The Composition of Strawberry Aroma Is Influenced by Cultivar, Maturity, and Storage

Charles F. Forney[1], Willy Kalt[2], and Michael A. Jordan[3]
Agriculture and Agri-Food Canada, Atlantic Food and Horticulture Research Centre, 32 Main Street, Kentville, N.S., B4N 1J5, Canada

Strawberry (*Fragaria ×ananassa* Duch.) fruit have a unique, highly desirable flavor and are one of the most popular summer fruits. Sugars, acids, and aroma volatiles contribute to the characteristic strawberry flavor, which is dependent on the proper balance of these chemical constituents. While sugars and acids are responsible for the sweetness and tartness of the fruit, aroma volatiles provide the unique, fruity flavors that characterize a fresh strawberry.

The aroma of fresh strawberries is dependent on many factors. The large genetic variability in the nature of strawberry aroma results in differences in flavor among cultivars. In addition, the aroma changes dramatically during fruit ripening after harvest; therefore, it is important to preserve and enhance the ripe fruit aroma during postharvest handling. The loss of this desirable aroma or the development of objectionable aromas reduces the quality and marketability of fresh strawberries. In this review we will discuss the chemical nature of strawberry aroma and how it is affected by various factors, including cultivar, maturity, and postharvest environment.

CHEMICAL COMPOSITION OF AROMA

Volatile chemicals are responsible for the aroma and contribute to the flavor of fresh strawberries. These compounds comprise only 0.01% to 0.001% of the fruit fresh weight but have a major effect on its quality (Buttery, 1981). Fresh strawberries produce numerous volatile compounds; as many as 360 have been isolated (Latrasse, 1991) including esters, aldehydes, ketones, alcohols, terpenes, furanones, and sulfur compounds (McFadden et al., 1965).

Esters are quantitatively and qualitatively the most abundant class of these compounds; 131 different ones have been identified in strawberry aroma (Latrasse, 1991). Esters provide the fruity and floral notes and they comprise from 25% to 90% of the total volatiles in fresh ripe fruit (Douillard and Guichard, 1990; Ito et al., 1990; Pyysalo et al., 1979; Schreier, 1980). Other classes of compounds, which may comprise up to 50% of strawberry volatiles, include aldehydes (Schreier, 1980) and furanones (Larsen and Poll, 1992). Alcohols account for as much as 35% of the volatiles, but normally contribute little to strawberry aroma (Larsen and Watkins, 1995b). While terpenes normally comprise <10% of strawberry volatiles and sulfur compounds <2%, they both may contribute to strawberry aroma (Dirinck et al., 1981; Schreier, 1980).

The volatile profile obtained from strawberry fruit is influenced by the analytical methods used to characterize these compounds. Volatiles from whole, intact fruit can be collected using headspace techniques; these samples can be analyzed directly or concentrated using adsorbent or cold traps. Volatiles are also collected from homogenized fruit or juice, using either headspace or solvent extraction techniques. Volatile samples are normally analyzed by gas liquid chromatography using a variety of methods of sample introduction, including liquid injection, thermal desorption, and cold on-column injection. High performance liquid chromatography (HPLC) has been used for some compounds that are thermally labile.

Each combination of techniques results in a slightly different volatile profile. Analysis of headspace compounds is dependent on their individual vapor pressure. The more volatile ones are present in higher concentrations. This reflects the compound's contribution to the fruit aroma but does not give its true concentration in the tissue. Disruption of the fruit through homogenization removes barriers to diffusion and allows for the determination of true concentrations, but may cause enzymatic changes in the volatile profile. Significant quantities of 1-hexanol, *trans*-2-hexen-1-ol, 1-hexanal, and of *trans*-2-hexenal are formed during homogenization through the actions of lipoxygenase, oxygen, and linolenic and linoleic acids (Latrasse, 1991). These C_6 aldehydes and alcohols may comprise up to 55% of the volatile profiles from homogenized fruit (Schreier, 1980), but account for <0.1% of volatiles collected from whole fruit (Ito et al., 1990).

