Review:Synthesis and metabolism of tea aroma compounds

Long Yuanfu[1]，He Yufan[1]，Wu Siyu[1]，Mo Shiqin[2]，Zhang Zaibao[1,*]

1 School of Life and Health Sciences, Huzhou University, Huzhou, Zhejiang, China

2 Changxing Bai Suiye Tea Industry Co., Ltd., Huzhou, Zhejiang, China* Corresponding author: Zhang Zaibao,zaibaozhang79@163.com

Synthesis and metabolism of tea aroma compounds

Abstract tea aroma is an important index of tea quality evaluation, and its formation mainly derives from the metabolites formed in the process of tea growth and processing. These metabolites mainly include phenolic compounds, amino acids and aromatic compounds. The type and content of these compounds are very important for the formation of tea aroma type, but also an important factor affecting the quality of tea. Both the preharvest growth and postharvest processing of tea affected the formation and metabolism of tea aroma. Biological stresses (tea garden pests, pathogens) and abiotic stresses (light, temperature, mechanical damage) have important effects on the synthesis and release of aroma substances.

keywords tea aroma; volatile compounds; stresses

1 Composition and content of aroma substances in tea

The content of aroma substances in tea is very low, but there are many types, including volatile fatty acid derivatives (VFADs), volatile terpenes (VTs) and volatile phenylpropionic acid/benzene ring compounds (VPBs) [1]. Volatile aromatic substances, such as alcohols, aldehydes, ketones, carboxylic acids, esters, lactones, phenols and nitrogen, oxygen and sulfur compounds (Table 1), account for 0.03% to 0.05% of the dry matter mass of tea, and are the main factors affecting the aroma of tea [2]. According to different chemical structures and characteristics, alcohols can be divided into aliphatic alcohols, aromatic alcohols and terpene alcohols. Among them, aliphatic alcohols account for 12.76% of the aromatic oil in the dry matter of tea after processing, accounting for about 60% of the aromatic oil content of fresh tea leaves (these substances have low boiling points and will evaporate in large quantities with water vapor during tea processing). In oolong tea, the content of nerolidol was as high as 25.06% [3]. Aldehydes account for about 3% of the aromatic oil in fresh tea leaves and about 10.30% of the aromatic oil in dried tea leaves, meaning that the content of aldehydes in finished tea is higher than that in fresh tea leaves. Ketones account for 15.35% of the aromatic substances in tea. There is no significant difference in the content of ketone compounds among different types of tea, meaning that ketones are commonly present in tea and are not the main factor causing significant differences in the aroma of various types of tea [3]. Esters and lactones account for 12.44% of the aromatic substances in tea. Nitrogen-containing compounds (pyridine, indole, etc.) are components with roasted aroma produced through thermophysical and chemical processes [4], accounting for about 13.41% of the aromatic substances in tea. The remaining components exist in trace amounts in volatile aromatic substances, but the role of these substances in the formation of tea aroma is not negligible.

Table 1. Composition and content of volatile aromatic substances in tea aroma

	Main ingredients	content
alcohols	(Z)-3-Hexen-1-ol , benzyl alcohol, phenylethanol, phenylpropanol, linalool, geraniol, nerol, Vanillyl alcohol , nerolidol	12.76%
aldehydes	acetaldehyde, n-pentanal, n-butyraldehyde, hexenal, benzaldehyde, cinnamaldehyde, neraldehyde, vanillin	10.30%
ketones	acetophenone, α-ionone, β-ionone, jasmone, theanone	15.35%
esters	geraniyl acetate, vanillyl acetate, linalyl acetate, neryl acetate, phenylacetic acid methyl ester, methyl salicylate, methyl anthranilate	12.44%
lactones	jasmine lactone, dihydroanionolide	
nitrogen compounds	indole, pyridine, quinoline, 2,5-dimethylpyrazine, 2-formylpyrrole, phenylacetonitrile	13.41%
carboxylic acids	acetic acid, propionic acid, isovaleric acid, butyric acid, isobutyric acid, salicylic acid, palmitic acid	
phenols	2-ethylphenol, 4-ethylguaiacol, eugenol, thymol	
oxygen- and sulfur-containing compounds	anethole, anethole, 2-ethylfuran, 1,1-dimethoxyethane, dimethyl sulfide, thiophene, 2,5-dimethylthiazole, benzothiazole	

