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Aromas and Flavours of Fruits

Berta Gonçalves, Ivo Oliveira, Eunice Bacelar,
Maria Cristina Morais, Alfredo Aires,
Fernanda Cosme, Jorge Ventura-Cardoso,
Rosário Anjos and Teresa Pinto

Additional information is available at the end of the chapter

Abstract

Aromas and flavours play an important role in horticultural crops' quality, namely in fruits. Plant breeders have made considerable advances producing cultivars with higher yields, resistant to pests and diseases, or with high nutritional quality, without paying enough attention to flavour quality. Indeed, consumers have the perception that fruit aromas and flavours have declined in the last years. Attention is given nowadays not only to flavoured compounds but also to compounds with antioxidant activity such as phenolic compounds. Fruit flavour is a combination of aroma and taste sensations. Conjugation of sugars, acids, phenolics, and hundreds of volatile compounds contribute to the fruit flavour. However, flavour and aroma depend on the variety, edaphoclimatic conditions, agronomical practices and postharvest handling. This chapter reviews the aromas and flavours of the most important fruits and discusses the most recent advances in the genomics, biochemistry and biotechnology of aromas and flavours.

Keywords: fruits, flavour quality, volatile compounds, genomics of flavour, biochemistry of flavour, biotechnology of flavour

1. Introduction

Quality in horticulture can be defined as the traits of a given commodity, regardless of its yield [1]. Here, we not only include visual appearance, ability to endure postharvest processing but also chemical and nutritional composition and flavour. Great advances have been made in horticultural breeding, obtaining fruits with characteristics that are those that growers (e.g. yield,

resistance to pests and diseases, appearance), distributors (handling and processing resistance) and retailers (handling and processing resistance, appearance) desire but, most of the times, failing to achieve top nutritional and flavour characteristics [2]. In parallel to this increase in breeding, knowledge regarding chemical composition and flavour traits has too been rising, also followed by insights on physiological, metabolic and biochemical pathways taking place in plants. However, increasing flavour of fruits by breeding is still not an easy task, due to the multitude of factors affecting the compounds responsible for this characteristic, like climate, production systems and pre- and postharvest processing [3]. Flavour is the interaction between taste, orthonasal and retronasal olfaction perceptions, commonly denominated as 'taste and aroma', which is one of the major quality traits of fruits and together with texture is responsible for repeated purchases of a given commodity [4]. The aroma fraction of flavour can even influence the perception of other traits, as recorded for sweetness and sourness [5]. Furthermore, flavour, which is the interaction of taste and aroma, hence dependent on chemical traits, is strongly linked to the individual preferences of consumers and can be seen as the 'modern concept of quality' [6]. Knowing the preferences of consumers and aiming to fulfil those expectations regarding the flavour of fruits, besides increasing the probability of producers to easily sell their commodities, they will also be linked to an expected improvement in nutritional uptake, as better-tasting fruits will likely replace less healthy snack foods [1]. New tools, namely those related to molecular techniques, allow the identification of genes responsible for biosynthesis of compounds and open new perspectives for the improvement of flavour, by cloning those genes, increasing that specific pathway or silencing the expression of a gene responsible for an undesired compound [2].

In this chapter, we will review the aroma and flavour compounds of the major fruits (fresh fruits and nuts) and, finally, review the latest advances in genomics, biochemistry and biotechnology of aromas and flavour compounds.

2. Fresh fruits

Volatile compounds are produced as indicators of fruit ripening, and they can be classified as primary (present in intact tissues) or secondary compounds (result of tissue disruption) [7]. Different fruits produce different volatile compounds, although their precursors are phytonutrients and the resulting volatile compounds are usually esters, alcohols, aldehydes, ketones, lactones and terpenoids [8].

The volatile compounds responsible for the aroma and/or flavour of the fruits are affected by several factors, starting with the genetic factors, environmental conditions, production practices, maturity degree and ending with postharvest handling and storage settings. These factors should be taken into account when comparing fruits' volatile profiles, since they can explain differences between species and cultivars. Furthermore, they can lead to modifications in the pathways involved in volatile biosynthesis. Volatiles with critical importance in aroma and flavour characteristics are biosynthesized from amino acids, lipids and carbohydrates, via a limited number of major biochemical pathways [9]. The first limiting step for volatile formation is the availability of primary precursors, including fatty acids and amino acids, compounds highly regulated during fruit development in terms of amount and

composition [10]. This limiting step has been studied and the formation of volatile compounds can be significantly increased, both qualitatively and quantitatively, if fruits are incubated in vitro with adequate metabolic precursors [11].

Some of the fruits with a higher amount of production and more commonly consumed worldwide are apples, bananas, cherries, oranges and grapes, which are shortly addressed here. In apples, over 300 volatile compounds were described [12], although they can be considered cultivar specific [13] and maturation dependent, from aldehydes to alcohols and esters [14]. The latter chemical class is predominant in ripe apples, and straight and branched esters can be found, namely ethyl, butyl and hexyl acetates, butanoates and hexanoates [15]. There is a clear increase of volatile compound production in apple skin, rather than in the internal tissues, due to a higher abundance of fatty acid substrates or increased metabolic activity [16]. The relative amount of each compound is, as referred earlier, linked to a specific cultivar and cannot only be used for cultivar discrimination but also to monitor ripening of fruits [17]. In apples, branched chain esters are produced from the breakdown of leucine, isoleucine and valine, while straight chain esters are synthesised from membrane lipids [18]. The hydroperoxides that result from these reactions are converted to aldehydes, then to alcohols and finally to esters. This sequence leads to the flavour of immature apples ('green notes') due to C6 aldehydes and alcohols to the 'fruity notes' given by the increased ester production [19]. For banana, about 250 volatile compounds have been described, although the really odorant are less than 40 [20]. Olfactometric methods have described several aromas and linked those to some compounds, namely 'banana' to 3-methylbutyl esters and acetate esters, 'grassy' to aldehydes and alcohols and 'spicy' to phenols [20, 21]. Major volatile compounds that contribute to banana aroma are volatile esters, such as isoamyl acetate and isobutyl acetate [22] but also isoamyl alcohol, butyl acetate and elemicine [23]. As for other fruits, the ripening process changes the volatile profile, with increased concentration of acetates and butanoates [24] and is cultivar dependent [25]. Recently, Bugaud and Alter [26] have found that 3-methybutyl esters were the most abundant volatile compounds, with 2-methylpropyl butanoate and 3-methylbutyl butanoate linked to 'banana' note; the presence of 3-methyl acetate to 'fermented' and 'chemical' notes, while the presence of 'grassy' (freshly cut green grass) aroma decreased as the total amount of volatiles increased with ripening, namely esters. For cherries, over 100 volatile compounds have been identified, including free and glycosidically volatile compounds, belonging to the chemical classes of carbonyls, alcohols, acids, esters, terpenes and norisoprenoids [27]. Major compounds include hexanal, (E)-2 hexenal and benzaldehyde and are associated with green/grassy notes. For some cultivars, other minor compounds gain increased importance, due to their low odour detection threshold such as (Z)-3-hexenal, decanal, nonanal, (E,Z)-2,6-nonadienal and (E,E)-2,4-nonadienal in 'Lapins', 'Rainier', 'Stella', 'Hongdeng' and 'Zhifuhong' cultivars [28, 29]. Some ketones have also been found in cherries, although they have relatively low importance in overall aroma [28], while alcohols, being the most abundant benzyl alcohol, 1-hexanol and (E)-2-hexen-1-ol, are responsible for green notes and the fresh green odour. Additionally, 1-Octen-3-ol has been described as one of the most predominant volatile compound in 'Hongdeng', 'Hongyan' and 'Rainier' sweet cherry cultivars [29]. The content of esters in cherries increases during ripening, but their relative abundance is low. The most common are ethyl acetate, butyl acetate, hexyl acetate, (Z)-2-hexenyl acetate and (E)-2-hexenyl acetate, with methyl benzoate described as among

the most powerful volatiles in some cultivars, such as 'Rainier' [28]. Terpenoid compounds are also present in cherries at low levels, limonene, linalool and geranylacetone being the most common [30]. However, when analysing the glycosidically bound aroma compounds in three sweet cherry cultivars ('Hongdeng', 'Hongyan' and 'Rainier'), Wen et al. [29] show that terpenoids are the second major class, after alcohols. In oranges, more than 300 volatile compounds have been reported, the major ones being limonene, β-myrcene and linalool [31], but valencene can also be of great importance, depending on the cultivar [32]. However, these compounds, although representing the large majority of the volatiles, are not the ones more responsible for the aroma, as their contribution is limited due of high odour-detection thresholds. Other minor compounds, like aldehydes (octanal, decanal, undecanal, (Z)-3-hexenal and (E)-2-decenal), esters (ethyl butanoate, ethyl 2-methylbutanoate and ethyl isobutyrate) and other terpenes (β-sinensal, geranial and neral) are those with a significance for the overall flavour of oranges [31]. Most of the grape cultivars have no scent, although the wines obtained from them are full of aromas [33, 34]. A great number of compounds have been recorded, including monoterpenes, C13 norisoprenoids, alcohols, esters and carbonyls [35, 36]. If linalool and geraniol have been identified as major aroma compounds in both red and white grapes [37], the volatile profile can be useful for the discrimination of grape cultivars [36]. Major free volatile compounds are hexanal, (E)-2-hexenal [36] while glycosidically bound include terpene and benzenic glycosides [34]. In more aromatic grape cultivars, like Muscat, major free compounds include linalool, geraniol, citronellol, nerol, 3,7-dimethyl-1,5-octadien-3,7-diol and 3,7-dimethyl-1,7-octadien-3,6-diol while those glycosidically bound were geraniol, linalool, citral, nerol, citronellol, α-terpineol, diendiol I, diendiol II, trans-furan linalool oxide, cis-furan linalool oxide, benzyl alcohol and 2-phenylethanol. Other monoterpenes that can also add to Muscat aroma were rose oxide, citral, geraniol, nerol and citronellol [38]. As for the other fruits, the volatile profile of grapes changes during ripening, and apparently a greater number of volatile compounds exist pre-veraison than post-veraison, as recorded for Riesling and Cabernet Sauvignon grapes, that also recorded differences (esters and aldehydes were the major class of compounds from Riesling grapes and alcohols for Cabernet Sauvignon) at veraison (**Table 1**) [39].

