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REVIEW

Genomic research on the king of fruit (*Durio* spp.): a systematic literature review

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Abstract Durian, a tropical fruit in the Malvaceae family, is prized for its nutrient-rich pulp, including carbohydrates, fats, fibers, vitamins, minerals, polyphenols, and essential fatty acids. Economically, durian has gained global trade prominence, with Thailand, Malaysia, and China leading production and consumption. This systematic literature review focuses on durian genomics, highlighting its impact on breeding through rigorous criteria and analysis phases. The PRISMA method produced 32 eligible papers for further analysis. The durian genomic research can be categorized into seven themes, i.e., genetic identification, genetic diversity, molecular markers development, gene expression, genomic sequencing, genome-wide analysis, and bioinformatics. Genomic research emphasizes genetic diversity and sequencing, employing simple sequence repeat (SSR) markers for conservation and breeding assessments. Restriction-site associated DNA (RAD) and PacBio sequencing unravel the complex durian genome, revealing unique gene expansions and evolutionary events such as polyploidization. Phylogenetic analyses within Malvales elucidate durian's evolutionary history and relationships, with research concentrated in Indonesia and China, reflecting regional significance. These insights inform conservation strategies, refine agricultural practices, and guide breeding efforts by elucidating durian's genetic diversity and adaptations. Integration of bioinformatics aids in gene synteny comparisons and resistance gene analog identification, advancing understanding of durian genetics and agronomy. These findings underscore genomics' pivotal role in unraveling durian fruit ripening mechanisms, which is essential for enhancing fruit quality and guiding future breeding strategies. The research gaps of durian genomic research include molecular markers development for fruit quality and analysis of local durian genetic diversity using whole genome sequencing, gene identification, and genome-wide analysis.

Keywords Bioinformatics · Durian · Genetic diversity · Gene expression · Molecular marker

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Introduction

Durian belongs to the genus *Durio* of the Malvaceae family. The genus *Durio* extends from the west tropical regions of Sri Lanka, India, Myanmar, Thailand,

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Peninsular Malaysia, Borneo, and Sumatra to the east tropical regions of Papua New Guinea and the Philippines. Borneo is considered the durian's center of diversity, with 15 endemic species. The tropical fruit includes approximately 30 species of large trees that grow naturally in the region (Kostermans 1958; Navia and Chikmawati 2018).As much as 24 out of 30 *Durio* species have been recorded to be found in Malaysian states (Peninsular Malaysia with 13 species, Sabah 13 species, and Sarawak 16 species), eight species in Sumatra (Indonesia), one species in Myanmar (Burma) and one species in Sri Lanka. Nine of these species produce edible fruits with starchy pulp, which are *D. testudiarum, D. oblongus, D. graveolens, D. lowianus, D. oxyleanus, D. grandifloras, D. dulcis, D. kutejensis,* and *D. zibethinus.* Of these nine species, only *D. zibethinus* is cultivated commercially (Ghazalli et al. 2022; Thorogood et al. 2022). More than 100 cultivars of *D. zibethinus* have been developed over the past 50 years (Cheon et al. 2017). To date, the top ten durian-producing countries are Thailand, Malaysia, Cambodia, Philippines, Indonesia, Vietnam, Brunei, Sri Lanka, Hongkong, and China. Durian has been distributed to India, Myanmar, Australia, Guinea, Jamaica, Honduras, Panama, and Hawaii (Foodalternatives 2024).

Durian is a nutritious fruit rich in fiber, vitamins, and various healthy plant compounds. According to Aziz and Jalil (2019), 100 g of durian pulp contains 65 g water, 1.47 g protein, 23.3 g carbohydrate, 5.33 g fat, 3.8 g fibers, 1.12 g ash, 6 mg calcium, 0.43 mg iron, 39 mg phosphorus, 0.21 mg copper, 30 mg magnesium, 2 mg sodium, 0.33 mg manganese, 436 mg potassium, 0.28 mg zinc, 23 µg β-carotene, 0.37 mg vitamin B1, and 19.7 mg vitamin C. Durian also has beneficial polyphenols, such as tannins, flavonoids, and phenolic acids, as well as other bioactive compounds like ascorbic acid (Aziz and Jalil 2019). In addition, durian pulp is rich in essential fatty acids, such as palmitic acid, stearic acid, octadecenoic acid, palmitoleic acid, myristic acid, oleic acid, and linoleic acid (Ho and Bhat 2015). Fully ripened durian fruit has a distinctive flavor and aroma due to the chemical reaction of volatile compounds, including alcohols, ketones, esters, sulfur, and aldehydes (Belgis et al. 2016). The durian fruit's medicinal properties include antidiabetic, anticancer (Leontowicz et al. 2007), and antioxidant activities (Leontowicz et al. 2008; Ashraf et al. 2010). Additionally, durian pulp has been reported to reduce symptoms of anxiety, stress, and depression (Rahman et al. 2023).

The durian export market has grown rapidly during the last two decades. According to the most recent data, the volume of durian traded globally increased more than tenfold between 2003 and 2022, peaking at 930,000 tonnes in 2021. Thailand and Malaysia are the world's two primary durian producers, accounting for up to 90% of total production. In 2016, Thailand produced 600 million kg of durian, whereas Malaysia produced roughly 400 million kg. The Philippines was the world's third-largest producer, with 71.5 million kg. Meanwhile, China is the world's largest importer of durian, with an annual average of 740,000 tonnes in 2020–2022, accounting for almost 95% of global imports. China acquires durians from Thailand, Malaysia, the Philippines, and Vietnam (FAO 2023).

Breeding programs are important for developing new plant cultivars with enhanced traits such as yield, biotic stress resistance, abiotic stress tolerance, and improved nutritional properties (Thudi et al. 2021). Traditional breeding relies on phenotypic selection, crossbreeding, backcrossing, and mutagenesis. Generally, conventional breeding programs would take years to produce new cultivars and longer years for tree plants like durian (Xu et al. 2020). To accelerate the breeding program, genomic research has been integrated into the activity, such as marker-assisted selection, genomic selection, qualitative trait loci mapping, genome-wide association research, gene editing, genetic diversity and conservation, transcriptomic, and proteomics (Budhlakoti et al. 2022). This integration would generate an accelerated breeding cycle, precision and accuracy breeding, enhanced traits, and is cost-effectiveness (Kim et al. 2020). Plant genomic research provides the foundational knowledge and tools that drive modern breeding programs (Bohra et al. 2020). Integrating genomics into breeding accelerates the development of improved plant cultivars, enhancing agricultural productivity and sustainability (Nerkar et al. 2022).

Durian breeding programs aim to improve the quality, yield, and resilience of durian cultivars to meet market demands and adapt to environmental challenges (Mansyah and Sutanto 2020). Most newly released durian superior cultivars are produced by local cultivars' characterization and evaluation without crossing or mutagenesis activities (Hau et al.

2023). On the other hand, durian has become an interesting genomic research object due to its diversity and abundance (Nawae et al. 2023). The objective of the current systematic literature review (SLR) is to provide a comprehensive summary and critical analysis of existing research on durian genomic research. In addition, this review summarizes existing knowledge, identifies research gaps, provides critical perspectives, and suggests future direction of durian genomic research.

