or their combinations, were used as edible coatings to maintain fruit quality and extend shelf life. Chitosan, the polysaccharide obtained from seafood, appeared to be an ideal preservative for fresh berries. Some studies were thus conducted on the responses of volatiles in strawberries to chitosan coating. A large delay was noted in build-up of ‘off’ flavors, attributed to acetaldehyde and ethanol, in strawberries dipped in chitosan acetate solution at 1% or 1.5% (w/w), and coated fruits exhibited enhanced levels of ethyl butanoate, ethyl...
hexanoate, and acetate esters.\textsuperscript{89} Another study also reported that pure chitosan promoted production of esters and dimethyl furfural after coating, and coatings containing lemon essential oil added terpenes (limonene, \(\gamma\)-terpinene, p-cymene, and \(\alpha\)-citral) to fruit volatiles, and thus also accelerated fermentation and modified the typical composition of the fruit volatiles.\textsuperscript{89} Strawberry volatiles may be enriched under the influence of chitosan with lemon essential oils or other volatile compounds.\textsuperscript{90}

Ozone treatment was reported to reduce the incidence of decay and affect the development of volatiles. However, no ‘off’ flavor was observed in fruits treated by ozone at 1.5 \(\mu\)L L\(^{-1}\) concentration,\textsuperscript{91} which was contrary to previous reports that an ‘off’ flavor occurred under an ozone atmosphere.\textsuperscript{92} Combined treatment (UV-C light, gaseous O\(_3\), superatmospheric O\(_2\), and high CO\(_2\)) of strawberries caused sensory property loss because of off-flavor development.\textsuperscript{92}

Ultra-violet radiation is mainly used to control decay, and studies have concentrated on its antimicrobial effect, particularly on cell-wall metabolism.\textsuperscript{93,94} Recently, volatile ester contents in 3/4 ripe ‘Aromas’ strawberry were increased remarkably increased by 4.35 kJ m\(^{-2}\) UV-C treatment compared to control. Transcript levels of ADH and AAT also exhibited a notable increase on the second and fourth days after treatment.\textsuperscript{95} This research also revealed that UV-C treatment seemed to induce accumulation of the allergenic protein Fra a1.\textsuperscript{95} However, the linalool content remained consistent, while both furanole and mesifuran concentrations decreased in response to the UV-C treatment.\textsuperscript{96}

FUTURE PROSPECTS AND CONCLUSIONS

Although the characteristic volatile compounds in strawberry have been identified and quantified, research on the biosynthetic pathways and precursor validation of strawberry volatiles is still limited. Recently, it was reported that the nonvolatile compounds turned to volatiles after hydrolysis of the bonds between the sugar and the aglycone.\textsuperscript{97} Nevertheless, there are still some gaps between the volatile biosynthesis and performance; for example, the process by which d-fructose-1,6-diphosphate converts into HMMF is still unclear and the biosynthesis of sulfur compounds is still unknown. Recently our laboratory focused on volatile profiles in response to exogenous hormone and abiotic stress. At the proteomic level, it was found that the expression of pyruvate decarboxylase (PDC) 2 and acetyl-CoA carboxylase (ACC) was down-regulated by application of exogenous forchlorfenuron (CPPU). This result provided evidence that CPPU suppressed volatile biosynthesis in strawberries.\textsuperscript{93} In CA and low-temperature conditions, the expression of FaQR and PDC2 coincided with the accumulation of volatiles during storage.\textsuperscript{93} These results revealed a new trend of studying strawberry volatile metabolism at the proteomic, metabolomic and transcriptomic levels.

In conclusion, aroma is a significant factor contributing to strawberry flavor, which is an important quality that influences consumer acceptability. Strawberry aroma is one of the most complex aromas, with more than 360 volatile compounds. Furanones, esters, terpenoids, sulfur compounds, and benzenoids are regarded as the main characteristic volatile compounds. This review is a comprehensive and updated overview of the features and metabolisms of the major volatile compounds in strawberry, and the effects of postharvest treatment factors, such as temperature, atmosphere, exogenous hormone, edible coating, ozone, UV radiation, on volatiles in strawberries. However, the research gap between volatile biosynthesis and performance needs to be filled.

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