

Review and Progress

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Molecular Regulation of Durian Fruit Aroma: Genetic Network of Sulfur-Containing Volatile Biosynthesis

Chuchu Liu ^{1,2} ✉, Zhonggang Li ¹¹ Cuixi Academy of Biotechnology, Zhuji, 311800, Zhejiang, China² Tropical Medicinal Plant Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China✉ Corresponding email: chuchu.liu@cui.orgInternational Journal of Horticulture, 2025, Vol.15, No.4 doi: [10.5376/ijh.2025.15.0019](https://doi.org/10.5376/ijh.2025.15.0019)

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Abstract This study describes the molecular regulatory mechanism of aroma formation in durian (*Durio zibethinus*) fruit and explores the biosynthetic pathway of sulfur-containing volatiles and their genetic network. The key role of sulfur-containing compounds in imparting a unique odor to the fruit, the core gene family involved in aroma biosynthesis, and the functions of transcription factors (such as MYB and bHLH) in the regulatory network, constructed a regulatory network model reflecting complex interactions. This study also explored the effects of environmental factors such as temperature and light and the fruit development stage on the changes in aroma components, and the mechanism of synergistic effects of external signals and internal regulatory factors. Emerging technologies such as molecular breeding, gene editing, and systems biology have important application prospects for improving the aroma quality of durian.

Keywords Durian aroma; sulfur-containing volatiles; Biosynthetic pathways; Genetic regulation; Molecular breeding

1 Introduction

Durian, Latin for *Durio zibethinus*, is a tropical fruit. Durian has a strong and distinctive smell, which is produced by a mixture of sulphur and onion. This special smell is characteristic of durian and makes durian play an important role in the cultural recognition and economic value of fruits in Southeast Asia (Teh et al., 2017). It is the various volatile compounds, especially sulfur-containing compounds, that give durian its distinctive smell and are more abundant and diverse in both content and variety than durian relatives such as *Durio kutejensis* (Belgis et al., 2017; Abdul Rahman et al., 2023). Durian's strong smell makes it stand out in the fruit category.

The unique smell of durian mainly comes from some sulfur-containing volatile compounds. These substances give durian its strong and special aroma. Studies have shown that an enzyme called methionine gamma-lyase (MGL) is highly active in durian fruit, and it plays a big role in shaping the fruit's smell (Teh et al., 2017; Ascharyaphotha et al., 2021). Compounds like propyl mercaptan, diethyl disulfide, and 3,5-dimethyl-1,2,4-trithiane are linked to the strong, and sometimes unpleasant, odor of durian (Belgis et al., 2017). The way these smell compounds are made is quite complex. Right now, scientists are trying to figure out how they are produced and controlled.

This study will explore how sulfur-containing aromatic compounds are produced and regulated in durian, and explore the genes and biochemical systems involved in sulfur-containing aromatic compounds. Understanding the source of these compounds and how they affect the smell of fruits in this study can provide a reference for the development of new varieties of durian with better aroma. This research could also provide useful insights into how fruit aromas work and how plants manage their volatile compounds.

2 Chemical Composition and Characteristics of Durian Aroma

2.1 Main categories and proportions of volatile compounds

Durian aroma is a complex mixture of volatile organic compounds (VOCs), including esters, alcohols, aldehydes, ketones and sulfides. Esters and alcohols are the main substances that play a key role in forming the overall aroma of the durian. Sujang et al. (2023) found that wild durians in Sarawak, Borneo, for example, had three to nine

times higher levels of ester compounds in some genotypes (such as *Durio graveolens* and *Durio dulcis*) than other volatile substances. Among durian varieties in Indonesia, the researchers detected 44 volatile compounds, with the highest proportion of esters and alcohols (Belgis et al., 2017; Khaksar et al., 2024).

The proportions of these compounds can vary greatly between different varieties of durians and even within the same variety, which can affect the intensity and quality of the aroma. Belgis et al. (2017) found that the odor is much milder if the content of sulfur and ester compounds is relatively low. This difference in volatile components is also an important clue for optimizing aroma characteristics in breeding efforts (Mungmai et al., 2023).