Methods used to collect and analyze volatiles can cause the loss of certain compounds. This may explain the inconsistencies in the detection of the furanones: furaneol [2,5-dimethyl-4-hydroxy-3(2*H*)-furanone] and mesifurane [2,5-dimethyl-4-methoxy-3(2*H*)-furanone] in strawberry fruit. Pérez et al. (1992) were not able to detect furanones in 'Chandler' fruit when volatiles were collected through purge and trap of whole fruit, eluted from the trap with carbon disulfide, and analyzed using gas chromatography (GC) with cool on-column injection. However, both compounds were detected when volatiles were extracted and analyzed using HPLC (Sanz et al., 1995). Furaneol breaks down at elevated temperatures and is unstable at low pH (Shu et al., 1985). Pickenhagen et al. (1981) reported that heating during volatile extraction, as well as glass capillary columns, reduced recovery of furaneol.

Among the hundreds of volatile compounds produced by fresh strawberries, only a small portion contribute to the fruit's aroma and flavor. The characteristic aroma is a blend of a number of volatile compounds; no single "character-impact" compound is responsible for strawberry aroma. The contribution of a compound to the aroma is dependent on its odor threshold and concentration in the fruit. From

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[1] Storage Physiologist. E-mail address: forneyc@em.agr.ca

[2] Food Chemist.

[3] GC-MS Technician.

these two values an aroma value (concentration/threshold) can be calculated (Larsen and Poll, 1992). Aroma values >1 should contribute to the fruit's aroma, and the greater the value, the greater the compound's contribution. Larsen and Poll (1992) calculated aroma values for volatiles from 'Senga Sengana' strawberries using threshold values determined from the headspace over water solutions of each compound and concentrations determined from solvent extracts from fresh juice. They determined that ethyl butanoate, furaneol, and ethyl hexanoate contributed the most to the aroma; methyl butanoate, linalool, 2-heptanone, and 2-methyl butanoic acid were also important. Using similar techniques, Schieberle and Hofmann (1997) reported that mesifurane, *cis*-3-hexenal, methyl butanoate, ethyl butanoate, ethyl 2-methylpropanoate, and 2,3-butanedione were the most odor-active compounds in fresh juice from Spanish strawberries of an unknown cultivar.

The contribution of individual compounds to strawberry aroma can also be evaluated by sniffing GC effluent of individual peaks and characterizing their aroma. Using this technique, we have evaluated the headspace aroma trapped on Tenax adsorbent traps from whole fresh fruit and have found that ethyl hexanoate gave the most consistent high intensity aroma in all five cultivars sampled. High intensity peaks were produced by ethyl 3-methylbutanoate in 'Kent', 'Cavendish', and 'Micmac' fruit and by 3-methylbutyl acetate in 'Kent' and 'Micmac' fruit (Forney et al., unpublished data). Pérez et al. (1992), using similar techniques to rank the contribution of headspace volatiles from whole 'Chandler' fruit to the fruit's aroma, determined that ethyl butanoate, ethyl 2-methylbutanoate, and ethyl hexanoate were major contributors.

CULTIVAR DIFFERENCES

Strawberry cultivars vary both quantitatively and qualitatively in the volatiles they produce. We found a 35-fold difference in the quantity of volatiles evolved from different cultivars of ripe strawberries (Fig. 1A). The chemical composition of these volatiles was dominated by methyl and ethyl esters but the abundance of each ester varied with cultivar. Aromas of 'Configra' and 'Chandler' fruit were dominated by ethyl esters comprising 80% and 60%, respectively, of the total volatiles (Dirinck et al., 1981; Pérez et al., 1992). In fruit of other cultivars, including 'Hokowase', 'Kent', 'Senga Gigana', and 'Annapolis', methyl esters accounted for >70% of the total volatiles (Dirinck et al., 1981; Forney and Jordan, 1995; Miszczak et al., 1995; Ueda and Bai, 1993).

Among strawberry esters, butanoates and hexanoates predominate. Butanoates comprise 88%, 57%, 32%, 77%, and 51%, while hexanoates comprise 8%, 30%, 18%, 11%, and 40% of the total esters in 'Annapolis', 'Cavendish', 'Honeoye', 'Kent', and 'Micmac' fruit, respectively (Fig. 1B) (Forney and Jordan, 1995). Quantitatively, methyl and ethyl butanoate and methyl and ethyl hexanoate comprise the bulk of the volatile esters produced by fresh strawberries.

