Current Status and Advances in Loquat Genomics: From Genome Mapping to Molecular Breeding

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Abstract This study provides an overview of the current status and advances in loquat genomics, with a focus on genome mapping, molecular breeding technologies, and the genetic mechanisms underlying key traits. As an important economic crop, loquat faces challenges such as environmental stresses, diseases, and breeding difficulties. In recent years, through high-quality genome assembly and the integration of multi-omics technologies (genomics, transcriptomics, and metabolomics), scientists have identified multiple key genes and QTL loci associated with fruit quality, stress resistance, and flowering and fruiting time. The article also discusses the role of marker-assisted selection (MAS) and genome editing tools like CRISPR-Cas9 in improving breeding efficiency. Furthermore, research indicates that the domestication process of loquat exhibits a two-stage pattern, with genetic diversity concentrated in wild varieties. Looking forward, the application of multi-omics technologies and artificial intelligence is expected to enable more efficient and precise loquat breeding to address challenges posed by climate change and market demands.

Keywords Loquat genomics; molecular breeding; High-quality genome assembly; Marker-assisted selection (MAS); Multi-Omics integration

1 Introduction

Loquat (*Eriobotrya japonica*) is a significant fruit crop within the Rosaceae family, valued for its unique flavor and nutritional benefits. It holds a prominent place in horticulture and global markets, particularly in Asia and Europe, where it is cultivated extensively (Wang et al., 2021; Jing et al., 2022). The fruit's economic importance is underscored by its role in local economies and its potential for export, contributing to the agricultural diversity and food security in these regions (Wang et al., 2017; Zhang etal., 2022).

Despite its economic significance, loquat breeding and production face several challenges. One major issue is the plant's susceptibility to environmental stresses, such as cold temperatures, which can severely impact yield and fruit quality. Additionally, loquat exhibits gametophytic self-incompatibility, complicating breeding efforts and necessitating careful selection of compatible cultivars for effective pollination. The presence of diseases, such as leaf spot caused by *Alternaria* species, further complicates cultivation and requires ongoing management strategies.

The study aims to provide a comprehensive review of the current status and advances in loquat genomics, focusing on genome mapping and molecular breeding. By exploring recent genomic studies, such as the identification of key genes involved in fruit size and development, and the characterization of self-incompatibility mechanisms, the paper seeks to highlight the progress made in understanding loquat's genetic makeup. The scope of this study includes the application of genomic insights to improve breeding strategies, enhance stress resistance, and ultimately increase the productivity and quality of loquat crops.

2 Loquat Genomics: An Overview

2.1 Evolutionary history and genetic diversity

Loquat (*Eriobotrya japonica*) is a subtropical fruit tree that has undergone significant evolutionary changes. It shares a common ancestor with other members of the Rosaceae family, such as apple and pear, and has experienced a whole-genome duplication event prior to its divergence from these relatives (Jiang et al., 2020; Jing

et al., 2022). The genetic diversity within loquat is notable, with wild loquats exhibiting higher levels of genetic variation compared to cultivated varieties. This diversity is crucial for understanding the domestication process and for breeding purposes (Wang and Paterson, 2021; Zhao, 2024). Studies have shown that loquat underwent a two-staged domestication process, initially in West-northern Hubei province and later refined in other regions of China, which has resulted in a rich genetic pool. The genetic diversity among loquat accessions has been further explored using microsatellite markers, revealing significant variation that is geographically structured (Blasco et al., 2014).

2.2 Current status of genomic resources in loquat

The genomic resources for loquat have advanced significantly with the development of high-quality genome assemblies. The first chromosome-level genome assembly of wild loquat has been completed, providing a comprehensive resource with over 45 000 predicted protein-coding genes. This assembly has facilitated the identification of key genes involved in fruit quality and development, which are essential for molecular breeding efforts. Additionally, the development of genetic maps using AFLP and SSR markers has provided a framework for further genetic studies and breeding programs (Gisbert et al., 2009; Manghwar et al., 2019). The availability of genic SNP markers has also enhanced the ability to conduct genetic diversity analyses and marker-assisted selection in loquat (Li et al., 2015).

