Review Article

Research Advances on Biosynthesis, Regulation, and Biological Activities of Apocarotenoid Aroma in Horticultural Plants

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Received 1 March 2020; Accepted 3 April 2020; Published 4 May 2020

Guest Editor: Yunus Alparslan

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Apocarotenoids, which play important roles in the growth and development of horticultural plants, are produced by the action of carotenoid cleavage oxygenase (CCO) family members or nonenzymatic cleavage actions. Apocarotenoids are commonly found in leaves, flowers, and fruits of many horticultural plants and participate in the formation of pigments, flavors, hormones, and signaling compounds. Some of them are recognized as important aroma components of fruit and flower with aromatic odor, such as ββ-ionone, β-damascenone, and 6-methyl-5-hepten-2-one in tomato fruit, and have low odor thresholds with β-ionone having odor threshold of only 0.007 ppb. In this review, the main apocarotenoid aroma components in horticultural plants were listed, and factors influencing their production were discussed at first. Then, the biosynthetic pathway of apocarotenoid aromas was briefly introduced, and the CCDs gene family was highlighted, and the nonenzymatic production of apocarotenoid aromas was also mentioned. Next, chemical and molecular regulations of apocarotenoid aromas and their biological activities were summarized. Finally, further exploration aspects needed were suggested. We anticipate that this review can afford some crucial information for comprehensive application of apocarotenoid volatile compounds in horticultural plants.

1. Introduction

Aromas of horticultural plants are composed of unique volatile compounds. Although different horticultural plants may have many similar aromas, each plant still has its own inherent aromas, which is determined by the proportion of main components and the existence of unique compounds [1]. Aromatic compounds in horticultural plants include monoterpenes, sesquiterpenes, phenolic derivatives, lipid derivatives, and amino acid derivatives, as well as apocarotenoids [1–4]. Apocarotenoids, such as β-ionone, play important roles in the growth, development, and signaling control of horticultural plants, and they were long assumed to be the products of the oxidative cleavage of carotenoids by the action of carotenoid cleavage oxygenase family members (CCOs) [5, 6]. Apocarotenoids are commonly found in leaves, flowers, and fruits of many horticultural plants and participate in the formation of pigments, flavors, hormones, and signaling compounds [5, 7–12]. Some of them have aromatic odor and low odor thresholds, which are recognized as important aroma components of fruits, flowers, vegetables, and other horticultural products [13–15]. Moreover, several apocarotenoid aroma compounds are extremely powerful and also can act as beneficial substances for human health [16]. Compared with monoterpenes, sesquiterpenes, phenolic derivatives, lipid derivatives, and amino acid derivatives, the identification, biosynthesis, regulation, and biological activities of apocarotenoids were studied later, and it has attracted widespread attention with the deepening of CCO research studies.

2. Apocarotenoid Aroma Components and Influential Factors

Carotenoid degradation (or catabolism) involves a multitude of nonenzymatic and enzymatic processes in horticultural plants and products, which can lead to form various
apocarotenoid aromas or their precursors apocarotenoid glycosides (AGs) [17]. Although AGs can function as a valve regulating carotenoid steady-state levels in leaves contributing to carotenoid homeostasis, they can be used as a flavor reserve and as detoxificants and can be hydrolyzed during development or processing to generate apocarotenoid volatile aroma compounds [13, 18]. For example, AGs usually contribute to fruit and wine aroma in grapevines (Vitis vinifera) [18, 19]. The production of apocarotenoid aromas or their precursors AGs is influenced by lots of genetic and environmental factors, which result in rich and colorful aroma components in horticultural plants and products.

2.1. Apocarotenoid Aroma Components and Classification. Apocarotenoids, such as β-cyclocitrinal, β-ionone, geranial, geranyl acetone, theaspiron, α-damascenone, β-damascenone, and 6-methyl-5-hept-2-one (MHO), all contribute to the aromas of different flowers and fruits of horticultural plants and are highly valued by the flavor and fragrance industry [8, 20, 21]. Their structures reveal an isoprenoid-based origin and are also named norisoprenoids. These apocarotenoid aromas are characterized in different parts of different horticultural plants (Table 1) and contribute to good quality of many horticultural products.

The aroma components of apocarotenoids can be divided into cyclic and linear types (Figure 1). Cyclic apocarotenoids, including β-ionone, β-cyclocitrinal, theaspiron, α-damascenone, and β-damascenone, have very low odor thresholds (our ability to sense it), such as β-ionone whose odor threshold is only 0.007 ppb. Therefore, although they are usually not abundant in fruits or flowers, they are extremely important to the quality of fruits and flowers and have a strong impact on people’s perception of the aroma of horticultural products. Linear apocarotenoids, such as 6-methyl-5-hept-2-one (MHO), geranyl acetone, and geraniol, are also important aroma components in fruits and flowers, but their odor thresholds are much higher than those of cyclic apocarotenoids, such as MHO whose odor threshold is 2000 ppb [3, 49, 50].

2.2. Factors Influencing Apocarotenoid Aromas. Due to the complex nature of apocarotenoid aromas, many factors influence these aroma components including the genetic makeup, developmental stages, cultural practices, postharvest handlings, storage conditions, and so on. To date, we have limited information about how these factors affect apocarotenoid aroma compositions and their contents resulting to different horticultural product quality.

2.2.1. Genetics. Apocarotenoid aromas vary with different cultivars or different organs in horticultural plants. In mandarin hybrid fruit, seven carotenoid-derived volatiles were found in ‘Temple’: nerol, neral, geranial, neryl acetate, α-ionone, geranyl acetone, and β-ionone. In contrast, only two of these, neryl acetate and geranyl acetone, were found in ‘Murcott’ [51]. In the juice of four varieties of citrus (Powell Navel orange (Citrus sinensis L.), Clemenules mandarin (C. reticulata Blanco.), Fortune mandarin (C. reticulata Blanco.) and Chandler Pummelo (C. maxima Merr.), ‘Clemenules’ showed the highest levels of β-ionone [28]. In apple fruits, β-damascenone and estragole in ‘Zaofengtian,’ which were not detected in ‘Vista Bella’ or ‘Liaofu,’ could be unique components to ‘Zaofengtian’ [52]. The volatiles of 6-methyl-5-hept-2-one and β-ionone specifically existed in ‘Sui hong’ papaya fruit at harvest and during 15 d storage period at 25°C, but they were not detected in ‘Sui huang’ papaya fruit [39]. The content of β-ionone, dihydro-β-ionone, and total apocarotenoids in ‘Luntaixiaobaixiang’ (LT) and ‘Baixing’ (BX) were significantly higher than those in ‘Hongyuxing’ (HY), ‘Danxing’ (DX), and ‘Yechengheiyexietying’ (YC), especially the β-ionone. Similarly, the contents of apocarotenoids in peels were significantly higher than those in the pulps of cultivars tested [22]. Reidel et al. [27] analyzed the volatile compounds of different organs of Prunus cerasifera and P. cerasifera ‘Pissardi’ and found that stem, flowers, and ripe fruits of P. cerasifera ‘Pissardi’ and flowers, gynoecium-androecium-chalice, green fruits, and ripe fruits of P. cerasifera emit apocarotenoid aromas. In carrot roots, Yahya et al. [26] found that the volatile norisoprenoids farnesyl acetone, α-ionone, and β-ionone accumulated in ‘Nairobi,’ ‘Rothild,’ and ‘Purple Haze’ cultivars but not in ‘Yellowstone’ and ‘Creme de Lite’ in a pattern reflecting their carotenoid content.