In addition to these esters, other volatile compounds are present in specific cultivars that gave them characteristic flavors. Ethyl 3-methylbutanoate and 3-methylbutyl acetate are predominant aroma volatiles in 'Kent' and 'Micmac' strawberries and hexyl acetate is an important contributor to aroma in 'Honeoye' fruit (Forney et al., unpublished data). Furaneol is an important contributor to strawberry flavor in many cultivars, including 'Senga Sengana', 'Parker', and 'Benton' (Larsen and Poll, 1992; Sanz et al., 1995). The monoterpene linalool is found in fruit of 'Senga Sengana' and 'Annelie' (Hirvi and Honkanen, 1982; Larsen and Poll, 1992). Other contributors to strawberry aroma in various cultivars include butanoic acid, 2-methylbutanoic acid, methyl and ethyl 2-methylbutanoate, γ-decalactone, and 2-heptanone (Fischer and Hammerschmidt, 1992; Larsen and Poll, 1992; Schieberle, 1994).

MATURITY EFFECTS

Many rapid qualitative and quantitative changes occur in strawberry fruit volatiles during ripening. Volatile content increases rapidly as fruit ripen and is closely correlated with color development (Forney et al., 1998; Miszczak et al., 1995). The fruit ripen rapidly in the field, turning from white to fully red in about 1.5 d. Volatile concentration is 5-fold as great in red-ripe fruit (6.8 μmol·m^{-3}) as in fruit that is 75% red (1.3 μmol·m^{-3}) at time of harvest (Forney and Jordan, 1995). Similarly, Ito et al. (1990) reported that total volatiles increase 14-fold during the 3 d in which 'Nyoho' strawberries go from white to full red. During color development many qualitative changes also occur. The concentrations of methyl esters increase ≈7-fold while those of ethyl esters change very little as fruit ripen (Fig. 2) (Forney et al., 1998). In 'Chandler' strawberries, Pérez et al. (1992) found that C_6 alcohols accounted for 25% of the fruit volatiles 36 d after bloom, but only ≈5% after 46 d. They suggest that C_6 alcohols could account for the "green" odor of immature strawberries. In addition to the increase in esters, furaneol, mesifurane, and furaneol glucoside increased with ripening in seven cultivars of strawberries (Sanz et al., 1995).

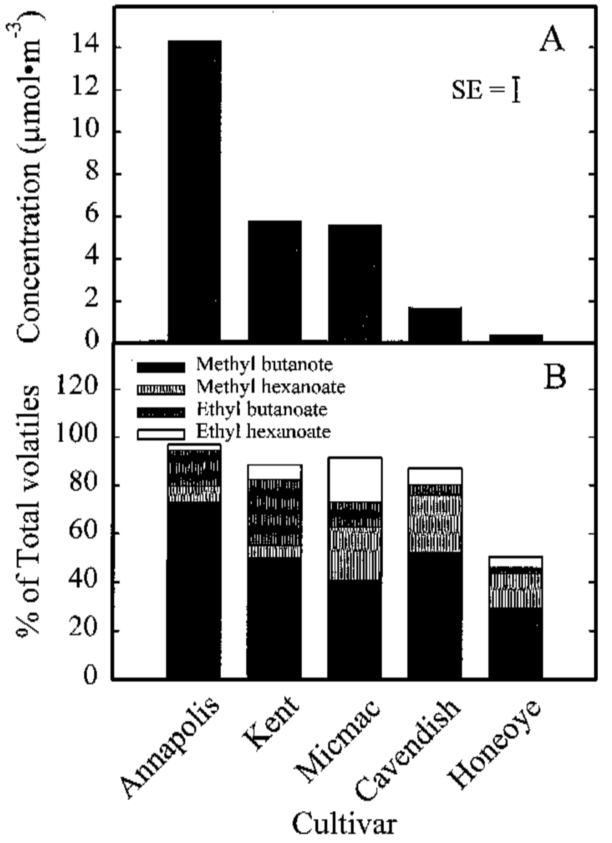

Fig. 1. Total concentration of volatile compounds (**A**) and major ester composition (**B**) in ripe fruit from five strawberry cultivars. Volatiles in the headspace of 4-L glass jars, each containing 100 g of whole, fresh fruit, were trapped on Tenax adsorbent traps, thermally desorbed, and analyzed by gas chromatography–mass spectrometry. The error bar represents the SE where n = 12 and df = 40. (Adapted from Forney and Jordan, 1995.)