2.2 Unique structure of sulfides and their contribution to aroma

Durian's unique smell, sulfide is the key factor. The unique molecular structure and strong olfactory activity of sulfide make it stand out in the overall aroma composition. 3, 5-dimethyl-1,2, 4-trithiane and ethyl-2-methylbutyrate are the most representative sulfur-containing compounds, and their combination is thought to be the source of the durian's unique "sulfur+fruit flavor" (Weenen et al., 1996). Although these substances are present in extremely low concentrations in the fruit, they have strong odor penetration and therefore play a decisive role in the overall aroma (Weenen et al., 1996; Cannon and Ho, 2018).

The synthesis of these sulfur-containing substances is not easy and involves the up-regulation of methionine gamma-lyase (MGL) and metabolic pathways associated with ethylene (Teh et al., 2017; Suntichaikamolkul et al., 2021). The synergy of these metabolic pathways contributes to the production of volatile sulfides (VSCs), which produce an odor that is an important marker that distinguishes durians from other tropical fruits.

2.3 Synergistic effect between different aroma components

The fragrance of durian is not a simple superposition of several volatile components, but the result of the interaction between various compounds. In particular, the interaction between sulfides and other VOCs such as esters and alcohols makes the aroma of durian richer and the sensory experience more complex. Weenen (1996) pointed out that combinations such as 3,5-dimethyl-1,2,4-trisulfane and ethyl-2-methylbutyrate not only enhance the aroma intensity, but also bring the iconic "durian flavor".

This "synergistic effect" affects how people feel about the strength of the smell and the overall taste. Some sulfides can make the fruity and sweet notes stand out more, so the whole smell becomes nicer and more balanced (Belgis et al., 2017; Sujang et al., 2023). Because these compounds work together, researchers can use this to breed durian varieties that are more popular and better match different people's taste preferences.

3 Biosynthetic Pathways of Sulfur Volatiles

3.1 Identifying the key precursors

At the heart of durian's unmistakable aroma are two key amino acids: methionine and cysteine. Methionine stands out as the major player-it serves as the starting point for producing volatile sulfur compounds (VSCs), which are largely responsible for the fruit's signature smell. Researchers have found that methionine-related pathways are significantly upregulated in the durian genome, which helps explain its dominant role in aroma production (Voon et al., 2007; Teh et al., 2017). Cysteine also contributes to the mix, though its role appears less prominent than methionine's. Still, it plays a supporting part in creating those sulfur-rich volatiles.

In many durian varieties, compounds like propyl mercaptan and diethyl disulfide have been found. They come from the breakdown of methionine and cysteine. These sulfur-containing substances make the durian smell stronger and more unique. Their origins and changes also show that the process of making these sulfur compounds in durian is quite complex.

3.2 Work of enzymes

The smell of durian comes from a group of special enzymes. One of the most important is methionine γ -lyase (MGL). This enzyme breaks down methionine and releases sulfur compounds that smell strong. These compounds are the main reason durian has such a strong odor (Teh et al., 2017; Zang et al., 2024). Studies have found that

MGL activity is very high in durian, showing that it plays a big role in making the smell. There are also enzymes called thiotransferases that help in this process. They move sulfur from one molecule to another. This helps create more complex and stronger-smelling sulfur compounds (Lu et al., 2024). When these enzymes work together, they turn simple substances into the key ingredients that give durian its special aroma.

3.3 Formation of precursors to final aroma

Methionine turns into a substance called methyl mercaptan. This thing smells strong and has a lot of sulfur in it. An enzyme called methionine gamma-lyase does this step (Teh et al., 2017). Then, methyl mercaptan keeps getting changed by other enzymes. In the end, it becomes some smell-related compounds we know, like diethyl disulfide and 3,5-dimethyl-1,2,4-trisulfonamide (Belgis et al., 2017). This whole process gives durian its strong and special smell. Besides methionine, cysteine also takes part in this process. Under the work of sulfur transferase and some other enzymes, cysteine breaks down into things like hydrogen sulfide. These also make the durian smell like sulfur (Lu et al., 2024).

4 Genetic Networks and Molecular Regulatory Mechanisms

4.1 Core gene families behind sulfur compound production

Durian has a special smell. This is mainly because of a group of genes in its body called the MGL gene family. There are many of these genes in durian. Compared to other similar fruits, durian has a lot more of them. This helps explain why durian has so many volatile sulfur compounds (VSCs) (Figure 1) (Teh et al., 2017). These sulfur compounds are the main reason durian smells so strong and special. The increase in these genes is not very common. But this is what gives durian its unique smell. It is very good at making strong sulfur smells because of this.