2. The Relationship Between Tea Aroma and Tea Quality

Among the color, aroma, and flavor of tea, aroma is one of the most important factors affecting tea quality. The combined effect of the types and contents of volatile aromatic substances in tea is the key to restricting the aroma quality of tea [5]. The precursor substances of tea aroma determine the characteristics and properties of aroma, including aromatic hydrocarbons and their oxides, terpenes (monoterpenes and sesquiterpenes), amino acids, carotenoids, sugars, etc. in fresh tea leaves, as well as enzymes necessary for the formation of aroma during processing [6-7]. The unique aroma types formed by the combination of different aromatic substances in different proportions are one of the characteristics of the aroma of various teas. The types and proportions of substances that make up the aroma of the six major tea categories are different, and their aroma characteristics are also different. For example, the main aroma components of green tea are chlorophyll, linalool and its oxides, indole, etc. Fresh tea leaves are processed through methods such as fixation (pan-frying or steaming), rolling, and drying (or baking, sun-drying) to form the floral and fruity aroma and roasted aroma of tea [2,8]. Black tea is a fermented tea and generally has floral and fruity aroma. The main aroma components are geraniol, benzyl alcohol, linalool and its oxides, etc. Some of these are originally present in fresh tea leaves, while others are formed by precursor substances (esters, terpenes, etc.) during processing [9-10]. Fresh black tea leaves undergo four basic processes: withering, rolling, fermentation and drying. The changes in various components are very complex, such as polyphenol compounds. The degradation and oxidation of substances eventually form the unique red soup and red leaves, sweet and mellow aroma of black tea [11]; Oolong tea is a semi-fermented tea, and neroli is the characteristic component of oolong tea aroma [12]; Black tea has different characteristic aromas depending on the place of origin, such as Hunan Xiangjian with pine resin, Sichuan Nanlu Biancha with oily aroma, and Yunnan Pu'er with agarwood aroma [13]; Yellow tea converts sugar into caramel under dry heat, and low-boiling-point aromatic substances will volatilize or isomerize at higher temperatures, forming a fresh aroma; White tea is a lightly fermented tea, and the abundant white hairs on the surface are an important factor that gives it aroma quality characteristics, constituting the sweet and pure aroma of white tea [14]. The different composition and proportion of aroma substances between different tea varieties, as well as the differences in processing methods, form the representative characteristic aromas between different teas. Even among the same type of tea, the difference in aroma will affect the quality of the tea. Therefore, the aroma characteristics of tea determine the quality of tea and meet different needs.

3. Tea aroma formation and metabolism

Volatile fatty acid derivatives (VFADs), volatile terpenes (VTs), volatile carotenoid derivatives and volatile phenylpropionic acid/benzene ring compounds (VPBs) are characteristic aromatic compounds commonly found in tea trees[1]. There are also some non-aromatic substances (such as amino acids) that play an important role in the formation of tea aroma substances. The metabolic changes of these compounds during the pre-harvest (tea growth process) and post-harvest (processing) process are key factors in the formation of tea aroma[6].

Aroma substances of tea

Most fatty acid derivatives are aldehydes and esters, while unsaturated fatty alcohols (such as quinol) are abundant in fresh tea leaves. Quinol and its precursor quinol not only contribute to the grassy aroma of tea, but quinol also provides precursors for the formation of other aroma compounds. Fatty acid metabolism in tea mainly occurs through two pathways: enzymatic reactions and auto-oxidation. Unsaturated fatty acids are catalyzed by lipoxygenases to generate peroxides, which are then catalyzed by peroxidases to form quinol and aldehydes. Finally, dehydrogenases catalyze the reduction of aldehydes to the corresponding alcohols (Figure 1).

图 1. 青叶醛、青叶醇的生物合成
Fig 1. Biosynthesis of trans-2-hexenal and (Z)-3-hexene-1-ol leaf

Terpenes are an important class of volatile aroma components in tea and belong to hydrocarbons. The terpenes present in tea trees are mainly monoterpenes and sesquiterpenes, which often exist in the form of glycosides (such as linalool and nerol), thus reducing their volatility. Therefore, under normal circumstances, they do not produce aroma in fresh leaves[15]. There are two pathways for the biosynthesis of terpenes: the mevalonate pathway (MVA) and the methyl erythritol phosphate pathway (MEP)[18]. Both of these pathways can produce isopentenyl pyrophosphate (IPP) and dimethylallyl pyrophosphate (DMAPP), which further synthesize terpenes. The key enzyme in the MVA pathway is 3-hydroxy-3-methylglutaryl-CoA reductase (HMGR), which catalyzes the formation of mevalonic acid for further synthesis of IPP; 1-deoxy-D-xylitol-5-phosphate reductase (DXR) catalyzes the formation of 2-C-methyl-D-erythritol-4-phosphate (MEP), which is also a key rate-limiting step in the MEP pathway [16-17].

In the shikimic acid pathway, volatile phenylpropionic acid/phenyl ring derivatives can be generated through a series of processes. In tea, VPBs are also an important class of aroma compounds, such as benzyl alcohol and phenylethyl alcohol, which can give tea a "fruity" aroma. The biosynthesis of these substances is regulated by the level of precursor substances (such as phenylalanine), but their biosynthetic pathways and corresponding formation mechanisms still need further research to clarify.