POSTHARVEST ENVIRONMENT

Volatile content of fresh strawberries increases during storage. Volatiles in 'Kent' fruit harvested fully red increased 7-fold after 4 d at 15 °C (Fig. 3) (Miszczak et al., 1995). Volatile content in fruit harvested pink also peaked after 4 d, increasing ≈200-fold. Volatile concentrations in pink fruit reached levels similar to those in freshly harvested, red-ripe fruit after being held for 4 d at 15 °C. In this study, ethyl esters increased during storage to a greater extent than did methyl esters. After 4 d at 15 °C, ethyl ester content of 'Kent' fruit increased from 7% to 44% of total volatiles. Similar increases in volatile content were observed by Forney and Jordan (1995). During 5 d at 1 °C plus 2 d at 15 °C, volatile content of 'Kent','Annapolis', 'Micmac', 'Cavendish', and 'Honeoye' fruit were 5.7, 1.9, 1.7, 1.4, and 1.3 times as high, respectively.

Storage temperature influences strawberry volatile production.

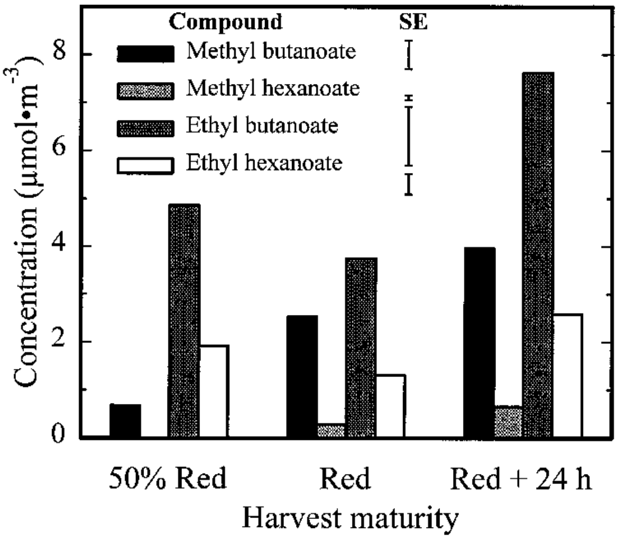

Fig. 2. Concentrations of four major esters in strawberries harvested at three stages of maturity. Fruit were harvested when 50% red (50% Red), on the day the fruit turned fully red (Red), or on the following day (Red+24 h). Volatiles in the head space of 4-L glass jars, each containing 100 g of whole, fresh fruit, were trapped on Tenax adsorbent traps, thermally desorbed, and analyzed by gas chromatography-mass spectrometry. Values are averages for five cultivars. Error bars represent the SE where n = 15 and df = 75 (Adapted from Forney et al., 1998.)

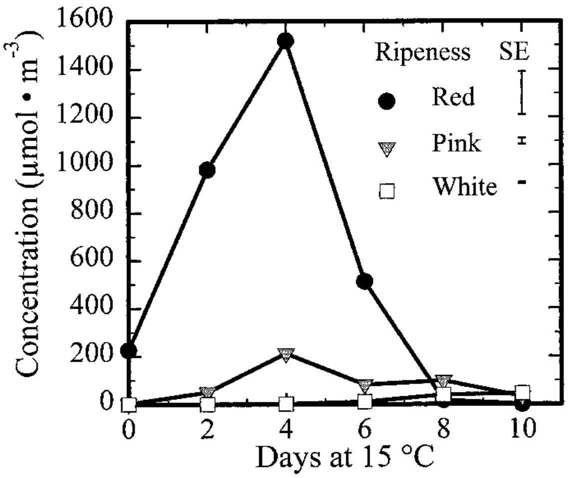

Fig. 3. Total concentration of volatile compounds in head space over 'Kent' strawberry fruit in storage. Fruit were harvested fully red, pink, or white and held at 15 °C for 10 d. Volatiles in the headspace of 1-L glass jars, each containing 10 whole, fresh fruit, were trapped on Tenax adsorbent traps, thermally desorbed, and analyzed by gas chromatography-mass spectrometry. Error bars represent the SE where n = 3 and df = 10. (Adapted from Miszczak et al., 1995.)