2.2.2. Developmental Stages. In tomato fruit, biosynthesis of the apocarotenoids β-ionone, geranyl acetone, and 6-methyl-5-hept-2-one increased 10- to 20-fold as fruits reached a fully ripened stage [53]. Three apocarotenoids, including β-damascenone, β-ionone, and dihydro-β-ionone, were the major aroma compounds in apricot fruits, with β-ionone representing 90% of the three total apocarotenoid aroma volatiles. As the most abundant aroma compounds in apricot, the contents of these three apocarotenoids increased dramatically during fruit ripening [23]. The content of β-ionone increased from 155 to 1875 μg/kg FW in peels and from 30 to 1026 μg/kg FW in pulps of all cultivars tested [19]. During flower development in Boronia megastigma (Nees), β-ionone levels reached a maximum in opening flowers (stage 3) with the levels reducing to less than half of that in the open flowers (stage 4), and this contrasted with the large increases in β-carotene in open flowers [25].

2.2.3. Culture Practices. Variation in N supply had a greater impact on the volatile compositions of grape berries than did variation in P or K supply. Reducing N supply to ‘Pinot noir’ grapevines resulted in lower total (free + bound) β-damascenone and Cα compounds in berries in all three consecutive years, and low K supply resulted in lower total β-damascenone in two of three years. Nutrient supply had a relatively small impact on monoterpenes and other volatile compounds in ‘Pinot noir’ berries [54].

2.2.4. Postharvest Handling. Harvested flowers of Boronia megastigma incubated at between 12 and 25°C for up to 24 h showed increased levels of extract of up to 25% with
increases in some compounds including \( \beta \)-ionone [55]. Fresh-cut cantaloupe melon fruit treated with ascorbic acid and sodium azide had higher concentrations of \( \beta \)-ionone and geranyl acetone and retained these compounds better with storage time at both 4°C and 22°C [56].

### 2.2.5. Storage Conditions

Although \( \beta \)-ionone had the highest concentration in raspberry fruits of both 'Sevillana' and 'Maravilla' cultivar, opposing trends in the volatile compound compositions for the cultivars during storage at low temperature (0.5°C, 90–95% RH) were observed and caused important changes in the volatile compound profile of raspberry. Under low temperature storage, significant decreases in \( \mathrm{C}_{13} \) norisoprenoids (including 1,1,6-trimethyl-1,2-dihyronaphthalene, \( \beta \)-damascenone, dihydro-\( \beta \)-ionone, \( \alpha \)-ionone, and \( \beta \)-ionone) and increases in terpenes were observed in 'Sevillana.' These changes are most likely responsible for the aromatic differences between the cultivars because of the presence of terpenes in 'Sevillana' and \( \mathrm{C}_{13} \) norisoprenoids in 'Maravilla' [43]. Storage of cantaloupe melon fruit at 4°C caused a considerable synthesis of the apocarotenoid compounds \( \beta \)-ionone and geranyl acetone and decrease in concentration of esters over a period of 24 h [56].
Figure 1: Molecular structure of several apocarotenoid aromas in tomato fruit: (a) β-ionone; (b) β-damascenone; (c) 6-methyl-5-hepten-2-one; (d) geranyl acetone.

3. Biosynthetic Pathway and Related Genes

As a subclass of isoprenoids, the biosynthesis of carotenoids and apocarotenoids is mainly originated from lycopene which is produced from two universal isoprenoid precursors, isopentenyl pyrophosphate (IPP) and dimethylallyl pyrophosphate (DMAPP). These precursors are produced by the 1-deoxy-D-xylulose-phosphate (DXP) pathway in plastid and the mevalonate (MVA) pathway in cytoplasm (Figure 2) [57].

The key enzymes to form apocarotenoids in horticultural plants are CCOs, which can decompose the carotenoid polyene chain-specific double bonds [5, 6, 16, 61]. CCOs include carotenoid cleavage dioxygenases (CCDs) and nectaris-epoxide-carotenoid dioxygenase (NCEDs). CCOs in Arabidopsis thaliana contain nine homologous genes, AtCCD1, AtCCD4, AtCCD7, AtCCD8, AtNCED2, AtNCED3, AtNCED5, AtNCED6, and AtNCED9, which are located on different chromosomes [62]. There are five groups by clustering with CCOs amino acid sequences of different plants, namely, CCD1, CCD4, CCD7, CCD8, and NECDs [5], while Chen et al. [6] divided 90 CCO genes from 12 species into six groups (i.e., CCD1, CCD4, CCD7, CCD8, NCED, and CCD-like) and found that some CCD8 genes from Sorghum bicolor, Zea mays, and Oryza sativa were not grouped with the CCD8 genes from the other nine species, but clustered in the CCD-like group.

Previous studies have shown that the CCOs related to the formation of apocarotenoid aroma components, which are important for fruit and flower quality, are mainly CCD1 and CCD4 branches [58]. They use different carotenoids as substrates and have different specificities and cleavage sites, thus contributing to the formation of the diversity of apocarotenoid aroma components in horticultural plants (Figure 2) [40, 57–60]. CCD7 and CCD8 branches are mainly involved in the biosynthesis of an important hormone, strigolactone [10, 63, 64], while NECD branch is the key rate-limiting step in ABA biosynthesis [65–67].