2.3 Comparison with genomic efforts in related species

Comparative genomics has revealed that loquat shares a close evolutionary relationship with other Rosaceae species, such as apple and pear, with a divergence time of approximately 6.76 million years ago (Figure 1) (Jiang et al., 2020). The genomic efforts in loquat have paralleled those in related species, with similar approaches being used to map genetic traits and understand self-incompatibility mechanisms (Carrera et al., 2009; Gisbert et al., 2009). The transferability of SSR markers from apple and pear to loquat has been demonstrated, highlighting the potential for cross-species genomic studies within the Rosaceae family. Moreover, the identification of S-RNases in loquat has provided insights into the self-incompatibility systems that are common across Pyrinae species, further aligning loquat genomic research with that of its relatives (Wang et al., 2017).

Figure 1 Picture of a loquat variety, Seventh Star (*Eriobotrya japonica*) (Adopted from Jiang et al., 2020)

3 Genome Mapping in Loquat

3.1 Early efforts and conventional mapping approaches

Early efforts in loquat genome mapping primarily relied on conventional techniques such as quantitative trait locus (QTL) mapping and the use of simple sequence repeat (SSR) markers. These methods were instrumental in identifying genetic markers associated with key traits like fruit weight and flesh color. For instance, QTL mapping has been used to identify loci associated with fruit weight, providing a foundational understanding of the genetic basis of this trait in loquat (Yuan et al., 2020; Peng et al., 2022b). Additionally, SSR markers have been employed to study genetic diversity and relationships among loquat varieties, which are crucial for breeding programs (Wang et al., 2021).

3.2 Advances in next-generation sequencing (NGS) technologies
The advent of next-generation sequencing (NGS) technologies has significantly advanced loquat genomics. NGS has enabled high-throughput sequencing and comprehensive transcriptome analysis, facilitating the identification of thousands of differentially expressed genes (DEGs) involved in fruit development and ripening (Song et al., 2016). This technology has also allowed for the assembly of high-quality reads into unigenes, providing a deeper understanding of the genetic networks regulating loquat fruit development. The integration of NGS with other omics approaches, such as metabolomics, has further enhanced the ability to map complex traits and identify candidate genes for molecular breeding (Peng et al., 2022b).

3.3 High-quality reference genome and assembly techniques
Recent efforts have focused on generating high-quality reference genomes for loquat, which are essential for accurate genome mapping and molecular breeding. The first high-quality chromosome-level genome assembly of wild loquat has been completed, revealing insights into the genomic evolution and domestication of the species (Jing et al., 2022). This reference genome includes a comprehensive set of predicted protein-coding genes and has facilitated the identification of genomic regions associated with important traits such as fruit quality and size. Advanced assembly techniques, combined with large-scale transcriptome and metabolome analyses, have provided valuable resources for elucidating the genetic basis of domestication and for guiding future breeding efforts in loquat.

4 Genomic Insights into Key Traits in Loquat
4.1 Genes and QTLs for fruit size and quality
Recent genomic studies have significantly advanced our understanding of the genetic basis of fruit size and quality in loquat. The identification of 95 EjSAUR genes, which are involved in auxin signaling, has been pivotal in understanding fruit size regulation. Specifically, the *EjSAUR22* gene has been identified as a key player in fruit expansion, responding to auxin and influencing cell size. Additionally, a multi-omics approach has identified major loci associated with fruit weight, including homologs of *ETHYLENE INSENSITIVE 4* (*EjEIN4*) and *TORNADO 1* (*EjTRN1*), which are crucial for fruit development (Peng et al., 2022b). Furthermore, the EjBZR1 gene has been shown to repress fruit enlargement by binding to the EjCYP90 promoter, highlighting its role in regulating brassinosteroid biosynthesis and cell expansion (Nadeem et al., 2018; Su et al., 2021). These insights provide a foundation for molecular breeding aimed at improving fruit size and quality in loquat.