Although the flavour of fruits is the interaction of taste and aroma, the chemical composition of fruits (organic acids, sugars, amino acids, pro-vitamins, minerals and salts) can also influence aroma perception and ultimately, flavour. For sugars, glucose, sucrose and fructose are

Fruit	Main volatile compounds	References
Apple	Acetaldehyde, ethyl butanoate, ethyl methyl propanoate, 2-methyl butanol, ethyl 2-methyl butanoate, 2-methyl butyl acetate, hexyl acetate, butyl acetate, hexyl butanoate, hexyl hexanoate, (E)-2-hexenal, (Z)-2-hexenal	[42–44]
Banana	(E)-2-hexenal, acetoin, 2, 3-butanediol, solerol, hexanal, isoamyl acetate, 3-methylbutyl acetate, 3-methylbutyl butanoate	[44, 45]
Cherry	Hexanal, (E)-2 hexenal, benzaldehyde, (E)-2-hexen-1-ol	[27–29]
Orange	Limonene, β-myrcene, linalool, hexanal, ethyl butanoate	[32, 46, 47]
Grape	Linalool, geraniol, (E)-2-hexenal, hexanal, phenylethyl alcohol, octanoic acid	[36, 37]

Table 1. Key volatile compounds present in some fruits largely consumed worldwide.

the most important sugars affecting the perception of sweetness (ranking fructose > sucrose > glucose) [40] and their proportion in a given fruit will change flavour. However, this relationship is not completely understood, as measurement of sugars as soluble solids, in orange, does correlate to sweetness but in mango does not [4]. The main organic acids in fruits are malic, citric and tartaric, citric being the most sour and tartaric the least [40]. Citric acid is linked to citrus fruits, tartaric to grapes and malic to apples, and they are responsible for the sour flavour detected on those fruits. Other fruits, like melon or banana, have reduced acidity [41]. The presence of minerals and salts can change the perception of acidity, by combining with organic acids, influencing the buffering capacity [40]. Many research studies on the flavour of fruits give us a good overview of this particular trait of these commodities. However, much is still to be done, since many cultivars are yet still less studied. Furthermore, the link between taste and aroma compounds and the consumer perception of those is still not well understood, and this should be the ultimately goal to achieve consumer-oriented commodities.

3. Nuts

Global consumption of nuts grew in the last years and it is expected to grow continuously on a yearly basis [48]. In 2015, almonds, cashews, walnuts and hazelnuts were the most preferred nuts by the consumers [49] but other nuts, such as pine nuts, pecans, chestnuts, Brazil nuts, macadamias and pistachios, are also an appreciated food, especially in the regions where they are regularly produced. They are generally consumed as whole nuts (fresh, roasted or salted) or used in a variety of commercial products and processed food [50]. Europe and North America are the largest nut consumer regions, accounting for almost 50% of the worldwide consumption [48]. Nuts have been a regular part of the human diet since pre-agricultural times [51] due to their nutritional value, sensory properties [49] and potential health properties [50, 52], and their consumption can reduce cardiovascular disease risk, the incidence of cancer and type 2 diabetes mellitus [53], as well as obesity and ageing effects [54].

Nut quality related to consumer purchase decisions is based on nut appearance such as size, colour, cleanness and freedom from decay and defects [55] but textural properties [54, 56] such as aroma and flavour also play an important role in consumer acceptability [57]. Sweetness, oiliness and roasted flavour are commonly associated with good overall nut sensory attributes [55], some compounds generated during the roasting process responsible for the typical nut flavour [58]. Roasting is a common practice used by the nut industry and involves several physical-chemical processes [59], which can modify the odour, flavour and quality of the final product [60], including negative effects, such as rancidity [61].

In general, nuts are characterised by their high content in unsaturated fatty acids [49, 50, 57] which make them highly sensitive to oxidation during the roasting process leading to the formation of harmful free radicals [61], which are responsible for undesirable odours and flavours [62]. As a result, the roasting process negatively affects the nutritional quality of nuts but also may influence both the formation of health-promoting components and those with potentially adverse health effects [63]. So, selecting the appropriate roasting conditions, mainly temperature and time, is crucial for achieving higher nut quality [55], which is also dependent on the genotype. For example, in walnuts, roasting treatments under 180°C,

for 20 min, produced 17 times higher levels of compounds that indicated oxidation, when compared to raw walnuts [63]. In comparison, the compounds that indicated oxidation only increased by 1.8 times for hazelnuts and 2.5 times for pistachios [63]. According to the same authors [63], the roasting process at low/middle temperatures (120–160°C) preserves constitutional compounds and sensory properties of different nuts (macadamia nuts, hazelnuts, almonds, pistachios and walnuts). Nevertheless, as it occurs with other foods, the characteristic flavour of nuts is dependent on the volatile compounds.

During roasting and other heat processes, additional volatile compounds are formed from reactions among food compounds. In roasted nuts, a wide range of volatiles contribute to the typical and desirable roast flavour. According to Xiao et al. [64], in raw almonds, a total of 41 volatile compounds were identified, including aldehydes, ketones, alcohols, pyrazines and other volatile compounds. The benzaldehyde was the predominant volatile compound present in the raw samples and is associated with a marzipan-like flavour [64]. Roasting resulted in about a 90% decrease in the benzaldehyde level and in the formation of up to 17 new volatile compounds that were not found in raw almonds. Many of these compounds are typically generated during the complex and well-known Maillard (non-enzymatic browning) reaction that occurs during roasting. Volatile compounds like pyrazines, furans and pyrroles have been previously identified as key compounds of roasted almond aroma and concentration of many of these volatile compounds increased with roasting time [64]. It was theorised that one of the reasons for the uncertainty surrounding the characterisation of the 'nutty' term is that nuts have aroma qualities that may be typical to only their own species and that there is no common aroma quality present among all nuts [65]. In a research conducted by Clark and Nursten [66], over 200 aroma compounds were identified as having nutty aromas. This work indicated benzaldehyde, 3,4-methylenedioxybenzaldehyde and 4-methylbenzaldehyde as responsible for nutty aromas in almonds, while 2,4-octadienal and 4-pheynyl-4-pentenal were linked to the same attribute in walnuts and 2-ethyl-3-methylpyrazine in roasted peanuts. In the harvest year, edaphoclimatic conditions of orchards and storage conditions have also been mentioned as key factors determining overall nut quality. In order to evaluate the influence of time and temperature conditions on the oxidative degradation of hazelnuts, Ghirardello et al. [63] observed that storage of nuts at low temperatures reduced the effects of lipid oxidation during 8 months, but refrigeration was necessary to preserve high nut quality for up to 1 year.

4. Grapes and wine

Grapes belong to the large group of fleshy fruits [67]. According to Peynaud and Riberéau-Gayon [68], grapes were classified as: (1) *Vitis vinifera* or European grape, subdivided into several cultivars; (2) American vines, *Vitis riparia*, *Vitis rupestris*, *Vitis labrusca*; (3) Hybrids and *Vitis rotundifolia* or Muscadine grapes; and (4) Asian vines, *Vitis amurensia*. The composition and concentration of grapes' aroma compounds are influenced by many factors such as grape variety [69–71], degree of ripening [72], sunlight [73–76] and vintage.

In grapes, volatile aroma compounds are found both as 'free' and as 'bound' to a sugar moiety, if 'bound', they are not odour active, but, upon hydrolysis of the glycoside, they may then be volatilised [77]. The amount of 'free' volatile aroma compounds makes it possible to classify

the grape cultivars into neutrals or aromatic [78, 79]. The aromatic grape cultivars presented a varietal character resulting from higher concentration in the amount of 'free' volatile aroma compounds, namely terpenes, norisoprenoids and isoprenoids [80]. The importance of these 'free' volatile aroma compounds is related not only to their high concentrations but also to their lower perception thresholds. Therefore, grape flavour depends on the content and composition of several groups of compounds [81]. Among the compounds responsible for the aromatic quality are monoterpenes and C_{13}-norisoprenoids. These compounds are indigenous from the grape and responsible for intense fruity and floral attributes in wines, contributing to the wine varietal aroma [82–84]. Other volatile compounds present in grapes are terpene hydrocarbons, pyrazines [38, 85–87] and some C_6–aldehydes and alcohols [88].