Carotenoids directly participate in the composition of tea aroma. The oxidative degradation of carotenoids in tea mainly occurs during processing and storage [19], and the formation of tea aroma depends on its transformation products. The oxidative degradation of carotenoids in tea is carried out through two pathways: biodegradation and physical degradation. Its degradation products are mainly C9-C13 isoprene aroma substances [20]. Among them, the degradation products of C13 include β-ionone, β-damascene, etc. [22], and these substances have very low thresholds in aqueous solution [21]. Using gas chromatography-olfaction determination and aroma extract dilution analysis, Schuh et al. analyzed the main aroma substances of Darjeeling black tea and found that the aroma threshold of β-damascene was as low as 0.004 μg/L [22]. Although these volatile substances are present in very low amounts in tea, they have a unique influence on the aroma quality of tea. Therefore, it is believed that β-damascene plays a very important role in the formation of the aroma of Darjeeling black tea.

In addition to some aromatic substances participating in the formation of tea aroma, some non-aromatic substances (such as amino acids) can also undergo Strecker degradation and Maillard reaction under heat to transform into aromatic substances, or react with sugars to produce caramel aroma substances [15, 23]. Catechins in tea trees can produce ortho-quinones through oxidation, and amino acids formed after protein hydrolysis can react with them to produce a similar apple aroma. Sugars can also emit a sweet aroma or roasted chestnut aroma during the roasting process of tea [12].

Multiple reactions involved in the formation of tea aroma

Tea processing involves various types of reactions: oxidative degradation of carotenoids and fatty acids, carbonyl-amine reaction (Maillard reaction [23]), caramelization, glycoside hydrolysis and microbial fermentation. The products formed by these reactions constitute important components of tea aroma. Ionone series compounds can participate in the formation of tea aroma and can be formed by the degradation of carotenoids during tea processing. Through oxidative degradation, carotenoids can produce a series of aroma substances, including β-ionone, β-damasone, tea spirone and their oxidized derivatives. These are compounds with floral and fruity aromas and are key aroma substances in oolong tea and black tea [24-25]. Fatty acid substances can lead to the breakage of fatty acid chains through enzymatic oxidation or non-enzymatic oxidation pathways. The degree and rate of oxidation are related to the degree of unsaturation of fatty acids [23]. For example, unsaturated fatty acids undergo a series of enzymatic reactions to eventually form corresponding alcohols, which can then participate in the formation of tea aroma. The Maillard reaction is common in food processing and is also a common browning process in tea drying. During tea processing, amino and carbonyl groups undergo Maillard reactions at high temperatures. Many heterocyclic compounds, such as furan, pyrrole, thiophene, and their derivatives, are also mainly derived from Maillard reactions [23]. Sugars can undergo caramelization at high temperatures. Maillard and caramelization reactions during tea processing can promote the formation of pyrazine and furan derivatives, which in turn can give tea a roasted aroma. Terpenoids and linalools in tea are bound aroma compounds. These two types of compounds are mainly present in the form of glycosides in fresh tea leaves [26], and can participate in the formation of alcoholic aromas in tea. In addition to bound compounds, alcoholic aromas are also formed from free compounds, but bound compounds contribute more to alcoholic aromas. Glycoside aroma precursors can be hydrolyzed by glycosidases, thereby releasing the corresponding alcoholic aromas [27]. In addition, acid hydrolysis can also effectively hydrolyze glycoside aroma precursors and release volatile aglycones[28]. The aglycones released by acid hydrolysis and enzymatic hydrolysis can be detected by gas chromatography (GC) and GC-mass spectrometry (GC-MS) to infer the types and contents of glycosides[29]. Microbial fermentation mainly occurs in the production process of black tea, and it can produce characteristic aroma substances. Taking the pile fermentation process of Pu'er tea as an example, this process uses sun-dried green tea as raw material. Various extracellular enzymes secreted by microorganisms can lead to a series of reactions, which change some chemical components in the tea leaves and form quality characteristics with aged aroma and bright red and yellow liquor.

Aliphatic alcohols, aromatic alcohols, and terpenoids are important components of tea aroma. A small portion exists in free form, while the vast majority are stored in cells by combining with monosaccharides and disaccharides to form glycosides. Because glycosides have stronger water solubility and weaker activity than their free glycoside ligands, aromatic compounds in tea usually accumulate in glycoside form. Glycosidases participate in the formation of alcohol-based aromas in tea. The isolation, purification, and characterization of glycosidases can help study the formation mechanism of alcohol-based aroma components. Glycoside aroma precursors (primrose glycosides, glucosides) can be hydrolyzed by β-glucosidases (β-primrose glycosidase, β-glucosidase) to release various free volatile aroma substances [6-7]. To date, through the separation and identification of aroma substances in tea, a variety of monoterpene alcohol glycosides and aromatic alcohol glycosides have been discovered. They are mostly present in the form of disaccharides and monosaccharides. Among them, the disaccharides are mostly β-primrose glycosides, and the monosaccharides are mostly β-glucosides[27]. The content of β-primrose glycosides is relatively high. In fresh tea leaves, glycosidases and their substrates are compartmentalized by cells and do not react. Due to a series of reasons (such as picking, mechanical damage, insect feeding, and pathogen infection), endogenous glycosidases in tea leaves bind to their substrates, and glycoside aroma precursors are hydrolyzed, releasing volatile aglycones[6], thus exhibiting aroma characteristics.