A SLR is a rigorous and thorough procedure for identifying, assessing, and integrating research findings related to a topic or research issue (Xiao and Watson 2019). SLR aims to offer a comprehensive and impartial synopsis of the current body of knowledge (Shaffril et al. 2021). Despite being time-consuming and resource-intensive, SLR has various advantages, including a full and unbiased report. SLR strives to encompass all pertinent research on a subject, offering a comprehensive overview of the existing data (Rethlefsen et al. 2021). The methodical technique and predetermined criteria minimize the likelihood of selection bias and enhance the reliability of the results. The meticulous and systematic technique guarantees uniformity and clarity in the process of selecting, evaluating, and combining research (Shaffril et al. 2021). Thorough documentation of the process enables others to reproduce the review or validate its conclusions. By combining the findings of numerous research, SLR can provide more substantial and widely applicable conclusions. The results obtained through SLR are frequently utilized to drive research guidelines, policy determinations, and the establishment of best practices (Mengist et al. 2020). The SLR technique can be used to identify topics with a dearth of evidence, suggesting potential avenues for future research. SLR offers valuable insights into the robustness and constraints of the current body of evidence by evaluating the quality of the research included (Xiao and Watson 2019).

Methodology

Research question and database resources

The research question of this present systematic review was determined through the PICo method: *P (Problem)* was genomic research, *I (Interest)* was breeding program, and *Co (Context)* was durian. Thus, the research question applied in this review was: How does/far durian genomic research impact the fruit breeding program?

Three primary life science journal databases, i.e., Scopus, Web of Science, and PubMed, were used in this SLR. Scopus is one of the main databases of citations and abstracts comprising peer-reviewed publications. By January 2024, Scopus covered over 94 million documents from 29.2 thousand journals worldwide. Scopus contains diverse subject areas, including biological and agriculture sciences covered by the durian genomic research. The second database is PubMed, which is managed by the US National Library of Medicine. PubMed contains about 36 million citations for biomedical literature from MEDLINE, life science journals, and online books.

Eligibility and exclusion criteria

The qualification criteria used in the review were type of literature, language, and year of publication (Table 1). For the current review, only scientific research articles containing experimental data published in reputable journals were selected. Thus, conference proceedings, review articles, books, and book series were all excluded from the review. Research articles that were written in English and published after 2014 were selected for further review (Table 1). The eligible articles were also analyzed using Mixed Method Appraisal Tool (MMAT, Hong et al. 2018).

Table 1 Eligibility and exclusion criteria of the systematic literature review

Criterion	Eligibility	Exclusion
Literature type	Research Journal	Conference proceedings, review papers, books, book series, thesis, dissertation, abstract-only publication
Language	English	Others
Year of publication	After 2014	Prior to 2014

Systematic review protocol

The systematic review was carried out using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) (Page et al. 2021). The most recent eligible articles included in the SLR were the ones published in January 2024. The overall systematic review protocol is illustrated in Fig. 1. The search procedure was determined in the initial phase, where the following keywords were used: bioinformatics, durian, durio, gene, genetics, genomic, marker, and molecular. As many as 1087 articles were obtained, and any duplication was removed from the research database, resulting in 268 scientific research articles.

Data analysis and abstraction

The selected articles were evaluated and analyzed. In order to determine pertinent subjects and sub-themes, the abstract of the articles was screened prior to evaluating the full articles. The bibliographical analysis was conducted using VOSviewer (Perianes-Rodriguez et al. 2016), while content analysis was used in qualitative examination to identify common themes related to durian genomic research's impact on plant breeding. Sub-themes were then established to expand the understanding of each theme.

Result and discussion

Bibliometric analysis

Figure 2 shows the bibliometric analysis of 32 durian genomic-related research with several related keywords. The node size represents the occurrence frequency. The arch between nodes characterizes their co-occurrence in the same article. Spaces between two nodes represent the co-occurrence of the two keywords. The long space between two nodes indicates a small amount of the two keywords co-occurrence, and vice versa. The bibliometric analysis revealed that the most used keywords in durian genomic research were "phylogenetic" and "genetic diversity." The high occurrence of these two keywords may indicate that these two are likely to be the most attractive research subjects for durian. The information gained from research related to the keywords will open more opportunities for further genomics research and breeding activities. The bibliometric analysis also suggested that phylogenetic was related to plastome and genome assembly, whereas genetic diversity was associated with DNA fingerprinting, Borneo Island, and Lai.

SLR result

This present review was extracted from 32 research articles on durian genomic research. The inclusive workflow of the research and the major results are presented in Fig. 3. The durian genomic research could be categorized into seven themes, namely genetic identification, genetic diversity, genome sequencing, bioinformatics, GWAS (genome-wide association studies), gene expression, and marker development (Table 2). Genetic diversity and genome sequencing were the themes most explored, whereas genetic identification and marker development were the least explored. Out of (at least) 30 species of recognized durian, 8 species, i.e., *D. ziberthinus*, *D. kutejensis*, *D. lowianus*, *D. oxleyanus*, *D. acutifolius*, *D. dulcis*, *D. testudinarum*, and *D. tanjungpurensis*, were the subjects of durian genomic research. Being labeled as the most commercial species, the genomic aspect of *D. ziberthinus*, was the most explored. In terms of research location, durian genomic research was primarily conducted in South Asia and China, which are also regions known as the center of fruit production (Fig. 4).

Genetic diversity

Genetic diversity encompasses the range of genetic data in a population, species, or ecosystem. It quantifies the diversity of alleles, distinct versions of genes, found within the gene pool of a population (Mukhopadhyay and Bhattacharjee 2016). This diversity emerges as a result of mutations, genetic recombination during sexual reproduction, and various other evolutionary mechanisms (Coates et al. 2018). Genetic variety is vital in the long-term viability and ability to adjust a population or species. The raw material for natural selection is provided, enabling populations to adapt to environmental changes, diseases, and other difficulties (Govindaraj et al. 2015). Conservation biology places great importance on the preservation of genetic variety. Preserving the adaptive potential of endangered species helps guarantee