AtCCD1 can catalyze the cleavage of linear and cyclic carotenoids at the 9-10 and the 9′-10′ positions, and 1-2 ionone molecules or different oxy-functionalized derivatives were produced based on the different properties of carotenoid substrates. In vitro, AtCCD1 can use phytoene, zeaxanthin, and neoxanthin as reaction substrates [68, 69]. In addition, studies also have shown that CCD1 can cleave lycopene double bonds at 5, 6 (5′, 6′) and 7, 8 (7′, 8′) positions [70, 71]. At present, the homologous genes of CCD1 have been identified in carambola [72], saffron [73], petunia [41], tomato [47], grape [74], nectarine [75], melon [76], citrus [77], strawberry [78], rose [79], osmanthus [80], and other horticultural plants. In tomato fruits, all apocarotenoids could be produced directly from carotenoid precursors through the action of LeCCD1A and LeCCD1B except for β-damascenone. However, some studies suggest that C40 carotenoids in plastids are firstly decomposed into C13 and C27 apocarotenoids by CCD7 or CCD4, and then the C27 apocarotenoids transported to the cytoplasm were further cleaved under the action of CCD1 to produce aroma components [81–83]. Therefore, the differential expression of CCD1 did not affect the composition and content of carotenoids in fruits of different citrus varieties, but might affect the apocarotenoid aroma compositions of fruits [84].

Compared with CCD1, the research of CCD4 is mainly focused on the relationship between CCD4 and carotenoid contents (i.e., fruit or flower color), and few studies involved apocarotenoid content. Brandi et al. [40] found that PpCCD4 played an important role in peach flesh color and aroma formation. The carotenoid content of white flesh mutant was lower than that of yellow flesh peach, while the apocarotenoid aroma concentration was higher than that of yellow flesh peach. In citrus fruits, CCD4b1 is responsible for the biosynthesis of C30 apocarotenoids β-citraurin (3-hydroxy-β,apo-8′-carotenal) which are key pigments in fruit coloration [85]. AtCCD4 plays an important role in dark-induced decomposition of carotenoids [86]. RNA interference (RNAi) studies have shown that CmCCD4a contributes to the formation of chrysanthemum white petals by decomposing carotenoids [87]. Two CmCCD4a RNAi vectors were introduced into white chrysanthemum (‘Jimba’) by Agrobacterium tumefaciens, which could effectively inhibit the expression of CmCCD4a in petals and result in yellow petals [88]. Like cultivated chrysanthemum, wild chrysanthemum with white ray petals contains CmCCD4a homologous gene, while wild chrysanthemum...
with yellow ray petals does not contain CmCCD4a homologous gene [89].

The expression levels of MdCCD4, CmCCD4a, RdCCD4, OqCCD4, and AtCCD4 were all detected in their respective flowers. The expression levels of RdCCD4 in rose flowers were 42, 150, and 240 times higher than those in leaves, stems, and roots, respectively. A small amount of carotenoids accumulated in perianth slices of pink and white lily cultivars was not regulated by transcription level of synthetic related genes, which may be related to the reduction of carotenoid content by CCD4 cleavage [90].

Besides catabolism by related CCD gene family members (CCDs), the unstable carotenoid can also generate apocarotenoid aromas through nonenzymatic cleavage at different sites by reactive oxygen species produced in oxidizing environments such as high (or low) temperature, strong light, metal catalysts, and water stress. All of the in-chain double bonds within carotenoid molecular can be attacked, leading

Figure 2: Biosynthetic pathway of apocarotenoid aroma in horticultural plants. GAP, glyceraldehyde-3-phosphate; DXS, 1-deoxy-D-xylulose-5-phosphate synthase; DXR, 1-deoxy-D-xylulose-5-phosphate reductase; MEP, 2-C-methyl-D-erythritol-4-phosphate; CMK, 2-phospho-4-(cytidine 5′-diphospho)-2-C-methyl-D-erythritol kinase; CDP-ME, 4-(cytidine 5′-diphospho)-2-C-methyl-D-erythritol; MCS, 2-C-methyl-D-erythritol-2,4-cyclodiphosphate synthase; CDP-MEP, 2-phospho-4-(cytidine 5′-diphospho)-2-C-methyl-D-erythritol; HDS, 4-hydroxy-3-methyl-2-E-butenyl-4-disphosphate; MECCP, 2-C-methyl-D-erythritol-2,4-cyclodiphosphate synthase; HDR, 4-hydroxy-3-methyl-2-E-butenyl-4-disphosphate reductase; HMBPP, 4-hydroxy-3-methyl-2-E-butenyl-4-disphosphate; DMAPP, dimethylallyl pyrophosphate; IPP, isopentenyl pyrophosphate; IPPI, isopentenyl pyrophosphate isomerase; GPPS, geranyl pyrophosphate synthase; AACT, aceto acetyl-CoA thiolase; HMGS, 3-hydroxy-3-methylglutaryl-CoA synthase; HMG-CoA, 3-hydroxy-3-methyl glutaryl-CoA; HMG-CoA reductase; MVA, mevalonate; MK, mevalonate kinase; MVAP, mevalonate phosphate; PMK, 5-phospho mevalonate kinase; MVAPP, mevalonolactone pyrophosphate; GPP, geranyl pyrophosphate synthase; IPP, farnesyl pyrophosphate; GGPPS, geranylgeranyl pyrophosphate synthase; GGPP, geranylgeranyl pyrophosphate; PDS, phytocene desaturase; ZDS, ω-carotene desaturase; Z-ISO, CRTISO, ω-carotene isomerase; LCY-B, lycopene-β-cyclase; CHY-B, carotene-β-hydroxylase; CHY-E, carotene-ε-hydroxylase; ZEP, zeaxanthin epoxidase; VDE, violaxanthin de-epoxidase; NXS, neoxanthin synthase; NCED, 9-cis-epoxycarotenoid dioxygenase; CCD, carotenoid cleavage dioxygenase [36, 57–60].
to produce different apocarotenoid components, and the number of apocarotenoid species formed enzymatically exceeds the number of those that are enzymatically formed [91].

4. Chemical and Molecular Regulation

Apocarotenoid aromas occur in all sorts of horticultural plants and products with different components and concentrations. On account of their beneficial effects, the predominant components can be regulated through chemical treatment, gene overexpression or silencing, and transcription factor expression.

4.1. Enzyme Inhibitor. An inhibitor of CCD enzymes, Abamine SG, decreased the levels of both isoprenoid and nonisoprenoid volatiles such as 3-hydroxy-β-damascenone and 3-hydroxy-5,6-epoxy-β-ionone in ‘Redhaven Bianca’ peach fruit (white-fleshed bud sport mutant of yellow-fleshed ‘Redhaven’) [40].