Besides glycoside hydrolysis, many aromatic compounds are formed through resynthetic pathways. In the past decade, most of the relevant genes have been cloned and their functions verified in vitro. In 2002, Mizutani et al. [29] isolated and purified β-primrose glycosidase from fresh tea leaves. Based on its partial amino acid sequence, they designed degenerate primers and cloned the β-primrose glycosidase sequence from tea leaves. The enzyme gene was introduced into Escherichia coli for expression. The results showed that the enzyme sequence had 50%-60% similarity to the β-primrose glycosidase sequence in other plants. The enzyme could hydrolyze β-primrose glycosides in vitro to generate primrose sugar and the corresponding ligand, but could not act on 2-phenylethyl-β-D-glucoside. This result indicates that β-primrose glycosidase can only specifically recognize β-primrose glycosides and only hydrolyzes the glycosidic bond between primrose sugar and the ligand.

4. The Influence of Post-Harvest Processing Stages on the Aroma Composition of Tea

ividedinto six types, including non-fermented green tea, slightly fermented white tea, semi-fermented oolong tea, fully fermented black tea, post-fermented yellow tea, and dark tea[30]. Tea is subjected to multiple stresses (damage, low temperature, water loss, etc.) during the production process. For example, the production of black tea requires seven steps: indoor withering, rolling, breaking up clumps, replenishing fermentation, drying, refining and baking. Among them, the withering process requires attention to time, temperature, light and other conditions. Low temperature (26°C) withering is conducive to aroma formation [31]. Shortening the withering time is not conducive to increasing the activity of enzymes (polyphenol oxidase, β-glucosidase), which to some extent inhibits the formation of tea aroma substances [31-32]. During the fermentation process, polyphenol oxidase is released from the epidermal cells of the leaves and encounters polyphenol compounds to produce an enzymatic reaction [33]. It is also accompanied by the degradation of carotenoids, oxidation and reduction of catechins, decarboxylation of amino acids and decomposition of fatty acids [1]. The synthesis of indole is terminated. After refining and baking, the quality of tea is purified, the leaf color is reddish-brown, and the grassy smell is transformed into a sweet taste and floral and fruity aroma. The production process of oolong tea is relatively complex. It involves a series of processing steps, including withering (sunlight or hot air), indoor resting, stirring, pile fermentation, fixation, initial rolling, initial drying, rolling, breaking up clumps, and drying. The leaves rub against each other, leaf cells are damaged, moisture is released, enzyme activity is increased, internal contents are transformed, and the formation of aroma substances (nerolidol, geraniol, linalool and their oxides) is promoted[34]. The grassy smell is removed, and a high aroma is formed, which is fragrant. The stress involved mainly includes mechanical damage from stirring and fixation, water loss from withering and ultraviolet radiation[1]. Damage stress forces water to evaporate, promotes a series of enzymatic reactions, and is a key factor affecting the aroma formation of oolong tea[35]. In addition, low temperature stress is also an important factor inducing the formation of various aroma components in tea. The dual stress (damage and low temperature) not only regulates the formation of volatiles, but also has a synergistic effect[36]. Green tea is processed through withering, fixation, rolling, and drying after picking to produce finished tea, which forms a green aroma and floral aroma[37]. During the withering stage, green and floral aroma compounds accumulate in large quantities[37], which may be related to the large amount of abscisic acid induced by dehydration stress during the withering process[38]. The formation of floral and green aroma in green tea is not only related to the withering stage, but also affected by the fixation and drying stages. The manufacturing process of white tea is relatively simple. White tea is processed by picking tender green leaves, withering indoors, piling, and drying to form a unique downy aroma. During the withering process of white tea, the components contained in the fresh leaves undergo a series of enzymatic and chemical reactions, such as the degradation of glycosides, the peroxidation and degradation of fatty acids, resulting in the generation of a large amount of aroma substances[39].

5. Stress and the synthesis of tea aroma

Tea leaves are subject to various stresses before and after picking (Figure 2), such as climate conditions, soil factors, feeding by leaf-eating pests and infection by pathogens. These stress factors promote the formation, accumulation and release of aroma compounds in tea leaves. On the one hand, the accumulated volatile aromatic substances are conducive to improving the aroma quality of tea leaves, and on the other hand, they are also conducive to the generation of stress response mechanisms in tea trees [1].

