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REVIEW

Applications of omics in deciphering the unique traits of durian, the king of fruits

Chee-Wei Yew[1] · Ching-Ching Wee[1]

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Abstract

Durio zibethinus, commonly known as the "king of the fruits," is widely cultivated in Southeast Asia, contributing significantly to the region's economy. In addition to commercial cultivars, numerous local edible durian species are also found in these countries. With the rapid advancement of omics technologies, extensive studies have been conducted on durians using various omics approaches. To date, omics studies have primarily focused on commercial durians (*D. zibethinus*), with relatively less emphasis on endemic, minimally commercialized local durians (*Durio* sp.). As such, this review summarizes all omics studies performed on both commercial cultivars and local durians of different species. In addition, it explores their applications in evolutionary studies, understanding the fruit ripening mechanism, identifying genetic markers for breeding, and uncovering their pharmaceutical and industry potential, as well as post-harvest processing. Furthermore, the current limitations of durian omics studies and future research prospects are discussed.

Key message

This review highlights omics-based insights into durian's evolution, ripening, breeding, and industrial value, offering integrated approaches for future research and biotechnology applications.

Keywords Applications · Durian · Omics · Musang King · Monthong

Introduction

Durian (*Durio zibethinus*), known as the "king of the fruits," is a highly prized tropical fruit cultivated in Southeast Asia, in countries such as Thailand, Malaysia, and Indonesia (Subhadrabandhu and Ketsa 2001). Recent statistics indicate that global durian trade has expanded significantly, increasing more than tenfold from 80,000 tonnes in 2003 to 870,000 tonnes in 2022 (FAO 2023). Durian holds immense importance in agriculture and industry owing to its economic value, nutritional properties, and medicinal potential (Aziz and Mhd Jalil 2019).

A total of 28 species in the *Durio* genus were reported in 2020 (Ketsa et al. 2020), including several local and underutilized durian species such as *D. dulcis*, *D. grandiflorus*, *D. graveolens*, *D. kutejensis*, *D. oxleyanus*, and *D. testudinarius*. These local durians are primarily found in East Malaysia (Sabah and Sarawak), Brunei, and Kalimantan. Among them, *Durio kinabaluensis* is endemic to Sabah. Unlike commercial durians, these local species are not widely cultivated in orchards but rather grown in village backyards or found in the wild. Documentation on their morphology (Ng et al. 2020; Sujang et al. 2023) and genetic profile is scarce, with limited information available mainly on social media platforms and personal blogs.

With advancements in omics technologies, multi-omics research encompassing genomics, transcriptomics, proteomics, and metabolomics, has become instrumental in enhancing the understanding of durian biology, from growth and development to its nutritional (Ho and Bhat 2015) and medicinal properties (Aziz and Mhd Jalil 2019). This review aims to provide an updated overview of omics and multi-omics research on durian and its potential applications in improving agronomic traits and marker-assisted breeding. A literature search was conducted using Scopus, PubMed, and Google Scholar databases to identify published research on

✉ Ching-Ching Wee
ccwee@ums.edu.my

[1] Biotechnology Research Institute, Universiti Malaysia Sabah, 88400 Kota Kinabalu, Sabah, Malaysia

durian omics. In addition, the National Center for Biotechnology Information (NCBI) was searched to retrieve publicly available durian sequencing data. This is particularly important for gathering comprehensive data, as it was found that not all sequencing data are published in peer-reviewed manuscripts despite the data having been deposited in GenBank.

Types of omics performed on durians

Omics technologies (Fig. 1), including genomics, transcriptomics, proteomics, and metabolomics, are widely employed to investigate the genes, mRNA, proteins, and metabolites, respectively, within an organism. These approaches facilitate the identification of traits pertaining to quality and disease resistance. To date, omics studies have primarily focused on different cultivars of commercial durians (*D. zibethinus*), with relatively less emphasis on local durian species (Tables 1 and 2). Commercial durian cultivars include Musang King (MK) from Malaysia, and Phuangmanee (PM), Chanee (CH), Monthong (MT), Kanyao (KY), and Chanthaburi 1 (a hybrid bred of CH and MT) from Thailand.

Genomics

The genome, encompassing both nuclear and organelle genomes, serves as the genetic blueprint of an organism. Deciphering this blueprint via genome sequencing and analysis provides valuable insight into the genetic structure (Misra et al. 2017), identifies genes linked to specific traits (Zhao et al. 2018), detects genetic variations within and across species (Hufford et al. 2021), and aids evolutionary studies (Soltis and Soltis 2021). There are two types of large-scale sequencing technologies: short-read and long-read sequencing. Short-read sequencing platforms, such as Illumina and MGI Tech, generate reads averaging 100–150 bp in length (Kim et al. 2021). In contrast, long-read sequencing platforms such as PacBio and Oxford Nanopore produce significantly longer reads, typically exceeding 15 kb (Bayega et al. 2018). However, when it comes to eukaryotic genomes, long-read sequencing can only assemble the genome up to the scaffold level. Achieving chromosome-level assemblies