In addition to MGL gene, ethylene related ACS gene (aminocyclopropane-1-carboxylate synthase) was also up-regulated in durian. There is a potential link between ethylene production and sulfur compound biosynthesis that may be related to the Yang Cycle, which involves methionine cycling, showing how layered and complex this odor-related gene network really is (Teh et al., 2017).

4.2 The Role of Transcription Factors Like MYB and bHLH

For genes to work, they need instructions. That's where transcription factors come in, especially ones from the MYB and bHLH families. These proteins act like switches, turning on genes that help make volatile organic compounds (VOCs), which are responsible for smell. In fruits like durian, MYB and bHLH transcription factors affect genes involved in making terpenes, phenylalanine-related compounds, fatty acids, and sulfur-containing volatiles (Lu et al., 2024; Wang and Zhang, 2024).

But in durian, controlling these sulfur compounds is not easy. MYB and bHLH don't work alone — they team up with other proteins and even epigenetic factors to control gene expression at different levels. This complex setup helps adjust the production of durian's special smell, depending on its growth stage and the environment (Lu et al., 2024).

4.3 Construction of gene regulatory network

The researchers linked some key genes, like MGL and ACS, with the transcription factors that control them. They wanted to make a regulatory network map to see how durian makes its special smell. In this map, the MGL gene plays a main role in making sulfur volatiles. The ACS gene is related to ethylene control. The transcription factors MYB and bHLH affect how MGL and ACS work. The activity of these genes also changes with the plant's growth and the environment (Teh et al., 2017; Lu et al., 2024).

The gene network also looks at how other metabolic paths interact and give feedback. For example, the paths that make terpenoids and phenylalanine. These also add to the durian's total smell. By showing all these links, we can see how the durian's genes work together to make this strong and complex scent (Liang, 2024; Lu et al., 2024).