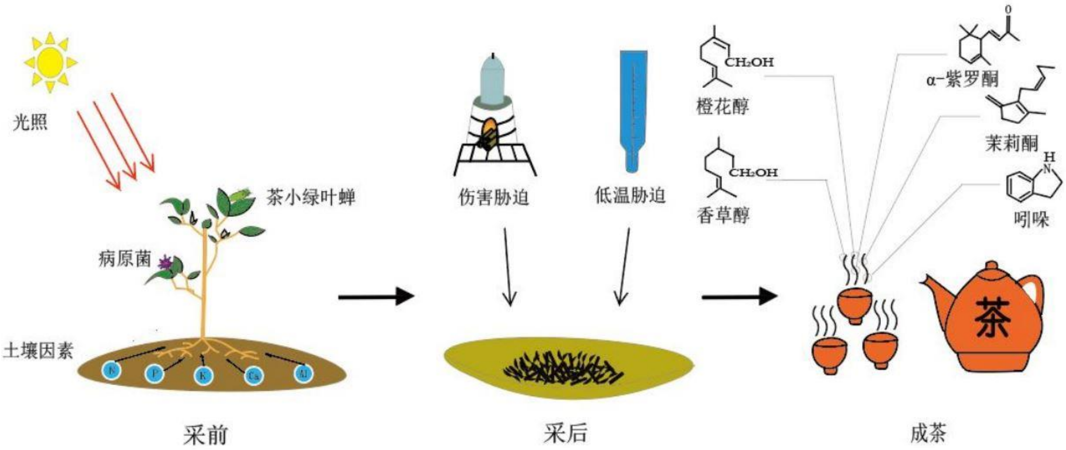

图 2. 胁迫与香气的关系

Fig 2. Relationship between stress and aroma

The effects of biological stress on tea aroma formation

Under normal conditions, most volatile compounds exist in plants primarily in liquid form [40]. When plants are subjected to biological stresses such as those from the external environment, they usually synthesize and release some volatile substances, which may have the function of mitigating the negative effects of stress on plants. Biological stress is particularly important for the formation and release of plant volatiles. During the growth of tea trees, some tea garden pests (such as tea green leafhoppers, tea geometrid moths, tea aphids, tea leafrollers, etc.) will attack tea trees [41]. In addition, some tea diseases such as tea anthracnose, leaf blight, and leaf swelling will also affect the yield, appearance, and quality of tea. These biological stress factors will lead to the production of aroma substances such as linalool, geraniol, α-farnesene, and indole in tea.

Attacks by the green leafhopper [1,42] can increase the release of (S)-linalool in tea leaves, and damage caused by continuous feeding is a key factor in the formation and release of (S)-linalool induced by green leafhopper attacks. In addition, green leafhopper feeding can also induce the release of some monoterpenes, such as 2,6-dimethyl-3,7-octadien-2,6-diol (diendiol I). The production of Diendiol I is a marker of green leafhopper infestation of tea leaves. Plant hormones, especially jasmonic acid, are involved in the formation and release of volatile substances in plants. Since damage stress from some tea garden pests can enhance the release of jasmonic acid in tea leaves, the formation of diendiol I may depend on jasmonic acid signaling [36].

Infection by pathogens can also affect the formation of tea aroma. For example, tea infected with tea anthracnose[43] has increased activity of phenylalanine ammonia-lyase and activated lipoxygenase metabolic pathway, which ultimately leads to the formation and release of volatile substances[44]. Tea cake disease is a low-temperature and high-humidity disease[45]. When tea trees are infected with tea cake disease, the content of some tea volatiles (terpenes, aromatic compounds, etc.) increases significantly. These substances have a certain inhibitory effect on the infection of pathogens[1].

The effects of abiotic stress on tea aroma formation

Not only do biological factors promote the formation of tea aroma, but many more abiotic factors can positively regulate tea aroma before and after harvest. In the pre-harvest stage, abiotic factors such as soil, temperature, light, and mechanical damage during processing can lead to a variety of plant responses.

Tea trees are perennial deep-rooted plants, and their growth is adaptable to a wide range of soil textures. They are generally planted in loose, well-drained sandy soil [46]. However, they have high requirements for soil acidity and alkalinity. Tea trees prefer acidic soil, and their soil pH range is mostly between 4.0 and 6.5. If the soil is too acidic and the pH is below 4.0, it will cause the tea seedlings to be infected with hydrogen ion poisoning, causing the tea leaves to turn from green to dark and then to red. In severe cases, it will lead to the death of the tea tree. If the soil is too alkaline, i.e., the pH is above 6.5, it will cause the tea leaves to turn yellow and be infected with chlorosis. In severe cases, it will cause the roots to turn black, thus leading to decay and death. pH mainly affects the aroma quality of tea by influencing the absorption of elements such as nitrogen, phosphorus, potassium, aluminum, and calcium by the roots of the tea tree. For example, when potassium is rich [46], it is beneficial to regulate water evaporation and can also increase the content of flavor and aroma components in tea.