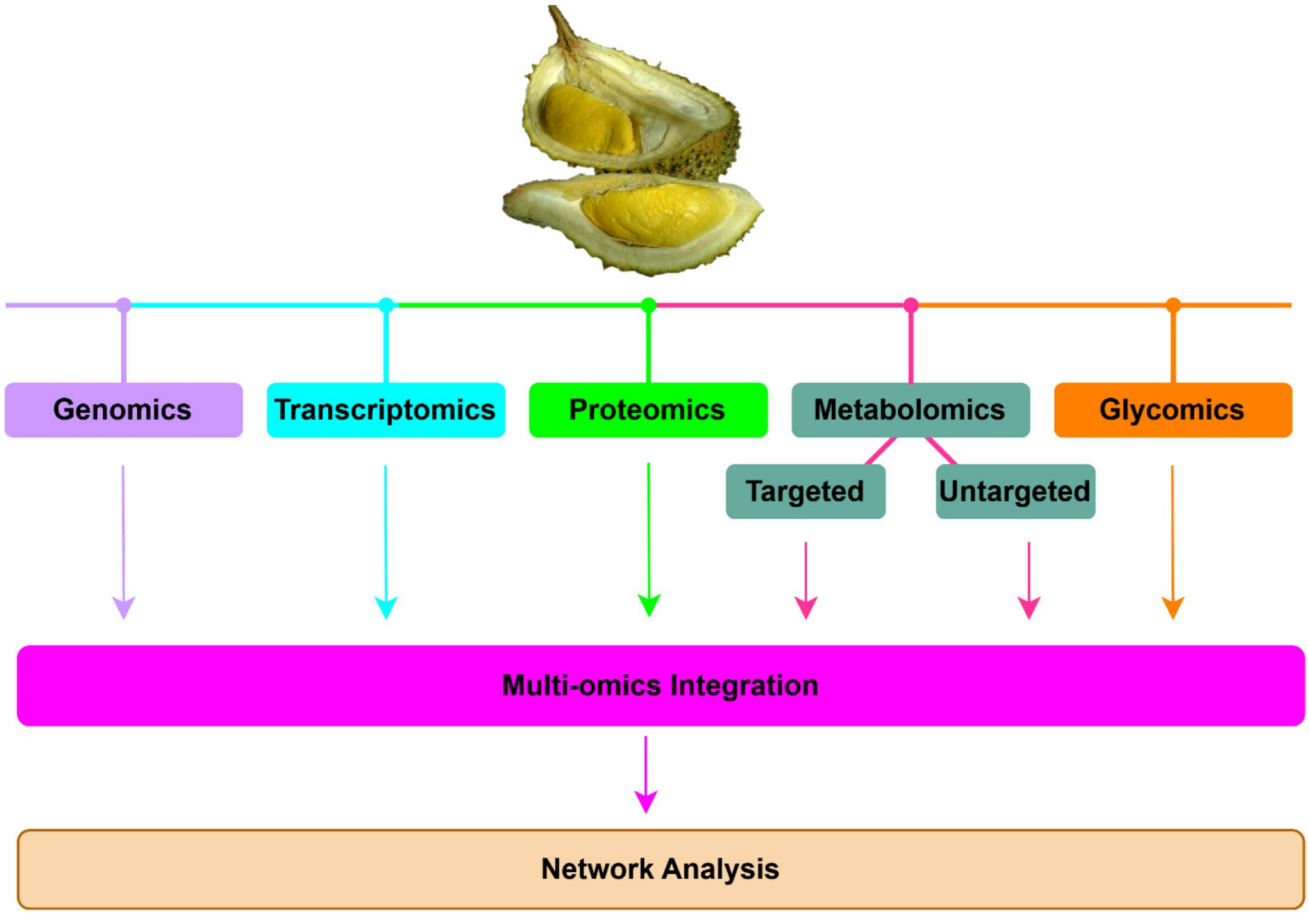

Fig. 1 Different types of omics performed on durian

Table 1 A summary of the application of omics in characterizing durian traits

Species	Cultivar(s)	Origin	Part	Platform/method	Main findings	References
Genomics						
D. zibethinus	MK	TH	Leaves	*In silico*	Identification of 2586 resistance gene analogs (RGAs) in durian through genome-wide analysis	Cortaga et al. 2022
D. testudinarius		ID	Leaves	*In silico*	Development of simple sequence repeat markers using existing *D. testudinarius* genomic data from NCBI	Magandhi et al. 2025
Transcriptomics						
D. zibethinus	D24	MY	Aril	Illumina▪	Genes associated with cell wall softening were significantly upregulated during fruit ripening	Husin et al. 2022
D. zibethinus	D24	MY	Aril	Illumina▪	Identification of 280 unknown transcripts and novel exons involved in fruit development and ripening, providing new insights into durian gene expression and potential genetic improvement strategies	Husin 2024
D. zibethinus	D24, D99, D160, D168, D197, D200	MY	Aril	Illumina°	The five most common pathways identified by KEGG in the comparative transcriptomics study of six Malaysian durian cultivars were fatty acid biosynthesis, starch and sucrose metabolism, carotenoid biosynthesis, phenylpropanoid biosynthesis, and galactose metabolism	Jantan et al. 2024
D. zibethinus	MT	TH	Aril	*In silico*	*Dz*HD-ZIP1.8 is bound to *Dz*MGL, which is the key enzyme controlling volatile sulfur compounds production	Pinsorn et al. 2024
D. zibethinus	CN, PM, MK, KY	TH	Aril	*In silico*	*Dz*ARF2A mediates fruit ripening by regulating ethylene biosynthetic genes in an auxin-dependent manner	Khaksar and Sirikantaramas 2020
D. zibethinus	MT, MK, PM	TH	Aril	*In silico*	Development of nine gene-based InDel markers associated with drought-responsive genes in durians, which successfully distinguished 24 Thai durian genotypes into four groups on the basis of genetic distance	Sathapondecha et al. 2024
Species	Cultivar(s)	Origin	Part	Method(s)	Main findings	References
Proteomics						
D. zibethinus	MK	MY	Aril	2D-PAGE, MALDI-TOF/TOF–MS/MS	Freezing downregulated 15 proteins and upregulated 3 proteins (cysteine synthase isoform, *S*-adenosylmethionine synthase, and isoflavone reductase-like protein) in Musang King durian pulp after 1 year of storage	Tan et al. 2021
D. zibethinus	Unknown	TH	Seed	N-terminal sequencing, MS	*Dz*TI-4 found in durian seeds utilizes a unique β1–β2 loop to bind to trypsin, showing it a potential nontoxic alternative to soybean trypsin inhibitor in cell culture	Deetanya et al. 2024
Metabolomics						
D. zibethinus	D2, D24, D101	MY	Aril	GC–MS	Different durian cultivars have unique volatile profiles responsible for their distinct aromas	Chin et al. 2007
D. zibethinus	D2, D24, MDUR78, D101, Chuk	MY	Aril	GC-TOFMS	PCA analysis on the basis of 29 volatile flavor compounds successfully differentiates the five Malaysian durian cultivars	Voon et al. 2007a
D. zibethinus	MK, D24, D88, IOI, XO, Red Prawn, Black Thorn	MY	Aril	HPLC*, GC–MS	The highest β-carotene content was detected in Black Thorn, which has orange pulp	Tan et al. 2020
D. zibethinus	D200, MK, MT	MY, TH	Aril	GC–MS, UHPLC, HPAEC-PAD*	The aril of Black Thorn (27) contained the fewest volatile compounds compared with Musang King (36) and Monthong (38)	Xiao et al. 2022a
D. zibethinus	MK	MY	Aril	GC-O, GC–MS	Ethyl propyl sulfide, dipropyl sulfide, methyl propyl trisulfide, and hexyl hexanoate were detected in durian for the first time, paving a new way for understanding the aroma production mechanism	Xiao et al. 2022b
D. zibethinus	D24	MY	Aril	GC–TOFMS	The ester compounds decrease significantly after 1 week of storage at 4 °C	Voon et al. 2007b

Table 1 (continued)

Species	Cultivar(s)	Origin	Part	Method(s)	Main findings	References
D. zibethinus	D24	MY	Aril	GC-TOFMS	Freeze-drying and spray-drying significantly altered durian pulp's volatile profile, reducing volatiles by 71–97% and 98–99%, respectively	Chin et al. 2008
D. zibethinus	D24	MY	Aril	GC–TOFMS	Gum Arabic provides the highest volatile retention in spray-dried durian powder	Chin et al. 2010
Species	Cultivar(s)	Origin	Part	Method(s)	Main findings	References
D. dulcis		MY	Aril	GC–MS	*D. dulcis* is rich in esters, ketones, sulfur compounds, and volatile alcohols	Hasmadi et al. 2021
D. graveolens	Yellow-fleshed	MY	Aril	GC*	Unsaturated fatty acids (69.7%) were higher than saturated fatty acids (30.3%), with oleic acid (22.2%) being the most abundant unsaturated fatty acids	Nasarud-din et al. 2013
D. kutejensis, *D. lowianus*		MY	Aril	HPLC*	*D. kutejensis* had a higher total carotenoid content than *D. lowianus*	Khoo et al. 2008
D. dulcis		MY	Aril	GC–MS	*D. dulcis* exhibits the strongest sweet and grassy aroma while *D. kutejensis* has the mildest aroma	Sujang et al. 2023
D. graveolens	Yellow-fleshed, orange-fleshed, red-fleshed					
D. kutejensis						
D. oxleyanus						
D. zibethinus	Terung iban					
D. zibethinus	MT	TH	Aril	GC–MS, GC-GC–MS*	The key sulfur-containing volatiles responsible for the aroma of Monthong durian is ethaethiol (with the highest odor activity value), methanethiol, propane-1-thiol, and hydrogen sulfide	Li et al. 2017
D. zibethinus	CN, MT	TH	Aril	CE–TOF/MS, HPLC	Metabolite profiles in durian are influenced by cultivar differences and harvest years	Pinsorn et al. 2018
D. zibethinus	MT	TH	Aril	HPLC*	Ripe durian pulp possesses the highest levels of γ-EC and considerable glutathione content, but their level decreased significantly in processed products	Singcha et al. 2024
D. zibethinus	KY, CN, MT, CH1	TH	Aril	GC–MS	Chanthaburi, a hybrid bred of "Chanee" and "Monthong," had fewer volatiles than other Thai durian cultivars but inherited ester compounds from its parent cultivars	Aschari-yaphotha et al. 2021
D. zibethinus	MT	TH	Aril	GC–MS, GC-GC–MS	Identification of 24 new odor-active compounds with ethyl(2S)-2-methylbutanoate, ethyl cinnamate, and 1-(eth-ylsulfanyl)ethanethiol contributing to the highest aroma impact	Li et al. 2012
Species	Cultivar(s)	Origin	Part	Method(s)	Main findings	References
D. zibethinus	MT	TH	Aril	UHPLC-ESI-QTOF-MS/MS, GC–MS	Early immature durian fruit is a novel source of bioactive procyanidin with antioxidant and anti-glycation properties	Pewlong et al. 2025
D. zibethinus	MT, KT, CN, KY	TH	Aril	LC–MS/MS*	Ethionine was confirmed present in durian pulp and iden-tified as a precursor to ethanethiol, contributing to its odor	Fischer and Steinhaus 2019
D. zibethinus	MT	TH	Aril	GC–MS	Heating and NaCl treatment reduce sulfur volatiles and increase non-sulfur compounds	Laohakun-jit et al. 2007
D. zibethinus	CN, MT	TH	Aril	GC–MS	Monthong shows temporary suppression of sulfur-contain-ing volatiles with ethephon and 1-MCP treatment, while 1-MCP treatment inhibits sulfur production in Chanee	Maninang et al. 2011
D. zibethinus	MT, CH1	TH	Aril	GC–MS	Alcohol acetyltransferase (AAT) enzymes extracted from Monthong and Chanthaburi 1 cultivars show a higher affinity for 3-methyl-1-butanol and hexanol as alcohol substrates	Aschari-yaphotha et al. 2024
D. zibethinus	CN, MT	TH	Aril	CE–TOF/MS, LC-QTOF/MS, HPLC*, IC*, SH-GC–MS*	Higher cysteine content might lead to an increased pro-duction of VSCs in Chanee	Pinsorn et al. 2023

Table 1 (continued)

Species	Cultivar(s)	Origin	Part	Method(s)	Main findings	References
D. zibethinus	Unknown	ID	Aril	GC–MS	Tempoyak fermented with *Pediococcus acidilactici* UP02 showed an increase in non-sulfur compounds, non-volatile acidity, and organic acids contents	Yuliana and Garcia 2009
D. zibethinus	Unknown	ID	Aril	GC–MS	Freeze-drying significantly affected the volatilome of durian, with losses of key volatile compounds ranging from 78–95% (30 h) and 0–100% (36 h), impacting the flavor profile	Darniadi et al. 2021
D. kutejensis, D. zibethinus		ID	Aril	GC–MS	*D. kutejenisis* has fewer sulfur and ester compounds than *D. zibethinus*, resulting in a milder aroma	Belgis et al. 2017
D. zibethinus	Atabrine	PH	Aril	GC–MS	Fermented durian showed a significant decrease in sulfur volatiles, such as diethyl trisulfide and *N*-dimethylthio-isophinyl-3-amino, while generating new esters, alcohols, and carboxylic acids, influencing the final aroma profile	Neti et al. 2011
Species	Cultivars	Origin	Part	Method(s)	Main findings	References
D. zibethinus	Criwik	ID	Leaves	GC–MS	Identification of 11 bioactive compounds, including squalene, ethyl iso-allocholate, neophytadiene, and phytol which are known for their pharmaceutical properties	Sawitri et al. 2025
D. zibethinus	MT	TH	Peduncles	HPLC-RI*, LC–MS/MS (QTRAP)*, QTOF, NMR	Asparagine could serve as a potential new biochemical marker for determining durian maturity	Charoensumran et al. 2021
D. zibethinus	MT	ID	Shell	UPLCLTQ-Orbitrap-MS/MS	Durian shell extract contains phenolic compounds that exhibit strong antioxidant properties, reduce oxidative damage in HepG2 cells, and inhibit apoptosis through mitochondrial pathway regulation	He et al. 2023
D. zibethinus	D175	MY	Shell	UHPLC–MS/MS	Identification of 20 bioactive compounds through UHPLC–MS/MS profiling of 100% ethanolic durian shell extract highlights its potential for pharmacological applications	Hatim et al. 2024
D. zibethinus	D197, D168, D24, D13	MY	Shell	GC–MS	Butanoic acids are the major compound in the essential oils of durian peels in all four cultivars	Zamakshshari et al. 2022
D. zibethinus	RI6	VN	Shell	HPLC*, LC/MS, QTOF	Identification of flavonoid-rich fraction F2, with the highest quercetin content, which possesses strong bioactivities	Nguyen et al. 2024a, b
D. zibethinus, *D. kutejensis*	Unknown	ID	Wood Bark	HRESIMS*, HREIMS*, HPLC*	Two new triterpenoids (methyl 27-*O*-trans-caffeoylcyl-icodiscate and methyl 27-*O*-cis-caffeoylcylicodiscate) and one new phenolic compound were identified from *D. zibethinus*. In addition, two new triterpenoids (3β-*O*-trans-caffeoyl-2R-hydroxyolean-12-en-28-oic acid and 3β-*O*-trans-caffeoyl-2R-hydroxytaraxest-12-en-28-oic acid) were identified from *D. kutejensis*	Rudiyansyah and Garson 2006

°|log2(FC)|≥1 and *p*.adj≤0.05.

▪|log2(FC)|≥1.5 and *p*.adj≤0.05.