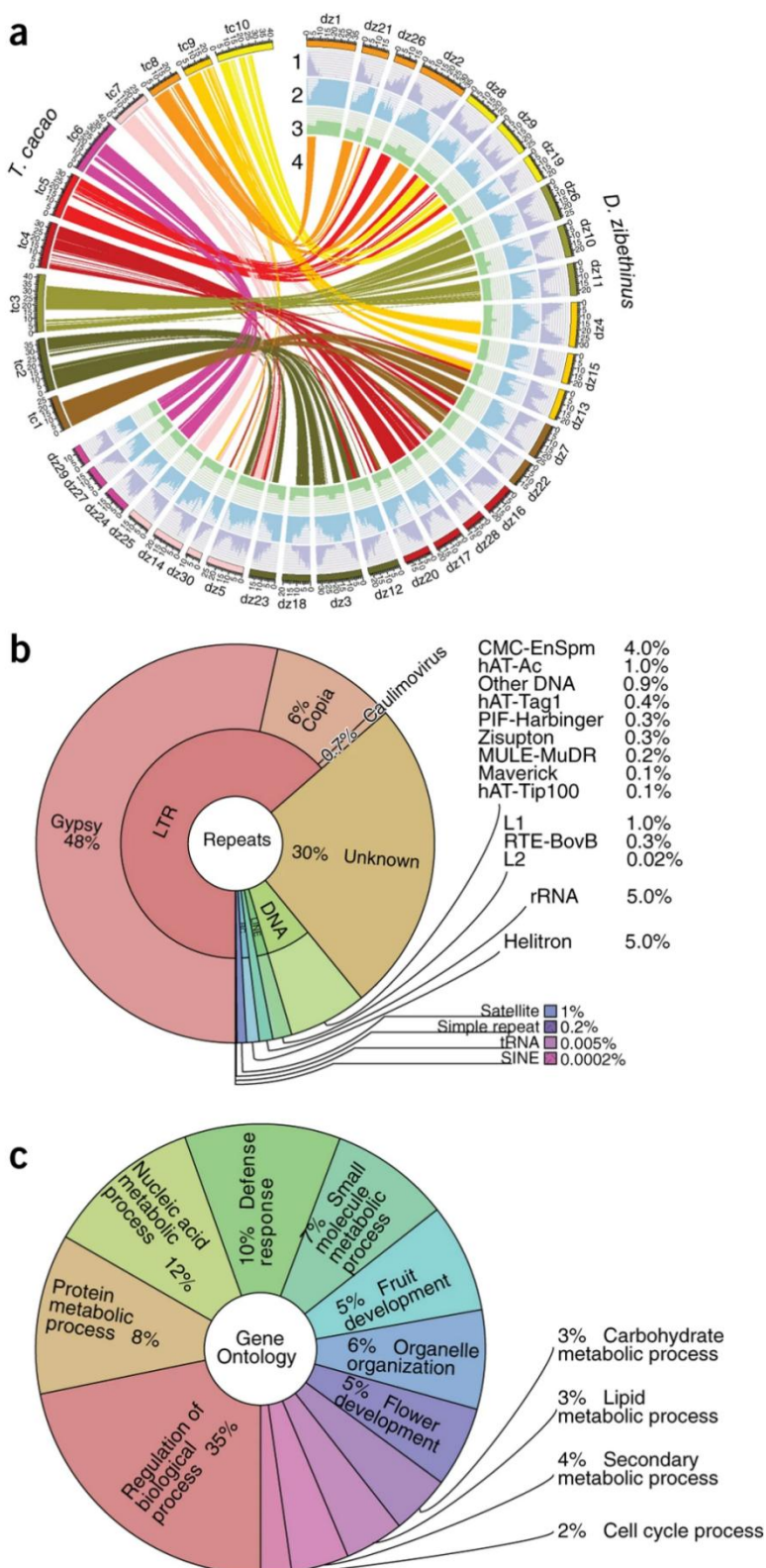


Figure 1 Characterization of the *D. zibethinus* genome (Adopted from Teh et al., 2017)

Image caption: (a) Circos plot of the multidimensional topography of the *D. zibethinus* genome (right), comprising 30 pseudomolecules that cover~95% of the assembly. Concentric circles, from outermost to innermost, show (1) gene density, (2) repeat element density, (3) GC content, and (4) syntenic regions with *T. cacao* (left), the closest sequenced relative in the Malvaceae family that did not undergo a recent WGD event. (b) Distribution of repeat classes in the durian genome. (c) Distribution of predicted genes among different high-level Gene Ontology (GO) biological process terms (Adopted from Teh et al., 2017)

5 Environmental and Developmental Regulatory Factors

5.1 How temperature and light influence aroma biosynthesis

Environmental conditions-especially temperature and light-play a major role in shaping the aroma of durian by affecting how volatile compounds are made inside the fruit. For starters, temperature can directly impact how active certain enzymes are, particularly those involved in creating sulfur-based volatiles, which are a big part of durian's signature smell. One key enzyme, methionine γ -lyase (MGL), seems to work even harder at higher temperatures, boosting the production of those potent sulfur compounds (Teh et al., 2017).

Light contributes to photosynthesis and also affects the expression of genes associated with fragrance, affects the activity of genes involved in the biosynthesis of volatile compounds, and subtly adjusts the aroma characteristics of fruits (Lu et al., 2024).

Light and temperature affect not only the activity of enzymes, but also the metabolic pathways of entire genes. Light can alter the expression of transcription factors, which are the main controllers of the aroma-related gene network. As pointed out by Hadi et al. (2013), the interaction between light and heat can significantly alter the concentration and composition of sulfur volatiles, thereby altering the smell of durian. Environmental influences are key, managing durian growing conditions well to produce the best Durian aroma.

5.2 Changes in aroma compounds

Each stage of durian growth smells different, and its aroma changes dramatically as the fruit matures. In the early stages, the foundation is mainly established, and genes responsible for breaking down carbohydrates and amino acids are particularly active, setting the stage for later aroma production (Husin et al., 2023).

But as the fruit ripens, something interesting happens: genes involved in sulfur volatile biosynthesis kick into high gear. That's when you start getting higher levels of powerful compounds like 3,5-dimethyl-1,2,4-trisulfane, which contributes heavily to durian's famously intense smell (Weenen et al., 1996; Teh et al., 2017).