The growth and development of tea trees also have certain requirements for temperature. Temperature restricts the growth rate of tea trees. It is usually divided into the maximum temperature, the optimal temperature and the minimum temperature. When the temperature gradually increases, its physiological reaction will gradually accelerate[47], and the tea tree grows faster. When the optimal temperature is reached, the growth rate of tea trees reaches its fastest. Then, as the temperature gradually increases, its physiological reaction will decrease. When the maximum temperature is exceeded, the tea tree will be damaged due to lack of water. Therefore, excessively high or low temperatures are not conducive to the growth and development of tea trees[48]. Low temperature can affect the light reaction of photosynthesis, inhibiting the photosystem II in thylakoids. Low temperature stress can significantly promote the synthesis of aromatic substances in fresh tea leaves[49]. High temperature conditions will reduce the enzyme activity in the tea tree, causing the tea tree to stop growing or even wither. Therefore, in actual production, measures such as early spring cultivation of tea gardens, summer and autumn mulching between rows, and application of organic fertilizer are often used to improve the soil temperature of tea gardens in order to achieve the best environment for tea tree growth.

As an important environmental factor, light can cause stress response in tea trees, which leads to the formation and release of aroma substances in tea[50]. Light quality, light intensity and light duration not only affect the metabolic status of tea trees, but also affect other physiological processes and developmental stages of tea trees. Tea trees are shade-tolerant plants with a low light compensation point, so in actual production, shading treatment (almost no light treatment) is often used to improve the flavor quality of tea. In addition, shading treatment also accelerates the conversion of related ascending metabolites, especially the conversion of shikimic acid, prephenylacetic acid and phenylpyruvic acid (PPA) to VPBs. In terms of light quality, tea trees absorb a large proportion of blue-violet light and red light. Generally, the photosynthetic rate under red light is higher than that under blue-violet light, which is conducive to the synthesis of sugars. Blue-violet light can accelerate the formation of amino acids and proteins, while red light has an important influence on the formation of tea polyphenols and carbohydrates, which is the basis for the accumulation of substances[51]. Blue and red light can significantly increase the formation of most volatiles in tea leaves before harvest, including VFADs, VPBs, and VTs, thereby enriching the aroma of the tea.

Tea is subjected to multiple stresses during production and processing[1], such as low temperature and water loss. In the processing of green tea, different fixation and drying processes have different effects on the formation and release of aroma in the finished green tea; the relatively complex processing of oolong tea gives it a special honey aroma and floral and fruity aroma.

6. Problems and Prospects

Tea aroma is an important component of tea quality, and its formation is closely related to both the pre-harvest growth stage and the post-harvest processing stage. This article reviews the biosynthesis of tea aroma substances and the regulatory mechanisms of tea under stress responses. It introduces several characteristic aroma substances in tea and their biosynthetic pathways. Furthermore, this article also explores the effects of biotic stress (tea garden pests, pathogens) and abiotic stress (light, temperature, mechanical damage) on the formation of tea aroma substances.

Currently, the isolation, purification, synthesis pathways, and enzymatic or non-enzymatic reactions involved in the aroma substances produced during tea processing require further investigation. For example, the mechanisms by which catechins and caffeine participate in aroma reactions remain unclear. In future research, we hope to artificially control stress mechanisms to alter the composition and content of aroma substances in tea, aiming to obtain our desired aroma and improve tea quality.

References

[1]YAN Zhen, WANG Dengliang. Progress in Understanding the Stress Response Mechanisms and Functions of Aroma Compounds in Tea[J]. Food Science, 2021, 42(15): 337-345.

[2]WAN Xiaochun. Biochemistry of Tea. 3rd Ed. 2003, Beijing: China Agriculture Press.

[3]LV Shidong. Study on volatile components of tea by GC-MS combined with stoichiometry[D]. Kunming University of Science and Technology, 2014.

[4]ZHAO Hetao, WANG Chunyuan. The composition of main aromatic substances in tea in China and their changes during processing[J]. Natural Products Research and Development, 1990(03): 42-48.

[5]WANG Rangjian, YANG Jun, KONG Xiangrui. Research progress on volatile terpenoids in tea plant[J]. Acta Tea Sinica, 2018, 59(03): 149-154.

[6]ZHOU Jie, DING Peng, WANG Guiyu, et al. Advancesin Glycosidically Bound Aroma Precursors in Tea(*Camellia Sinensis*). Journal of Xinyang Normal University (Natural Science Edition), 2018, 31(01): 152-159.