*Targeted metabolomics

MK, Musang King; PM, Phuangmanee; CN, Chanee; MT, Monthong; KY, Kanya; CH1, Chanthaburi 1; KT, Krathum; MY, Malaysia; TH, Thailand; IN, Indonesia; VN, Vietnam; CE–TOF/MS, capillary electrophoresis-time of flight mass spectrometry; GC, gas chromatography; GC–MS, gas chromatography–mass spectrometry; GC-GC–MS, two-dimensional heart-cut gas chromatography–mass spectrometry; GC-O, gas chromatography–olfactometry; GC–TOFMS, gas chromatography–time of flight mass spectrometry; HPAEC-PAD, high-performance anion exchange chromatography with pulsed amperometric detection; HPLC, high-performance liquid chromatography; HRESIMS, high-resolution electrospray ionization mass spectrometry; HREIMS, high-resolution electron ionization mass spectrometry; IC, ion chromatography; LC–QTOF/MS, liquid chromatography–quadrupole time-of-flight mass spectrometry; LC–MS/MS (QTRAP), liquid chromatography–tandem mass spectrometry (ion-trap triple quadrupole); LC–MS-QTOF, liquid chromatography–mass spectrometry analysis with quadrupole time-of-flight; LC/MS, liquid chromatography–mass spectrometry; MALDI-TOF/TOF–MS/MS, matrix-assisted laser desorption/ionization time-of-flight mass spectrometer; MS, mass spectrometry; NMR, nuclear magnetic resonance; PS-MS, paper spray mass spectrometry; QTRAP, ion-trap triple quadrupole; QTOF, quadrupole time-of-flight; SHGC-O, static headspace gas chromatography–olfactometry; SH-GC–MS, static headspace gas chromatography–mass spectrometry; SPME–GC–MS, headspace solid-phase microextraction coupled to fast gas chromatography–mass spectrometry; TLC, thin layer chromatography; UHPLC, ultra-high-performance liquid chromatography; UHPLC-ESI-QTOF-MS/MS, ultra-high-performance liquid chromatography coupled with electrospray ionization quadrupole time-of-flight mass spectrometry; UHPLC–MS/MS, ultra-high-performance liquid chromatography coupled with mass spectrometry; UHPLC-LTQ-Orbitrap-MS/MS, ultra-high-performance liquid chromatography coupled with linear ion trap quadrupole orbitrap mass spectrometry

Table 2 Integration of multi-omics for in-depth analyses of durian traits

Species	Cultivar(s)	Origin	Part	Omics	Platform(s)/ Method(s)	Main findings	References
D. zibethinus	MT	TH	Aril	G, T, NeA	*In silico*	*Dz*CAMTA3 and *Dz*CAMTA8 coordinate durian fruit ripening by acting as ethylene-induced transcriptional activators while antagonistically interacting with auxin to regulate key ripening pathways	Iqbal et al. 2021
D. zibethinus	MT	TH	Aril	M, T	CE–TOF/MS, GC–TOF/MS, HPAEC-PAD*, BGI●	Durian ripening is characterized by increased sucrose, malate, succinate, and most amino acids, supported by transcriptomic analysis showing increased expression of key genes involved in sugar metabolism, glycolysis, tricarboyxlic acid (TCA) cycle, and amino acid pathways	Sangpong et al. 2021
D. zibethinus	MK, MT, PM	TH, MY	Aril, stalk, leaves,	G, T, M*	Illumina, PacBio, Hi-C, GC–MS●	There is a potential association between ethylene biosynthesis and the production of volatile sulfur compounds in durian	Teh et al. 2017
D. zibethinus	MT	TH	Aril	T, M	*In silico*, LC–MS/MS	*Dz*MYB1 interacts with *Dz*bHLH1 and regulates flavonoid biosynthesis by activating the expression of chalcone synthase, chalcone isomerase, and flavanone 3-hydroxylase	Weerawanich et al. 2024
D. zibethinus	MT	TH	Aril	T, NeA	*In silico*	Ethylene and auxin regulate durian fruit ripening by regulating the expression of *Dz*ERF9 (a positive regulator of ACS and ACO) and *Dz*ERF6 (a negative regulator of ACS and ACO)	Khaksar and Sirikantaramas 2021
D. zibethinus	MT	TH	Aril	T, M	*In silico*, LC–MS/MS	*Dz*MYB2 and DzMYB3 act as an activator and repressor, respectively, in phenylpropanoid regulation	Weerawanich and Sirikantaramas 2024
D. zibethinus	MT, CN, PM	TH	Aril	G, T	*In silico*	*Dz*NCED5a regulates ABA biosynthesis in durian ripening	Tantisuwanichkul and Sirikantaramas 2024
D. zibethinus	MT	TH	Aril	G, T	*In silico*	*Dz*AGL6-1 regulates carotenoid biosynthesis in durian by activating PSY expression	Tantisuwanichkul et al. 2024
D. zibethinus	MT, CN	TH	Aril	G, T	*In silico*	*Dz*Dof2.2 regulates auxin biosynthesis, contributing to the faster ripening of Chanee compared with Monthong	Khaksar et al. 2019
Species	Cultivar(s)	Origin	Part	Omics	Platform(s)/ method(s)	Main findings	References
D. zibethinus	MT, KY, CN, PM	TH	Aril	G, T	*In silico*	Phytohormone-associated cytochrome P450s (CYP88 and CYP707) regulate fruit ripening by regulating gibberellin and abscisic acid biosynthesis, contributing to differences in post-harvest ripening speed among fast- (CN and PM) and slow-post-harvest (MT and KY) ripening cultivars	Suntichaikamolkul et al. 2021
D. zibethinus	CN	TH	Aril	G, T	*In silico*	*Dz*LAP1 exhibits Cyc-Gly dipeptidase activity and may play a role in sulfur metabolism and ethylene-related volatile production during fruit ripening	Panpetch and Sirikantaramas 2021
D. zibethinus	PM, MT, KD	TH	Leaves	G, T	Illumina, 10× Genomics	The draft pangenome showed that genome evolution patterns are different between Malaysian and Thai durians	Nawae et al. 2023
D. zibethinus	PM, MT, KD	TH	Leaves	T, NeA	Illumina▪	The durian cultivar Puangmanee exhibits the highest resistance to *Phytophthora palmivora*, likely owing to the high expression of genes encoding chitin response proteins	Nawae et al. 2024

Table 2 (continued)

Species	Cultivar(s)	Origin	Part	Omics	Platform(s)/ method(s)	Main findings	References
D. zibethinus	KY	TH	Leaves	G, T	Illumina, Oxford Nanopore, PacBio, Dovetail Genomics	High expression of shikimate *O*-hydroxycinnamoyl transferase (HCT), caffeoyl-CoA *O*-methyltransferase caffeoyl-CoA *O*-methyltransferase (CCoA-omet), and peroxidase (PER) in the fruit peel during fruit ripening suggests their role in durian thorn formation through lignin biosynthesis	Li et al. 2024a, b
D. zibethinus	Unknown	MY	Seed	Ld, Gly, M	HPLC-RI*, GC–FID, SEC-MALS	Durian seed gum is primarily composed of galactose and glucose	Amid et al. 2012

$|\log_2(FC)| \geq 1.5$ and $p.adj \leq 0.05$

$|\log_2(FC)| \geq 2$ and $p.adj \leq 0.05$

MK, Musang King; PM, Phuangmanee; CN, Chanee; MT, Monthong; KY, Kan Yao; MY, Malaysia; TH, Thailand. G, genomics; T, transcriptomics; P, proteomics; M, metabolomics; NeA, network analysis; Ld, lipidomics; Gly, glycomics; CE–TOF/MS, capillary electrophoresis-time of flight/mass spectrometry; GC–FID, gas chromatography–flame ionization detection; GC–MS, gas chromatography–mass spectrometry; GC–TOF/MS, gas chromatography-time of flight/mass spectrometry; HPAEC-PAD, high-performance anion exchange chromatography with pulsed amperometric detection; HPLC-RI, high-performance liquid chromatography with refractive index detection; LC–MS/MS, liquid chromatography–tandem mass spectrometry; SEC-MALS, size exclusion chromatography with multi-angle light scattering

*Targeted metabolomics

requires additional approaches, such as chromosome conformation capture (Hi-C) technologies from Dovetail Genomics (Moll et al. 2017) and optical mapping from Bionano (Belser et al. 2018).

The first draft genome of *D. zibethinus* cultivar Musang King from Malaysia was reported by Teh et al. (2017). This genome was sequenced using the PacBio RSII platform, with scaffolding performed using Dovetail Genomics, generating a total of 30 chromosome-scale pseudomolecules that summed up to 738 Mbp. This work discovered important durian-specific paleopolyploidization events, which have expanded into four copies. Furthermore, re-analysis of this genome found hexaploidization instead of four in the durian lineage (Wang et al. 2019). Since these genes produce volatile sulfur compounds (VSCs), this genomic structure explains the generation of the characteristic durian aroma, which is considered malodorous by some consumers, but is a unique aroma by durian lovers. In 2019, the Musang King genome was integrated into the MaGenDB database (http://magen.whu.edu.cn) alongside genome data from 12 other Malvaceae species (Ji et al. 2025; Wang et al. 2020).

Although the Musang King is a draft genome, it serves as the reference genome for the subsequent resequencing and comparative genomic studies on other cultivars. Pangenome analyses of three Thai durian cultivars (Kradumthong, Monthong, and Puangmanee) found a total of 49,631 genes, of which 39 genes are either present or absent (PAV genes) among these cultivars (Nawae et al. 2023). Meanwhile, the Musang King genome was found to harbor a much higher number of copy number variations of these PAV genes, indicating that the underlying gene structure determines the uniqueness of each cultivar. In 2024, the cultivar Kan Yao, originating from Thailand, was sequenced and de novo assembled to obtain a 777.8 Mb haploid genome made up of 28 pseudochromosomes. This was achieved through the use of a combination of four sequencing technologies, i.e., PacBio, Oxford Nanopore, Illumina, and Dovetail Genomics (Li et al. 2024a, b). Interestingly, a large portion of duplicated genes is enriched in the lignin biosynthesis module of the phenylpropanoid pathway, which could have resulted in the formation of the hard thorns of durian fruits. At the same time, a high-quality chromosome-scale haploid genome of the same Kan Yao cultivar was resolved by Ji et al. (2025). Two haploid genomes, consisting of up to 53,125 functional genes, were assembled and characterized as two haplotypes from which structural variations could be determined. In addition, 19 out of 28 chromosomes were assembled with no gaps. These findings have thus turned the current genetic variations analyses into genomic structure analyses. It serves not only as a benchmark for genomic analyses but also as a reference from which genetic markers could be derived for the molecular breeding of durians.