During ripening, grapes develop a characteristic flavour and/or aroma by synthesising volatile compounds [89, 90]. For example, linalool and geraniol have been shown to contribute to the aroma of 'Concord' grapes, closely resembling the aroma of methyl anthranilate [91, 92]. The aroma compounds, which are secondary metabolites of the plant metabolism, are distributed between the pulp and skin of the grape berry, with the highest concentration in the grape skin [92, 93]. Wu et al. [94] characterised the aromas of table grapes, and they found that in 20 grape cultivars, a total of 67 volatile compounds, 61 in the mesocarp and 64 in the skin and the total contents of volatiles of mesocarp and skin largely depended on the levels of esters and terpenes, respectively (**Figure 1**).

Vitis labrusca and *Vitis rotundifolia* cultivars have a distinct and pronounced odour; the foxy aroma of *V. labrusca* is attributed to methyl anthranilate [95]. Chemical compounds originated from several sources contribute to wine aroma. Grape volatile aroma compounds, such as monoterpenes, C_{13}-norisoprenoids, methoxypyrazines and thiols, if present, are of major importance for the wine varietal character [96]. The volatile compounds found in wine presented different sensory attributes like fruits such as cherry, pear or passion fruit [97]. As an example, in **Figure 2**, different fruit flavours' attributes perceived in red and white wines are identified.
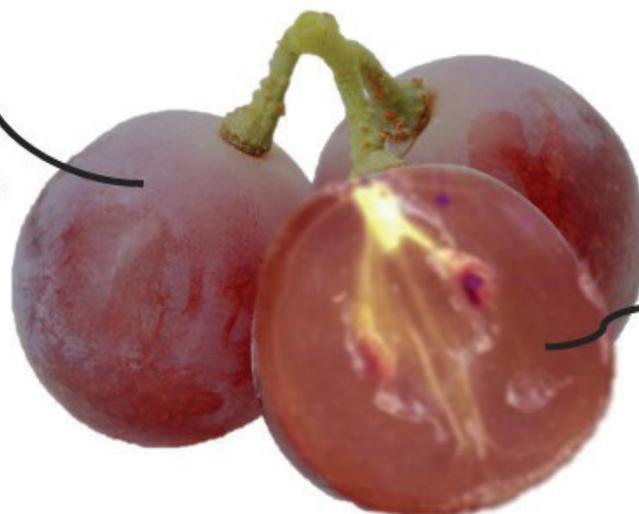
Figure 1. Grape berry flavours compounds localization.

Figure 2. Fruit flavours in the red and white wine.

5. Genomics, biochemistry and biotechnology of aromas and flavour

As already mentioned, the flavour of fruits is a complex set of interactions between two main sensations: taste and aroma [2]. Taste is mainly a set of sweet and sour sensations linked to the presence of sugars and organic acids (although other minor compounds affect bitterness, astringency or saltiness). However, the aroma is usually the predominant sensation, surpassing taste [98]. Indeed, if taste sensations, detected in mouth, are recognised by six classes of receptors (sweet, sour, salty, bitter, umami and fat-taste), for flavour complexity, where the olfactory system is essential, 350 olfactory receptor genes are known in humans [1].

The known decrease in flavour of fruits is strongly connected to the pressure on the producers: they are usually paid depending on physical characteristics of fruits (size, shape and colour) but not to chemical traits, so the selection of cultivars is performed to enhance those qualities; the ripening of fruits is delayed as much as possible to make sure that they are able to withstand harvest, handling, storage and shipping without damages, but without a normal

ripening, flavour sensations decreased [99]. Considering that flavour perception relies on the interaction of a considerable amount of compounds, it makes it one of the most challenging quality attributes to manipulate, which has led to a reduced attention given to this theme [40]. However, consumers' pressure is growing to bring back the typical flavour of old horticultural commodities, where the flavour sensations were almost instantly detected by odour, followed by the recognition of taste.

To achieve the goal of horticultural commodities of full flavour, some strategies can be followed, including changes in agricultural practices but also genetics tools, using the information on the known pathways of formation of those compounds linked to taste and aroma. Considering the first approach, one should cite the preharvest factors such as genome or growing conditions, harvest maturity or postharvest storage like those important in the final flavour of any horticultural commodity [40]. Some of them are somewhat easy to control (growers are able to choose the cultivar, cultural practices and postharvest procedures), while others, such as climate conditions, are outside human influence. The choice of the cultivar to grow and its link to flavour and how chemical components in the plant tissue are expressed are connected to genetic backgrounds [99]. Indeed, recent works comparing cultivars of sweet cherry [100], peach [101], gooseberry [102], fig [103] or pear [104], to cite a few, show how genetic backgrounds can influence chemical composition and ultimately flavour, recognised by sensory evaluation. However, although genetics have a major role when determining the flavour of freshly harvested fruits, the gene expression can be modified by pre- and postharvest factors [105] (**Figure 3**), as recently reported for peach [106]. Included in those preharvest factors are weather, soil preparation and cultivation, soil type, irrigation, fertilisation practices and crop loads, while for postharvest, it should be mentioned that storage temperature management, packaging under controlled or modified atmosphere, the use of edible coating, heat or physicochemical treatments are the factors [107]. The next step on flavour research was given when information on biosynthesis was obtained by using molecular and biochemical approaches. Knowing the metabolic pathways, namely the genes involved and the associated enzymes but also the regulatory elements (hormones and transcription factors) or which mechanisms are implicated in the storage or sequestration of volatile precursors, is key in allowing a biotechnological approach to their manipulation [108]. The genes that are linked to flavour can be mostly divided into two categories: those encoding for enzymes and those responsible for factors regulating pathway output [1]. If the knowledge for synthesis pathways and genes for those enzymes responsible has been increasing rapidly, the regulation of metabolic pathway output is not well understood, and the number of genes involved may be quite large, as found for strawberry, where 70 quantitative trait loci (QTLs) affecting volatiles and their precursors have been identified [109] or mandarin (206 QTLs) [110], for instance. As referred earlier, the compounds responsible for aroma can be divided in several classes, the most important being monoterpenes, sesquiterpenes, lipids-, sugars- and amino acid-derived compounds. Knowing how they are biosynthesized and what is involved, when and how are key steps to allow their manipulation. In fact, several steps of aroma volatile biosynthesis for which genes have been characterised and used as targets for genetic transformation are presented in **Figure 4** (adapted from [108]). The large part of the available research on the manipulation of flavour has been conducted on tomato, as it is a plant easy to transform, with an associated high economic importance [111] and information regarding this fruit is readily
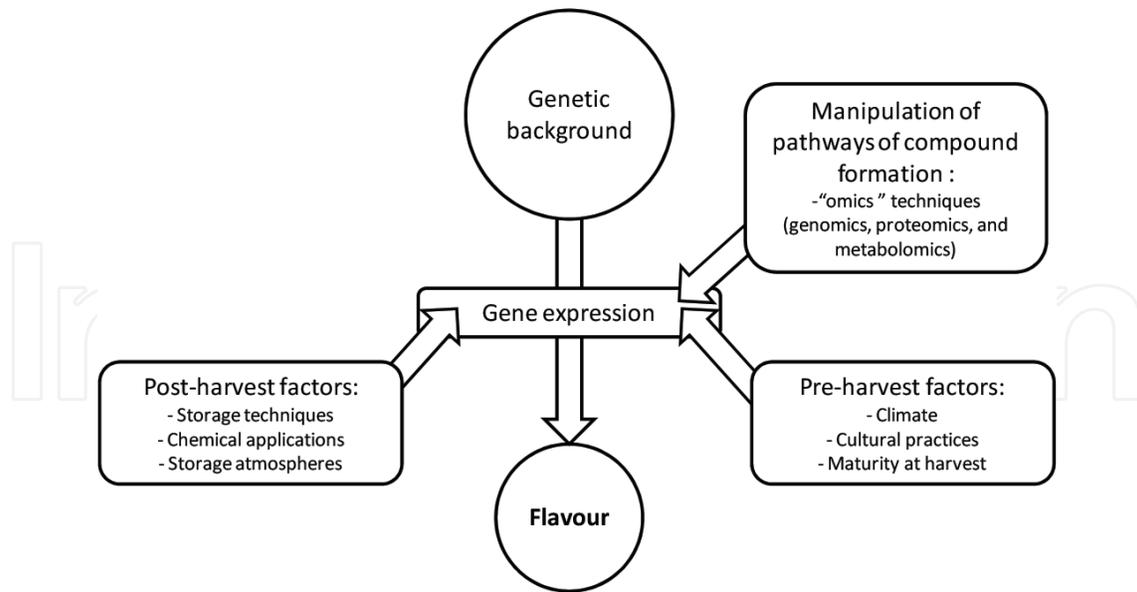
Figure 3. Factors affecting flavour formation in horticultural crops.