4.2. Overexpression of CCD Gene. The additional integration of the carotenoid cleavage dioxygenase gene from the plant Petunia hybrida (PhCCD1) led to the production of low amounts of β-ionone (0.073 ± 0.01 mg/g DCW) and changed the color of the strain of Saccharomyces cerevisiae from orange to yellow [92]. Carotenoid-accumulating E. coli strains were transformed either with pTHIO-StCCD4 or the void pTHIO-plasmid which served as negative control; StCCD4 catalyzed the cleavage of all-trans-β-carotene at the C9′–C10′ double bond, leading to β-ionone and all-trans-β-apo-10′-carotenal, both in vivo and in vitro [93]. Overexpression OfCCD4 from Osmanthus fragrans in E. coli increased CCD4 activity and the concentration of β-ionone [94].

4.3. Silencing of CCD Gene. In tomato fruit, silencing LeCCD1A and LeCCD1B could result in a significant decrease of β-ionone content in mature fruit [47]. Successful knockout of InCCD4 using the CRISPR/Cas9 system in the white-flowered cultivar Ipomoea nil cv. AK77 caused the white petals to turn pale yellow, and the total amount of carotenoids in the petals of ccd4 plants was increased 20-fold relative to nontransgenic plants [95], but the change of apocarotenoid aroma components deserved further study.

4.4. Transcriptional Regulation. OfWRKY3 in Osmanthus fragrans, which can bind to the W-box palindrome motif present in the OfCCD4 promoter, is a positive regulator of the OfCCD4 gene and might partly account for the biosynthesis of β-ionone in sweet osmanthus [96]. The expression pattern of OfERF61 closely resembled that of OfCCD4, and overexpression of OfERF61 upregulates the transcript levels of NbCCD4 in tobacco leaves, suggesting that ERF61 may participate in CCD4 regulation and β-ionone production in sweet osmanthus [97].

5. Biological Activities

As secondary metabolites, apocarotenoid aromas not only affect plant growth, development, and signaling control but also have numerous biological activities, including free radical scavenging, sunburn preventive, chemopreventive, antimicrobial, insect repellent, and attractive effects. Based on in vitro and in vivo experiments, some apocarotenoid aromas will finally be used to treat human ailments and protect the environment.

5.1. Free Radical Scavenging Activity. Both as fragrant acyclic terpenoids, C13 apocarotenoid geranyl acetone was significantly more effective as an ABTS (2,2′-amino-di-2-ethylbenzothiazoline sulphonic acid-6-ammonium salt) and DPPH (1,1-diphenyl-2-picrylhydrazyl) radical scavenger than monoterpene geraniol. According to the computational results, the presence of allylic H-atom (at the position 3′C) close to the -OH group seemed to be essential for the observed antiradical activity of geraniol, while the scavenging ability of geranyl acetone was associated with the presence of both allylic hydrogen and alkylic hydrogen in the close vicinity of the carbonyl functionality [98].

5.2. Sunburn Prevention Effect. To establish sunburn preventive activity, female Skh-1 mice were given oral β-damascenone followed by irradiation with UVR from fluorescent ‘sunlamps.’ The findings demonstrated that β-damascenone protected against sunburn by activating a seaceous gland-based pathway that fortified and thickened the cornified envelope plus sebum layer in a way that previously has been observed to occur only in keratinocytes [99].

5.3. Chemopreventive Effect. β-Ionone demonstrates potent anticancer activity both in vitro and in vivo [100]. β-Ionone showed promising chemopreventive effects during promotion of hepatocarcinogenesis by acting through distinct mechanism of actions: β-ionone may inhibit cell proliferation and modulate 3-hydroxy-3-methylglutaryl coenzyme A (HMGCoA) reductase, and geraniol can induce apoptosis and inhibit RhoA activation [101]. β-Ionone also effectively ameliorated the lung carcinogenesis, which is attributed to the antiproliferative and antioxidative potential through free radical scavenging property [102]. β-Ionone has potent ability to arrest cell cycle of SGC-7901 cells and decrease proliferation through a MAPK pathway by transcriptional downregulation of cell cycle proteins [103]. β-Ionone also can suppress DMBA-initiated mammary cancer in rats [100].

5.4. Antimicrobial Activity. Essential oils from lots of horticultural plants contain apocarotenoid volatiles, such as β-damascenone and β-ionone from underground parts (root and rhizome) of Gentiana asclepiadea [104], 2-hydroxy-β-ionone from Sisymbrium officinale [105], 6-methyl-5-hepten-2-one from Anthemis tenuisecta [106], and cis-
geranyl acetone from sterile stems of Equisetum arvense [107]. The disk diffusion method or minimum inhibitory concentration procedure was used for the evaluation of the antimicrobial activity of essential oil, and results demonstrated that all the essential oils exhibit great potential antimicrobial activity against all tested strains [104–107].

5.5. Insect Repellent. In plants, the oxidative cleavage of carotenoid substrates produces volatile apocarotenoids, including α-ionone, β-ionone, and dihydro-β-ionone, compounds that are important in herbivore-plant communication. β-Ionone has a strong repellent effect toward both the flea beetle and the spider mite and significant oviposition deterrence to whiteflies. In contrast, dihydro-β-ionone had attractant properties, especially to the crucifer flea beetle, while α-ionone did not show any significant activity [108]. AtCCD1 overexpression and induced β-ionone emission might find application in the control of pests for Brassica crops grown in greenhouse operations. Potentially, β-ionone could also be used on crops grown in open-air ecosystems if this allomone is released in sufficient quantities to discourage herbivore foragers [109].

5.6. Insect Attractant. β-Ionone can be used as baits to attract insects. Males of Euglossa mandibularis were consistently captured in scent traps baited with β-ionone in areas of Mixed Ombrophilous Forests or transition between this latter physiognomy and Montane Semideciduous Forest at Parque Nacional do Iguacu, Paraná state, Brazil [110]. Geranyl acetone may be a relatively common pheromone structure for species in the subfamily Spondylidinae. Asemum caseyi are attracted to geranyl acetone alone, while Asemum nitidum are attracted to blends of fuscumol and geranyl acetone [111]. By using this kind of aroma as pheromone to attract insects, less pesticide will be used and environmentally conscious production will be achieved.

6. Perspective

At present, many studies of apocarotenoid aromas were carried out on model plants or microorganisms. An optimized HS-SPME-GC/MS method for volatile apocarotenoid detection and quantification was validated with Arabidopsis in vitro and in planta [11]. This method can enable us to find more apocarotenoid aromas in horticultural plants and products. The strategy of Escherichia coli-based modular pathway optimization and enzyme engineering to over-produce natural α-ionone and β-ionone was developed, demonstrating the great potential of using microbes or horticultural plants in production of natural flavors and fragrances [57, 86]. Although many studies proved that essential oils containing apocarotenoid aromas from horticultural plants possess antimicrobial activity, little is known about the effect of individual apocarotenoid aromas in different essential oils [104–107].