Transcriptomics

Genomic analyses will identify genes and their variations in a genome, but the gene functions can only be inferred when the gene is heterogeneously expressed and analyzed in clearly-defined spatial–temporal conditions. Transcriptomic analyses are thus aimed at identifying and quantifying sets of differentially expressed genes out of the total genes in a genome. Hence, transcriptomics is the study of all RNAs, including isoforms, present in a cell or a population of cells (Choi et al. 2021). As long-read sequencing can capture full-length transcripts, it enables the unambiguous identification of different isoforms produced from alternative splicing

events (Wright et al. 2022). In fruit research, transcriptomics studies primarily focus on gene expression across different fruit cultivars, fruit organs, developmental stages, disease-resistance strains, and fruit ripening (Hu et al. 2021; Ochoa-Alejo et al. 2024; Yang et al. 2022).

While the Kan Yao cultivar was sequenced using both PacBio and long-read sequencing platforms, other durian transcriptome studies primarily used short-read sequencing platforms such as Illumina or MGI Tech (Supplementary File 2). Notably, there have been more transcriptomic studies on durian than genomic studies (Supplementary Files 1 and 2). Most durian transcriptomics studies primarily focus on gene expression studies (Tables 1 and 2) and typically use triplicate samples (Supplementary File 2), except for the study involving six Malaysian durian varieties (Jantan et al. 2024). However, the threshold used to identify differentially expressed genes varied across different studies (Tables 1 and 2).

The first durian transcriptome data originated from the Musang King (arils, roots, stems, and leaves), Monthong (aril), and Puang Manee (aril) cultivars (Teh et al. 2017). Comparative transcriptomic analysis has been conducted between (1) fruit arils and other plant organs such as roots, stems, and leaves; (2) durian arils and arils of other species; and (3) among different durian cultivars, including Musang King, Monthong, and Puang Manee fruit (Teh et al. 2017). These studies revealed that sulfur-related, ripening-associated, and flavor-related processes are significantly upregulated in durian arils compared with non-aril organs (Teh et al. 2017). Comparative analysis has also been conducted on the Monthong cultivar from Thailand across five ripening stages (Suntichaikamolkul et al. 2021). In the cultivar D24, transcriptomic analysis showed that cell-wall-softening genes, such as polygalacturonase and pectin-modifying enzymes, are upregulated during fruit ripening (Husin et al. 2022). In addition, transcriptomic analysis of six Malaysian durian cultivars, D24, D99, D160, D168, D197, and D200, at two developmental stages (matured and ripe) confirmed that fatty acid biosynthesis, starch and sucrose metabolism, carotenoid biosynthesis, phenylpropanoid biosynthesis, and galactose metabolism are the most common pathways identified using Kyoto Encyclopedia of Genes and Genomes (KEGG) analysis (Jantan et al. 2024). Volatile sulfur compounds (VSCs), such as ethanethiol produced via the methionine γ-lyase (*MGL*) gene family, are regulated by the transcription factor homeodomain associated with a leucine zipper motif (HD-ZIP) (Pinsorn et al. 2024). These pathways are hypothesized to have contributed to the development of the unique creamy texture and aromatic scent of durians during fruit ripening. Besides the differential expression study, transcriptomic analysis of the D24 cultivar enabled the identification of previously unknown transcripts and novel exons involved in fruit development and ripening (Husin 2024).

Transcriptome analysis of the Kan Yao cultivar on multiple samples from stem, leaf, flower, and different fruit tissues at different days after flowering has collectively identified ~92,000 transcripts, which derive from about 50,400 coding genes (Ji et al. 2025). Subsequent annotation found about 5400 noncoding genes, including 280 microRNAs. However, no further downstream analyses were performed, despite the findings from this work being valuable for future analysis of expressed genes regulating fruit development and ripening. To complement this, pan-transcriptomic analyses from the leaves of five cultivars, i.e., KD, MT, PM, MK, and Salika (SK), are useful to identify sets of expressed genes in all cultivars (named as core orthologous genes) (Nawae et al. 2023). Whereas, unique sets of genes that are only found in just one cultivar are an enrichment of accessory genes that determine the specific characteristics of each cultivar. These include plant invertase/pectin methylesterase inhibitor (which play a role in flower formation) and aminocyclopropane-1-carboxylic acid (ACS), involved in fruit ripening, and genes from the lignin biosynthesis pathway associated with thorn formation (Li et al. 2024a, b; Nawae et al. 2023; Teh et al. 2017). Nevertheless, these genes should be responsive for the common pathways of fruit growth and development in durians rather than being specific to either cultivar, thus, further research is needed to resolve this matter.

It is also intriguing to note that some cultivars expressed varying groups of pathogen-responsive genes that are inferred *in silico* to confer resistance to *Peronospora parasitica*, *P. syringae*, etc. (Nawae et al. 2023) in addition to heat shock proteins that are upregulated under heat stress (Li et al. 2024a, b). To validate the expression of pathogen-responsive genes, transcriptomic analyses were performed on living plants after being infected with *Phytophthora palmivora*, a devastating oomycete that leads to significant loss of crops in Southeast Asia (Nawae et al. 2024). It was found that the resistant cultivar Puangmanee, as compared with susceptible cultivars Monthong and Kradumthong, significantly expressed genes encoding chitin response proteins such as lysM domain receptor-like kinase and endochitinase. Chitin was released by zoospores of *Phytophthora* that then induced plant innate immunity. All infected cultivars expressed a high number of heat shock proteins, such as HSP70 and ERdj3B, which are postulated to maintain proper folding and functioning of resistance proteins against pathogens. Transcriptional reprogramming, as mediated by stress response transcription factors, for instance, WRKY40 and ERF1A, is triggered by the pathogen infection. Taken together, findings of the transcriptomic analyses should be applicable as a molecular reference for choosing cultivars in

accordance with the planting environment, naturally occurring pathogens in different countries with varying agricultural practices.

Overall, transcriptomics studies have contributed significantly to the understanding of the molecular basis of durian fruit development, ripening, and aroma production. However, it does not directly reflect which proteins are synthesized or how they function within the organism. Hence, proteomics studies are equally important as it complements transcriptomics data by revealing the actual proteins that are synthesized, their abundance, and their functional roles during fruit development and ripening.

Proteomics

Proteomics involves the large-scale identification and quantification of proteins in cells, tissues, or organisms. High-throughput proteomic techniques range from mass spectrometry (MS)-based methods to single-molecule (SMP) and single-cell proteomics (SCP) (Cui et al. 2022). A crucial step in proteomics studies is optimizing protein extraction in order to identify the optimum number of proteins present in the sample. For the Musang King cultivar, the acetone–phenol extraction method has been identified as the most effective (Tan et al. 2021). To date, proteomics studies on durians have been scarce (Table 1) despite their holding significant potential for enhancing our understanding of the molecular mechanisms underlying fruit development, ripening, and aroma production.

Transcriptomic determination of differentially regulated genes is limited to identifying expressed genes, for which the function of each gene and its isoform is predicted *in silico*. Proteomic analyses thus address this shortcoming by detecting and quantifying all expressed proteins in their final stage, judging that some proteins might have undergone protein modification after being translated (Li et al. 2024a, b). As such, the identified proteins are working macromolecules such as enzymes, receptors, stress response proteins, and transcription factors, etc. It is suggested that proteomic maps representing different distinguished stages of fruit development, fruit ripening, and post-harvest senescence should be constructed (Chin et al. 2019; Shi et al. 2014). Subsequent comparative analyses would help to unravel differentially expressed proteins and their associated roles in the molecular biology of fruit development or ripening (Jia et al. 2024; Palma et al. 2011).

It is foreseen that emphasis of proteomic analyses should be placed on protein–protein interactions, especially mediated by transcription factors (TFs) as the major upstream gene regulators (Tian et al. 2020). A recent work on the role of MYB transcription factor in fruit development of durian found that *Dz*MYB2 acts as an activator, but *Dz*MYB3 acts as a repressor in the phenylpropanoid regulation that produces flavonoids in durian pulp (Weerawanich and Sirikantaramas 2024). Predictably, a plant genome could harbor thousands of TF genes. Since TFs exert their regulatory roles by forming molecular associations with the target proteins into complexes, isolating the TF will retrieve all target proteins altogether. As multiple TF families and their members have different target proteins, purification of all TFs will pull out all target proteins from a proteome. Subsequently, the interaction between proteins in a complex and across complexes could be characterized as a protein–protein interaction network (Ding et al. 2013; Li et al. 2015). This would generate a proteome with details of functional interactions that lead to the studied mechanism.

Metabolomics

Metabolites are considered the final products of genes after expression and post-translational modification of their functional proteins. Metabolomics is the study of metabolites, which are intermediate or end products of metabolic pathways. It can be categorized into targeted approaches, which focus on specific known metabolites, and untargeted approaches, which profile the entire metabolome, including unknown compounds. Current development and utilization of high-throughput analytical methods, such as gas chromatography–mass spectrometry (GC–MS), liquid chromatography–mass spectrometry (LC–MS), and nuclear magnetic resonance (NMR), have identified a large number of primary and secondary metabolites. The underlying shortcoming of metabolomic analyses lies in the inability to separate complex mixtures of metabolites and simultaneously detect and quantify thousands of metabolites for high-throughput analysis. Besides, some metabolites appear to be low-abundance. These methods were reviewed previously for further reading (Letertre et al. 2020; Wang et al. 2015).

Primary metabolites are macromolecules (sugars, amino acids, organic acids, lipids, etc.) used in or produced by fundamental and essential molecular processes such as photosynthesis. Meanwhile, secondary metabolites (flavonoids, hydroxycinnamoyl derivatives, acylated glycosides, glutathione, etc., as well as phytohormones) are triggered to be produced in response to biotic and abiotic stressors such as heat, drought, infection, and consumption by herbivores, as an indispensable strategy of sessile plants in adaptation for survival. It has been estimated that there are approximately 8000 commonly shared primary metabolites among plants, but there could be up to a million secondary metabolites, and most of them are unique and only shared by plants from similar lineages. Owing to their specialized roles in plant defense and adaptation, secondary metabolites have been coined as specialized metabolites (Huang and Dudareva

2023; Kessler and Kalske 2018; Weng et al. 2021). Coupled with new mathematical modeling on the basis of population genetics and natural selection, hypotheses on plant chemodiversity have been proposed (Wittmann and Bräutigam 2025). It is important to point out that there is a huge number of metabolites whose specific functions remain unknown. Furthermore, these works do not provide an inference on specialized metabolites for the development of agronomic traits. It is therefore intriguing to discover the reason why so many metabolites are being synthesized that are costly in terms of energy and nutrients, especially in plants in the wild. Predictably, selection of commercial agronomic traits should then have reduced the chemodiversity of the resulting cultivars.