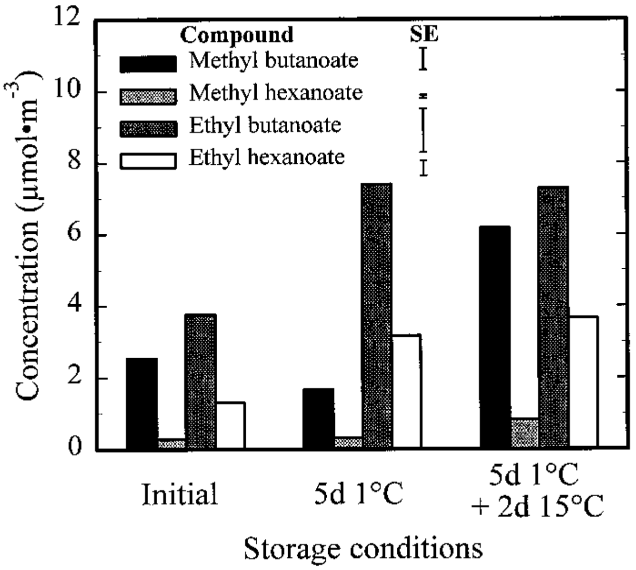

Fig. 4. Concentrations of four major esters in "red-ripe" strawberry fruit at harvest (Initial), after storage at 1 °C for 5 d (5d 1 °C), or after an additional 2 d at 15°C (5d 1 °C + 2d 15 °C). Volatiles in the head space of 4-L glass jars, each containing 100 g of whole, fresh fruit, were trapped on Tenax adsorbent traps, thermally desorbed, and analyzed by gas chromatography-mass spectrometry. Values are averages for five cultivars. Error bars represent the SE where n = 15 and df = 75. (Adapted from Forney et al., 1998.)

Holding pink 'Kent' strawberries at 10 and 20 °C had no consistent effect on the content of all volatile compounds (Miszczak et al., 1995). Production of methyl 3-methylbutanoate and 3-methylbutyl acetate was higher at 20 °C than at 10 °C, whereas the opposite was true for ethyl butanoate. We have found that ethyl butanoate and ethyl hexanoate increased during storage at 1 °C, while methyl butanoate and methyl hexanoate increased during storage at 15 °C (Fig. 4). These temperature-related changes in ester composition are consistent with what we have observed with strawberries ripening in the field (Fig. 2). With field temperatures ranging from 12 to 30 °C, concentrations of methyl esters increased more rapidly than did those of ethyl esters. Methyl butanoate and methyl hexanoate increased 6- and 20-fold, respectively, in fruit ripened from 50% red to red + 24 h, while ethyl butanoate and ethyl hexanoate concentrations increased <50%. The reason for this temperature effect on ester synthesis has not been explained. Understanding the mechanism underlying these changes could provide new methods to control strawberry flavor development both before and after harvest.

Exposure to light during storage also affects patterns of volatile synthesis in harvested strawberries. Miszczak et al. (1995) showed that storage in light (200 µmol·m^{-2}·s^{-1}) for 3 d at 10 or 20 °C increased the production of ethyl hexanoate, 3-methylbutyl acetate, ethyl 3-methylbutanoate, and methyl 3-methylbutanoate in pink 'Kent' strawberries.

Low-oxygen atmospheres and injurious levels of CO_2 can induce fermentation, causing ethanol accumulation in the fruit, which, in turn, produces off-odors. Normal mitochondrial oxidative phosphorylation can be disrupted because of a lack of O_2 or interference with normal mitochondrial function arising from membrane damage or changes in pH gradients (Ke et al., 1994). Disruption of respiratory metabolism results in the accumulation of pyruvate, which is converted to acetaldehyde and ethanol by pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) in the cytoplasm. In addition, elevated levels of CO_2 in the storage atmosphere tend to lower cytoplasmic pH (Siriphanich and Kader, 1986), which may stimulate the activity of these two enzymes (Ke et al., 1994). The resulting increased levels of ethanol may stimulate formation of ethyl esters, especially ethyl acetate (Ke et al., 1994; Larsen and Watkins, 1995b).