Apocarotenoid aromas are widely present in different parts (fruits, flowers, leaves, stems, and roots) of horticultural plants and possess different biological activities. The research on apocarotenoid aromas in horticultural plants is incomplete and unsystematic. The following aspects need further exploration: (1) characterization of more components of apocarotenoid aromas; (2) separation and purification of individual apocarotenoid aroma; (3) biological activities of individual apocarotenoid aroma to plants, animals, and humans; (4) dynamic changes of apocarotenoid aromas during growth; (5) relationship between concentration of apocarotenoid aromas and contents of carotenoids in fruits or flowers; (6) development of new products of apocarotenoid aromas; (7) production of fruits and flowers with elevated levels of apocarotenoid aromas; and (8) production of natural flavors and fragrances by transgenic engineering. With the development of science and technology, more research studies will be carried out to demonstrate the function of apocarotenoid aromas, and these volatile compounds will be exploited not only for plant protection but also for human and animal health.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

This research was funded by the National Natural Science Foundation of China (grant no. 31372042) and Excellent Youth Backbone Teachers of Yangzhou University (2014).

References

[1] M. El Hadi, F.-J. Zhang, F.-F. Wu, C.-H. Zhou, and J. Tao, “Advances in fruit aroma volatile research,” Molecules, vol. 18, no. 7, pp. 8200–8229, 2013.
[2] C. I. Cazzonelli and B. J. Pogson, “Source to sink: regulation of carotenoid biosynthesis in plants,” Trends in Plant Science, vol. 15, no. 5, pp. 266–274, 2010.
[3] H. J. Klee, “Improving the flavor of fresh fruits: genomics, biochemistry, and biotechnology,” New Phytologist, vol. 187, no. 1, pp. 44–56, 2010.
[4] D. A. Nagegowda, “Plant volatile terpenoid metabolism: biosynthetic genes, transcriptional regulation and subcellular compartmentation,” FEBS Letters, vol. 584, no. 14, pp. 2965–2973, 2010.
[5] M. H. Walter, D. S. Floss, and D. Strack, “Apocarotenoids: hormones, mycorrhizal metabolites and aroma volatiles,” Planta, vol. 232, no. 1, pp. 1–17, 2010.
[6] H. Chen, X. Zhao, H. Shao et al., “Genome-wide analysis of carotenoid cleavage oxygenase genes and their responses to various phytohormones and abiotic stresses in apple (Malus domestica),” Plant Physiology and Biochemistry, vol. 123, pp. 81–93, 2018.
[7] S. H. Schwartz, X. Qin, and M. C. Loewen, “The biochemical characterization of two carotenoid cleavage enzymes from Arabidopsis indicates that a carotenoid-derived compound inhibits lateral branching,” Journal of Biological Chemistry, vol. 279, no. 45, pp. 46940–46945, 2004.
[8] M. E. Auldridge, D. R. McCarty, and H. J. Klee, “Plant carotenoid cleavage oxygenases and their apocarotenoid products,” Current Opinion in Plant Biology, vol. 9, no. 3, pp. 315–321, 2006.
[9] X. Hou, J. Rivers, P. León, R. P. McQuinn, and B. J. Pogson, "Synthesis and function of apocarotenoid signals in plants," *Trends in Plant Science*, vol. 21, no. 9, pp. 792–803, 2016.

[10] R. Batra, P. Agrawal, S. Tyagi et al., "A study of CCD8 genes/proteins in seven monocots and eight dicots," *PLoS ONE*, vol. 14, Article ID e0213531, 21 pages, 2019.

[11] J. Y. Rivers, T. T. Truong, B. J. Pogson, and R. P. McQuinn, "Volatile apocarotenoid discovery and quantification in Arabidopsis thaliana: optimized sensitive analysis via HS-SPE-GC/MS," *Metabolomics*, vol. 15, Article ID 79, 13 pages, 2019.

[12] J. Y. Wang, I. Haider, M. Jamil et al., "The apocarotenoid metabolite zaxinone regulates growth and strigolactone biosynthesis in rice," *Nature Communication*, vol. 10, Article ID 810, 9 pages, 2019.

[13] P. Winterhalter and P. Schreier, "C13-Norisoprenoid glycosides in plant tissues: an overview on their occurrence, composition and role as flavour precursors," *Flavour and Fragrance Journal*, vol. 9, no. 6, pp. 281–287, 1994.

[14] P. Winterhalter and R. Rouseff, *Carotenoid-Derived Aroma Compounds*, American Chemical Society, Washington, DC, USA, 2002.

[15] E. Lewinsohn, Y. Strit, E. Bar et al., "Not just colors-carotenoid degradation as a link between pigmentation and aroma in tomato and watermelon fruit," *Trends in Food Science & Technology*, vol. 16, no. 9, pp. 407–415, 2005.

[16] A. Ningrum, "Role of carotenoid cleavage dioxygenases (CCD3) for the aroma formation in plants," *Agro Food Industry Hi-Tech*, vol. 27, no. 6SI, pp. 22–26, 2016.

[17] K. Lätari, F. Wüst, M. Hübner et al., "Tissue-specific apocarotenoid glycosylation contributes to carotenoid homeostasis in Arabidopsis leaves," *Plant Physiology*, vol. 168, no. 4, pp. 1550–1562, 2015.

[18] A. K. Hjelmeland and S. E. Ebeler, "Glycosidically bound volatile aroma compounds in grapes and wine: a review," *American Journal of Enology & Viticulture*, vol. 66, no. 1, p. 11, 2015.

[19] P. Winterhalter and P. Schreier, "The generation of norisoprenoid volatiles in starfruit (Averrhoa carambola L.): a review," *Food Reviews International*, vol. 11, no. 2, pp. 237–254, 1995.

[20] V. F. Cataldo, J. López, M. Cárcamo, and E. Agosin, "Chemical vs. biotechnological synthesis of C13-apocarotenoids: current methods, applications and perspectives," *Applied Microbiology and Biotechnology*, vol. 100, no. 130, pp. 5703–5718, 2016.

[21] S. Lakshminarayan, "Role of carotenoid cleavage dioxygenases in volatile emissions and insect resistance in arabi- dopsis," Master thesis, The University of Western Ontario, London, UK, 2013.

[22] W. Xi, H. Zheng, Q. Zhang, and W. Li, "Profiling taste and aroma compound metabolism during apricot fruit development and ripening," *International Journal of Molecular Sciences*, vol. 17, no. 7, p. 998, 2016.