Among all the omics analyses performed on commercial durians, metabolomics has been studied extensively on the aril (Table 1). Metabolites should have contributed to the much sought-after unique combination of flavors of durian arils, i.e., dry (non-soggy), thick and golden/yellowish pulp, coupled with its creamy, custard-like texture that tastes bittersweet, as well as its distinctive pungent aroma, despite it being a malodor by those who despise durians. Nevertheless, it is observed that the majority of studies focused on the pungent smells, judging from the common use of GC–MS, which is limited to unveiling small volatiles. As a rule-of-thumb, sulfur-containing metabolites, such as ethionine, are responsible for the common durian odor, whereas other volatiles, such as esters, add a unique aroma which differentiates commercial cultivars (Aschariyaphotha et al. 2021; Chin et al. 2007; Fischer and Steinhaus 2019). Besides volatile compounds, sugar and amino acids also influence durian's aroma and flavor. Their distribution in cultivars D200, MK, and MT has been analyzed (Xiao et al. 2022a).

A special note should be made to the studies of durian species other than the commercial *D. zibethinus* varieties, especially on those originating from Borneo, which are reckoned as indigenous durians in Southeast Asia. These wild but edible species are *D. dulcis*, *D. graveolens*, *D. kutejensis,*, and *D. oxleyanus*. They are naturally diverse in their phenotypes—which range from light green to reddish pericarp, yellow, orange to red aril—and unique but overlapping chemical profiles (Belgis et al. 2017; Hasmadi et al. 2021; Sujang et al. 2024, 2023). Other metabolomics studies have investigated nutrient composition, such as fatty acid profiles in *D. graveolens* with yellow-flesh (Nasaruddin et al. 2013), and carotenoid content in *D. kutejensis* and *D. lowianus* (Khoo et al. 2008), as well as several Malaysian durian cultivars (Tan et al. 2020).

Unfortunately, although these works give valuable insights into the metabolite profiles of each local indigenous durian, the data are hardly comparable to the commercial varieties, as the studies did not include a comparative analysis with those of high market demand, such as Musang King and Monthong. Some local durians might have their species wrongly identified or have varied local names across different regions (Belgis et al. 2017; Hasmadi et al. 2021; Sujang et al. 2024). This research also focuses on volatiles that contribute to its pungent smell. Understanding the metabolites contributing to flavor, color, and texture allows for targeted breeding of desired fruit traits, which have thus remained elusive.

Multi-omics integration for a holistic understanding of durian

Multi-omics integrates various omics approaches, such as genomics, transcriptomics, proteomics, and metabolomics, to achieve a comprehensive understanding of biological systems and their interactions. In plants, multi-omics technologies have facilitated crop improvement (Yang et al. 2021), enhanced breeding efficiency (Mahmood et al. 2022), and led to the discovery of plant signaling molecules (Luo et al. 2022).

The Musang King reference draft genome (PRJNA400310) and transcriptome datasets for Musang King [SRX3188225 (roots), SRX3188222 (stems), SRX3188226 (leaves), and SRX3188223 (aril)] and Monthong [PRJNA683229 (mature and ripe) and PRJNA732556 (immature1, immature 2, and midripe)] are available in the NCBI database, making them valuable references for downstream analyses. Omics integration has been applied in durian, particularly for genomics–transcriptomics and transcriptomics–metabolomics analysis. A common workflow involves genome-wide identification of target genes, followed by transcriptomic analysis to detect fruit- or ripening-specific differentially expressed genes before conducting quantitative reverse transcription polymerase chain reaction (RT-qPCR) validation across different cultivars.

Using these resources, genome-wide identification studies have been conducted for various gene families, including cytochrome P450 (Suntichaikamolkul et al. 2021), carotenoid cleavage oxygenases (CCO) (Tantisuwanichkul and Sirikantaramas 2024), DNA-binding with one finger (Dof) (Khaksar et al. 2019), calmodulin-binding transcription activators (CAMTA) (Iqbal et al. 2021), resistance gene analogs (RGAs) (Cortaga et al. 2022), MADS-box proteins (Tantisuwanichkul et al. 2024), and leucylaminopeptidase (LAP) (Panpetch and Sirikantaramas 2021). Transcriptome-wide studies have identified ethylene response factors (ERFs) (Khaksar and Sirikantaramas 2021), MYB activators (Weerawanich et al. 2024; Weerawanich and Sirikantaramas 2024), and auxin response factors (ARFs) (Khaksar and Sirikantaramas 2020).

Similarly, as current research has been emphasizing the agronomic traits of the durian pulp, multi-omic analyses endeavor to depict the mechanism of fruit development and ripening. These studies have highlighted the role of phytohormones, i.e., gibberellin, jasmonic acid, and abscisic acid, in fruit ripening, in addition to ethylene and auxin (Suntichaikamolkul et al. 2021; Tantisuwanichkul and Sirikantaramas 2024). Coupled with transcription factors, cultivar-specific Dof was found to be involved in auxin biosynthesis (Khaksar et al. 2019). Durian ripening is characterized by increased sucrose, malate, succinate, and amino acids, supported by transcriptomic data showing the upregulation of genes involved in sugar metabolism, glycolysis, the TCA cycle, and amino acid pathways (Sangpong et al. 2021). Functional studies have shown that *Dz*MYB1 regulates the phenylpropanoid pathway and flavonoid biosynthesis (Weerawanich et al. 2024), while *Dz*HD-ZIP1.8 controls volatile sulfur compound production (Pinsorn et al. 2024). Taken together, these results are important in drawing the regulatory mechanism of fruit ripening mediated by transcription factors and phytohormones.

Application of omics studies in durians

Omics studies have five main applications in durians: (1) evolutionary studies, (2) understanding the durian fruit ripening mechanism, (3) identifying genetic markers for breeding, (4) discovery of bioactive compounds for pharmaceutical and industrial applications, and (5) applications in the post-harvest processing. These applications are discussed in the following sections.

Evolutionary studies

Organelle genomes are useful for evolutionary studies, and several complete organelle genomes from tropical fruits have been reported, including mangosteen (Wee et al. 2022; Wee et al. 2023a, b), pineapple (Redwan et al. 2015), banana (Martin et al. 2013), and longan (Nguyen et al. 2024a, b). The chloroplast genome length (120–190 kb) (Sugiura 1995) is more conserved compared with the mitogenome (66 kb to 11.3 Mb) (Skippington et al. 2015; Sloan 2012). In higher plants, the plastome structure is highly conserved and consists of a typical quadripartite structure, with two inverted repeat (IR) regions separating the large single-copy (LSC) region from the small single-copy (SSC) region (Wicke et al. 2011).

The first durian chloroplast genome, from the cultivar Monthong, was reported in 2017 (Cheon et al. 2017). As of 1 March 2025, a total of 15 durian chloroplast genomes have been published, with genome sizes around 165 kb, except for *D. dulcis* (~141 kb; accession no. NC_073110) from Indonesia and the Monthong cultivar (~143 kb; accession no. MT321069) from Thailand (Table S1) (Shearman et al. 2020). Both chloroplast genomes lack inverted repeat (IR) regions, which are commonly found in higher plants. A similar scenario was observed in 24 other Thai cultivars when their Illumina reads were mapped against the Monthong chloroplast genome (MT321069) and a published chloroplast genome (MG138151), showing significant drops in read depth at the IR region (Shearman et al. 2020). Notably, most complete chloroplast genomes recorded in the NCBI database belong to local durians (Table S1), primarily sourced from Sarawak, Malaysia.

While 15 chloroplast genomes have been recorded in the NCBI database, some have not been included in published studies examining durian evolutionary history. Therefore, to address this gap, a phylogenetic tree was constructed using the chloroplast genomes of these seven durian species (*D. dulcis*, *D. graveolens*, *D. kutejensis*, *D. lowianus*, *D. oxleyanus*, *D. testudinarius*, and *D. zibethinus*) from different cultivars and origins (Table S1), excluding PP668208, which was identified as an outlier during analysis (Fig. S1). The analysis also included *Theobroma cacao* (NC_014676), from the same Malvaceae family as durian, and *Arabidopsis thaliana* (NC_000932). Protein-coding genes of each chloroplast genome were downloaded from the NCBI Organelle Genome database, and 71 protein-coding genes (Table S2) common to all 15 durian chloroplast genomes were concatenated and aligned using the MAFFT version 7 online tool (https://mafft.cbrc.jp/alignment/server/; accessed on 7 March 2025) (Katoh et al. 2019). Maximum likelihood (ML) analysis was performed using the RAxML-NG v1.2.2 tool (Kozlov et al. 2019) with 1000 bootstrap replicates, using the TVM+I+G4 model, selected through ModelTest-NG v0.1.7 (Darriba et al. 2020). The resulting phylogenomic tree was visualized and edited using FigTree v1.4.4 (Rambaut 2018).

The phylogenetic tree confirms the classification of *Durio* within the Malvaceae family, indicated by the blue line. The commercial *D. zibethinus* cultivars (Mothong, Ri6, and an unknown Malaysian cultivar) were closely grouped, reflecting their recent divergence from a common ancestor (Fig. 2). In contrast, Borneo durian species (*D. dulcis*, *D. graveolens*, *D. kutejensis*, *D. lowianus*, *D. oxleyanus*, and *D. testudinarius*) exhibited greater genetic differentiation, suggesting that wild Bornean durians represent a more diverse and ancient lineage. Interestingly, *D. dulcis* samples from Indonesia and Sarawak did not cluster together. Instead, the Indonesian *D. dulcis* grouped with *D. oxleyanus*, while the Sarawak *D. dulcis* clustered with *D. graveolens*. This suggests possible genetic differentiation within *D. dulcis*, which may be due to geographic isolation. Among the three *D. graveolens*