4.2 Genetic regulation of flowering and fruiting time
The genetic regulation of flowering and fruiting time in loquat is closely linked to the MADS-box gene family. A comprehensive genome-wide analysis has identified 125 EjMADS-box genes, which are crucial for flower and fruit development. These genes are categorized into various subfamilies, with several candidates like *EjMADS107/109* and *EjMADS24 / EjMADS46 / EjMADS49 / EjMADS55 / EjMADS61 / EjMADS67 / EjMADS77 / EjMADS86* being potentially involved in flower bud differentiation and fruit expansion (Figure 2) (Li et al., 2023). The expression patterns of these genes during different developmental stages suggest their conserved roles in regulating flowering and fruiting time, providing valuable targets for breeding programs aimed at optimizing these traits (Xu et al., 2012).

4.3 Disease resistance genes in loquat
Disease resistance in loquat is a critical trait for ensuring crop resilience and productivity. Genomic studies have identified several genes that may contribute to disease resistance. For instance, genes involved in sugar biosynthesis have been enriched in regions undergoing selective sweeps, indicating their potential role in disease resistance (Wang and Paterson, 2021). Additionally, transcriptomic analyses under cold stress conditions have revealed differentially expressed genes (DEGs) such as UDP-glycosyltransferase and glycosyltransferase, which are implicated in stress responses and may contribute to enhanced disease resistance (Zhang et al., 2022). These findings underscore the importance of integrating genomic data to identify and utilize disease resistance genes in loquat breeding programs.
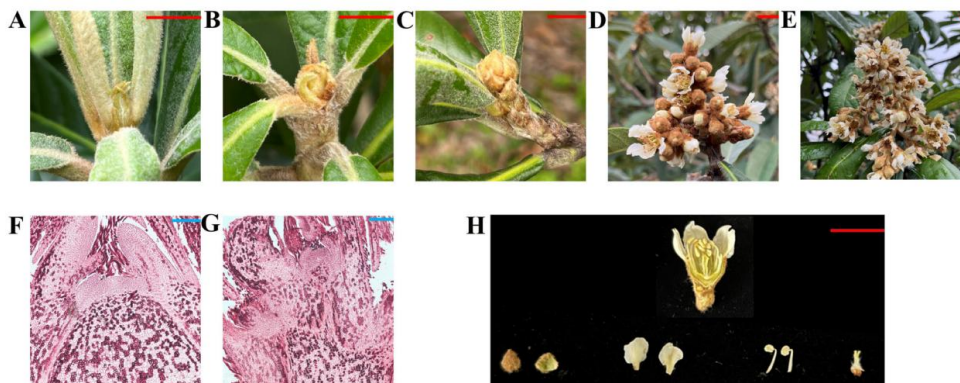
Figure 2 Stem apex tissue at different stages and flower organ tissue of loquat (Adopted from Li et al., 2023)

Image caption: (A) Vegetative bud. (B) Flower bud differentiation begins. (C) Visible flower bud. (D) The first flowering stage (the period when about 25% of the flowers of the whole tree are open). (E) Full-bloom stage (a period when about 75% of the flowers of the whole tree are open). (F) Paraffin section of vegetative bud. (G) Paraffin section of visible flower bud. (H) Flower organ tissue of loquat. The four flower organ tissues are sepals, petals, stamens, and pistils in the picture. The red bar represents 1 cm. The blue bar represents 200 μm (Adopted from Li et al., 2023)

5 Molecular Breeding in Loquat

Molecular breeding in loquat has seen significant advancements with the integration of genomic tools and technologies, enhancing the efficiency and precision of breeding programs. The application of molecular markers and genome editing technologies has revolutionized the way breeders can select and improve loquat cultivars, focusing on traits such as disease resistance, fruit quality, and yield.