available (e.g. [1]). However, some data regarding other horticultural commodities are available, and some are cited here. For instance, modulation of the soluble sugar content in strawberry has been achieved, by an antisense cDNA of ADP-glucose pyrophosphorylase (AGPase) small subunit (FagpS), a key regulatory enzyme for starch biosynthesis. The down-regulation of the AGPase gene led to an increase of the soluble sugar content, which primarily changed the taste sensation of strawberries but can ultimately also change aroma and flavour, as soluble sugars may be converted into volatile compounds [112]. For orange, the down-regulation of the D-limonene synthase (important as D-limonene is the most abundant volatile component
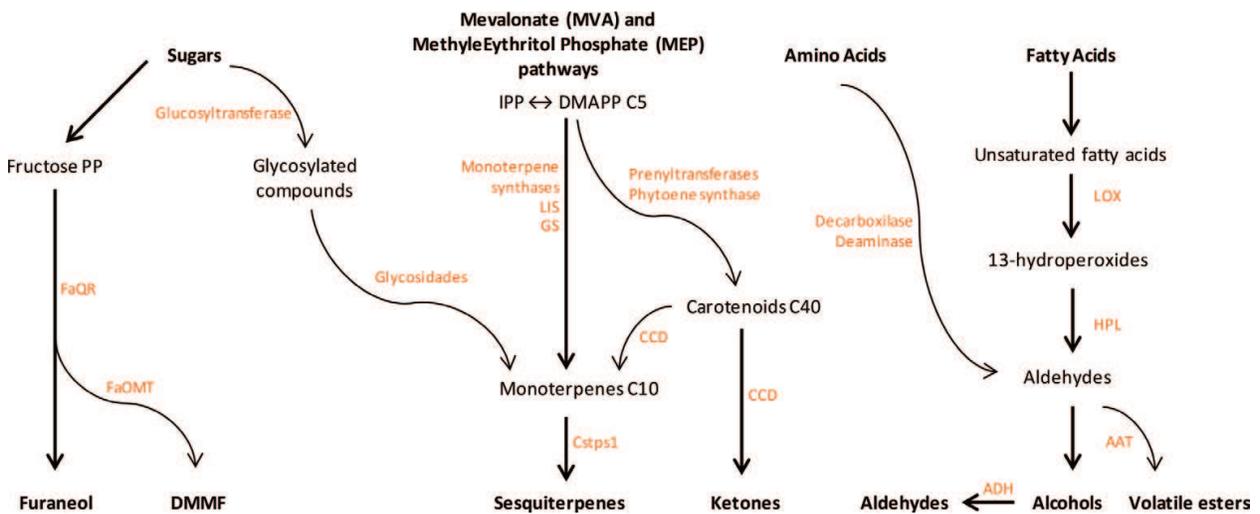

Figure 4. Representation of the steps of major groups of aroma volatiles biosynthesis. FaQR—*Fragaria × ananassa* quinone oxidoreductase; FaOMT—*Fragaria × ananassa* O-methyltransferase; DMMF—2,5-dimethyl-4-methoxy-3(2H)-furanone; IPP—isopentenyl pyrophosphate; DMAPP—electrophile dimethylallyl pyrophosphate; LIS—linalool synthase; GS—geraniol synthase; Cstps1—sesquiterpene synthase gene; CCD—carotenoid cleavage dioxygenases; LOX—lipoxygenases; HPL—hydroperoxide lyase; AAT—alcohol acyltransferase; ADH—alcohol dehydrogenase. Adapted from Pech et al. [108]). Metabolic ways (or pathways) and enzymes which genes have been up- or down-regulated, by genetic engineering, are in orange.

of all commercially grown citrus fruits) did not affect negatively fruit and juice intensity and discrimination but provided a clear insight to how the combined presence of several volatiles can influence fruit flavour [113]. Considering the compounds that are precursors of aromatic compounds, several strategies can be developed to modify their amounts, and will be shortly addressed, providing few but key examples. For fatty acids are derived into saturated and unsaturated short-chain alcohols, aldehydes and esters by the lipoxygenase (LOX) pathway. The first way to manipulate the volatile composition using fatty acids is to change their amounts present in plant organs. Recently, it was observed in pear that if incubated in vitro with metabolic precursors of volatile compounds, the formation of those was significantly increased, both qualitatively and quantitatively [11]. Some of the enzymes involved in the fatty acid conversion to volatiles can also be tuned to modify the final aroma. For desaturases, they have been identified in strawberry as being responsible for the production of lactones, a group of fatty acid-derived volatiles in peach, plum, pineapple and strawberry [114]. Another group of enzymes, phospholipases, are involved in the formation of polyunsaturated free fatty acids, the substrates for lipoxygenases [115]. The expression of phospholipases can be modified by the use of hexanal-based formulations [116] or by the application of chilling [117, 118]. Hydroxyperoxide lyase (HPL) forms very unstable hemiacetals from hydroperoxides generated by LOX, leading to the formation of aldehydes. HPL silencing in potato plants have reduced the content of the C6 compounds in the leaves, while increasing that of C5 [119]. Alcohol dehydrogenase (ADH) catalyses the interconversion of aldehydes and their corresponding alcohols and is a key enzyme in volatile ester biosynthesis [13]. Recent works show that the overexpression of an alcohol dehydrogenase (ADH) from mango led to a change in alcohols and aldehydes related to flavour [120], with previous works also showing that overexpression of an ADH increased the level of alcohols [121]. Alcohol acyl-transferases (AAT) catalyse the transfer of an acyl-CoA to an alcohol, resulting in the synthesis of a wide range of esters [122]. The reduction of AAT expression in apples resulted in reduced levels of key esters in ripe fruit, altered ratios of biosynthetic precursor alcohols and aldehydes, changing in a perceptible way, by sensory analysis, the ripe fruit aroma [123], and recent works show that they may be linked to the volatile ester and phenylpropene production in many different fruits [124]. The volatile formation pathway from amino acids is mainly due to the decarboxylases activity, but few are known to date. The catabolism of melon amino acid aminotransferase and branched-chain amino acid aminotransferase (BCAT) is connected to the amino acid-derived aroma compound formation [125]. Terpenoids are structurally diverse and the most abundant plant secondary metabolites, being of great significance, as they have vast applications in the pharmaceutical, food and cosmetics industries [126], with information regarding volatile terpenoids having been recently reviewed [127]. For carotenoid-derived compounds, the major enzymes involved are carotenoid cleavage dioxygenases (CCD), and the suppression of one gene encoding for CCD leads to the reduction of the production of β-ionone, geranylacetone and pseudoionone [128, 129]. Finally, for sugar-derived compounds, information is also available. One of the enzymes responsible for their conversion into volatiles is O-methyltransferase. This enzyme has been overexpressed in strawberries and a reduced expression of its encoding gene (FaOMT) changed furaneol to the 2,5-dimethyl-4-methoxy-3(2H)-furanone (DMMF) ratio, ultimately changing the aroma of the fruit [130]. Many other works have been looking to gain insights into this specific theme, providing important information on how to manipulate aroma and flavour components, and some of those can be found reviewed by Aragüez and Valpuesta Fernández [44] or Dudareva et al. [131].

6. Conclusions

The quality of horticultural commodities can be assessed in many ways, including by their aroma and flavour. This chapter overviews the large amount of information available regarding these characteristics in fruits. However, all this information is still not enough to fully understand the processes behind the formation of compounds, the interaction of those compounds with each other, but, more importantly, how they will finally influence the consumers' perception of aroma and flavour, and, ultimately, their tendency to buy such commodities. This is true to not only all fruits referred in this chapter but also to those not included here, and a continuous effort to identify volatile and non-volatile compounds for flavour and aroma in understudied species or cultivars must be undertaken. Furthermore, the improvement of flavour and aroma by adequate cultural practices must be achieved without a decline in other quality traits of crops. This must also be the goal of gene manipulation focused in metabolic and regulatory pathways of compound formation. The future appears to be bright concerning flavour in horticultural commodities, as we are likely to see multidisciplinary approaches, from genetic engineering to biochemical and metabolic characterisation, linked to sensory evaluations, which will result in flavour-rich and healthier fruits, with increased interest for both producers and consumers.

Conflicts of interest

The authors have no conflicts of interest.