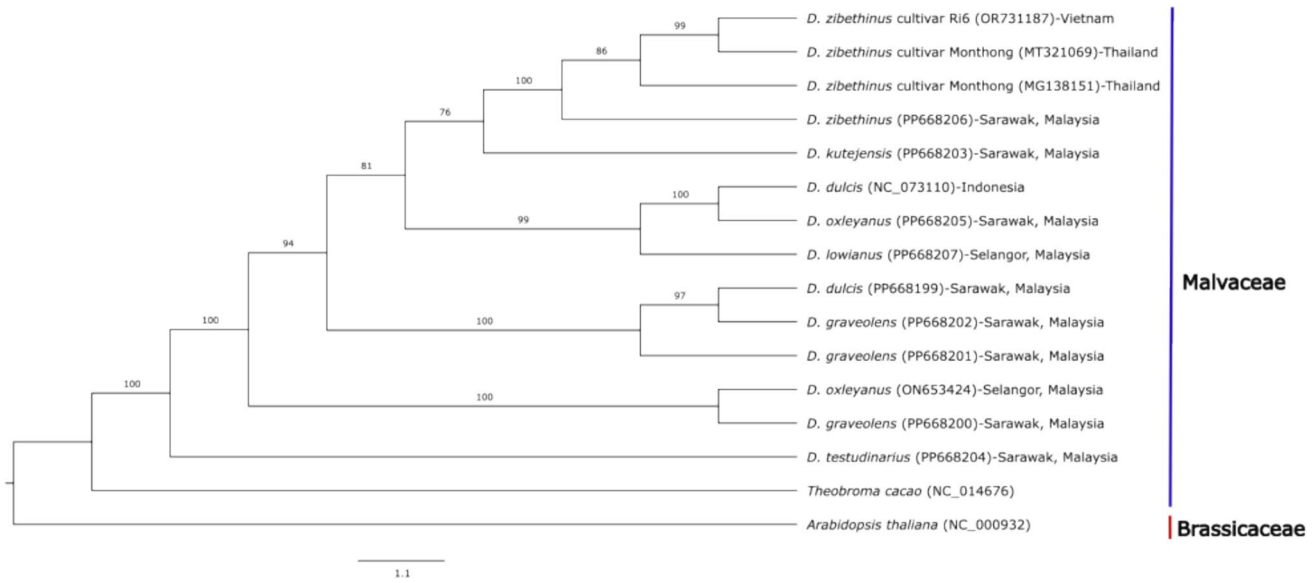

Fig. 2 Maximum likelihood phylogenetic tree of 14 *Durio* samples representing seven species on the basis of 71 protein-coding genes. The tree includes *D. dulcis*, *D. graveolens*, *D. kutejensis*, *D. lowianus*, *D. oxleyanus*, *D. testudinarius*, and *D. zibethinus*, with sample locations indicated in parentheses. *Theobroma cacao* and *Arabidopsis thaliana* were used as outgroups. Blue line: Malvaceae; red line: Brassicaeae

chloroplast genomes in GenBank, two closely clustered together, while the third clustered with *D. oxleyanus*, possibly reflecting different genotypes with different pulp colors (yellow, orange, and red) (Sujang et al. 2023). *D. testudinarius* appears to be the most genetically distinct, forming a separate branch within the tree. This unique placement might be because of its distinct fruit characteristics, such as small and spiky fruit. The placement of *Theobroma cacao* within Malvaceae aligns with previous studies (Cheon et al. 2017; Huy et al. 2024), further confirming its evolutionary relationship with *Durio*. However, as in the case of mangosteen (Wee et al. 2023a, b), the chloroplast genome alone is insufficient to differentiate durian species owing to the highly conserved nature of protein-coding genes. Therefore, it is recommended that future evolutionary studies incorporate mitochondrial genome data for improved resolution.

Understanding the durian fruit ripening mechanism

Fruits are classified into two categories, climacteric and non-climacteric, on the basis on their ripening behavior (Fukano and Tachiki 2021). Durian is a climacteric fruit, characterized by a rise in ethylene production concurrent with a burst in respiration rate (Tongdee et al. 1989). In contrast, non-climacteric fruits do not exhibit this pattern.

Fruit ripening involves the coordination of phytohormones and transcription factors (Giovannoni et al. 2017). The current understanding of fruit ripening mainly comes from studies on tomatoes, a model fruit owing to their short ripening stages (Giovannoni 1993). The two main phytohormones that control fruit ripening are ethylene (C_2H_4) and abscisic acid (ABA). Ethylene plays a crucial role in climacteric fruit ripening, and treatment with 1-methylcyclopropene (1-MCP) delays durian fruit ripening (Amornputti et al. 2016; Thongkum et al. 2018). ABA, conversely, is more essential for non-climacteric fruit ripening and is also involved in fruit development, seed growth, germination, and stress response (Yuan et al. 2018). Three key fruit-ripening transcription factors (TFs), colorless non-ripening (CNR) (Thompson et al. 1999), non-ripening (NOR) (Tigchelaar 1973), and ripening inhibitor (RIN) (Robinson 1968), regulate ripening upstream of ethylene production.

Recent omics studies have refined the understanding of durian fruit ripening (Fig. 3). *In silico* analysis using public durian genome and transcriptome data has identified key transcription factors, including auxin response factors (ARFs) (Khaksar and Sirikantaramas 2020), ethylene response factor (ERF) (Khaksar and Sirikantaramas 2021), the CAMTA family (Iqbal et al. 2021), and 9-cis-epoxycarotenoid dioxygenases (NCEDs) (Tantisuwanichkul and Sirikantaramas 2024). Their roles were validated through transient expressions in *Nicotiana benthamiana*, RT-qPCR analysis, and dual-luciferase reporter assay. Ethylene biosynthesis, regulated by 1-amino-cyclopropane-1-carboxylate synthase (ACS) and ACC oxidase (ACO), is controlled by *Dz*ERF9 (a positive regulator) and *Dz*ERF6 (a negative regulator), both influenced by C_2H_4 and auxin (IAA) (Khaksar and Sirikantaramas 2021). There is crosstalk between C_2H_4 and auxin (IAA), with *Dz*ARF2A mediating fruit ripening by regulating ethylene biosynthetic genes in an auxin-dependent manner (Khaksar and Sirikantaramas 2020), while *Dz*Dof2.2 regulates auxin biosynthesis (Khaksar

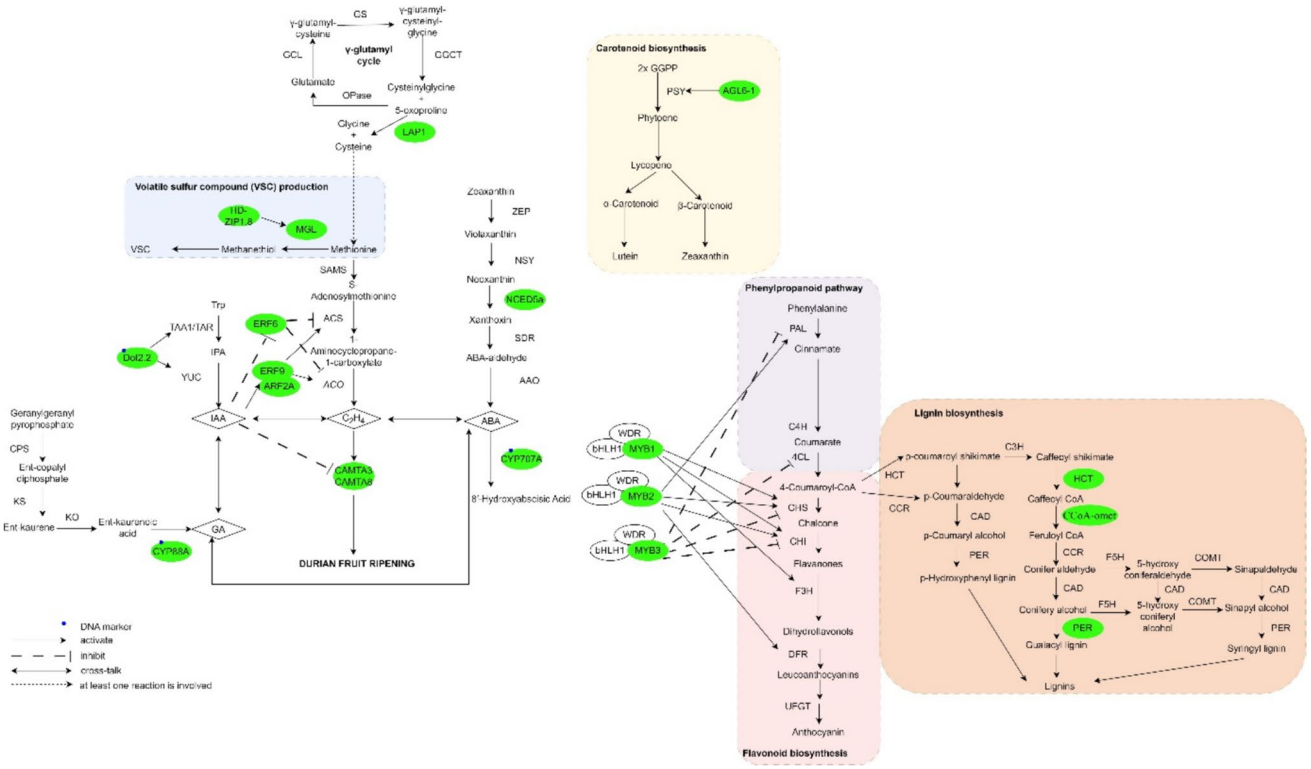

Fig. 3 A schematic illustration of the durian fruit ripening mechanism showing the coordination between phytohormones and transcription factors (TFs). Green boxes indicate the TFs discovered in durian omics analysis. 4CL, 4-coumaroyl-CoA ligase; AAO, abscisic aldehyde oxidase; ACO, 1-amino-cyclopropane-1-carboxylic acid oxidase; ACS, 1-amino-cyclopropane-1-carboxylate synthase; AGL, agamous-like; ARF, auxin response factor; bHLH, basic helix-loop-helix; C3H, p-Coumarate 3-hydroxylase; C4H, cinnamate-4-hydroxylase; CAD, cinnamyl alcohol dehydrogenase; CAMTA, calmodulin-binding transcription activator; CCoA-omet, caffeoyl-CoA *O*-methyltransferase; CCR, cinnamoyl-CoA reductase; CHI, chalcone isomerase; CHS, chalcone synthase; COMT, caffeic acid *O*-methyltransferase; CPS, copalyl diphosphate synthase; CYP, cytochrome P450; DFR, dihydroflavonol reductase; Dof, DNA-binding with one finger; ERF, ethylene response factor; F3H, flavanone 3-hydroxylase; F5H, ferulate-5-hydroxylase; GCL, glutamate cysteine ligase; GGCT, γ-glutamylcyclotransferase; GGPP, geranylgeranyl pyrophosphate; GS, glutamine synthetase; HCT, shikimate hydroxycinnamoyl transferase; HD-ZIP, homeodomain-leucine zipper; KO, kaurene oxidase; KS, kaurene synthase; LAP, leucylaminopeptidase; MGL, methionie γ-lyase; MYB, v-myb myeloblastosis viral oncogene homolog; NCED, 9-cis-epoxycarotenoid dioxygenase; NSY, neoxanthin synthase; OPase, oxoprolinase; PAL, phenylalanine ammonia-lyase; PER, peroxidase; PSY, phytoene synthase; SDR, short-chain dehydogenase/reductase; TAA1/TAR, tryptophan aminotransferase of *Arabidopsis* 1/tryptophan aminotransferase-related; UFGT, UDPG flavonoid *O*-glucosyltransferase; WDR, WD40-repeat protein; YUC, flavin monooxygenase; ZEP, zeaxanthin epoxidase

et al. 2019). In addition, *Dz*CAMTA3 and *Dz*CAMTA8 act as ethylene-induced transcriptional activators but also interact antagonistically with auxin to regulate key ripening pathways (Iqbal et al. 2021). The identification of putative phytohormone-associated cytochrome P450s, such as CYP88 and CYP707, involved in gibberellin (GAs) and ABA biosynthesis, respectively, further refines the current understanding of the durian ripening mechanism (Suntichaikamolkul et al. 2021).