5.1 Marker-assisted selection (MAS) and its applications

Marker-Assisted Selection (MAS) has become a cornerstone in loquat breeding, allowing for the precise selection of desirable traits by using molecular markers linked to specific phenotypic characteristics. Functional markers (FMs), which are closely associated with phenotypic traits, have been particularly useful in this regard. They enable breeders to directly select genes associated with important agronomic traits, thereby increasing the efficiency of developing new loquat varieties. This approach not only accelerates the breeding process but also enhances the accuracy of selecting traits related to biotic and abiotic stress resistance, ultimately contributing to the development of elite loquat cultivars (Salgotra and Stewart, 2020).

5.2 CRISPR-Cas9 and other genome editing tools

The advent of CRISPR-Cas9 and other genome editing tools has opened new avenues for precision breeding in loquat. These technologies allow for targeted modifications in the loquat genome, enabling the introduction of desirable traits with high precision and predictability (Varshney et al., 2016). CRISPR-Cas9, in particular, has been highlighted for its ability to create site-specific double-stranded DNA breaks, facilitating the rapid and precise editing of plant genomes. This technology surpasses traditional methods like zinc finger nucleases (ZFNs) and transcription activator-like effector nucleases (TALENs) in terms of ease and efficiency. The use of CRISPR-Cas9 in loquat breeding holds promise for improving traits such as disease resistance and fruit quality, and it is expected to play a crucial role in future breeding strategies (Bortesi and Fischer, 2015; Chen et al., 2019).

5.3 Integration of genomics with phenomics for breeding efficiency

Integrating genomics with phenomics represents a significant advancement in enhancing breeding efficiency for loquat. This integration involves combining genomic data with phenotypic information to better understand the genetic basis of complex traits. By leveraging high-throughput sequencing and functional genomics approaches, breeders can identify functional markers that are highly associated with phenotypic variation. This comprehensive approach allows for more informed selection decisions, ultimately leading to the development of superior loquat cultivars. The synergy between genomics and phenomics not only accelerates the breeding process but also improves the accuracy of trait selection, ensuring that new varieties meet the desired agronomic and quality standards (Hasan et al., 2021).

6 Case Study: Genomic Dissection of Loquat Fruit Ripening

6.1 Background and importance of fruit ripening in loquat cultivation

Loquat (*Eriobotrya japonica* Lindl.) is a non-climacteric fruit known for its rich nutritional profile, including essential minerals and carotenoids. The ripening process in loquat is crucial as it affects the fruit's taste, texture, and overall marketability. Understanding the molecular mechanisms underlying fruit ripening can significantly enhance loquat cultivation by improving fruit quality and extending shelf life. The ripening process involves complex physiological and biochemical changes driven by differentially expressed genes (DEGs) across various metabolic pathways, including carbohydrate metabolism and hormone signaling (Jing et al., 2020).