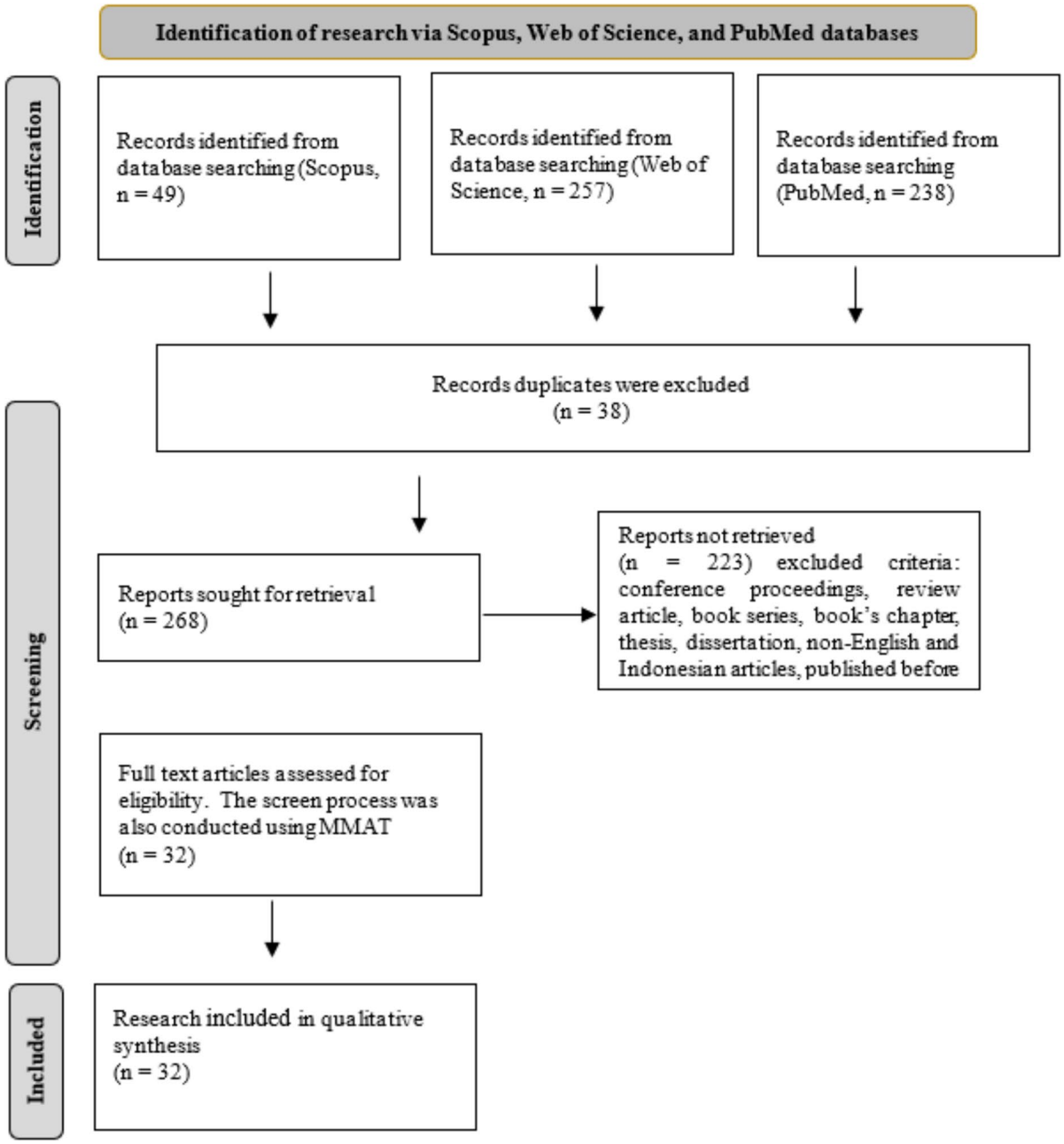

Fig. 1 The flow diagram of the systematic literature review. The flow diagram outlines the stages of literature selection, screening, eligibility assessment, and inclusion criteria applied to identify relevant research. The process begins with an initial search across databases, followed by removing duplicates and screening based on predetermined criteria. Eligible research articles are further evaluated for their quality and relevance to the review objectives using the MMAT method (Hong et al. 2018). Finally, selected articles are synthesized to provide insights into the topic under investigation. *n: number of publications

their long-term survival. Conservation initiatives frequently prioritize safeguarding ecosystems, preventing habitat fragmentation, and implementing breeding programs to uphold or reinstate genetic diversity (Hoban et al. 2022).

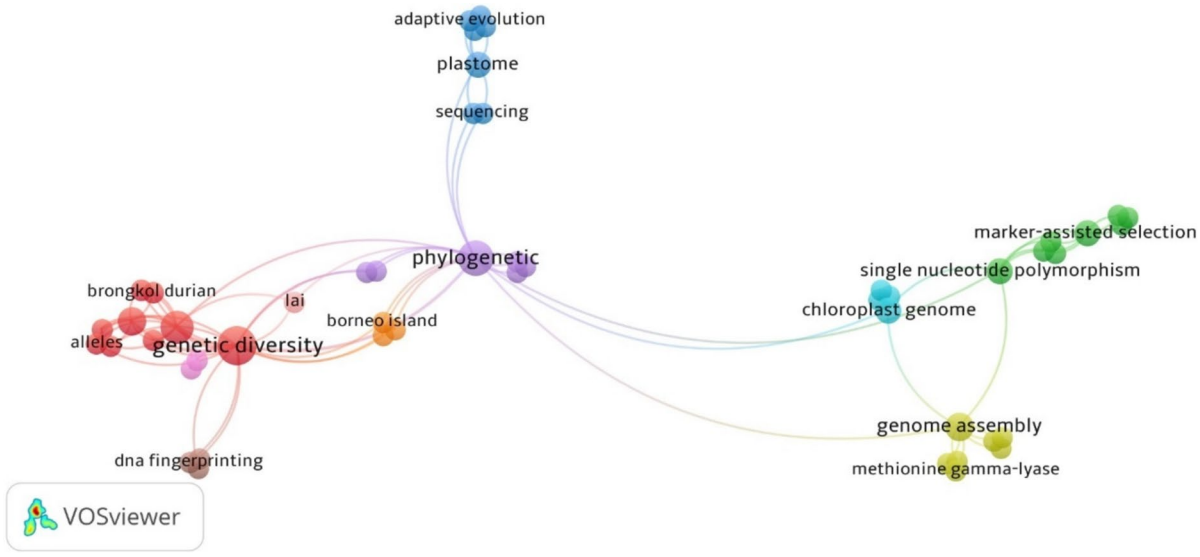

Fig. 2 Co-occurrence keywords of bibliometric analysis of the durian genomic research using Vosviewer

Genetic diversity can be affected by genetic drift and inbreeding. Genetic drift is the phenomenon where allele frequencies shift randomly due to chance events, while inbreeding decreases genetic diversity by increasing the occurrence of homozygous individuals (Cruzan 2022). The presence of genetic diversity is fundamental to the process of evolution. Through the mechanism of natural selection, populations are able to adapt to changing surroundings over time. The presence of diverse characteristics among individuals in a group serves as the foundation for natural selection, resulting in evolutionary modifications (Kanaka et al. 2023). Social activities, including overexploitation, pollution, habitat damage, and climate change, can potentially diminish genetic variety. Conservation efforts strive to reduce these effects and save genetic diversity for future generations (Kardosa et al. 2021).

Genetic diversity is crucial for the well-being, adaptability, and capacity for the evolution of people and ecosystems. Preserving and upholding genetic variety is crucial for the enduring existence of species and the proper operation of ecosystems (Hoban et al. 2022). Several genetic diversity research of durian have been done, with most of the research conducted in Indonesia, with one exception (conducted in China) (Table 3). Indonesia, a vast country with diverse ecogeographic conditions, naturally harbors a wide genetic diversity of durian. This diversity stems from the belief that Borneo Island is the center of origin for durian. Due to its cross-pollination system, the fruit has developed into numerous accessions.

The Indonesian durian genetic diversity research was conducted on a small scale, such as in a district with a small number of molecular markers, usually 10 to 14 markers (Riupassa et al. 2016; Prihatini et al. 2016; Handayani and Rahayu 2017; Hannum et al. 2020; Nasrika and Retnoningsih 2021; Numba 2023; Amrullah et al. 2023). The samples included in each research may come from a contest for the best fruit, which was held by the government, universities, and NGOs. Another Indonesian durian genomic research sample resource came from government or private *ex vitro* collection (Amom and Nongdam 2017).

Other aspects that should be noticed are the type of markers used in the Indonesian durian genomic diversity research, which was limited to RAPD (random amplified polymorphic DNA) and ISSR (inter simple sequence repeat). These markers were chosen to be applied in the research due to their simple operation and laboratory equipment requirement, making them low-cost methods (Kiran et al. 2010). However, both markers are dominant markers, which are less informative because they only differentiate the genome by size without revealing what or how many different alleles are in the genome (Nadeem et al. 2017). In addition, Chinese durian genomic diversity research was conducted using 32 genotypes of Hainan province durian.