Accumulation of ethanol and acetaldehyde is often associated with off-odors and flavors. In strawberry fruit held in 20% CO_2, ethanol concentrations increased 2-fold but there was no increase in acetaldehyde concentration (Larsen and Watkins, 1995b). Off-odors that developed in these fruit were correlated with fruit ethanol content, but, because of its high odor threshold, (100–800 mg·kg^{-1}), ethanol was not responsible for the off-odor (Larsen, 1994). Increased levels of ethyl acetate induced by stressful atmospheres appear to be the true cause of many anaerobic off-odors in fresh produce. Ethyl acetate has a low odor threshold (0.26–5 mg·kg^{-1}) (Larsen, 1994). It has a fruity, pineapple-like odor at low concentrations, but a more chemical-like odor that often is associated with anaerobic fruit at higher concentrations. When 'Pajaro' strawberries were stored in varying concentrations of CO_2 (0% to 20%) for up to 11 d at 0 °C, the concentration of ethyl acetate was best correlated with off-flavor scores (r = 0.85) (Larsen and Watkins, 1995b); r values for ethanol and acetaldehyde were 0.62 and 0.3, respectively.

MECHANISMS OF SYNTHESIS

Esters are the most important group of volatile compounds responsible for the aroma of strawberry fruit. However, research to determine the mechanisms by which these esters are produced has been limited. The primary enzyme believed to be responsible for ester production is alcohol acyltransferase (AAT), which Pérez et al. (1993) isolated and partially purified from 'Chandler' fruit. The enzyme had a broad pH range (5.5 to 9.3) and a temperature optimum of 35 °C at pH 8.0.

This enzyme catalyzes the esterification of an acyl moiety from acyl-CoA onto an alcohol (Fig. 5). The many sources of substrates for this reaction influence the composition of the esters produced. Pérez et al. (1993) reported that AAT had greatest activity with hexanol when acetyl-CoA was used as an acyl donor although methanol and ethanol were not tested as substrates. Although it had slightly greater activity with acetyl-CoA, AAT acted on other acyl-CoAs (propionate and butanoate). The specificity of this enzyme was correlated with the ester composition in ripe 'Chandler' fruit, suggesting that ester composition is dependent on the properties of the enzyme. Pérez et al. (1996) observed that the more flavorful fruit of 'Oso Grande' had higher AAT activity than did fruit of the less flavorful cultivar I-101, supporting the importance of this enzyme for flavor development in strawberry fruit.

The ability of strawberry fruit to produce esters varies with fruit maturity. Yamashita et al. (1977) demonstrated that immature 'Hokowase' strawberry fruit, collected 5 d after flowering, converted added pentanal to 1-pentanol, but produced no esters. However, the production of 1-pentyl acetate and 1-pentyl n-butanoate increased dramatically between 30 and 40 d after flowering, as fruit ripened. Similarly, Hamilton-Kemp et al. (1996) found that C_6 alcohols added to ripe strawberries were converted to their corresponding acetate esters. To explain this ability of ripe fruit to produce esters, Pérez et al. (1996) showed that AAT activity increased as strawberry fruit ripened on the plant and was first detected in most cultivars when fruit had begun to turn pink. In addition, AAT activity did not change when fruit were stored at 1 °C for 9 d (Pérez et al., 1996).

Alcohol dehydrogenase (ADH) is another enzyme that is involved with synthesis of aroma volatiles in strawberry fruit (Fig. 5). This enzyme is involved in the interconversion of alcohols and aldehydes to supply precursors for ester synthesis and the production of other volatile compounds. When C_6 aldehydes were supplied to ripe strawberries, they were readily converted to their corresponding alcohols and acetate esters (Hamilton-Kemp et al., 1996). Mitchell and Jelenkovic (1995) observed that the specific activity of NAD- and NADP-dependent ADH to various alcohols and aldehydes corresponded to the substrates found in ripe strawberries. This enzyme may play a key role in supplying the precursors that determine what esters a strawberry fruit produces.