6.2 Identification of candidate genes through transcriptomic analysis

Transcriptomic analysis has been instrumental in identifying candidate genes involved in loquat fruit ripening. High-throughput RNA sequencing has revealed thousands of DEGs during fruit development, with significant involvement in pathways such as cell-wall degradation and hormone signaling. Notably, genes related to auxin and ethylene response have been differentially expressed, indicating their roles in the ripening process. Additionally, several transcription factor families have been identified, which may regulate these pathways (Gisbert et al., 2009; Jing et al., 2020). The integration of genomics and transcriptomics has further identified key loci and genes, such as *Ethylene Insensitive 4* (*EjEIN4*), that are potentially involved in fruit development and ripening (Figure 3) (Peng et al., 2022a).
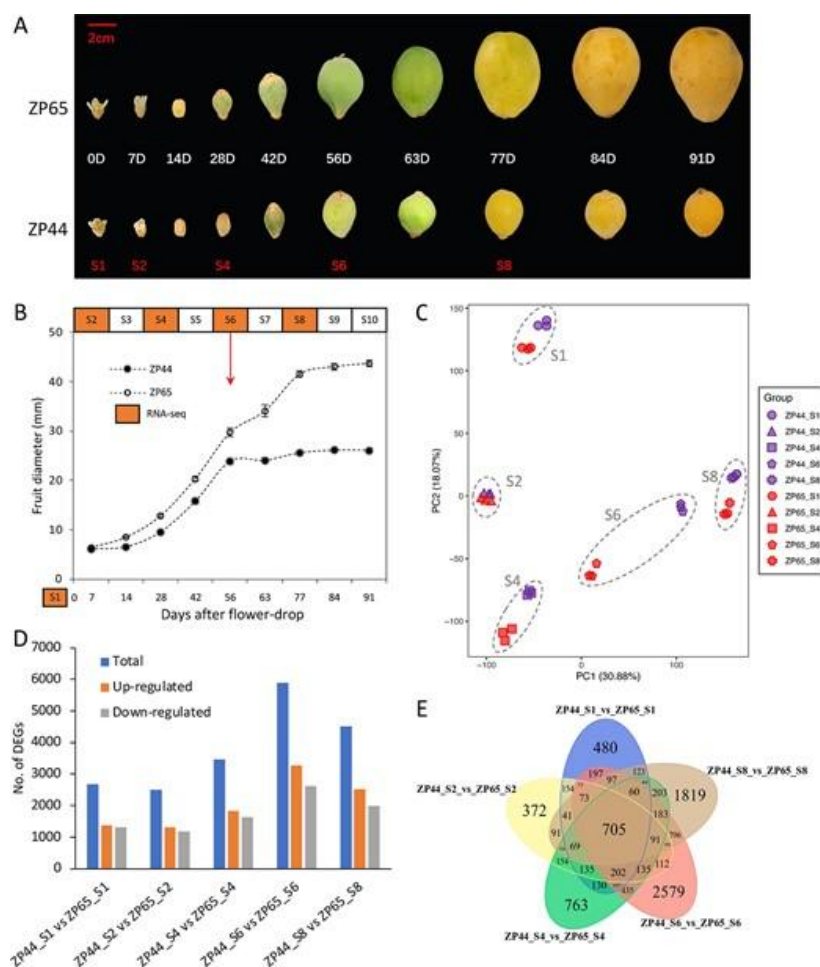

Figure 3 Observation of fruit development and DEGs identified from the RNA-seq experiment (Adopted from Peng et al., 2022a)

Image caption: (A) Observations of fruit development of ZP44 and ZP65 at 10 time points, including 0 days past anthesis (0D, S1), 7D (S2), 14D, 28D (S4), 42D, 56D (S6), 63D, 77D (S8), 84D, and 91D. (B) Comparison of fruit diameter (transverse diameter) between ZP44 and ZP65. The values are the mean fruit diameter of 15 fruits. Bars are standard errors. (C) Principal component analysis using transcriptome profiles of all 30 replicates. (D) Summary of DEGs between ZP44 and ZP65 at each stage. (E) Comparison of DEGs at each stage (Adopted from Peng et al., 2022a)

6.3 Functional validation of ripening-related genes

Functional validation of ripening-related genes in loquat has been achieved through various experimental approaches. For instance, the expression patterns of ethylene biosynthetic genes such as *ACS1* and *ACO1* have been analyzed, revealing their differential regulation in peel and pulp tissues during ripening. These studies suggest a non-climacteric ripening behavior, where ethylene action is necessary to maintain the expression of specific genes (Kumar et al., 2021). Additionally, the role of auxin-responsive genes, such as those in the SAUR family, has been explored, highlighting their contribution to cell expansion and fruit development (Wang and Paterson, 2021).