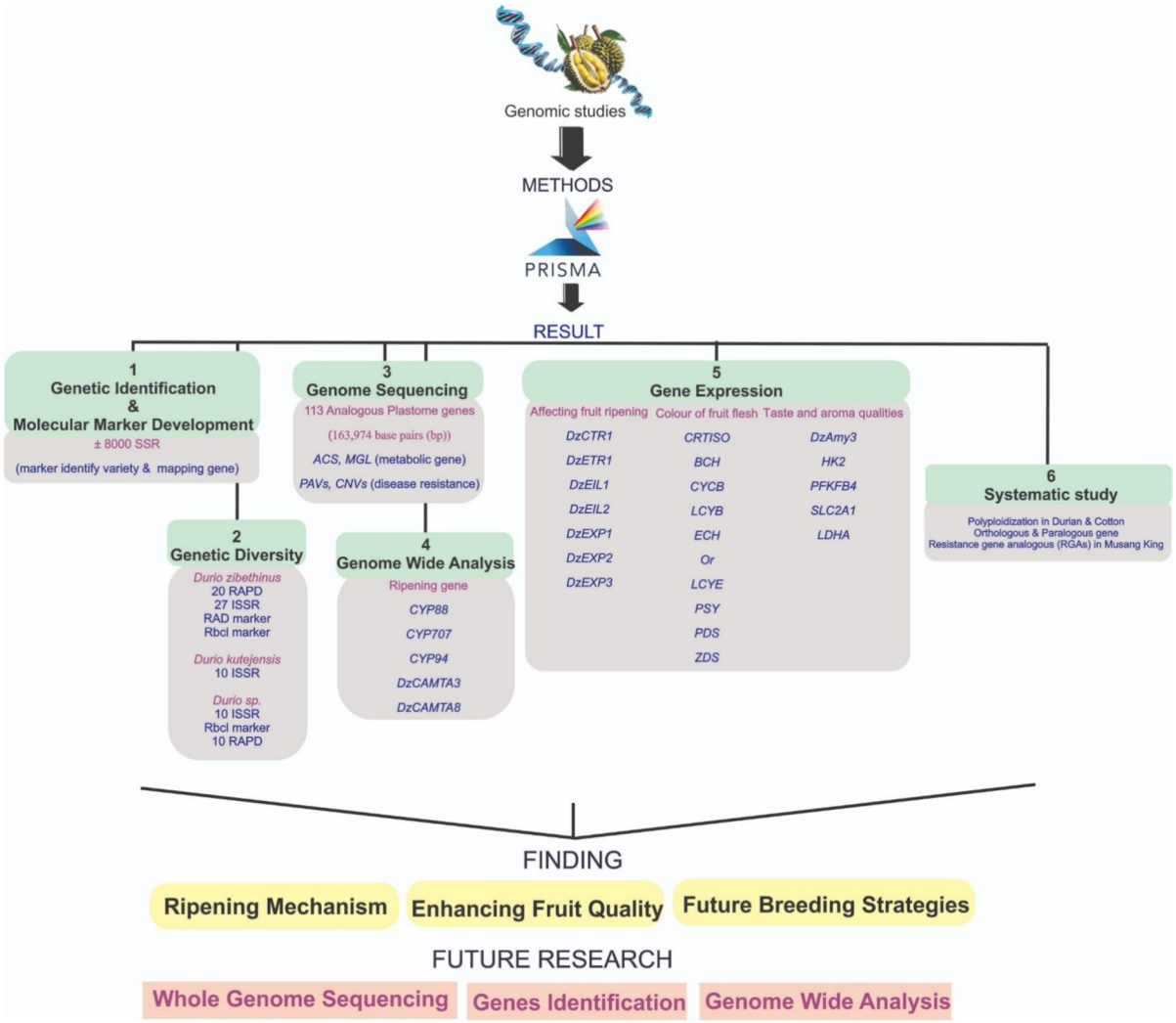

Fig. 3 The overall workflow and significant findings of systematics literature review of genomic research of durian (*Durio* spp.)

With a more sophisticated method of RAD (restriction-site associated DNA) sequencing, the research provided more informative results on the Chinese durian genome (Lin et al. 2022). While the number of samples and markers reveal the durian genomic diversity, capturing the whole picture of Indonesian durian genomic information is still challenging. More prominent, comprehensive research in terms of number of samples and marker type should be proposed to disclose informative facts about the Indonesian durian genome diversity.

Genomic sequencing

Multiple investigations have been undertaken to uncover the complete genomic sequencing of durian. In 2017, research was conducted on *D. ziberthinus* plastome sequencing in order to successfully determine the whole plastome genome of the king of fruits. The size of the durian plastome was 163,974 base pairs (bp), which comprised two inverted repeat segments, each 23,679 bp in length, divided by a large (95,704) single-copy region and a shorter (20,912 bp)

Table 2 The result of a systematic literature review of durian (*Durio* spp.) genomic research

References	Genetic identification	Genome sequencing	Bioinformatics	Genetic diversity	GWAS	Gene expression	Marker development	Species involved							
								Dz	Dk	Di	Do	Da	Dd	Dte	Dta
Azizi et al. (2022)	√						√	√							
Cheon et al. (2017)		√						√							
Cortaga et al. (2022)			√					√							
Handayani and Rahayu (2017)				√					√						
Hannum et al. (2020)				√				√							
Husin et al. (2022)					√			√							
Iqbal et al. (2021)					√			√							
Khaksar et al. (2019)					√			√							
Lin et al. (2022)				√			√	√							
Mursyidin et al. (2022)				√				√	√	√	√	√	√	√	
Mursyidin (2022)				√				√							
Nasrika and Retnoningsih (2021)				√				√							
Nawae et al. (2023)		√						√							
Numba (2023)				√				√	√						
Palapol et al. (2015)						√		√							
Paśko et al. (2019)						√		√							
Pasoongnoen et al. (2015)						√		√							
Prakoso and Retnoningsih (2021)				√				√							
Prihatini et al. (2016)				√				√							
Riupassa et al. (2016)				√				√	√						√
Shearman et al. (2020)		√						√							
Siew et al. (2017)				√				√							
Suntichaikamolkul et al. (2021)					√			√							
Teh et al. (2017)		√						√							
Thongkum et al. (2018)						√		√							
Wang et al. (2020)		√						√							
Wang et al. (2019)		√						√							
Wang et al. (2021)		√						√							
Wisutiamonkul et al. (2017a)						√		√							
Wisutiamonkul et al. (2017b)						√		√							
Wong et al. (2022)		√									√				

GWAS, genome wide association studies; Dz, *Durio ziberthinus*; Dk, *Durio kutejensis*; Dl, *Durio lowianus*; Do, *Durio oxleyanus*; Da, *Durio acutifolius*; *Dd*, *Durio dulcis*; Dte, *Durio testudinarum*; Dta, *Durio tanjungpuriensis*

single-copy region. The gene array of *D. zibethinus* was analogous to terrestrial plants' plastome. The plastome had a total of 113 genes, consisting of 30 tRNA genes, 79 protein-coding genes, and 4 rRNA genes. As many as 15 genes had one intron each and two with two introns each. In addition, 144 simple sequence repeats (SSR) could be found in the durian genome. The phylogenetic analysis demonstrated that *D. zibethinu*s (Helicteroideae) was the closest relative of the *Tilia* (Tilioideae) clade, with a bootstrap support of 100% (Cheon et al. 2017).

A recent endeavor to uncover the whole genetic makeup of durian has led to the creation of a preliminary genome of the durian cultivars found in Thailand. The extremely heterozygous durian genome was assembled at a chromosome-scale resolution by single-molecule sequencing and chromosome contact mapping procedures. Durian exhibited increased expression of ethylene-, sulfur-, and lipid-related pathways, as revealed by transcriptomic analysis on its fruits. The research identified instances of ancient whole genome duplication events that were common to both durian and cotton. Additionally, it was discovered that unique gene expansions in durian, particularly in the methionine g-lyase (MGL) gene, were connected with the formation of volatile sulfur compounds (VSCs). The expression of the ethylene-related gene aminocyclopropane-1-carboxylic acid synthase (ACS) and MGL increased in fruits coherently with the downstream metabolites (ethylene and VSCs), indicating a possible connection between the ethylene production and the methionine regeneration through the Yang cycle (Teh et al. 2017).