Substrate availability may also play a major role in the composition of esters produced by ripe strawberry fruit. Amino acids, sugars, and lipids all can act as precursors for ester substrates. Amino acid metabolism generates aliphatic and branched-chain alcohols, acids, carbonyls, and esters. Leucine gives rise to 3-methylbutyl acetate, and low levels of both leucine and 3-methylbutyl acetate were found in 'Chandler' strawberries (Pérez et al., 1992). Alanine increased 2-fold in strawberries between 30 and 36 d after bloom and could be a precursor of ethyl esters. Drawert and Berger (1981) found that feeding alanine to cultured segments of strawberry fruit enhanced formation of methyl hexanoate, ethyl hexanoate, ethyl butanoate, and ethyl decanoate.

Normal aerobic metabolism of sugars can produce precursors for ester production, and fermentation induced by anaerobiosis produces large quantities of acetaldehyde and ethanol. Associated with these increases are increases in the production of ethyl esters, including ethyl acetate, ethyl butanoate, and ethyl hexanoate (Larsen and Watkins, 1995a; Ueda and Bai, 1993).

Fatty acids from various lipids also appear to serve as ester precursors. Fatty acids are catabolized through two major pathways, β-oxidation and the lipoxygenase pathway (Sanz et al., 1997). β-Oxidation produces acyl-CoAs that can be used by AAT to produce esters. The lipoxygenase pathway is most active in disrupted plant cells and produces a variety of volatile C_6 and C_9 compounds, including 1-hexanol, *trans*-2-hexen-1-ol, 1-hexanal and *trans*-2-hexenal, which are found in large quantities in homogenized strawberry fruit tissue (Latrasse, 1991; Schreier, 1980). These lipoxygenase products are metabolized by the fruit into volatile esters (Hamilton-Kemp et al., 1996).

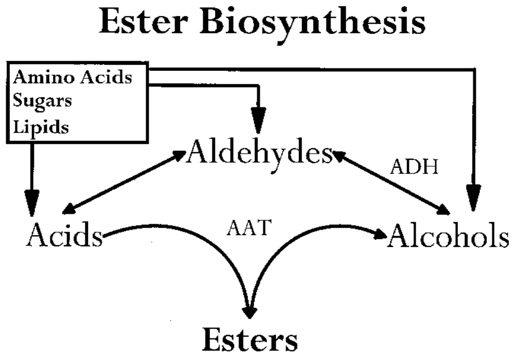

Fig. 5. Proposed pathways involved in the biosynthesis of volatile esters in ripe strawberry fruit. ADH = alcohol dehydrogenase, AAT = alcohol acyltransferase.

In addition to esters, furanones make an important contribution to the aroma and flavor of fresh strawberry fruit. However, our understanding of the mechanism of furanone biosynthesis is very limited. Sugars have been suggested as precursors for furanone synthesis, with fructose being the most likely candidate (Sanz et al., 1997; Zabetakis and Holden, 1997). Sanz et al. (1997) suggest that furaneol could be synthesized from an intermediate of the pentose phosphate cycle and that fructose-6-phosphate could be its precursor. The addition of 6-deoxy-D-fructose to tissue-cultured strawberry cells stimulated the production of furaneol-glucoside, suggesting its role as a precursor of furanone synthesis (Zabetakis and Holden, 1997). While furanone synthesis is believed to be enzyme-mediated, no enzyme has been identified to date. Identification of the biochemical pathway responsible for furanone synthesis and its regulation could provide new insights into strawberry flavor development.

CONCLUSIONS

The aroma of fresh strawberries is comprised of a complex mixture of volatile components, with methyl and ethyl esters predominating. Other compounds that contribute to aroma include furanones, aldehydes, terpenes, and sulfur compounds. Many factors influence the volatile composition, including cultivar, fruit maturity, and postharvest environment. We still have a limited understanding of the mechanisms controlling the synthesis of aroma volatiles. A better understanding of these mechanisms could provide us with the ability to manipulate strawberry fruit to optimize flavor at the time of consumption. Understanding properties of enzymes involved in the production of aroma volatiles may lead to genetic and environmental manipulations to improve strawberry flavor following shipping and marketing.

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