6.4 Implications for enhancing shelf life and market value

The insights gained from genomic and transcriptomic studies have significant implications for enhancing the shelf life and market value of loquat. By identifying and manipulating key genes involved in ripening, it is possible to develop loquat varieties with improved postharvest qualities. For example, controlling the expression of genes related to ethylene and auxin signaling could delay ripening, thereby extending shelf life and reducing postharvest losses (Halladakeri et al., 2023). Furthermore, understanding the genetic basis of ripening can aid in breeding programs aimed at improving fruit quality traits, such as taste and texture, ultimately increasing the market value of loquat (Wang et al., 2021).

7 Future Perspectives in Loquat Genomics and Breeding

7.1 Integration of multi-omics approaches

The integration of multi-omics approaches, including genomics, transcriptomics, and metabolomics, holds significant promise for advancing loquat breeding. By combining these diverse datasets, researchers can gain a comprehensive understanding of the genetic and molecular mechanisms underlying important traits such as fruit weight and quality. For instance, a study identified candidate loci associated with fruit weight by integrating whole-genome resequencing, transcriptome analysis, and metabolic profiling, highlighting the role of auxin in fruit development (Peng et al., 2022a). Such integrative approaches can facilitate the identification of key genes and pathways, providing valuable targets for molecular breeding and genetic improvement of loquat.

7.2 Big data analytics and artificial intelligence in genomic research

The application of big data analytics and artificial intelligence (AI) in genomic research is poised to revolutionize loquat breeding. With the increasing availability of high-throughput sequencing data, AI and machine learning algorithms can be employed to analyze complex datasets, identify patterns, and predict phenotypic outcomes. For example, the use of quantitative PCR for genotyping polyploid loquats demonstrates the potential of data-driven approaches in breeding programs (Wang et al., 2021). By leveraging AI, breeders can accelerate the selection of desirable traits, optimize breeding strategies, and enhance the efficiency of developing new loquat cultivars.

7.3 Addressing climate change challenges through genomic innovations

Climate change poses significant challenges to loquat cultivation, necessitating the development of resilient varieties. Genomic innovations offer a pathway to address these challenges by enabling the identification and manipulation of genes associated with stress tolerance. The construction of high-quality genome assemblies and the identification of genes involved in key metabolic pathways provide a foundation for breeding climate-resilient loquats (Arora and Narula, 2017; Jing et al., 2020). By focusing on traits such as drought and heat tolerance, genomics-assisted breeding can contribute to the development of loquat varieties that are better adapted to changing environmental conditions, ensuring sustainable production in the face of climate change.

8 Conclusion

The field of loquat genomics has made significant strides, particularly in genome mapping and molecular breeding. Recent advancements include the development of high-quality chromosome-level genome assemblies and the application of quantitative PCR for genotyping polyploid loquats, which are crucial for understanding genetic traits such as flesh color. Additionally, the construction of genetic linkage maps using AFLP and SSR markers has provided a framework for further genetic studies and breeding efforts. These developments have laid a solid foundation for future research and breeding programs aimed at improving loquat varieties.

Despite these advancements, several knowledge gaps remain. There is a need for more comprehensive studies on the genetic diversity and domestication processes of loquats, as current research has primarily focused on cultivated varieties. Furthermore, the integration of advanced genomic tools such as optical mapping and next-generation sequencing could enhance our understanding of loquat genetics and facilitate the identification of key quantitative trait loci (QTLs). Prioritizing research on these fronts will be essential for addressing the challenges in loquat breeding and improving fruit quality and yield.

Looking forward, the next decade of loquat genomics is poised to leverage cutting-edge technologies to accelerate breeding programs and enhance genetic research. The integration of genomics-assisted breeding techniques, such as marker-assisted selection and genomic selection, will likely become more prevalent, enabling the development of superior loquat cultivars with desirable traits. Additionally, advancements in sequencing technologies and bioinformatics will facilitate more detailed genetic analyses, leading to a deeper understanding of loquat biology and the potential for innovative breeding strategies. This vision underscores the importance of continued investment in genomic research and the adoption of new technologies to drive progress in loquat breeding and cultivation.

Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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