Another technique was employed to unveil the complete genomic sequences of durian. Utilizing lengthy PacBio reads, the *D. zibethinus* chloroplast genome was fully sequenced. The utilization of extended PacBio readings enabled the determination that the durian chloroplast genome was successfully assembled into a solitary 143 kilobase cyclic contig, encompassing a total of 111 genes. A total of 46 short (45–586 bp) direct repetitions and five short (63–169 bp) inverted repeats were identified. The assembly utilized long reads that covered the entire chloroplast, with overlaps exceeding 10 kilobases.

Additionally, numerous long reads were employed to connect the beginning and conclusion of the contig. The durian chloroplast was shown to be devoid of the extensive inverted repeats often present in chloroplast genomes. Furthermore, 24 more durian accessions were subjected to sequencing and compared to the existing assembly, revealing the absence of the big inverted repeat in these variations. Nine single nucleotide polymorphisms (SNPs) were observed among the different types (Shearman et al. 2020).

A reanalysis of the durian genome was performed by contrasting the genome with other genomes that have been thoroughly studied. It was revealed that durian and cotton had distinct polyploidization episodes. Hexaploidization occurred in durian approximately 19–21 million years ago (mya), whereas cotton's decaploidization took place 13–14 mya. Similar polyploidization may have arisen from the increased cotton gene's evolutionary rates due to diploidization and the inadequate understanding of the intricate nature of plant genomes. Decaploidization increased the cotton gene's evolutionary rates by 64% higher than durian. This process also accounted for a previous four-fold overestimation of the timing of the occurrence. However, the process of hexaploidization in durian did not significantly increase the rates of gene evolution, most likely because of its extended generation period. In addition, it is likely that differences in the evolution speed account for 98.4% of the cases when reassembled phylogenetic dendrograms of similar genes do not match the expected pattern (Wang et al. 2019).

The durian genome was studied to determine the genetic makeup of 13 members in the Malvaceae family. The ENCODE pipelines to analyze and incorporate 374 different sets of omics data into a customized genome browser was utilized along with the numerous dynamic charts to effectively convey information on the gene, RNA, and protein levels, including functional components and dynamic expression profiles. Furthermore, a practical comparison system was developed to facilitate the comparative examination of genes based on many characteristics within a single species or among closely related species. The utilization of this database and its accompanying tools may enable users to efficiently access extensive functional data for the purpose of biological exploration (Wang et al. 2020).

Comprehensive research of plastome evolution and phylogenetic relationships in 39 species of the Malvales order found that all species exhibited the quadripartite structure traits, as reflected in the angiosperm plastomes. However, notable independent expansions

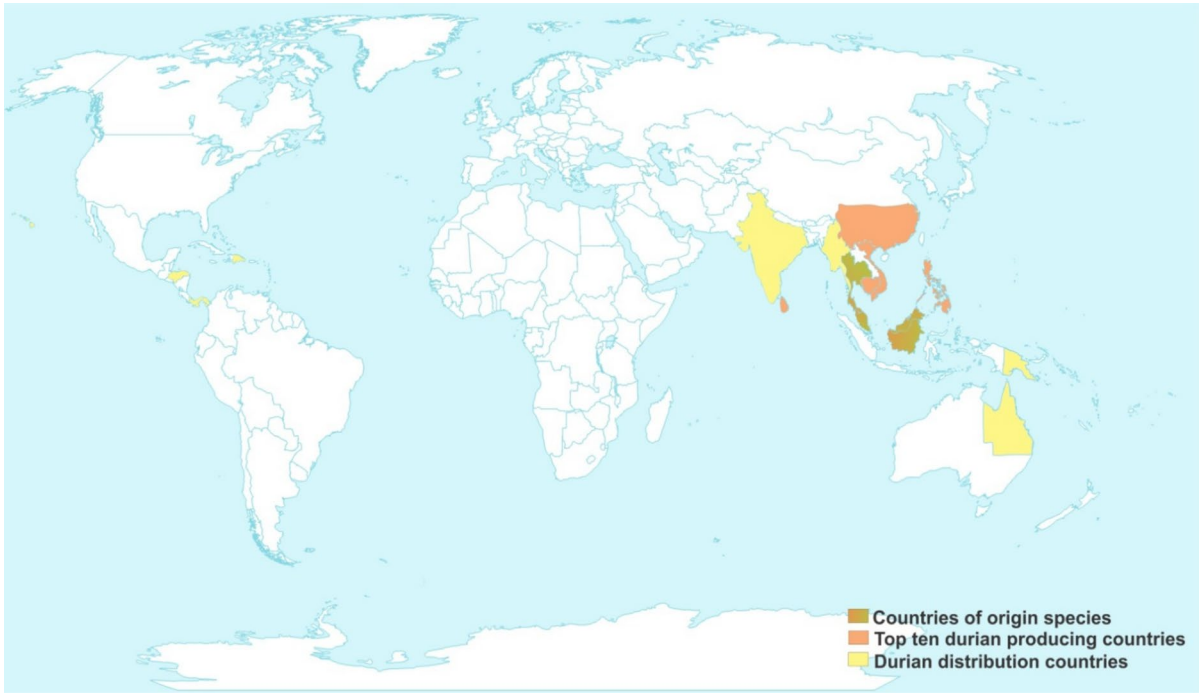

Fig. 4 Geographic Distribution of Durian (*Durio spp.*). Annotation: ( ): Countries of origin species (Borneo (Indonesia), Malaysia, and Thailand); ( ): Top ten durian-producing countries (Thailand, Malaysia, Cambodia, Philippines, Singapore, Indonesia, Vietnam, Brunei, Sri Lanka, and China); ( ): Durian distribution countries (India, Myanmar, Northern Australia, New Guinea, Jamaica, Honduras, Panama, and Hawaii). Sources: Foods alternative, 2024; Michael J. Brown. 1997

of the inverted repeat regions were observed in *Abelmoschus esculentus* and *D. zibethinu*s. In Malvaceae, a total of nine coding sequences were found to have locations that were positively chosen. Multiple diverse coding and non-coding areas were discovered in the Malvaceae plastomes, which could be useful for phylogenetic determination at lower taxonomic levels. The phylogenetic reformation, which relied on 78 protein-coding genes, provided robust support for almost all relationships within the subfamilies of Malvaceae. The expansion of the subfamilies within the Malvaceae family occurred throughout the early Eocene periods and later Cretaceous periods, which coincided with a period of global warming (Wang et al. 2021).

The resequencing analysis of multiple Thailand durian cultivars, including Kradumthong, Monthong, and Puangmanee, showed a significant genetic variation among these widely cultivated cultivars. The genome assemblies varied from 762.6 to 832.7%, whereas covered annotations for these genomes ranged from 92.4 to 95.7% of the embryophyte core proteins. The evolution rates of protein families in durian genomes were slower than those in cotton genomes. Protein families with functions related to protein phosphorylation and transcriptional regulation, which are implicated in responses to abiotic and biotic stress, exhibited a higher rate of evolution in durians. The phylogenetic reconstruction, presence or absence variations (PAVs), and copy number variations (CNVs) indicated that the genomic evolution of Thailand durians differed from that of the Malaysian durian (Musang King). The disease resistance gene profiles of CNV and PAV, as well as the methylesterase inhibitor expression domain-containing genes related to blooming and fruit maturation, were found to be distinct in Monthong compared to others. The genome assemblies and research of cultivated durians offer excellent resources for enhancing the comprehension of the genetic diversity of these fruits. This knowledge can potentially aid in producing new durian cultivars (Nawae et al. 2023).