[23] Q. Zhang, C. Feng, W. Li, Z. Qu, M. Zeng, and W. Xi, "Transcriptional regulatory networks controlling taste and aroma quality of apricot (Prunus armeniaca L.) fruit during ripening," *BMC Genomics*, vol. 20, Article ID 45, 15 pages, 2019.

[24] X. Du, C. E. Finn, and M. C. Qian, "Volatile composition and odour-activity value of thornless "Black Diamond" and "Marion" blackberries," *Food Chemistry*, vol. 119, no. 3, pp. 1127–1134, 2010.

[25] C. M. Cooper, N. W. Davies, and R. C. Menary, "Changes in some carotenoids and apocarotenoids during flower development in Boronia megastigma (Nees)," *Journal of Agricultural and Food Chemistry*, vol. 57, no. 4, pp. 1513–1520, 2009.

[26] M. Yahya, E. Bar, N. K. Dubey et al., "Formation of nor-isoprenoid flavor compounds in carrot (Daucus carota L.) roots: characterization of a cyclic-specific carotenoid cleavage dioxygenase 1 gene," *Journal of Agricultural and Food Chemistry*, vol. 61, no. 50, pp. 2244–2252, 2013.

[27] R. V. B. Reidel, P. L. Cioni, and L. Pistelli, "Volatile emission of different plant parts and fruit development from Italian cherry plums (Prunus cerasifera and P. cerasifera "Pissardii")," *Biochemical Systematics and Ecology*, vol. 75, pp. 10–17, 2017.

[28] M. C. González-Mas, J. L. Rambla, M. C. Alamar et al., "Comparative analysis of the volatile fraction of fruit juice from different citrus species," *PLoS One*, vol. 6, no. 7, Article ID e22016, 2011.

[29] S. Sdriri, J. L. Rambla, C. Besada, A. Granell, and A. Salvador, "Changes in the volatile profile of citrus fruit submitted to postharvest degreening treatment," *Postharvest Biology and Technology*, vol. 133, pp. 48–56, 2017.

[30] M. N. A. Khalil, M. I. Fekry, and M. A. Farag, "Metabolome based volatiles profiling in 13 date palm fruit varieties from Egypt via SPME GC-MS and chemometrics," *Food Chemistry*, vol. 217, pp. 171–181, 2017.

[31] R. V. B. Reidel, B. Mela, P. L. Cioni et al., "Aroma profile of Rubus ulmifolius flowers and fruits during different ontogenetic phases," *Chemistry & Biodiversity*, vol. 13, no. 12, pp. 1776–1784, 2016.

[32] P. Grupi, A. Coletta, and D. Antonacci, "Analysis of carotenoids in grapes to predict norisoprenoid varietal aroma potential of wine," *Journal of Biotechnology*, vol. 150, p. 321, 2010.

[33] J. Langen, P. Wegmann-Herr, and H.-G. Schmarr, "Qualitative determination of a-ionone, β-ionone, and β-damascenone and enantiodifferentiation of a-ionone in wine for authenticity control using multidimensional gas chromatography with tandem mass spectrometric detection," *Analytical and Bioanalytical Chemistry*, vol. 408, no. 23, pp. 6483–6496, 2016.

[34] J.-X. Shen, M. M. Rana, G.-F. Liu, T.-J. Ling, M. Y. Gruber, and S. Wei, "Differential contribution of jasmine floral volatiles to the aroma of scented green tea," *J. Food Quality*, vol. 2017, Article ID 5849501, 10 pages, 2017.

[35] M. Y. Wang, E. MacRae, M. Wohlers, and K. Marsh, "Changes in volatile production and sensory quality of kiwifruit during fruit maturation in Actinidia delicosa ‘Hayward’ and ‘A. chinensis ‘Hort16A’’,” *Postharvest Biology and Technology*, vol. 59, no. 1, pp. 16–24, 2011.

[36] A. C. Lindhorst and M. Steinhaus, "Aroma-active compounds in the fruit of the hardy kiwi (Actinidia arguta) cultivars Ananasnaya, Bojnice, and Dumbarton Oaks: differences to common kiwifruit (Actinidia delicosa ‘Hayward’)," *European Food Research and Technology*, vol. 242, no. 6, pp. 967–975, 2016.

[37] J. A. Pino and J. Mesa, "Contribution of volatile compounds to mango (Mangifera indica L.) aroma," *Flavour and Fragrance Journal*, vol. 21, no. 2, pp. 207–203, 2006.

[38] A. Bonneau, R. Boulanger, M. Lebrun, I. Maraval, and Z. Gunata, "Aroma compounds in fresh and dried mango fruit (Mangifera indica L. cv. Kent): impact of drying on volatile composition," *International Journal of Food Science & Technology*, vol. 51, no. 3, pp. 789–800, 2016.

[39] G. Jing, T. Li, H. Qu et al., "Carotenoids and volatile profiles of yellow- and red-fleshed papaya fruit in relation to the
expression of carotenoid cleavage dioxygenase genes,” 
*Post-harvest Biology and Technology*, vol. 109, pp. 114–119, 2015.

[40] F. Brandi, E. Bar, F. Mourguès et al., “Study of “Redhaven” peach and its white-fleshed mutant suggests a key role of CDD4 carotenoid dioxygenase in carotenoid and nor-isoprenoid volatile metabolism,” 
*BMC Plant Biology*, vol. 11, no. 1, p. 24, 2011.

[41] A. Simkin, B. A. Underwood, M. Auldridge, M. G. Taylor, and J. A. D. Zeevaart et al., “Specific oxidative cleavage of carotenoids by VP14 of maize,” 
*FEBS Letters*, vol. 588, no. 9, pp. 1802–1807, 2014.

[42] T. Vogel, B. C. Tan, D. A. Gage et al., “The Malus carotenoid cleavage dioxygenase 7 is involved in stress response and regulated by basic pentacysteine 1,” 
*Scientia Horticulturae*, vol. 192, pp. 264–270, 2015.

[43] S. H. Schwartz, B. C. Tan, D. A. Gage et al., “The Malus carotenoid cleavage dioxygenase 7 is involved in stress response and regulated by basic pentacysteine 1,” 
*Scientia Horticulturae*, vol. 192, pp. 264–270, 2015.

[44] P. Leng, B. Yuan, and Y. Guo, “The role of abscisic acid in fruit ripening and responses to abiotic stress,” 
*Journal of Experimental Botany*, vol. 65, no. 16, pp. 4577–4588, 2014.