As a fruit ripens, typical changes include color changes, cell wall softening, increased sweetness, aroma development, and metabolite shifts (Cherian et al. 2014). When the first durian draft genome was published in 2017, the upregulation of the *MGL* gene, coinciding with the production of volatile sulfur compounds (VSCs), was observed through transcriptomics and metabolomics analysis (Teh et al. 2017). Further *in silico* studies using existing transcriptomics data, combined with dual-luciferase assays, identified *Dz*HD-ZIP1.8 as the transcription factor regulating *DzMGL* gene expression (Pinsorn et al. 2024). In addition, *Dz*LAP1 may play a role in sulfur metabolism and ethylene-related volatile production during fruit ripening (Panpetch and Sirikantaramas 2021).

Fruit color changes primarily depending on pigments such as anthocyanins, carotenoids, and chlorophyll. The v-myb myeloblastosis viral oncogene homolog (MYB) is a known master regulator of phenylpropanoid and flavonoid biosynthesis (Pratyusha and Sarada 2022; Yan et al. 2021). In durian, both *Dz*MYB1 and *Dz*MYB2 function as activators, whereas *Dz*MYB3 acts as a repressor (Weerawanich et al. 2024; Weerawanich and Sirikantaramas 2024). Carotenoid content in durian is regulated by *Dz*AGL6-1, which

activates the promoter of the *PSY* gene (Tantisuwanichkul et al. 2024). Lignin biosynthesis, which contributes to thorn formation on the durian shell, has been linked to high expression levels of shikimate *O*-hydroxycinnamoyl transferase (HCT), caffeoyl-CoA *O*-methyltransferase (CCoA-omet), and peroxidase (PER) in the fruit peel, where thorns develop during fruit ripening (Li et al. 2024a, b).

Identifying genetic markers for breeding

A genetic marker is a specific DNA sequence or variation used to identify genes or traits in genetic studies and breeding programs (Kebriyaee et al. 2012). Genetic marker identification is crucial for trait selection and genetic mapping. There are two main categories of genetic markers: classical markers (morphological, cytological, and biochemical markers) and DNA/molecular markers. Examples of DNA markers include amplified fragment length polymorphism (AFLP), restriction fragment length polymorphism (RFLP), and single-nucleotide polymorphism (SNP) (Nadeem et al. 2018).

Metabolomics profiling is a powerful tool in durian breeding programs as it helps identify key metabolites associated with specific or desirable traits. For instance, *D. kutejensis* has a milder aroma owing to lower sulfur and ester compound levels compared with *D. zibethinus* (Belgis et al. 2017; Sujang et al. 2023). In addition, the four key sulfur-containing volatiles responsible for the aroma of Monthong durian are ethaethiol, methanethiol, propane-1-thiol, and hydrogen sulfide (Li et al. 2017). Asparagine and cysteine could serve as potential biochemical markers for determining durian maturity (Charoensumran et al. 2021) and VSC production, respectively (Pinsorn et al. 2023). These metabolites can be used as biochemical markers to select elite breeding lines with the best trait combinations.

Compared with classical markers, DNA markers are preferred owing to their high polymorphism, easy detection, environmental stability, and high reproducibility (Amiteye 2021). In durian, simple sequence repeat (SSR) markers have been discovered in the endemic durian kura-kura (Magandhi et al. 2025), while InDel markers on putative drought-responsive genes have been identified from the RNA sequencing data of commercial durians available in public databases (Bioproject accession no. PRJNA400310) (Sathapondecha et al. 2024). The identification of resistance gene analogs (RGAs), which may play a role in plant defense against pathogens (Cortaga et al. 2022), presents the potential for developing DNA markers to select durian cultivars with enhanced disease resistance. For instance, the durian cultivar Puangmanee (PM) exhibits the highest resistance to *Phytophthora palmivora*, likely owing to the high expression of genes encoding chitin response proteins, RUN1, RPV1, and RGA4, compared with two susceptible cultivars [Monthong (MT) and Kradumthong (KD)] (Nawae et al. 2024). *Dz*Dof2.2 and CYP genes (CYP88 and CYP707) can be used as DNA markers on the basis of their differential expression levels, which contribute to variations in ripening speed and post-harvest ripening speed among durian cultivars (Khaksar et al. 2019; Suntichaikamolkul et al. 2021).

Post-harvest processing

Durian is a climacteric fruit with a short shelf life at room temperature, typically lasting 2–5 days (Tifani et al. 2018). There are several factors affecting durian's metabolite and protein profiles (Fig. 4). To extend its storage duration and maintain quality, several methods have been applied, including heating and salting (to make tempoyak) (Rajagukguk and Arnold 2021), freezing (Razali et al. 2022, 2023), freeze-drying (Prasetia et al. 2023), and spray-drying (Chin et al. 2008). These processing techniques not only affect the fruit's longevity but also alter its metabolite composition, particularly its volatile compounds, which play a crucial role in durian's distinctive aroma. Notably, ripe durian pulp possesses the highest levels of γ -glutamylcysteine (γ-EC) and considerable glutathione content, but these levels decreased significantly in processed products (Singcha et al. 2024).

Different processing methods significantly impact the volatile composition of durian. Heating and salt treatment, for instance, reduce sulfur volatiles in Monthong (Laohakunjit et al. 2007). Similarly, fermentation decreases sulfur volatiles such as diethyl trisulfide and *N*-dimethylthioisophinyl-3-amino, while generating new esters, alcohols, and carboxylic acids, thereby modifying the final aroma profile (Neti et al. 2011). Tempoyak fermented with *Pediococcus acidilactici* UP02 exhibited increased levels of non-sulfur compounds, non-volatile acidity, and organic acids (Yuliana and Garcia 2009). Moreover, metabolite profiles in durian are influenced by cultivar differences and harvest years (Pinsorn et al. 2018), adding another layer of complexity to post-harvest quality management.

Storage temperature, duration, and chemical treatments also play a crucial role in durian's volatile composition. In the D24 cultivar, ester compounds decrease significantly after 1 week of storage at 4 °C (Voon et al. 2007b). In addition, chemical treatment (ethephon and 1-MCP) on Monthong temporarily suppresses sulfur-containing volatiles, which recover after dehiscence. However, in the Chanee cultivar, 1-MCP treatment inhibits sulfur production while ethephon enhances it after dehiscence (Maninang et al. 2011).

Drying methods such as freeze-drying and spray-drying also cause significant losses in durian volatiles.

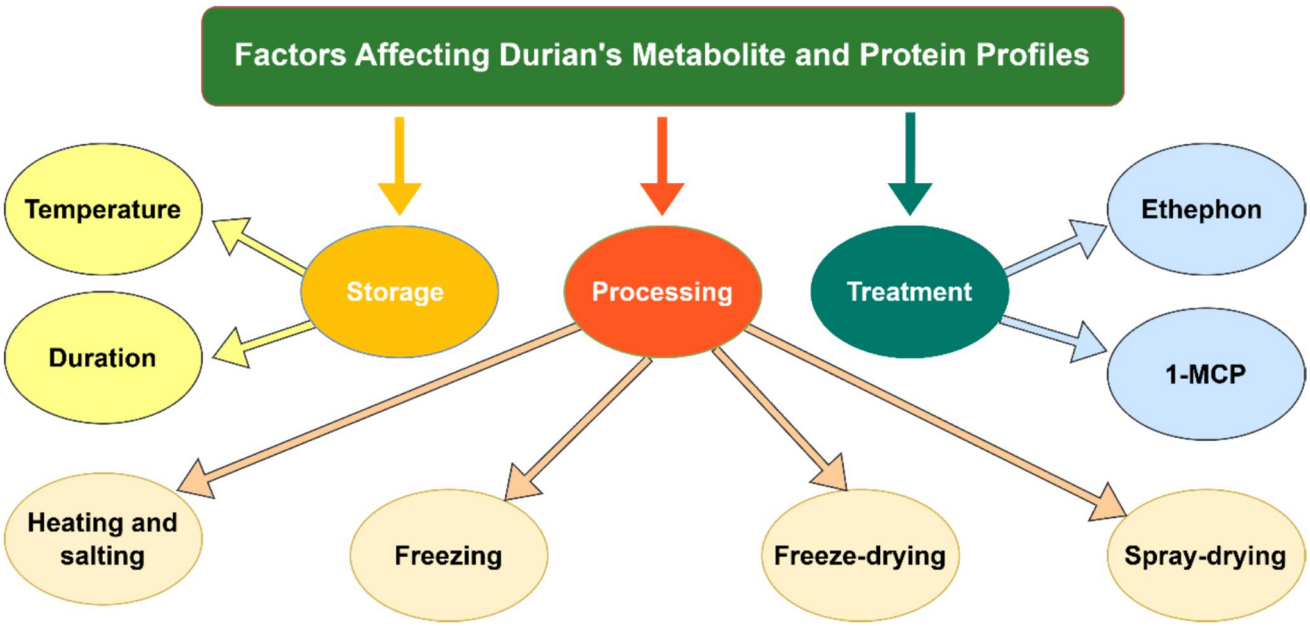

Fig. 4 Factors affecting durian metabolite and protein profiles

Freeze-drying for 30 h results in a 78–95% loss of key volatile compounds, with even greater losses observed with extended drying duration (Darniadi et al. 2021). Spray-drying leads to even higher volatile losses than freeze-drying (Chin et al. 2008). The addition of gum arabic provides the highest volatile retention in spray-dried durian powder (Chin et al. 2010). Apart from affecting the metabolite profile, freezing also impacts the protein profile of Musang King durian pulp, with 15 proteins downregulated and 3 proteins upregulated after 1 year of storage (Tan et al. 2021).