Author details

Berta Gonçalves[1]*, Ivo Oliveira[1], Eunice Bacelar[1], Maria Cristina Morais[1], Alfredo Aires[1], Fernanda Cosme[2], Jorge Ventura-Cardoso[1], Rosário Anjos[1] and Teresa Pinto[1]

*Address all correspondence to: bertag@utad.pt

1 Department of Biology and Environment, School of Life Sciences and Environment, CITAB, Centre for the Research and Technology of Agro-Environmental and Biological Sciences, University of Trás-os-Montes e Alto Douro, Vila Real, Portugal

2 Department of Biology and Environment, School of Life Sciences and Environment, CQ-VR, Chemistry Research Centre, University of Trás-os-Montes e Alto Douro (UTAD), Vila Real, Portugal

References

[1] Klee HJ. Improving the flavor of fresh fruits: Genomics, biochemistry, and biotechnology. New Phytologist. 2010;**187**:44-56. DOI: 10.1111/j.1469-8137.2010.03281.x

[2] Wyllie SG. Flavour quality of fruit and vegetables: Are we on the brink of major advances? In: Brückner B, Wyllie SG, editors. Fruit and Vegetable Flavour. Recent Advances and Future Prospects. Woodhead Publishing Series in Food Science, Technology and Nutrition. New York, Washington DC, USA: Woodhead Publishing; 2008. pp. 3-10. ISBN: 9781845694296

[3] Jiang Y, Song J. Fruits and fruit flavor: Classification and biological characterization. In: Hui, Y., editor. Handbook of Fruit and Vegetable Flavors. New Jersey, USA: John Wiley & Sons, Inc. Publication. 2010. pp. 3-23. ISBN: 978-0-470-22721-3

[4] Beaulieu J, Baldwin E. Flavor and aroma of fresh-cut fruits and vegetables. In: Fresh-cut Fruit and Vegetables Science, Technology and Market. Boca Raton, FL, USA: CRC Press; 2002. pp. 391-425. ISBN: 9781420031874

[5] Baldwin E, Scott J, Einstein M, Malundo T, Carr B, Shewfelt R, Tandon K. Relationship between sensory and instrumental analysis for tomato flavor. Journal of the American Society of Horticultural Science. 1998;**123**:906-915. DOI: 98A0967495

[6] Brückner B. Consumer acceptance of fruit and vegetables: The role of flavour and other quality attributes. In: Brückner B, Wyllie SG, editors. Fruit and Vegetable Flavour. Recent Advances and Future Prospects Woodhead Publishing Series in Food Science, Technology and Nutrition. New York, Washington DC, USA: Woodhead Publishing; 2008. pp. 11-17. ISBN: 9781845694296

[7] Drawert F, Heimann W, Emberger R, Tressl R. Über die Biogenese von Aromastoffen bei Pflanzen und Frü chten. IV. Mitt Bildung der Aromamstoffe des Apfels im Verlauf des Wachstums und bei der Largerung. Zeitschrift für Lebensmittel-Untersuchung und Forschung. 1969;**140**:65-87. DOI: 10.1007/BF01387242

[8] Goff S, Klee H. Plant volatile compounds; sensory cues for health and nutritional value. Science. 2006;**311**:815-819. DOI: 10.1126/science.1112614

[9] Sanz C, Olias, Perez A. Aroma biochemistry of fruits and vegetables. In: Phyto-chemistry of Fruit and Vegetables. New York, NY, USA: Oxford University Press Inc.; 1997. pp. 125-155. ISBN: 0198577907

[10] Song J, Bangerth F. Fatty acids as precursors for aroma volatile biosynthesis in pre-climacteric and climacteric apple fruit. Postharvest Biology and Technology. 2003;**30**: 113-121. DOI: 10.1016/S0925-5214(03)00098-X

[11] Qin G, Tao S, Zhang H, Huang W, Wu J, Xu Y, Zhang S. Evolution of the aroma volatiles of pear fruits supplemented with fatty acid metabolic precursors. Molecules. 2014;**19**:20183-20196. DOI: 10.3390/molecules191220183

[12] Beaulieu J. Effect of cutting and storage on acetate and nonacetate esters in convenient, ready-to-eat fresh-cut melons and apples. Hortscience. 2006;**41**:65-73

[13] Dixon J, Hewett E. Factors affecting apple aroma/flavour volatile concentration: A review. New Zealand Journal of Crop and Horticultural Science. 2000;**28**:155-173. DOI: 10.1080/01140671.2000.9514136

[14] Fellman J, Miller T, Mattinson D, Mattheis J. Factors that influence biosynthesis of volatile flavor compounds in apple fruits. Hortscience. 2000;**35**:1026-1033

[15] Song J, Forney C. Flavour volatile production and regulation in fruit. Canadian Journal of Plant Science. 2008;**88**:537-550. DOI: 10.4141/CJPS07170

[16] Defilippi B, Dandekar A, Kader A. Relationship of ethylene biosynthesis to volatile production, related enzymes and precursor availability in apple peel and flesh tissues. Journal of Agricultural and Food Chemistry. 2005;**53**:3133-3141. DOI: 10.1021/jf047892x

[17] Pathange L, Mallikarjunan P, Marini R, O'Keefe S, Vaughan D. Non-destructive evaluation of apple maturity using an electronic nose system. Journal of Food Engineering. 2006;**77**:1018-1023. DOI: 10.1016/j.jfoodeng.2005.08.034

[18] Rowan D, Hunt M, Alspach P, Whitworth C, Oraguzie N. Heritability and genetic and phenotypic correlations of apple (*Malus × domestica*) fruit volatiles in a genetically diverse breeding population. Journal of Agricultural and Food Chemistry. 2009;**57**:7944-7952. DOI: 10.1021/jf901359r

[19] Mattheis J, Fellman J. Preharvest factors influencing flavor of fresh fruit and vegetables. Postharvest Biology and Technology. 1999;**15**:227-232. DOI: 10.1016/S0925-5214(98)00087-8

[20] Pino J, Febles Y. Odour-active compounds in banana fruit cv. Giant Cavendish. Food Chemistry. 2013;**141**:795-801. DOI: 10.1016/j.foodchem.2013.03.064

[21] Jordán M, Tandon K, Shaw P, Goodner K. Aromatic profile of aqueous banana essence and banana fruit by gas chromatography–mass spectrometry (GC-MS) and gas chromatography-olfactometry (GC-O). Journal of Agricultural and Food Chemistry. 2001;**49**:4813-4817. DOI: 10.1021/jf010471k

[22] Wendakoon S, Ueda Y, Imahori Y, Ishimaru M. Effect of short-term anaerobic conditions on the production of volatiles, activity of alcohol acetyltransferase and other quality traits of ripened bananas. Journal of the Science of Food and Agriculture. 2006;**86**:1475-1480. DOI: 10.1002/jsfa.2518

[23] Boudhrioua N, Giampaoli P, Bonazzi C. Changes in aromatic components of banana during ripening and air-drying. Lebensmittel-Wissenschaft & Technologie. 2003;**36**:633-642. DOI: 10.1016/S0023-6438(03)00083-5

[24] Jayanty S, Song J, Rubinstein N, Chong A, Beaudry R. Temporal relationship between ester biosynthesis and ripening events in bananas. Journal of the American Society of Horticultural Science. 2002;**127**:998-1005

[25] Aurore G, Ginies C, Ganou-Parfait B, Renard C, Fahrasmane L. Comparative study of free and glycoconjugated volatile compounds of three banana cultivars from French West Indies: Cavendish, Frayssinette and plantain. Food Chemistry. 2011;**129**:28-34. DOI: 10.1016/j.foodchem.2011.01.104

[26] Bugaud C, Alter P. Volatile and non-volatile compounds as odour and aroma predictors in dessert banana (*Musa* spp.). Postharvest Biology and Technology. 2016;**112**:14-23. DOI: 10.1016/j.postharvbio.2015.10.003

[27] Serradilla M, Hernández A, López-Corrales M, Ruiz-Moyano S, de Guía Córdoba M, Martín A. Composition of the cherry (*Prunus avium* L. and *Prunus cerasus* L.; Rosaceae).

Nutritional Composition of Fruit Cultivars. 2016;**1**:127-147. DOI: 10.1016/B978-0-12-408117-8.00006-4

[28] Girard B, Kopp T. Physicochemical characteristics of selected sweet cherry cultivars. Journal of Agricultural and Food Chemistry. 1998;**46**:471-476. DOI: 10.1021/jf970646j

[29] Wen Y, He F, Zhu B, Lan Y, Pan Q, Li C, Reeves M, Wang J. Free and glycosidically bound aroma compounds in cherry (*Prunus avium* L.). Food Chemistry. 2014;**152**:29-36. DOI: 10.1016/j.foodchem.2013.11.092

[30] Serradilla M, Martín A, Ruiz-Moyano S, Hernández A, López-Corrales M, Córdoba M. Physicochemical and sensorial characterization of four sweet cherry cultivars grown in Jerte Valley (Spain). Food Chemistry. 2012;**133**:1551-1559. DOI: 10.1016/j.foodchem.2012.02.048

[31] Perez-Cacho P, Rouseff R. Processing and storage effects on orange juice aroma: A review. Journal of Agricultural and Food Chemistry. 2008;**56**:9785-9796. DOI: 10.1021/jf801244j

[32] Cuevas F, Moreno-Rojas J, Ruiz-Moreno M. Assessing a traceability technique in fresh oranges (*Citrus sinensis* L. Osbeck) with an HS-SPME-GC-MS method. Towards a volatile characterisation of organic oranges. Food Chemistry. 2007;**221**:1930-1938. DOI: 10.1016/j.foodchem.2016.11.156

[33] Gonçalves B, Falco V, Moutinho-Pereira J, Bacelar E, Peixoto F, Correia C. Effects of elevated CO_2 on grapevine (*Vitis vinifera* L.): volatile composition, phenolic content, and in vitro antioxidant activity of red wine. Journal of Agricultural and Food Chemistry. 2008;**57**:265-273. DOI: 10.1021/jf8020199