[7] ZHANG Zhengzhu, WAN Xiaochun, KANZO Sakata. Purification by Affinity Chromatography and Characterization of Tea Leaf -Glucosidase[J]. Journal of Tea Science, 2005, 25(1): 16-22.

[8]WANG Huafu. Flavor types and aromatic substances of tea[J]. Chinese tea, 1989(02): 16-17.

[9]PENG Yun, LI Guo, LIU Xueyan, et al. SPME/GC-MS Analysis of Aroma Quality of Black Tea from Different Producing Areas[J]. Science and Technology of Food Industry, 2021, 42(9): 228-235.

[10]ZHANG Chao, LU Yan, LI Jixin, et al. Advances in research on aroma components and mechanism of aroma formation in tea[J]. Fujian tea, 2005(03): 17-19.

[11] Introduction to the Processing of High Quality Black Tea[J]. Tea Bulletin, 2017, 44(03): 53.

[12]YAO Zhaopeng, HUANG Jianan. Tea review and inspection. 4th Ed. 2010, Beijing: China Agriculture Press.

[13]JI Jieli, YUAN Dandan, LIU Fei, et al. Research progress on the quality formation mechanism of dark tea[J]. Food and Drug, 2016, 18(01): 52-60.

[14]ZHANG Yinggen, CHEN Lin, CHEN Quanbin, et al. Aromatics-based Model for Quality Evaluation of White Teas. Journal of Tea Science, 2017, 58(04): 149-156.

[15]ZHANG Zhengzhu, SHI Zhaopeng, WAN Xiaochun. Terpenoids and Tea Aroma (Review)[J]. Journal of Anhui Agricultural University, 2000(01): 51-54.

[16]ZHANG Dongtao, SUN Jun, YE Naixing, et al. Research Progress of Enzymes Associated with Terpene Synthesis in *Camellia sinensis*. Journal of tea industry, 2015, 56(02): 68-79

[17]MA Liang, DING Peng, YANG Guangxiao, et al. Advances on the Plant Terpenoid Isoprenoid Biosynthetic Pathway and Its Key Enzymes. Biotechnology Bulletin, 2006(S1): 22-30.

[18]HE Zhirong, XIANG Wei, XU Yan, et al. Progress in the Research of Biosynthesis of Volatile Terpenoids and Their Glycosides in Tea Plant[J]. Journal of Tea Science, 2012, 32(1): 1-8.

[19]ZENG Xiaoxiong. Oxidative degradation of carotenoids in tea and its relationship with tea quality[J]. Tea communication, 1992(01): 31-33.

[20]CHEN Li, YE Yulong, WANG Chunyan, et al. Research progress on carotenoid aroma precursors in tea. Food and fermentation industry.

[21]WAN Xiaochun, LI Daxiang, ZHANG Zhengzhu, XIA Tao, LING Tiejun, CHEN Qi. Research Advance on Tea Biochemistry[J]. Journal of Tea Science, 2015, 35(1): 1-10.

[22]Schuh Christian, Schieberle Peter. Characterization of the key aroma compounds in the beverage prepared from Darjeeling black tea: quantitative differences between tea leaves and infusion[J]. Journal of Agricultural and Food Chemistry, 2006, 54(3): 916-924.

[23]ZHA Minyu, WU You, ZHANG Liang. Research advances on volatile aroma compounds of tea[J]. Journal of Food Safety and Quality Inspection, 2020, 11(13): 4298-4303.

[24]Kawakami Michiko, Kobayashi Akio. Carotenoid–derived aroma compounds in tea[J]. Am Chem Soc, 2001, 802(11): 145-159.

[25]Ravichandran Ramaswamy. Carotenoid composition, distribution and degradation to flavour volatiles during black tea manufacture and the effect of carotenoid supplementation on tea quality and aroma[J]. Food Chem, 2002, 78(1): 23-28.