Table 3 Summary of various genetic diversity research conducted on durian (*Durio* spp.) across different countries and species

References	Country	Species	Sample	Marker	Results
Prihatini et al. (2016)	Indonesia	*D. ziberthinus*	32 F1 hybrids	14 RAPD	112 out of 114 polymorphic alleles Similarity coefficient of 0.141–0.776
Riupassa et al. (2016)	Indonesia	*D. ziberthinus* *D. kutejensis* *D. tanjungpurensis*	58 genotypes of *ex vitro* collection	10 ISSR	161 out of 164 polymorphic alleles Genetic diversity index of 0.16–0.32 13 specific species loci
Handayani and Rahayu (2017)	Indonesia	*D. kutejensis*	8 cultivars from Batuah, East Kalimantan	10 ISSR	84 out of 92 polymorphic alleles Similarity coefficient of 0.34–0.58
Hannum et al. (2020)	Indonesia	*D. ziberthinus*	50 samples from Nias, West Sumatra	6 RAPD	100% (77) polymorphic alleles Similarity index of 0.00–0.89 (intra-population) and 0.22–0.43 (inter-population)
Prakoso and Retnoningsih (2021)	Indonesia	*D. ziberthinus*	25 superior cultivars from Brongkol, Central Java	7 ISSR	32 out of 36 polymorphic alleles Similarity coefficient of 0.29–0.95
Nasrika and Retnoningsih (2021)	Indonesia	*D. ziberthinus*	16 superior cultivars from Gunung Pati, Central Java	10 ISSR	50 out of 67 polymorphic alleles Similarity coefficient of 0.54–0.88
Lin et al. (2022)	China	*D. ziberthinus*	32 genotypes from Hainan, China	RAD sequencing, 232.148 SNP markers	Hainan durians can be classified into 2 clusters
Mursyidin et al. (2022)	Indonesia	*D. kutejensis* *D. lowianus* *D. excelsus* *D. acutifolius* *D. dulcis* *D. testudinarium*	19 genotypes	Rbcl	Nucleotide diversity of 0.024 Genetic divergence of 0.0006–0.0053 (intra-species) and 0.0000–0.011 (inter species)
Mursyidin (2022)	Indonesia	*D. ziberthinus*	51 superior cultivars from Kalimantan 48 sequences from Genebank	Rbcl	Nucleotide diversity of 0.056 Genetic divergence of 0.00–18.89
Amrullah et al. (2023)	Indonesia	*D. ziberthinus*	40 superior cultivars from Batang, Central Java	10 ISSR	100% (161) polymorphic alleles Similarity coefficient of 0.05–0.86
Numba (2023)	Indonesia	*D. ziberthinus* *D. kutejensis* *Boschia excelsa*	10 genotypes	10 RAPD	68 out of 78 polymorphic alleles 1 kb alleles produced from OPA02 primer potential gene associated with *Phytophthora palmivora* resistance

RAPD, rapid amplified polymorphic DNA; ISSR, inter simple sequence repeat; RAD, restriction-site DNA; SNP, single nucleotide polymorphism; Rbcl, ribulose biphosphate carboxylase

Genetic identification and molecular marker development

Genetic identification, also known as DNA profiling or genetic fingerprinting, is a method used to determine the identity of a species by analyzing its distinct genetic composition. The process involves examining specific segments of a species's DNA to generate a unique profile that can be compared with other samples for the purpose of identification.

Plant genetic identification has been used extensively in diverse fields, such as paternity and relation testing, genetic profiling, and conservation purposes. Durian genetic identification research is conducted in order to develop cultivar-specific markers. For example, a molecular marker based on nadhA gene was developed as an electrochemical biosensor specific to the Musang King cultivar (Azizi et al. 2022).

Research on China's durian genetic diversity by whole genome sequencing (WGS) of 32 genotypes through RAD sequencing method produced almost 8000 SSR markers, which differed in amplicon lengths and size. These markers can identify the cultivar, construct genetic mapping, and support molecular-assisted breeding and development programs. This research claimed to publish the first report of SSR markers in durian (Lin et al. 2022).

Genome-wide association

Fruit ripening was a crucial aspect of cultivating and breeding durian. However, this fruit reaches maturity fast and has a limited shelf life after being harvested, which makes it challenging to prolong the marketing time and export it to faraway markets. The developmental and ripening phases of fruits primarily impact their organoleptic qualities, including flavor, odor, and color appearance. Several studies have been conducted to examine the process of durian fruit ripening. The initial research was centered on cytochrome P450 (CYP), a substantial group of enzymes that governs numerous phytohormone and plant compound biosynthetic pathways. The thorough exploration of the transcriptome libraries and the whole durian genome resulted in the discovery of all CYPs, which are part of the process of durian fruit maturation. Validation of gene expression using RT-qPCR demonstrated a strong connection between the transcriptome libraries and the five stages of fruit ripening. The CYP88, CYP707, and CYP94 were potentially involved in the biosynthesis of gibberellin, abscisic acid, and jasmonic acid, respectively, and exhibited significant differences between fast and slow ripening accessions. This result strongly suggests that these hormones play crucial roles in fruit ripening. These P450s associated with phytohormones can collectively serve as supplementary molecular regulators that control ripening processes alongside auxin and ethylene. They also possess economic significance as important biological characteristics (Suntichaikamolkul et al. 2021).

The second research on durian fruit ripening focused on analyzing the Calmodulin-binding transcription activator (CAMTA) gene family in *D. zibethinus*. This research discovered 10 CAMTAs with conserved domains. The phylogenetic investigation of *DzCAMTAs* revealed that *DzCAMTA3* was closely related to its tomato ortholog, which has already been confirmed to play a role in the fruit ripening process through ethylene-mediated signaling. In addition, the examination of the whole transcriptome showed that *DzCAMTA3* and *DzCAMTA8* were the durian CAMTA genes with the most significant expression levels. These two *DzCAMTAs* exhibited a unique gene expression pattern related to the ripening process after harvest in Monthong, a durian cultivar indigenous to Thailand.

Furthermore, the reduced expression of *DzCAMTA3* and *DzCAMTA8* in response to exogenous auxin treatment was confirmed, indicating their sensitivity to auxin in a time-dependent manner. Thus, we infer that *DzCAMTA3* and *DzCAMTA8* interact cooperatively with ethylene in the process of durian fruit ripening. On the other hand, *DzCAMTA3* and *DzCAMTA8* have an antagonistic effect on auxin and can influence the post-harvest ripening process in durian. Moreover, the genes interacting with *DzCAMTA3* and *DzCAMTA8* possess notable CAMTA recognition motifs and control crucial pathways connected with fruit ripening (Iqbal et al. 2021).

Gene expression

It is known that durian is classified as a climacteric fruit high in bioactivity and nutritional content. As a climacteric fruit, the durian's ethylene content and respiration rate increase during fruit ripening (Thongkum et al. 2018). *D. zibethinus* has a thorny protective fruit skin with varying thicknesses and is estimated to have a total separate cell area of around 400 cm^2 per

fruit, making durian as the fruit with the highest separated cell area (Palapol et al. 2015).

A large cell area indicates an individual's high respiration process. In the case of durian, this affects the speed of fruit ripening, which is influenced by other genes expressed at various times in the fruit ripening process. Some of the main genes involved in fruit ripening are genes that influence ethylene (for ripening), affect the formation of carotenoids (for color), and influence changes in glucose and lactic acid (for flavor and aroma quality, respectively) (Paśko et al. 2019).

Genes affecting fruit ripening

In climacteric fruits such as durian, fruit ripening requires the help of ethylene. Ethylene biosynthesis starts with methionine produced by several enzymes, namely 1-aminocyclopropane-1-carboxylate synthase (ACS), S-adenosyl-methionine synthetase (SAM), and 1-aminocyclopropane-1-carboxylic acid oxidase (ACO). In durian, several genes related to flavor and aroma also play a role in fruit ripening. It is known that the expression of these fruit ripening-related genes is highly expressed on days 1–7 of the durian ripening process; DzETR2 is expressed highest while *DzEIL1* is expressed lowest, whereas *DzCTR1*, *DzETR1*, and *DzETR1* gene expressions extensively had a positive correlation with color and ethylene production. Meanwhile, fruit flesh hardness, total soluble solids (TSS), brightness level, and hue were negatively correlated with durian fruit ripening gene expression. It was also reported that *DzEIL1* gene did not significantly correlate with ethylene production and color (Thongkum et al. 2018).