[34] Liu J, Zhu X, Ullah N, Tao Y. Aroma glycosides in grapes and wine. Journal of Food Science. 2017;**82**:248-259. DOI: 10.1111/1750-3841.13598

[35] Dieguez S, Lois L, Gomez E, De Ia Pena M. Aromatic composition of the *Vitis vinifera* grape Albariño. Lebensmittel-Wissenschaft und-Technologie. 2003;**36**:585-590. DOI: 10.1016/S0023-6438(03)00064-1

[36] Aubert C, Chalot G. Chemical composition, bioactive compounds, and volatiles of six table grape varieties (*Vitis vinifera* L.). Food Chemistry. 2018;**240**:524-533. DOI: 10.1016/j.foodchem.2017.07.152

[37] Rosilllo L, Salinas M, Garijo J, Alonso G. Study of volatiles in grapes by dynamic head-space analysis application to the differentiation of some *Vitis vinifera* varieties. Journal of Chromatography A. 1999;**847**:155-159. DOI: 10.1016/S0021-9673(99)00036-9

[38] Fenoll J, Manso A, Hellin P, Ruiz L, Flores P. Changes in the aromatic composition of the *Vitis vinifera* grape Muscat Hamburg during ripening. Food Chemistry. 2009;**114**:420-428. DOI: 10.1016/j.foodchem.2008.09.060

[39] Kalua C, Boss P. Comparison of major volatile compounds from riesling and cabernet sauvignon grapes (*Vitis vinifera* L.) from fruit set to harvest. Australian Journal of Grape and Wine Research. 2010;**16**:337-348. DOI: 10.1111/j.1755-0238.2010.00096.x

[40] Kader A. Flavor quality of fruits and vegetables. Journal of the Science of Food and Agriculture. 2008;**88**:1863-1868. DOI: 10.1002/jsfa.3293

[41] Wyllie S, Leach D, Wang Y, Shewfelt R. Key aroma compounds in melons: Their development and cultivar dependence. In: Rouseff R, Leahy M, editors. Fruit Flavors: Biogenesis, Characterization and Authentication. Washington, DC: American Chemical Society; 1995. pp. 248-257. ISBN: 084123227X

[42] Berger R. Flavours and Fragrances-Chemistry, Bioprocessing and Sustainability. Berlin, Germany: Springer-Verlag; 2007. ISBN: 978-3-540-49339-6

[43] Villatoro C, Altisent R, Echeverria G, Graell J, Lopez M, Lara I. Changes in biosynthesis of aroma volatile compounds during on-tree maturation of "pink lady" apples. Postharvest Biology and Technology. 2008;**47**:286-295. DOI: 10.1016/j.postharvbio.2007.07.003

[44] Aragüez I, Valpuesta FV. Metabolic engineering of aroma components in fruits. Biotechnology Journal. 2013;**8**:1144-1158. DOI: 10.1002/biot.201300113

[45] Nogueira J, Fernandes P, Nascimento A. Composition of volatiles of banana cultivars from Madeira Island. Phytochemical Analysis. 2003;**14**:87-90. DOI: 10.1002/pca.691

[46] Feng S, Suh J, Gmitter Jr F, Wang Y. Differentiation between the flavors of sweet orange (*Citrus sinensis*) and mandarin (*Citrus reticulata*). Journal of Agricultural and Food Chemistry. 2017;**66**:203-211. DOI: 10.1021/acs.jafc.7b04968

[47] Moufida S, Marzouk B. Biochemical characterization of blood orange, sweet orange, lemon, bergamot and bitter orange. Phytochemistry. 2003;**62**:1283-1289. DOI: 10.1016/S0031-9422(02)00631-3

[48] USDA 2017. Available from: https://www.nutfruit.org/files/multimedia/1510229514_1497859419_Statistical_Yearbook_2016-2017.pdf

[49] Sathe S, Monaghan E, Kshiesagar H, Venkatachalam M. Chemical composition of edible nut seeds and its implications in human health. In: Alsalvar C, Shahidi F, editors. Tree Nuts Composition, Phytochemicals and Health Effects. Florida, USA: Taylor & Francis Group; 2008. pp. 12-29. ISBN 978-0-8493-3735-2

[50] Ros E. Health benefits of nut consumption. Nutrients. 2010;**2**:652-682. DOI: 10.3390/nu2070683

[51] Eaton S, Konner M. Paleolithic nutrition. A consideration of its nature and current implications. New England Journal of Medicine. 1985;**312**:283-289. DOI: 10.1056/NEJM-198501313120505

[52] Rehm C, Drewnowski A. Replacing American snacks with tree nuts increases consumption of key nutrients among US children and adults: Results of an NHANES modelling study. Nutrition Journal. 2017;**16**:17. DOI: 10.1186/s12937-017-0238-5

[53] Fischer S, Glei M. Potential health benefits of nuts. Ernährungs Umschau International. 2013;**60**:206-215. DOI: 10.4455/eu.2013.040

[54] Contador L, Robles B, Shinya P, Medel M, Pinto C, Reginato G, Infante R. Characterization of texture attributes of raw almond using a trained sensory panel. Fruits. 2015;**70**:231-237. DOI: 10.1051/fruits/2015018

[55] Kader AA. Ch 2: Impact of nut postharvest handling, de-shelling, drying and storage on quality. In: Harris LJ, editor. Improving the Safety and Quality of Nuts. Vol. 250. Woodhead Publishing Series in Food Sciences, Technology and Nutrition; 2008. pp. 22-34. Cambridge, UK: Woodhead Publishing; ISBN: 9780857097484

[56] Shakerardekani A, Karim R, Ghazali H, Chin N. Textural, rheological and sensory properties and oxidative stability of nut spreads – A review. International Journal of Molecular Sciences. 2013;**14**:4223-4241. DOI: 10.3390/ijms14024223

[57] Aceña L, Vera L, Guasch J, Busto O, Mestres M. Comparative study of two extraction techniques to obtain representative aroma extracts for being analysed by gas chromatography-olfactometry: Application to roasted pistachio aroma. Journal of Chromatography A. 2010;**1217**:7781-7787. DOI: 10.1016/j.chroma.2010.10.030

[58] Bolling B, McKay D, Blumberg J. The phytochemical composition and antioxidant actions of tree nuts. Asia Pacific Journal of Clinical Nutrition. 2010;**19**:117-123

[59] Saklar S, Katnas S, Ungan S. Determination of optimum hazelnut roasting conditions. International Journal of Food Science & Technology. 2001;**36**:271-281. DOI: 10.1046/j.1365-2621.2001.00457.x

[60] Alamprese C, Ratti S, Rossi M. Effects of roasting conditions on hazelnut characteristics in a two-step process. Journal of Food Engineering. 2009;**95**:272-279. DOI: 10.1016/j.jfoodeng.2009.05.001

[61] Chang S, Alasalvar C, Bolling B, Shahidi F. Nuts and their co-products: The impact of processing (roasting) on phenolics, bioavailability, and health benefits – A comprehensive review. Journal of Functional Foods. 2016;**26**:88-122. DOI: 10.1016/j.jff.2016.06.029

[62] Shahidi F, John J. Ch. 8: Oxidation and protection of nuts and nut oils. In: Decker EA, Elias RJ, McClements DJ, editors. Oxidation in Foods and Beverages and Antioxidant Applications. Woodhead Publishing Series in Food Science, Technology and Nutrition. Cambridge, UK: Woodhead Publishing; 2010. pp. 274-305. ISBN: 9780857090447

[63] Ghirardello D, Contessa C, Valentini N, Zeppa G, Rolle L, Gerbi V, Botta R. Effect of storage conditions on chemical and physical characteristics of hazelnut (*Corylus avellana* L.). Postharvest Biology and Technology. 2013;**81**:37-43. DOI: 10.1016/j.postharvbio.2013.02.014

[64] Xiao L, Lee J, Zhang G, Ebeler S, Niramani W, Seiber J, Mitchell A. HS-SPME GC/MS characterization of volatiles in raw and dry-roasted almonds (*Prunus dulcis*). Food Chemistry. 2014;**151**:31-39. DOI: 10.1016/j.foodchem.2013.11.052

[65] Miller A, Chambers E IV, Jenkins A, Lee J, Chambers D. Defining and characterizing the "nutty" attribute across food categories. Food Quality and Preference. 2013;**27**:1-7. DOI: 10.1016/j.foodqual.2012.04.017

[66] Clark R, Nursten H. Analysis of the sensory term "nutty" and a list of compounds claimed to be nutty. International Flavours and Food Additives. 1997;**5**:197-201

[67] Seymour GB. Banana. In: Seymour GB, Taylor JR, Tucker GA, editors. Biochemistry of Fruits Ripening. New York: Chapman & Hall; 1993. pp. 83-86. DOI: 10.1002/9781118593714.ch1

[68] Peynaud E, Ribereau-Gayon G. The grape. In: Hulme AC, editor. The Biochemistry of Fruits and their Products. Vol. 2. London: Academic Press; 1971. pp. 179-205. ISBN: 0123612020

[69] Augustyn O, Rapp A. Aroma components of *Vitis vinifera* L. cv. Chenin blanc grapes and their changes during maturation. South African Journal of Viticulture. 1982;**3**:47-51. DOI: 10.21548/3-2-2381