[45] S. Z. Awan, J. O. Chandler, P. J. Harrison et al., “Promotion of germination using hydroxamic acid inhibitors of 9-cis-epoxycarotenoid dioxygenase,” 
*Frontiers in Plant Science*, vol. 8, Article ID 357, 13 pages, 2017.

[46] F. Chauffour, M. Bailly, F. Perretta et al., “Multi-omics analysis reveals sequential roles for ABA during seed maturation,” 
*Plant Physiology*, vol. 180, no. 2, pp. 1198–1218, 2019.

[47] S. H. Schwartz, X. Qin, and J. A. D. Zeevaart et al., “Characterization of a novel carotenoid cleavage dioxygenase from plants,” 
*Journal of Biological Chemistry*, vol. 276, no. 27, pp. 25208–25211, 2001.

[48] H. Schmidt, R. Kurtz, W. Eisenreich, and W. Schwab, “The carotenoid AtCCD1 from Arabidopsis thaliana is a dioxygenase,” 
*Journal of Biological Chemistry*, vol. 281, no. 15, pp. 9845–9851, 2006.

[49] T. J. Vogel, B.-C. Tan, D. R. McCarty, and H. J. Klee, “The carotenoid cleavage dioxygenase 1 enzyme has broad substrate specificity, cleaving multiple carotenoids at two different bond positions,” 
*Journal of Biological Chemistry*, vol. 283, no. 17, pp. 11364–11373, 2008.

[50] F.-C. Huang, P. Molnár, W. Schwab et al., “Cloning and functional characterization of carotenoid cleavage
dioxigenase 4 genes,” *Journal of Experimental Botany*, vol. 60, no. 11, pp. 3011–3022, 2009.

[73] F. Bouvier, C. Suire, J. Mutterer, and B. Camara, “Oxidative remodelling of chromoplast carotenoids,” *The Plant Cell*, vol. 15, no. 1, pp. 47–62, 2003.

[74] S. Mathieu, N. Terrier, J. Procureur, F. Bigey, and Z. Günata, “A carotenoid cleavage dioxygenase from *Vitis vinifera* L.: functional characterisation and expression during grape berry development in relation to C13-norisoprenoid accumulation,” *Journal of Experimental Botany*, vol. 56, no. 420, pp. 2721–2731, 2005.

[75] S. Baldermann, M. Naim, and P. Fleischmann, “Enzymatic carotenoid degradation and aroma formation in nectarines (*Prunus persica*),” *Food Research International*, vol. 38, no. 8-9, pp. 833–836, 2005.

[76] M. Ibdah, Y. Azulay, V. Portnoy et al., “Functional characterisation of *CcCD1*, a carotenoid cleavage dioxygenase from melon,” *Phytochemistry*, vol. 67, no. 15, pp. 1579–1589, 2006.

[77] M. Kato, H. Matsumoto, Y. Ikoma et al., “The role of carotenoid cleavage dioxygenases in the regulation of carotenoid profiles during maturation in citrus fruit,” *Journal of Experimental Botany*, vol. 57, no. 10, pp. 2153–2164, 2006.

[78] C. García-Limones, K. Schnabele, R. Blanco-Portales et al., “Functional characterisation of *FaCCD1*: a carotenoid cleavage dioxygenase from strawberry involved in lutein degradation during fruit ripening,” *Journal of Agricultural and Food Chemistry*, vol. 56, no. 19, pp. 9277–9285, 2008.

[79] F.-C. Huang, G. Horváth, P. Mohár et al., “Substrate promiscuity of *RcCD1*, a carotenoid cleavage oxygenase from *Rosa damascena*,” *Phytochemistry*, vol. 70, no. 4, pp. 457–464, 2009.

[80] S. Baldermann, M. Kato, M. Kurosawa et al., “Functional characterization of a carotenoid cleavage dioxygenase 1 and its relation to the carotenoid accumulation and volatile emission during the floral development of *Osmanthus fragrans* Lour,” *Journal of Experimental Botany*, vol. 61, no. 11, pp. 2967–2977, 2010.

[81] E. Auldridge, A. Block, J. T. Vogel et al., “Characterization of three members of the Arabidopsis carotenoid cleavage dioxygenase family demonstrates the divergent roles of this multifunctional enzyme family,” *The Plant Journal*, vol. 45, no. 6, pp. 982–993, 2006.

[82] D. S. Floss, W. Schliemann, J. Schmidt, D. Strack, and M. H. Walter, “RNA interference-mediated repression of *MtCCD1* in mycorrhizal roots of medicago truncatula causes accumulation of C27 apocarotenoids, shedding light on the functional role of *CCD1*,” *Plant Physiology*, vol. 148, no. 3, pp. 1267–1282, 2008.

[83] D. S. Floss and M. H. Walter, “Role of carotenoid cleavage dioxygenase 1 (*CCD1*) in apocarotenoid biogenesis revisited,” *Plant Signalling & Behavior*, vol. 4, no. 3, pp. 172–175, 2009.

[84] M. Kato, H. Matsumoto, Y. Ikoma et al., “Accumulation of carotenoids and expression of carotenoid biosynthetic genes and carotenoid cleavage dioxygenase genes during fruit maturation in the juice sacs of ‘tamami’, ‘kiyomi’ tangor, and ‘wilking’ Mandarin,” *Journal of the Japanese Society for Horticultural Science*, vol. 76, no. 2, pp. 103–111, 2007.

[85] M. J. Rodrigo, B. Alquezar, E. Alós et al., “A novel carotenoid cleavage activity involved in the biosynthesis of citrus fruit-specific apocarotenoid pigments,” *Journal of Experimental Botany*, vol. 64, no. 14, pp. 4461–4478, 2013.

[86] A. J. Ytterberg, J.-B. Peltier, and K. J. van Wijk, “Protein profiling of plastoglobules in chloroplasts and chromoplasts. A surprising site for differential accumulation of metabolic enzymes,” *Plant Physiology*, vol. 140, no. 3, pp. 984–997, 2006.

[87] A. Ohmiya, S. Kishimoto, R. Aida, S. Yoshioka, and K. Sumitomo, “Carotenoid cleavage dioxygenase (*CmCCD4a*) contributes to white color formation in chrysanthemum petals,” *Plant Physiology*, vol. 142, no. 3, pp. 1193–1201, 2006.

[88] A. Ohmiya, K. Sumitomo, and R. Aida, “‘Yellow jimba’: suppression of carotenoid cleavage dioxygenase (*CmCCD4a*) expression turns white Chrysanthemum petal yellow,” *Journal of the Japanese Society for Horticultural Science*, vol. 78, no. 4, pp. 450–455, 2009.