During durian maturation, genes related to vitamin and cofactor metabolism become more active, which affects the final mixing of aroma compounds (Husin et al., 2023). This is a dynamic, time-intensive process that not only increases in the composition of volatiles, but also changes in complexity and characteristics. This is why the aroma also changes over time when studying durian ingredients, which is also a focus of research (Panpetch and Sirikantaramas, 2021).

5.3 Teamwork between external conditions and internal signals

It's not just outside factors like weather that shape durian's aroma-what's happening inside the fruit matters just as much. The biosynthesis of volatile compounds is a kind of balancing act between external environmental signals (like temperature and light) and internal genetic regulators.

External factors can activate or inhibit certain genes, especially those involved in the production of volatile compounds. Light and heat affect not only enzyme activity, but also transcription factors, which in turn control how fragrance-related genes are expressed (Teh et al., 2017). At the same time, plant hormones like ethylene work from the inside out, coordinating the process of methionine regeneration and regulating enzymes like ACS (aminocyclopropane-1-carboxylate synthase), which are closely involved in the synthesis of sulfur compounds.

What's fascinating is how all these signals interact-light and temperature tweak gene expression, which then influences hormonal signaling, which circles back to affect enzyme activity and compound synthesis. Hadi et al. (2013) emphasized that this crosstalk is what ultimately shapes the durian's aroma profile. By better understanding this intricate dance between inside and out, farmers and scientists can fine-tune conditions to grow fruit with just the right level of that famous (or infamous) durian punch.

6 Applications of Biotechnology and Future Prospects

6.1 Improving durian aroma with molecular breeding and gene editing

Modern biotechnologies like molecular breeding and gene editing are opening exciting new doors for enhancing the aroma of durian fruit. Thanks to the work of researchers like Teh et al. (2017), we now have a deeper understanding of the genetic blueprint behind sulfur-containing volatiles-those potent compounds responsible for durian's iconic smell.

The researchers linked key genes like MGL and ACS with the transcription factors that control them. They aimed to build a regulatory network to show how durian creates its special smell. In this model, the MGL gene plays a main role in making sulfur compounds, while the ACS gene is involved in ethylene control. The expression of MGL and ACS is affected by two transcription factors, MYB and bHLH, and their activity also changes depending on plant growth stages and environmental conditions (Teh et al., 2017; Lu et al., 2024).

The network also includes how other metabolic pathways interact, such as those for making terpenoids and phenylalanine. These also help shape the overall aroma. By mapping out these connections, we can better see how the durian genome controls such a complex and strong smell (Lu et al., 2024; Liang, 2024).

6.2 Fine-tuning aroma through genetic regulation

Besides changing single genes, scientists are now also looking more into the systems that control how volatile compounds are made in fruit. These systems include transcription factors, epigenetic control, and some complex feedback loops (Mayobre et al., 2021; Lu et al., 2024). If we can understand better how these systems work, we can control the fruit's smell more exactly.

Studies like those by Weenen et al. (1996) and Hadi et al. (2013) have helped identify key regulatory genes tied to sulfur volatile production. Adjusting the expression of these genes-either ramping them up or dialing them back-can help craft a more refined and appealing aroma profile.

Wu et al. (2022) and Lu et al. (2024) showed that transcription factors and epigenetic signals can regulate the entire family of aromatic-related genes, not only in the sulfur pathway, but also in the biosynthesis of terpenes and fatty acids. This is essential for improving the smell of durian and can be applied to other fruits where aroma is a major selling point (Figure 2) (Araguez and Fernandez, 2013).

6.3 Potential of aromatic compounds

Durian's unique scent is not only a cultural icon, but also a valuable asset in the food and spice industries. The sulfur-rich aroma compounds in durian will stimulate the creation of new flavor additives, snacks or cooking products (Peng, 2019). By separating and mixing these different volatile compounds, food scientists can make flavor enhancers that taste like durian. This gives a chance to create special products for certain regions or for people who enjoy strong and unique flavors (Weenen et al., 1996).

With a growing global interest in unusual and exotic flavours, durian aroma compounds could become hot commodities. With modern technological tools such as metabolic engineering, it is now possible to produce these compounds on a large scale, making them more accessible and more economical for commercial use (Araguez and Fernández, 2013). On this basis, market applications can be expanded, which increases economic benefits for durian growers and puts new flavored products on the shelves around the world (Zhu et al., 2015; Peng, 2019).