[70] Razungles A, Gunata Z, Pinatel S, Baumes R, Bayonove C. Etude quantitative de composes terpeniques, norisoprenoides et de leurs precurseurs dans diverses varietes de raisins. Sciences des Aliments. 1993;**13**:59-72

[71] Garcia E, Chacia J, Mart Ma J, Izquierdo P. Changes in volatile compounds during ripening in grapes of Airat, Macabeo and Chardonnay white varieties grown in La Mancha region (Spain). Food Science and Technology International. 2013;**9**:33-41

[72] Augustyn O, Rapp A, Van wyk C. Some volatile aroma components of *Vitis vinifera* L. cv. Sauvignon blane. South African Journal of Viticulture. 1982;**3**:53-60. DOI: 10.21548/3-2-2382

[73] Belancic A, Agosin E, Ibacache A, Bordeu E, Baumes R, Razungles A, Bayonove C. Influence of sun exposure on the aromatic composition of chilean Muscat grape cultivars Moscatel de Alejandria and Moscatel rosada. American Journal of Enology and Viticulture. 1997;**48**:181-186

[74] Razungles A, Baumes R, Dufour C, Sznaper C, Bayonove C. Effect of sun exposure on carotenoid and C13-norisoprenoid glycosides in Syrah berries (Vitis vinifera L.). Sciences des Aliments. 1998;**18**:361-373

[75] Ristic R, Downey M, Iland P, Bindon K, Francis I, Herderich M, Robinson S. Exclusion of sunlight from shiraz grapes alters wine colour, tannin and sensory properties. Australian Journal of Grape and Wine Research. 2007;**13**:53-65. DOI: 10.1111/j.1755-0238.2007.tb00235.x

[76] Scafidi P, Pisciotta A, Patti D, Tamborra P, Di Lorenzo R, Barbagallo M. Effect of artificial shading on the tannin accumulation and aromatic composition of the Grillo cultivar (*Vitis vinifera* L.). BMC Plant Biology. 2013;**13**:175-186. DOI: 10.1186/1471-2229-13-175

[77] Hjelmeland A, Ebeler S. Glycosidically bound volatile aroma compounds in grapes and wine: A review. American Journal of Enology and Viticulture. 2015;**66**:1-11. DOI: 10.5344/ajev.2014.14104

[78] Rosilllo L, Salinas MR, Garijo J, Alonso G. Study of volatiles in grapes by dynamichead-space analysis application to the differentiation of some Vitis vinifera varieties. Journal of Chromatography A. 1999;**847**:155-159. DOI: 10.1016/S0021-9673(99)00036-9

[79] Bellincontro A, Nicoletti I, Valentini M, Tomas A, De Santis D, Corradini D, Mencarelli F. Integration of nondestructive techniques with destructive analyses to study post-harvest water stress of winegrapes. American Journal of Enology and Viticulture. 2009;**60**:57-65

[80] Gunata Z, Bayonove C, Baumes R, Cordonnier R. The aroma of grapes. I. Extraction and determination of free and glycosidically bound fractions of some grape aroma components. Journal of Chromatography. 1985;**331**:83-90. DOI: 10.1016/0021-9673(85)80009-1

[81] Jordão A, Vilela A, Cosme F. From sugar of grape to alcohol of wine: Sensorial impact of alcohol in wine. Beverages. 2015;**1**:292-310. DOI: 10.3390/beverages1040292

[82] Peynaud E, Blouin J. In: Le gout du vin. Le grand livre de la degustation. 3rd ed. Paris: Dunod; 1996. ISBN: 9782100700806

[83] Peinado R, Moreno J, Bueno J, Moreno J, Mauricio J. Comparative study of aromatic compounds in two young white wines subjected to pre-fermentative cryomaceration. Food Chemistry. 2004;**84**:585-590. DOI: 10.1016/S0308-8146(03)00282-6

[84] Yuan F, Qian M. Development of C 13-norisoprenoids, carotenoids and other volatile compounds in *Vitis vinifera* L. Cv. Pinot noir grapes. Food Chemistry. 2016;**192**:633-641. DOI: 10.1016/j.foodchem.2015.07.050

[85] Capone S, Tufariello M, Siciliano P. Analytical characterisation of Negroamaro red wines by "Aroma wheels". Food Chemistry. 2013;**141**:2906-2915. DOI: 10.1016/j.food-chem.2013.05.105

[86] Guillaumie S. Genetic analysis of the biosynthesis of 2-methoxy-3-isobutylpyrazine, a major grape-derived aroma compound impacting wine quality. Plant Physiology. 2013;**162**:604-615. DOI: 10.1104/pp.113.218313

[87] Genovese A, Lamorte S, Gambuti A, Moio L. Aroma of Aglianico and Uva di Troia grapes by aromatic series. Food Research International. 2013;**53**:15-23. DOI: 10.1016/j.foodres.2013.03.051

[88] Kalua C, Boss P. Evolution of volatile compounds during the development of cabernet sauvignon grapes (*Vitis vinifera* L.). Journal of Agricultural and Food Chemistry. 2009;**57**:3818-3830. DOI: 10.1021/jf803471n

[89] Aharoni A, Lewinsohn E. Genetic engineering of fruit flavours. In: Hui YH, editor. A Handbook of Fruit and Vegetable Flavors. New Jersey, USA: John Wiley & Sons, Inc. Publication; 2010. pp. 101-114. ISBN: 978-0-470-22721-3

[90] Patil V, Chakrawar V, Narwadkar P, Shinde G. Grape. In: Salunkhe DK, Kadam SS, editors. Handbook of Fruit Science and Technology: Production, Composition, Storage and Processing. New York: Marcel Dekker; 1995. pp. 1-38. ISBN: 9780585157146

[91] Bolin H, Salunkhe D. Physicochemical and volatile flavor changes occurring in fruit juices during concentration and foam – mat drying. Journal of Food Science. 1971;**36**:665-667. DOI: 10.1111/j.1365-2621.1971.tb15156.x

[92] Olmo H. Grapes. In: MaCrae R, Robinson RK, Sadler MJ, editors. Encyclopedia of Food Science Food Technology and Nutrition. London: Academic Press; 1993. p. 2252. ISBN: 0122268504

[93] Fernandez E, Cortes S, Castro M, Gil M, Gil M. Distribution of free and glycosidically bound monoterpenes and norisoprenoids in the skin and pulp of Albarino grapes during 1998 maturation. In: Funel AL, editor. Oenologie 99. 6e Symposium International d'Oenolologie, Bordeaux. Paris: Tec & Doc; 1999. pp. 161-164

[94] Wu Y, Duan S, Zhao L, Gao Z, Luo M, Song S, Xu W, Zhang C, Ma C, Wang S. Aroma characterization based on aromatic series analysis in table grapes. Scientific Reports. 2016;**6**:31116. DOI: 10.1038/srep31116

[95] Kanellis AK, Roubelakis-Angelakis KA. Grape. In: Seymour G, Taylor J, Tucker G, editors. Biochemistry of Fruit Ripening. London: Chapman &Hall; 1993. pp. 189-234

[96] Ugliano M, Bartowsky E, McCarthy J, Moio L, Henschke P. Hydrolysis and transformation of grape glycosidically bound volatile compounds during fermentation with three Saccharomyces yeast strains. Journal of Agricultural and Food Chemistry. 2006;**54**:6322-6331. DOI: 10.1021/jf0607718

[97] Puckette M, Hammack J. Wine Folly, The Essential Guide to Wine. New York: Kindle; 2015. p. 240. ISBN: 9781592408993

[98] Sanz C, Pérez A. Plant metabolic pathways and flavor biosynthesis. In: Hui YH, editor. A Handbook of Fruit and Vegetable Flavors. John Wiley & Sons, Inc.; 2010. pp. 129-155. ISBN: 978-0-470-22721-3

[99] Giovannoni J. Molecular biology of fruit maturation and ripening. Annual Review of Plant Physiology and Plant Molecular Biology. 2001;**52**:725-749. DOI: 10.1146/annurev. arplant.52.1.725

[100] Amidei R, Castellari L, Missere D, Grandi M, Lugli S. Fruit sensory test of new sweet cherry cultivars. Acta Horticulturae. 2017;**1161**:593-598. DOI: 10.17660/ActaHortic. 2017.1161.94

[101] Belisle C, Adhikari K, Chavez D, Phan U. Development of a lexicon for flavor and texture of fresh peach cultivars. Journal of Sensory Studies. 2017;**32**:e12276-e12287. DOI: 10.1111/joss.12276

[102] Vítova E, Sůkalová K, Mahdalová M, Butorová L, Matějíček A, Kaplan J. Influence of volatile compounds on flavour of selected cultivars of gooseberry. Chemical Papers. 2017;**71**:1895-1908. DOI: 10.1007/s11696-017-0184-x

[103] Sortino G, Barone E, Tinella S, Gallotta A. Postharvest quality and sensory attributes of *Ficus carica* L. Acta Horticulturae. 2017;**1173**:353-358. DOI: 10.17660/ActaHortic. 2017.1173.61