Application of 1-methylcyclopropene (1-MCP) for ethylene inhibition and ethephon as a fruit ripening stimulant showed different gene expression in Monthong durian. The expression of *DzETR1* and *DzETR2* in durian pulp was influenced by the production of ethephon during fruit maturation. Administration of 1-MCP inhibited *DzETR1* and *DzETR2* gene expression, which suppressed ethylene production. *DzCTR1* expression regulated durian ripening, where the expression of this gene increased when given ethephon and decreased when given 1-MCP. In durian, the *DzEIL1* and *DzEIL2* genes encode EIN3-like protein, slightly affecting gene expression when given ethephon.

Meanwhile, administration of 1-MCP still significantly inhibited *DzEIL1* and *DzEIL2* gene expression. During fruit ripening, ethylene production was inhibited by 1-MCP and induced by ethephon. Thus, it can be inferred that the durian fruit maturation is stimulated by ethylene, which is controlled by the DzETR2 gene via EIL and other transcription factors.

The expansin gene is also involved in fruit ripening, which is related to dehiscence. In addition to being triggered by ethylene production, the process also affects several genes, such as *DzEXP1*, *DzEXP2*, and *DzEXP3*. Expansin is a group of proteins from four subfamilies: α-expansin (EXPA) and β-expansin (EXPB), which affect cell wall tension, expansin-like A, and expansin-like B. The α-expansin gene is found in fruit flesh and tissue.

Expansin genes (*DzEXP1* and *DzEXP2*) are involved in the cell separation process, and both are correlated with fruit flesh softening. Applying 1-MCP can inhibit the expression of the expansin gene, stimulate the softness of the fruit flesh, and the cracking of the durian fruit skin for 6 days, so ethylene production will increase on the seventh day. Meanwhile, plants without treatment will experience increased ethylene production on the first day. The highest *DzEXP1* expression was found in fruit without treatment on the fourth day, fruit applied with ethephon on the third day, and fruit treated with 1-MCP on the ninth day. Fruit flesh softening was inhibited around 6 days after 1-MCP application, while control fruit flesh softened on the fourth day. On the other hand, ethephon application accelerated fruit pulp softening on the first day. Fruit peel rupture was delayed for 4 days on 1-MCP application, whereas ethephon application induced fruit peel rupture by one day. Cell wall polymer separation induces fruit development with the increase of expansin gene expression, which is accompanied by softening of the fruit pulp and rupturing of the fruit peel. As such, the *DzEXP1* and *DzEXP2* genes impact fruit pulp softening and fruit peel breaking.

Genes that affect the color of fruit flesh

The color of durian pulp results from the accumulation of α-carotene and β-carotene, which are components of vitamin A. Several carotenoid genes are involved in the development and ripening process of durian, such as carotene isomerase (CRTISO),

beta-carotene hydroxylase (BCH), chromoplast-specific lycopene beta-cyclase (CYCB), lycopene beta-cyclase (LCYB), epsilon-carotene hydroxylase (ECH), cauliflower Orange (Or), lycopene epsilon-cyclase (LCYE), phytoene synthase (PSY), phytoene desaturase (PDS), and zeta-carotene desat urese (ZDS). As a comparison, in durian, which has white flesh (var. Monthong) and yellow flesh (var. Chanee), the PSY and LCYB genes were highly expressed 10 days after anthesis in the Monthong and Chanee cultivars, then the expression weakened during fruit development. LCYB gene expression was higher in the Monthong cultivar than in Chanee during fruit development and ripening. PDS gene expression increased during fruit development and ripening in both cultivars. However, PDS gene expression was less in the Chanee cultivar except in week 12, during which the expression was higher than in the Monthong cultivar. ZDS gene expression increased during fruit development and ripening, with the expression pattern rising in the Chanee cultivar 10 weeks after anthesis, while in the Monthong cultivar only increased slightly. ZDS gene expression in the Chanee cultivar was higher than in the Monthong cultivar, which correlated with the high carotenoid content in the Chanee cultivar.

The expression of the CRTISO and LCYE genes had the same pattern as that of ZDS, where the expression increased during fruit development but decreased during fruit ripening in both cultivars. The expression of the CYCB gene in the Monthong cultivar was highly expressed 12 weeks after anthesis before fruit development and ripening. In contrast, the Chinese cultivar did not experience increased expression and tended to be weakly expressed. Finally, the expression of the BHC and ECH increased during fruit development. Still, it decreased during fruit ripening, where the expression in the Chanee cultivar was weaker than in the Monthong cultivar.

The expression of ZDS and CRTISO increased in the Chanee cultivar during development. CRTISO expression decreased from perfect fruit condition to ripening, which was in line with carotenoid concentrations in the late phase of both cultivars. ZDS and CRTISO have the same expression pattern. Thus, these genes can coordinate together, and their expression abundance correlates with the carotenoid content and yellow color of the fruit flesh. The ZDS gene acts as a regulator in the catalysis of ζ-carotene to tetra-cis-lycopene (pro-lycopene) as a substrate for the enzyme encoding CRTISO. Lycopene was detected in durian flesh from Malaysia, although it was detected not in the Chanee and Monthong cultivars.

LCYB gene regulates the conversion of lycopene into α-carotene and β-carotene. The BHC gene governs the conversion of α-carotene to lutein and β-carotene to zeaxanthin. The high expression of LCYB and CYCB genes in the Monthong cultivar compared to Chanee indicates that Monthong can produce higher levels of β-carotene. Nevertheless, it was also implied that the β-carotene content of Monthong was lower than Chanee due to the conversion of β-carotene into zeaxanthin as a result of the high expression of the BCH gene in Monthong.

The LCYE gene controls the conversion of lycopene to α-carotene. LCYE gene expression in Chanee was higher than in Monthong, which was also consistent with increased α-carotene. Meanwhile, weak BCH and ECH gene expression in Chanee resulted in high lutein content. Research indicates that α-carotene is a flux control medium towards lutein rather than influencing the expression levels of BCH and ECH genes. It was assumed that the accumulation of α- and β-carotene during durian fruit development and maturation was regulated by the ZDS, LCYB, and LCYE genes.

Genes that influence glucose and lactic acid changes

Durian fruit is known to have a unique taste and aroma, which is related to changes in glucose and lactic acid. The enzyme α-amylase converts the starch content in durian fruit into sugar, which gives a sweet flavor when the fruit is ripe. The gene that plays a role in α-amylase expression is DzAmy3, an α-type plastid from the Monthong durian cultivar. DzAmy3 initiates the breakdown of starch granules in plastids into soluble starch.

Several main components that play a role in durian aroma include sulfides, esters, and alcohol, which are expressed through glycolysis. Several genes involved in this process include Hexokinase (HK2), 6-phosphofructo-2-kinase 4 (PFKFB4), SLC2A1 (Glut 1) (facilitated glucose transporter member 1), and lactate dehydrogenase A (LDHA). Furthermore, the research result also revealed the high expression of the PFKFB4 and HK2 genes.

Bioinformatics

Bioinformatics is an indispensable tool in plant genomics research, facilitating data analysis, interpretation, and hypothesis generation to advance our understanding of plant biology and improve crop productivity and sustainability (Ong et al. 2016; Byrne et al. 2018). Bioinformatics in plant genomics involves applying computational techniques and tools to analyze and interpret plant genomic data. With the advent of high-throughput sequencing technologies, such as next-generation sequencing (NGS), robust genomic data can be generated. Bioinformatics is crucial in handling, analyzing, and extracting meaningful information from these data (Araújo et al. 2021).