Bioactive compounds discovery for pharmaceutical and industrial applications

Bioactive compounds in plants are secondary metabolites with antioxidants, anti-inflammatory, and antimicrobial properties. These include alkaloids, flavonoids, tannins, terpenes, and saponins (Bernhoft 2010). Among various omics approaches, metabolomics is the most widely used omics technique for identifying bioactive compounds in plants.

In durian, multiple studies have identified key bioactive compounds from different parts of the plant, including the leaves (Sawitri et al. 2025), aril (Pewlong et al. 2025), and shell (Hatim et al. 2024; He et al. 2023; Nguyen et al. 2024a, b; Zamakshshari et al. 2022). For instance, procyanidin is found in early immature durian fruits exhibiting antioxidant and anti-glycation properties (Pewlong et al. 2025).

Interestingly, the durian shell, which is typically treated as waste, has been found to contain valuable bioactive compounds with pharmacological potential. Recent studies have highlighted the medical value of durian shell extracts from various cultivars and regions. The ultra-high-performance liquid chromatography coupled with mass spectrometry (UHPLC–MS/MS) profiling of the D175 cultivar from Malaysia identified 20 bioactive compounds, suggesting their potential for pharmacological applications (Hatim et al. 2024). Similarly, fraction F2, obtained through silica gel column chromatography of the durian shell's crude ethanolic extract from the RI6 cultivar in Vietnam, was found to have the highest concentration of flavonoids and quercetin, contributing to its anti-inflammatory and anti-xanthine oxidase activities (Nguyen et al. 2024a, b). In addition, durian shell extract from the Monthong cultivar in Thailand demonstrated strong in vitro antioxidant properties, reducing oxidative damage in HepG2 cells and inhibiting apoptosis through mitochondrial pathway regulation (He et al. 2023).

In terms of antimicrobial properties, the durian shell extract from the D168 cultivar in Malaysia exhibited antibacterial activity against *Bacillus subtilis*, *Staphylococcus aureus*, and *Pseudomonas aeruginosa* (Zamakshshari et al. 2022). These findings underscore the potential of durian shell as a valuable source of bioactive compounds for pharmaceutical and industrial applications.

Challenges and perspectives

There are several challenges in durian genome sequencing, including its large genome size (around 1 Gb), the presence of repetitive DNA elements, polyploidy, and high sequencing cost. In addition, big data complexities make genome assembly more challenging. As a result, most durian

sequencing efforts rely on cost-effective short-read sequencing (Supplementary Files 1 and 2). To date, only Musang King from Malaysia and Kan Yao from Thailand have been sequenced using a combination of both long and short-read sequencing. These reference genomes serve as valuable resources for future comparative genomics studies.

Beyond genome sequencing, integrating multi-omics approaches such as genomics, transcriptomics, proteomics, and metabolomics, can provide a comprehensive understanding of molecular interactions underlying durian traits. Currently, only three network analyses have been reported (Table 2). Network analysis has been applied to fruit ripening, helping to identify hub genes regulating metabolism and enabling the construction of a regulatory network model (Wee et al. 2023a, b). Conducting similar analysis in durian could uncover regulatory mechanisms governing key pathways, as well as address challenges such as climate change and disease outbreaks in durian cultivation.

Collaboration with agricultural stakeholders is also crucial. Their on-field experience in managing climate change, pest control, and hybrid breeding selection can significantly contribute to developing elite durian cultivars. Furthermore, incorporating artificial intelligence (AI) and machine learning (ML) can enhance durian quality prediction, classification (Lim and Chuah 2018), and disease management (Daud et al. 2023), thereby improving cultivation and commercialization efforts.

Currently, most omics studies focus on commercial durians, whereas research on local durians remains limited (Tables 1 and 2). Studies on local durians have primarily examined physicochemical, phytochemical, and nutritional properties, as well as chemical composition, contributing to sensory attributes (Belgis et al. 2016; Faridah et al. 2021; Hoe and Siong 1999; Sujang et al. 2024). However, the genetic potential of Borneo's indigenous durian cultivars remains largely unexplored. There is a need for omics-based genetic profiling and characterization of these local cultivars to uncover their hidden genetic treasures. Such research would support breeding programs aimed at developing superior durian germplasm for future cultivation.

Durian cultivars are propagated vegetatively by grafting a scion from a superior tree to a rootstock that is planted from a seed, disregarding its cultivar (Chau et al. 2004; Mad and Dodd 1990). Grafted trees will produce fruit much faster, at about 7 years, as compared with ~15 years by trees grown from seeds (Ketsa et al. 2020). Owing to this long maturation time, conventional crossing of desire breeds is strenuous, which is aggravated by its self-incompatibility, nocturnal blooming, and chiropterophilous pollination by bats only (Ei and Ismail 2022; Ng et al. 2020; Sheherazade et al. 2019). Generative propagation by seeds is rarely practiced for a superior cultivar, as sexual reproduction usually produces offspring of varying phenotypes. It is therefore predictable that the cultivar collection in each country might have its scions originate from just a few individuals. This means that the superior cultivars are natural diverse stocks selected from the wild by farmers who cross-bred those carrying favorable agronomic traits. Pan-genome analyses could therefore identify the presence–absence variations (PAVs), and structural variations that dissect complex traits across different cultivars on flowering time, stress tolerance, and even resistance to plant pathogens. Wild durians from Borneo have much more diverse phenotypes than the cultivated ones, especially in terms of the pulp color, texture, flavors, pungency, and the shape, color, size, spikiness, and dehiscence of their husk. This represents an enormous genomic diversity that merits detailed investigation on pan-genomes as well as gene/protein regulatory networks that manifest these unique traits, for conservation as well as commercialization purposes (Juarah et al. 2021; Sudarmono et al. 2023).

The metabolome is the closest to the manifestation of genotype, as its phenotype is observable and measurable. This could be deviated when the same plants respond differently to biotic and abiotic stress under varying agronomic practices (Jan et al. 2021; Marone et al. 2022). For example, durians planted in insular Southeast Asia, such as Malaysia and Indonesia, will have faced a tropical monsoon climate, which consists of an alternate rainy and dry season with relatively stable rainfall and humidity. In Malaysia, daily temperatures range from 25 to 32 °C, and the mean annual rainfall ranges from 2000 mm to 4000 mm. A short dry spell of approximately 15 days would have induced flowering of durian trees after 50 days. A high annual rainfall that is over 3000 mm was reported to have reduced the production of durians (Eguchi et al. 2025a, 2025b). Whereas, countries located in the mainland Southeast Asia, such as Thailand and Vietnam, would have experienced a more extreme tropical savanna climate that has hotter and drier seasons. Likewise, the island of Hainan, China, also has a tropical monsoon climate, but the average temperature is relatively lower (ranging from 17 to 28 °C) compared with Malaysia (25 to 32 °C) (Tinghui 2009). Besides, the majority of the durian trees have been planted for decades in natural hilly areas where an irrigation system is not necessary, as compared with modern orchards where trees are planted on man-made raised mounds with irrigation (Pinsorn and Sirikantaramas 2025). The fruiting trees could have an age range from 7 years to decades. Under these conditions, it is thus plausible that the resulting fruits of the same cultivars' manifest phenotype plasticity (Stotz et al. 2021), yet despite this, there is no study investigating this phenomenon. Taking the cultivation of Musang King in Vietnam as an example. MK originates from Malaysia. When it was

planted in Vietnam, up to 30% of the harvested fruits were reported to have hardened flesh. This suggested that mitigation was needed to improve irrigation, fertilization, or other agronomic management that enhances plant tolerance or adaptability to environmental stresses (Duong et al. 2025; Mariani and Ferrante 2017). In order to ensure consistency in fruit quality, it is important to decipher these epigenetic and environmental effects (epigenome), which are particularly mediated by phytohormones and transcription factors that trigger gene expression (transcriptome) and its resulting set of metabolites (metabolomics) via multi-omic approaches (Giovannoni et al. 2017; Lloyd and Lister 2022).

In terms of harvesting and post-harvesting practice, Malaysian and Indonesian durians are allowed to turn ripe on the tree (~130 days after anthesis, DAA) and allowed to drop into a netting below each tree, then the fruits are collected. These durians usually have about 3–4 days of short shelf life till their husk is dehiscent and cracks open. These durians are supplied fresh to the local market, Singapore, and Hong Kong, as fresh durians are preferred. For other overseas markets, especially mainland China, whole durians are cryo-frozen with liquid nitrogen and transported at about −20 °C. In contrast, this harvesting practice is not practiced in Thailand, instead, the mature but unripe fruits are harvested at 100–110 DAA and then kept at low oxygen storage and shipment till the whole fruit turns ripe on the shelf in a few weeks' time (Ketsa 2018; Razali et al. 2023; Wiangsamut 2024). Unripe fruits will have hard, unfavorable pulp, whereas overripe fruit will have its husk dehiscent and cracked open, rendering rapid deterioration of fruit quality. As durian is a climacteric fruit, it is well established that there is a burst of ethylene before it turns ripe (Ketsa and Daengkanit 1998). The regulatory role of ethylene in inducing production of favorable agronomic traits (aroma, sweetness, etc.) should be further explored as an essential metabolite biomarker for ripening (Sospeter et al. 2025). A specialized omics study that builds on genetic mutagenesis of a specific master regulator in ethylene induction could be investigated; however, there is no established durian mutagenesis model, as is the case with tomatoes (Palma et al. 2019).

Both post-harvest practices have advantages over the other; thus, the key to success is harvesting at the right maturity stage. Unfortunately, there is a discrepancy in the current practice, which relies on DAA but also generalized and anomalous maturity indices, such as fruit weight, lipid content, total sugar, total carotenoid content, total phenolic content, and other subjective physical (color change) or sensory (aroma) judgement for varying cultivars, among previous reports (Wattanasan et al. 2025; Yongyut et al. 2025). For example, fruits (unspecified cultivars) at 113 DAA are considered fully mature and ready to drop (Pascua and Cantila 1992), whereas Monthong takes 120–127 DAA to reach full maturity (ripen) (Sangwanangkul and Siriphanich 2000). Meanwhile, the maturity stage at 80%, 85%, 90%, and 100% is estimated for DAA at 110, 115, 120, and 130, respectively (Youryon and Supapvanich 2022). To avoid this discrepancy, standardized maturity indices are needed, especially those that constitute the underlying molecular regulation and signature metabolites. This information could be derived from metabolomic studies that search for volatiles classified as sulfur-containing compounds, esters, and alcohols that produce the unique aroma and taste of durian pulp (Wattanasan et al. 2025). Going further, some abundant or unique volatiles could be used as the biomarkers for each cultivar as a biological barcode for cultivar identification.

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Declarations

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