[104] Taiti C, Marone E, Lanza M, Azzarello E, Masi E, Pandolfi C, Giordani E, Mancuso S. Nashi or Williams pear fruits? Use of volatile organic compounds, physicochemical parameters, and sensory evaluation to understand the consumer's preference. European Food Research and Technology. 2017;**243**:1917-1931. DOI: 10.1007/s00217-017-2898-y

[105] Forney C, Mattheis J, Baldwin E. Effects on flavor. In: Modified and Controlled Atmospheres for the Storage, Transportation, and Packaging of Horticultural Commodities. Boca Raton: CRC Press/Taylor & Francis; 2009. pp. 119-158. ISBN: 9781420069570

[106] Liu H, Cao X, Liu X, Xin R, Wang J, Gao J, Wu B, Gao L, Xu C, Zhang B, Grierson D, Chen K. UV-B irradiation differentially regulates terpene synthases and terpene content of peach. Plant, Cell & Environment. 2017;**40**:2261-2275. DOI: 10.1111/pce.13029

[107] Fallik E, Ilic Z. Pre-and postharvest treatments affecting flavor quality of fruits and vegetables. In: Mohammed WS, editor. Preharvest Modulation of Postharvest Fruit and Vegetable Quality. Cambridge, USA: Academic Press; 2018. pp. 139-168. ISBN: 9780128098073

[108] Pech J, Latché A, van der Rest B. Genes involved in the biosynthesis of aroma volatiles in fruit and vegetables and biotechnological applications. In: Bruckner B, Wyllie SG, Editors. Fruit and Vegetable Flavour: Recent Advances and Future Prospects. Cambridge: Woodhead; 2008. p. 254-271. ISBN: 9781845694296

[109] Zorrilla-Fontanesi Y, Rambla J, Cabeza A, Medina J, Sánchez-Sevilla J, Valpuesta V, Botella M, Granelli A, Amaya I. Genetic analysis of strawberry fruit aroma and identification of O-methyltransferase FaOMT as the locus controlling natural variation in mesifurane content. Plant Physiology. 2012;**159**:851-870. DOI: 10.1104/pp.111.188318

[110] Yu Y, Bai J, Chen C, Plotto A, Yu Q, Baldwin E, Gmitter F. Identification of QTLs controlling aroma volatiles using a 'Fortune'x 'Murcott'(*Citrus reticulata*) population. BMC Genomics 2017;**18**:646. DOI: 10.1186/s12864-017-4043-5

[111] Davidovich-Rikanati R, Azulay Y, Sitrit Y, Tadmor Y, Lewinsohn E. Tomato aroma: Biochemistry and biotechnology. In: Havkin Frenkel D, Belanger F, editors. Biotechnology in Flavor Production. Oxford, UK: Blackwell Publishing; 2008. pp. 118-129. ISBN: 9781118354056

[112] Park J, Lee Y, Chung W, Lee I, Choi J, Lee W, Ezura H, Lee S, Kim I. Modification of sugar composition in strawberry fruit by antisense suppression of an ADP-glucose pyrophosphorylase. Molecular Breeding. 2006;**17**:269-279. DOI: 10.1007/s11032-005-5682-9

[113] Rodríguez A, Peris J, Redondo A, Shimada T, Costell E, Carbonell I, Rojas C, Peña L. Impact of *D*-limonene synthase up-or down-regulation on sweet orange fruit and juice odor perception. Food Chemistry. 2017;**217**:139-150. DOI: 10.1016/j.foodchem. 2016.08.076

[114] Sánchez-Sevilla J, Cruz-Rus E, Valpuesta V, Botella M, Amaya I. Deciphering gamma-decalactone biosynthesis in strawberry fruit using a combination of genetic mapping, RNA-Seq and eQTL analyses. BMC Genomics. 2014;**15**:218. DOI: 10.1186/1471-2164-15-218

[115] Feussner I, Wasternack C. The lipoxygenase pathway. Annual Review of Plant Biology. 2002;**53**:275-297. DOI: 10.1146/annurev.arplant.53.100301.135248

[116] Jincy M, Djanaguiraman M, Jeyakumar P, Subramanian K, Jayasankar S, Paliyath G. Inhibition of phospholipase D enzyme activity through hexanal leads to delayed mango (*Mangifera indica* L.) fruit ripening through changes in oxidants and anti-oxidant enzymes activity. Scientia Horticulturae. 2017;**218**:316-325. DOI: 10.1016/j.scienta.2017.02.026

[117] Wang J, Zhou X, Zhou Q, Cheng S, Wei B, Ji S. Low temperature conditioning alleviates peel browning by modulating energy and lipid metabolisms of 'Nanguo'pears during shelf life after cold storage. Postharvest Biology and Technology. 2017;**131**:10-15. DOI: 10.1016/j.postharvbio.2017.05.001

[118] Sivankalyani V, Noa S, Feygenberg O, Hanita Z, Dalia M, Alkan N. Transcriptome dynamics in mango fruit peel reveals mechanisms of chilling stress. Frontiers in Plant Science. 2016;**7**:1-17. DOI: 10.3389/fpls.2016.01579

[119] Salas J, Sanchez C, Garcia-Gonzalez D, Aparicio R. Impact of the suppression of lipoxygenase and hydroperoxide lyase on the quality of the green odor in green leaves. Journal of Agricultural and Food Chemistry. 2005;**53**:1648-1655. DOI: 10.1021/jf040331l

[120] Singh R, Srivastava S, Chidley H, Nath P, Sane V. Overexpression of mango alcohol dehydrogenase (MiADH1) mimics hypoxia in transgenic tomato and alters fruit flavor components. Agri Gene. 2018;**7**:23-33. DOI: 10.1016/j.aggene.2017.10.003

[121] Speirs J, Lee E, Holt K, Yong-Duk K, Steele S, Loveys B, Schuch W. Genetic manipulation of alcohol ehydrogenase levels in ripening tomato fruit affects the balance of some flavor aldehydes and alcohols. Plant Physiology. 1998;**117**:1047-1058. DOI: 10.1104/pp.117.3.1047

[122] D'Auria J. Acyltransferases in plants: A good time to be BAHD. Current Opinion in Plant Biology. 2006;**9**:331-340. DOI: 10.1016/j.pbi.2006.03.016

[123] Souleyre E, Chagne D, Chen X, Tomes S, Turner R, Wang M, Maddumage R, Hunt M, Winz R, Wiedow C, Amiaux C, Gardiner S, Rowan D, Hamiaux C. The AAT1 locus is critical for the biosynthesis of esters contributing to ripe apple'flavour in 'Royal Gala'and 'Granny Smith'apples. The Plant Journal 2014;**78**:903-915. DOI: 10.1111/tpj.12518

[124] Yauk Y, Souleyre E, Matich A, Chen X, Wang M, Plunkett B, Dara A, Espley R, Tomes S, Chagné D, Atkinson R. Alcohol acyl transferase 1 links two distinct volatile pathways that produce esters and phenylpropenes in apple fruit. The Plant Journal. 2017;**91**:292-305. DOI: 10.1111/tpj.13564

[125] Gonda I, Bar E, Portnoy V, Lev S, Burger J, Schaffer A, Tadmor Y, Gepstein S, Giovannoni J, Katzir N, Lewinsohn E. Branched-chain and aromatic amino acid catabolism into aroma volatiles in *Cucumis melo* L. fruit. Journal of Experimental Botany. 2010;**61**:1111-1123. DOI: 10.1093/jxb/erp390

[126] Muhlemann J, Klempien A, Dudareva N. Floral volatiles: From biosynthesis to function. Plant Cell and Environment. 2014;**37**:1936-1949. DOI: 10.1111/pce.12314

[127] Abbas F, Ke Y, Yu R, Yue Y, Amanullah S, Jahangir M, Fan Y. Volatile terpenoids: Multiple functions, biosynthesis, modulation and manipulation by genetic engineering. Planta. 2017;**246**:803-816. DOI: 10.1007/s00425-017-2749-x

[128] Simkin A, Schwartz S, Auldridge M, Taylor M, Klee H. The tomato carotenoid cleavage dioxygenase 1 genes contribute to the formation of the flavor volatiles beta-ionone, pseudoionone, and geranylacetone. Plant Journal. 2004;**40**:882-892. DOI: 10.1111/j. 1365-313X.2004.02263.x

[129] Ilg A, Bruno M, Beyer P, Al-Babili S. Tomato carotenoid cleavage dioxygenases 1A and 1B: Relaxed double bond specificity leads to a plenitude of dialdehydes, mono-apocarotenoids and isoprenoid volatiles. FEBS Open Biology. 2014;**4**:584-593. DOI: 10.1016/j. fob.2014.06.005

[130] Lunkenbein S, Salentijn E, Coiner H, Boone M, Krens F, Schwab W. Up- and down-regulation of *Fragaria × ananassa* O-methyltransferase: Impacts on furanone and phenylpropanoid metabolism. Journal of Experimental Botany. 2006;**57**:2445-2453. DOI: 10.1093/jxb/erl008

[131] Dudareva N, Klempien A, Muhlemann J, Kaplan I. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. New Phytologist. 2013;**198**:16-32. DOI: 10.1111/nph.12145