[89] S. Yoshioka, K. Sumitomo, Y. Fujita et al., “Significance of *CmCCD4a* orthologs in apetalous wild chrysanthemum species, responsible for white coloration of ray petals,” *Euphytica*, vol. 171, no. 2, pp. 295–300, 2010.

[90] M. Yamagishi, S. Kishimoto, and M. Nakayama, “Carotenoid composition and changes in expression of carotenoid biosynthetic genes in tepals of Asiatic hybrid lily,” *Plant Breeding*, vol. 129, no. 1, pp. 100–107, 2010.

[91] P. Schaub, F. Wüst, J. Koschmieder et al., “Nonenzymatic β-carotene degradation in provitamin A-biofortified crop plants,” *Journal of Agricultural and Food Chemistry*, vol. 65, no. 31, pp. 6588–6598, 2017.

[92] J. López, K. Essus, I. Kim et al., “Production of β-ionone by combined expression of carotenogenic and plant *CCD1* genes in *Saccharomyces cerevisiae*,” *Microbial Cell Factories*, vol. 14, no. 1, p. 13, 2015.

[93] M. Bruno, P. Beyer, and S. Al-Babili, “The tomato carotenoid cleavage dioxygenase 4 catalyzes a single cleavage of β-ionone-containing carotenones and non-epoxidated xanthophylls,” *Archives of Biochemistry and Biophysics*, vol. 572, pp. 126–133, 2015.

[94] X. Zhang, J. Pei, L. Zhao, F. Tang, X. Fang, and J. Xie, “Overexpression and characterization of *CCD4* from *Osmanthus fragrans* and β-ionone biosynthesis from β-carotene in vitro,” *Journal of Molecular Catalysis B: Enzymatic*, vol. 134, pp. 105–114, 2016.

[95] K. Watanabe, C. Oda-Yamamizo, K. Sage-Ono, A. Ohmiya, and M. Ono, “Alteration of flower colour in *Ipomoea nil* through CRISPR/Cas9-mediated mutagenesis of carotenoid cleavage dioxygenase 4,” *Transgenic Research*, vol. 27, no. 1, pp. 25–38, 2018.

[96] Y. Han, M. Wu, L. Cao et al., “Characterization of *OfWRKY3*, a transcription factor that positively regulates the production and the production and regulation of its key floral constituents, β-ionone and linalool,” *Horticulture Research*, vol. 6, no. 1, p. 12, 2019.

[97] A. Stobiecka, “Comparative study on the free radical scavenging mechanism exerted by geraniol and geranylacetone using the combined experimental and theoretical approach,” *Flavour and Fragrance Journal*, vol. 30, no. 5, pp. 399–409, 2015.

[98] A. N. Uddin, I. Labuda, and F. J. Burns, “A novel mechanism of filaggrin induction and sunburn prevention by
β-damascenone in Skh-1 mice,” Toxicology and Applied Pharmacology, vol. 265, no. 3, pp. 335–341, 2012.

[100] J.-R. Liu, X.-R. Sun, H.-W. Dong et al., “β-ionone suppresses mammary carcinogenesis, proliferative activity and induces apoptosis in the mammary gland of the Sprague-Dawley rat,” International Journal of Cancer, vol. 122, no. 12, pp. 2689–2698, 2008.

[101] M. T. Cardozo, A. de Conti, T. P. Ong et al., “Chemo-preventive effects of β-ionone and geraniol during rat hepatocarcinogenesis promotion: distinct actions on cell proliferation, apoptosis, HMGCoA reductase, and RhoA,” The Journal of Nutritional Biochemistry, vol. 22, no. 2, pp. 130–135, 2011.

[102] S. Asokkumar, C. Naveenkumar, S. Raghunandhakumar et al., “Antiproliferative and antioxidant potential of beta-ionone against benzo(a)pyrene-induced lung carcinogenesis in Swiss albino mice,” Molecular and Cellular Biochemistry, vol. 363, no. 1-2, pp. 335–345, 2012.

[103] H.-W. Dong, S. Zhang, W.-G. Sun et al., “β-Ionone arrests cell cycle of gastric carcinoma cancer cells by a MAPK pathway,” Archives of Toxicology, vol. 87, no. 10, pp. 1797–1808, 2013.

[104] V. Mihailovic, N. Vukovic, N. Niciforovic et al., “Studies on the antimicrobial activity and chemical composition of the essential oils and alcoholic extracts of Gentiana asclepiadea L.” Journal of Medicinal Plants Research, vol. 5, no. 7, pp. 1164–1174, 2011.

[105] I. Blažević, A. Radonić, J. Mastelić et al., “Hedge mustard (Sisymbrium officinale): chemical diversity of volatiles and their antimicrobial activity,” Chemistry & Bioactivity, vol. 7, no. 8, pp. 2023–2034, 2010.

[106] E. F. Hanbali, F. Mellouki, M. Akssira, H. Boira, and M. A. Blázquez, “Composition and antimicrobial activity of essential oil of Anthemis tenuisecta ball,” Journal of Essential Oil Bearing Plants, vol. 10, no. 6, pp. 499–503, 2007.

[107] N. Radulović, G. Stojanović, and R. Palić, “Composition and antimicrobial activity of Equisetum arvense L. essential oil,” Phytotherapy Research, vol. 20, no. 1, pp. 85–88, 2006.

[108] L. A. Cáceres, S. Lakshminarayan, K. K.-C. Yeung et al., “Repellent and attractive effects of α-, β-, and dihydro-β-ionone to generalist and specialist herbivores,” Journal of Chemical Ecology, vol. 42, no. 2, pp. 107–117, 2016.

[109] S. Wei, A. Hannoufa, J. Soroka et al., “Enhanced β-ionone emission in Arabidopsis over-expressing AtCCD1 reduces feeding damage in vivo by the crucifer flea beetle,” Environmental Entomology, vol. 40, no. 6, pp. 1622–1630, 2011.

[110] L. R. R. Faria and F. C. V. Zanella, “Beta-ionone attracts Euglossa mandibularis (Hymenoptera, Apidae) males in western Paraná forests,” Revista Brasileira de Entomologia, vol. 59, no. 3, pp. 260–264, 2015.

[111] S. T. Halloran, R. M. Collignon, J. S. McElfresh, and J. G. Millar, “Fuscumol and geranylacetone as pheromone components of californian longhorn beetles (Coleoptera: cerambycidae) in the Subfamily Spondylidinae,” Environmental Entomology, vol. 47, no. 5, pp. 1300–1305, 2018.