Most durian genomic research, such as genetic diversity genome-wide association and genomic sequencing, employs bioinformatics approaches. For the bioinformatics theme, two studies were included in the current review since our research analyzed deposited sequences from the public genome databases.

The first research reanalyzed the sequence of the durian genome by comparing it to the cotton genome to determine the gene synteny. Through the analysis of the differences in syntenic genes resulting from polyploidization in durian and cotton, orthologous and paralogous genes were found in each of the two genomes (Wang et al. 2019). The second research was conducted using the reference genome of the durian cultivar Musang King to examine the fruit's resistance gene analogs (RGAs). A total of 2586 RGAs was characterized and functionally annotated, which was the most thorough examination of durian RGAs, offering a priceless resource for research on this significant tropical fruit crop's genetics, agronomy, and other biological aspects (Cortaga et al. 2022).

General discussion

This systematic review was one of the first reviews of durian genomic research. Using the PRISMA method, the current review captured several highlighted results. Genomic research is a trending research topic for most crops since it facilitates research in other fields, such as physiology, evolution, and breeding. In addition, many researchers have conducted speed breeding to accelerate plant new cultivar assembly, including through genomic research (Samantara et al. 2022). The application of genomic research in plant breeding has produced a superior cultivar, such as those developed for potato, rice, maize, chili, and other horticulture commodities (Ebert 2020). Unlike those crops, durian breeding is limited to new cultivars originating from local accession without crossing or hybridization. The agronomic characteristics of durian—long vegetative, stage, and regeneration time—make the hybridization activities require abundant resources.

On the other hand, as the plant is a natural cross-pollination species, the genetic constituents of durian are widely diverse. Thus, durian breeders choose to characterize and evaluate the local accession rather than conducting crossing activities. However, durian genomic research is still an interesting topic to be explored. The complete information on the durian genomic aspect may lead to further understanding of improved agronomic practice, post-harvest handling, pest and disease management, as well as breeding program.

This research has several inherent limitations. Gusenbauer and Haddaway (2020) recommended 14 databases for searching relevant articles. However, due to access constraints during the review synthesis, only three databases were used: Scopus, Web of Science, and PubMed, supplemented by Springer Link, Emerald, Sage, and Taylor Francis. The quality process assessment relied on MMAT, ensuring that the selected articles used in this present review originated from qualified research. The articles were expected to reveal differences in quality when assessed using various quality evaluation methodologies. In the future, examining more papers than the 32 publications reviewed in this research using different assessment methodologies should be considered. The quality evaluation aims to identify documents relevant to the review's purpose rather than focusing on finding flawless articles that should be highlighted (Shaffril et al. 2021).

Future research direction

Similar to vegetable crops, the fruit crop genomic research has lagged behind staple food crops, such as wheat and rice. However, genome sequencing technologies contributed greatly to the understanding of the evolution process as well as the genetic dissection of important characters (Li et al. 2022). The

genomic insight of fruit crops for the last 15 years has been expanded by the development of publicly accessible genomic databases. The application of unique genetic features of fruit crop characters, along with new genomic-assisted tools, namely genomic selection and gene editing, are directing scientists and breeders to pursue plant breeding efforts (Wang et al. 2023). The future of molecular research on durian will likely focus on several themes that can contribute to the better understanding, improvement, and sustainable production of this distinctive and highly valued tropical fruit. Molecular research in durian could open doors to innovations in genetics, breeding, crop management, and even novel applications in the food industry. One of the foundational areas of molecular research in durian is the complete genomic sequencing of the durian genome. While some progress has been made, further refinement and comparison with other related species (e.g., mangosteen, rambutan) could help uncover unique genetic features of durian. Sequencing the entire genome will also provide a blueprint for understanding the molecular pathways responsible for key traits like flavor, aroma, and texture. This insight would be vital for improving durian breeding procedures as applied to other fruit crops (Wang et al. 2023).

Several foci of durian genomic mapping are resequencing the whole durian genome to develop the reference genome and identifying gene clusters responsible for essential characteristics in which transcriptomics plays an important role. Transcriptomics involves analyzing RNA molecules to understand how genes are expressed in different tissues and under diverse situations. This research could reveal which genes are activated during fruit ripening, how the plant responds to environmental stressors, or how it deals with pathogens. Such research will provide insights into how to enhance durian's productivity and resilience. The research should then focus on understanding the gene expression patterns during fruit ripening, investigating the molecular response to abiotic stressors like drought or extreme temperatures, and identifying genes involved in resistance to fungal diseases (e.g., durian dieback). The identified genes then can be confirmed spatially using several tools such as in situ hybridization (Miya et al. 2025) and functionally using clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) (Zhang et al. 2021).

Advanced gene-editing tools like CRISPR/Cas9 are revolutionizing plant genomics. These technologies allow precise modification of genes associated with essential traits without introducing foreign DNA. In durian, CRISPR could improve fruit quality, enhance disease resistance, or extend shelf life, providing a non-GMO (genetically modified organisms) approach to crop improvement.

Using molecular markers (such as SNPs or microsatellites) can considerably accelerate the breeding process by identifying desired features at the DNA level, even before the plant yields fruit. This will allow breeders to focus on the most promising genetic lines for specific traits like yield, pest resistance, or fruit quality, speeding up traditional breeding cycles. This research area should focus on developing molecular markers linked to desirable traits (e.g., fruit size, pest resistance, drought tolerance). The developed marker can then be applied to marker-assisted selection (MAS) for breeding durians with improved characteristics.

Molecular research on durian is poised to change this highly valued fruit's cultivation, quality, and sustainability. Researchers can tackle the challenges facing durian farmers and producers by applying advanced molecular tools and technologies such as genomics, CRISPR gene editing, metabolomics, and transcriptomics. These innovations will improve the economic value of durian and contribute to a more sustainable and efficient agricultural industry in the face of changing environmental conditions (Fig. 5).

Conclusion

This review was conducted to comprehensively assess the influence of genomic research on the durian breeding program. The research provides valuable contributions to practical applications and the existing knowledge base. Interested parties, such as researchers, breeders, and academics, might use the review to inspire additional genetic investigations that can aid in developing new cultivars. The findings guide combining local knowledge with scientific research to create a climate change adaptation policy and discuss the implications of durian genome research on producing commodities. The results provide researchers with valuable information regarding the particular areas of durian genome research that should be prioritized

Steps of durian molecular breeding	Year 1	Year 2	Year 3	Year 4	Year 5
Identification of parental lines and important traits	Characterization and evaluation of morphological characters and genetic diversity with molecular marker				
Genomic mapping and sequencing	Reference genome construction, genome-wide analysis				
Transcriptomics	Identification of expressed gene clusters responsible for important characters				
Confirmation of the function of genes		Yeast *in situ* hybridization/ CRISPR			
Gene editing			CRISPR technology to target specific genes		
Development of molecular markers		Development of molecular markers linked to desirable traits (marked assisted selection [MAS])			
Selection				Selection of genome editing results using MAS	

Fig. 5 Roadmap of future durian molecular research in supporting the fruit breeding program

in future research. The review determined that durian genetic investigations had a limited impact on assembling novel plant cultivars. The durian breeding program may require 10–20 years to develop a new cultivar through crossing and traditional breeding due to the plant's lengthy life cycle. Newly published durian cultivars typically originate from local accessions rather than through crossbreeding methods. To break the loop, durian genome investigations using biotechnological approaches have been started. Genomic research like GWAS and gene mining can aid in developing a precise breeding program for durian. Molecular markers are designed to help with the selection of parents and offspring.

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Declarations

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