7 Current Challenges and Future Outlook

7.1 The tough job of figuring out gene function and building regulatory maps

One of the biggest hurdles in cracking the molecular puzzle behind durian's aroma is figuring out what each gene actually does-especially those involved in producing sulfur-containing volatiles. While the durian genome has already been mapped at the chromosome level, it's clear that the key players-like MGL (methionine γ -lyase) and ACS (aminocyclopropane-1-carboxylate synthase)-don't operate in isolation. They're part of a complex network of interactions, many of which are still not fully understood (Lee et al., 2012; Teh et al., 2017).

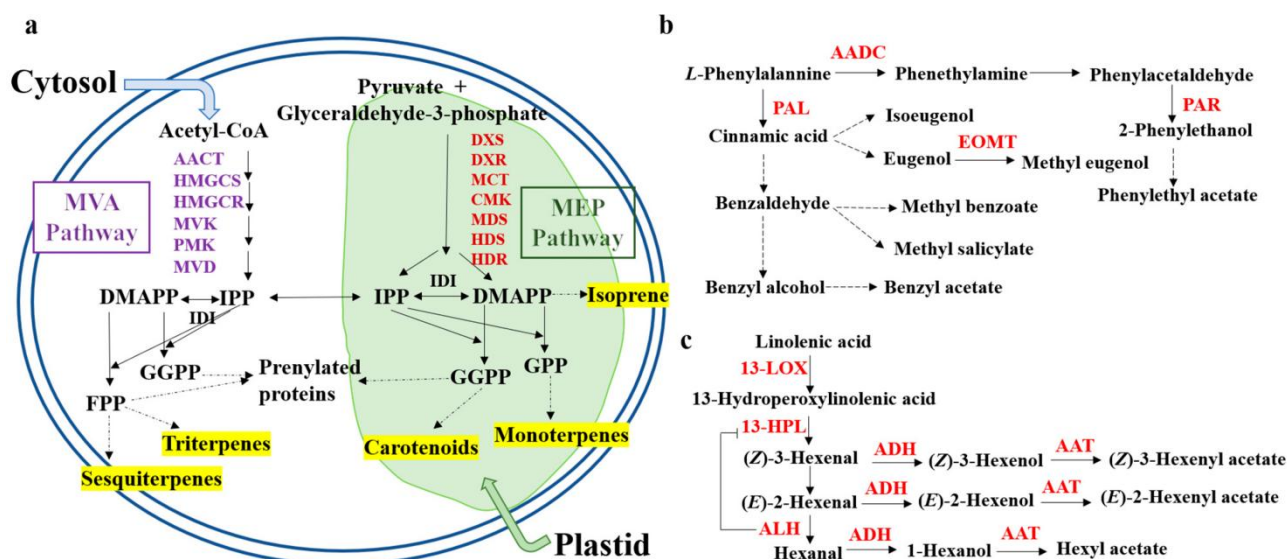


Figure 2 Synthetic pathways of terpenoids (a), phenylpropane (b), and fatty acid derivatives (c) related to the formation of aroma components (Adopted from Lu et al., 2024)

Image caption: AACT, acetyl-CoA C-acetyltransferase; HMGCS, hydroxymethylglutaryl-CoA synthase; HMGR, hydroxymethylglutaryl-CoA reductase; MVK, mevalonate kinase; PMK, phosphomevalonate kinase; MVD, mevalonate diphosphomevalonate decarboxylase; DXS, 1-deoxy-D-xylulose-5-phosphate synthase; DXR, 1-deoxy-D-xylulose-5-phosphate reductoisomerase; HDS, 4-hydroxy-3-methylbut-2-enyl-diphosphate synthase; HDR, 4-hydroxy-3-methylbut-2-en-1-yl diphosphate reductase; IDI, isopentenyl-diphosphate delta-isomerase; GPP, geranyl diphosphate synthase; GGPP, geranylgeranyl diphosphate synthase; DMAPP, dimethylallyl diphosphate; IPP, isopentenyl diphosphate; AADC, aromatic L-amino acid decarboxylase; PAL, phenylalanine ammonia-lyase; EOMT, eugenol O-methyltransferase; PAR, phenylacetaldehyde reductase; 13-LOX, 13-lipoxygenase; 13-HPL, 13-hydroperoxidase lyase; ADH, ethanol dehydrogenase; AAT, alcohol acyltransferase (Adopted from Lu et al., 2024)

Verifying the roles of these genes isn't easy. Recreating the exact natural conditions where these aroma compounds are produced is tricky, making it hard to run controlled experiments that confirm how specific genes behave in real-time.