[26]Wang Huafu, You Xiaoqing. Free and glycosidically bound monoterpene alcohols in Qimen black tea[J]. Food Chemistry, 1996, 56(4).
[27]DENG Huili, SUN Yun, LAI Zhongxiong. Progress on the effects of β-primeverosidase on tea alcoholic aroma. Subtropical Agricultural Research, 2015, 11(02): 139-143.
[28]KU Xiuping, LIU Kun, DENG Weiwei, et al. Research progress of glycoside aroma precursors and related endogenous glycosidases in tea. Tea Industry Bulletin.
[29]Mizutani M et al. Cloning of β-primeverosidase from tea leaves, a key enzyme in tea aroma formation. Piant Physiology, 2002, 130: 2164-2176.
[30]Susanne Baldermann, Ziyin Yang, Tsuyoshi Katsuno, et al. Discrimination of Green, Oolong, and Black Teas by GC-MS Analysis of Characteristic Volatile Flavor Compounds[J]. American Journal of Analytical Chemistry, 2014, 5(9).
[31]XIA Tao, TONG Qiqing, DONG Shangsheng, et al. Studies on the Change of β-Glucosidase Activity During the Withering and Fermentation of Black tea. Tea Science, 1996(01): 63-66.
[32]XIA Tao, TONG Qiqing. Effects of freeze withering on polyphenol oxidase and β-glucosidase activity of tea leaves. Journal of Zhejiang Agricultural University, 1997, 23(1): 108-110
[33]TAO Linlin, ZHANG Yanan, YAN Zhen, et al. Research progress of fermentation technology in black tea processing[J]. Guangdong Tea Industry, 2020(01): 2-6.
[34]ZHANG Wanting, ZHANG Lingzhi, WANG Dengliang. Research progress on the influence of oolong tea processing technology on aroma components[J]. Guangdong Tea Industry, 2010(Z1): 21-27.
[35]CHENG Liu, WU Yun. Processing technology of oolong tea in dachouding tea farm[J]. Guangdong tea industry, 2010(Z1): 43-44.
[36]ZENG Lanting, Naoharu Watanabe, YANG Ziyin. Understanding the biosyntheses and stress response mechanisms of aroma compounds in tea (Camellia sinensis) to safely and effectively improve tea aroma[J]. Critical Reviews in Food Science and Nutrition, 2018, 5.
[37]LIU Zhenzhen, CHEN Xiaohua, LI Chongyong, et al. Study on the important aroma components of Hanzhong green tea and their changes during processing[J]. Tea communication, 2021, 48(01): 71-79.
[38]CHAO Jeong-Yong, MIZUTANI Masaharu, SHIMIZU Bun-ichi, et al. Chemical Profiling and Gene Expression Profiling during the Manufacturing Process of Taiwan Oolong Tea "Oriental

Beauty"[J]. Bioscience, Biotechnology, and Biochemistry, 2007, 71(6).
[39]CHEN Zhida. Research on the material basis and quantitative evaluation of the flavor quality of white tea. Hangzhou: Zhejiang University, 2019.
[40]Eran Pichersky, Jonathan Gershenzon. The formation and function of plant volatiles: perfumes for pollinator attraction and defense[J]. Current Opinion in Plant Biology, 2002, 5(3): 237-243.
[41]CHEN Zongmao, XU Ning, HAN Baoyu, et al. Chemical Communication Between Tea Plant-Herbivore-Natural Enemies[J]. Journal of Tea Science, 2003, 23(s1): 38-45.
[42]SUN Yichao, CAO Fanrong. Effects of Leafhopper Infection on Defensive Response of Tea Plants[J]. Guangdong Tea Industry, 2018(02): 2-5.
[43]ZHANG Zhengzhu, LI Yingbo, QI Li, WAN Xiaochun. Antifungal activities of major tea leaf volatile constituents toward Colletorichum camelliae Massea[J]. Journal of agricultural and food chemistry, 2006, 54(11): 3936-3940.
[44]CHEN Shenglong, ZHANG Liping CAI Xiaoming, et al. (E)-Nerolidol is a volatile signal that induces defenses against insects and pathogens in tea plants[J]. Horticulture Research, 2020, 7: 52.
[45]LIU Hui, ZHOU Yufeng, ZHOU Luona, et al. Research progress on interaction mechanism between pathogenic bacteria of tea cake and tea plant[J]. Guizhou Agricultural Sciences. 2021, 49(01).
[46]DENG Xihai, JIANG Qiao, ZHOU Lingyun. Habitat Environment and Chemical Composition of Major High Quality Black Teas in the World[J]. Soils,2008,40(4):672-675
[47]YE Cui. Effect of temperature change on plant growth period. Tianchang Anhui, 2020, 54(10): 7-8.
[48]SHENG Zhonglei, ZHANG Ying, LI Zhonglin, et al. Effects of microenvironment on the growth and development of tea tree cuttings[J]. Agricultural Engineering Technology, 2018, 38(32): 24-25.
[49]ZHOU Hanchen, SHAMALA Lubobiferdinand, YI Xingkai, et al. Analysis of terpene synthase family genes in Camellia sinensis with an emphasis on abiotic stress conditional[J]. Scientific Reports, 2020, 10(1): 933.
[50]TAO Hanzhi, WANG Xinzhang. The Relationship between Photosynthesis and Light Quality in Tea Plants[J]. Plant Physiology Communication, 1989(1): 19-23.
[51]FANG Shimao, HUANG Wenjing, LIU Zhongying, et al. Research progress of light quality

withering on quality formation of tea. Agricultural technology services, 2020, 37(10): 40-45.