Constructing a comprehensive genetic network that captures how all these genes interact and regulate each other. Events like paleopolyploidization and durian-specific gene duplication only make things more complicated, introducing redundancy and potential shifts in gene function (Ho and Bhat, 2015; Teh et al., 2017). And to map it all out accurately, researchers need cutting-edge bioinformatics tools and solid transcriptomic data-not just to build the models, but to interpret them in a meaningful way.

7.2 Multiomics and systems biology

The research of durian aroma should not only stay on genes, but also be studied from the perspective of the whole biology. Integrate different kinds of "omics" data: genomics, transcriptomics, metabolomics, and so on, each offering unique insights, but put them together to have a unified, coherent understanding of how aromas are formed.

The real problem is that there's too much data, and it's all really different. Some are in different formats. Some come from different time points. And there are all kinds of different molecules. This makes it hard to put the data together. We can use some strong algorithms and computer tools to help (Lu et al., 2024), but if we want to find the key genes and pathways, we have to do this step.

Systems biology simulates how individual substances work together to simulate how the pathways of terpenoids, phenylalanine, and fatty acids interact to form the aroma of durian (Lu et al., 2024). But building accurate predictive models of these interactions is difficult, with well-collated data and computational power, which is somewhat lacking in current durian studies.

7.3 Emergence of new technologies

Because of breakthroughs in biotechnology, the future of research is full of hope. Tools such as CRISPR-Cas9 make it possible to precisely tune the genes responsible for aroma, allowing researchers to more directly test gene function and design durian scents with customized odor signatures (Teh et al., 2017), which can reduce durian's distinctive odors at the DNA level.

High-throughput phenotypic analysis makes it faster and easier to screen durian varieties for specific aroma characteristics. Breeders can more effectively identify and breed better-smelling durians (Belgis et al., 2017). But also with the power of artificial intelligence and machine learning, these tools can help make sense of large and complex omics datasets, reveal hidden gene interactions, and even predict how changes in individual genes affect aromas. By using artificial intelligence to model these networks, researchers can create smarter breeding strategies to scientifically improve the quality of durians to meet consumer expectations.

8 Concluding Remarks

Research into durian has uncovered some fascinating insights into how its famously bold aroma is made-especially the biosynthesis and regulation of sulfur-containing volatiles, which are the main drivers of that unmistakable scent. Early genomic studies of *Durio zibethinus* have pinpointed key metabolic pathways, along with amplified genes-most notably methionine γ -lyase (MGL)-that are closely linked to the production of volatile sulfur compounds (VSCs). What's more, the upregulation of pathways related to sulfur metabolism, ethylene signaling, and lipid processes hints at a deeply interconnected regulatory network behind durian's aroma. When comparing different durian varieties, it's clear that both the diversity and amount of sulfur compounds make a major impact on how each fruit smells. Certain compounds, in fact, are directly tied to those distinct, sometimes polarizing, odor profiles.

Learning how durian makes those strong-smelling sulfur things isn't just for fun or science. It can also help us make durian smell and taste better. If we find the right genes and see how they work, we can keep the good smells and get rid of the bad ones. Once we know this, breeders can use the info to grow new durian types that more people will enjoy. This could also help durian sell in more places. And it's not only about durian. We can use the same method for other fruits too. That's why this research is helpful not just for durian, but for farming and food tech in general.

Further research could be conducted to see which genes and chemical reactions are involved in this process, particularly transcription factors and epigenetic regulation that control gene expression. Now the genome and transcriptome technology is more and more advanced, the future may find more ways of regulation, may also find new directions for improvement. In practice, molecular markers can be used to help breeders pick out durians with specific scents. Gene editing can also further regulate the production of sulfur. Through these methods, the durian's flavor can be improved and it can be more popular in the international market.

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Conflict of Interest Disclosure

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