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Genetic Studies of *Punica granatum*: From Molecular Markers to Trait Improvement

Zhongmei Hong
CRO Service Station, Sanya Tihitar SciTech Breeding Service Inc., Sanya, 572025, Hainan, China
Corresponding email: zhongmei.hong@hitar.org

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Abstract This study reviewed the significant progress in the genetic research of *Punica granatum* and the research on genes related to traits, introduced how high-throughput sequencing and multi-omics methods were used to identify genes related to fruit peel color, disease resistance and environmental adaptability, and also summarized the achievements of the construction of genetic linkage maps and quantitative trait locus (QTL) analysis. These research results provide assistance for future molecular marker-assisted breeding. This study aims to provide theoretical support and practical suggestions for the molecular breeding and germplasm resource conservation of *Punica granatum*.

Keywords *Punica granatum*; Genetic diversity; SSR markers; AFLP markers; Genome-wide analysis; Trait improvement; Breeding programs; Punicalagin biosynthesis

1 Introduction

Punica granatum is a fruit-bearing deciduous shrub or small tree that has been cultivated by people for a long time. It originated from regions ranging from Iran to northern India and is now widely cultivated in the Mediterranean, the Middle East and some parts of Asia. *Punica granatum* is rich in nutrients, have medicinal value, and are also rich in antioxidants, vitamins and minerals, making them very popular. Wild *Punica granatum* are also regarded as a functional food beneficial to health (Khadivi et al., 2020).

Understanding the genetic differences among different groups of *Punica granatum* is beneficial for protecting this precious species well. Zarei and Sahraroo (2018) discovered significant genetic variations among *Punica granatum* germplasm resources through microsatellite labeling, which is crucial for resource conservation and breeding efforts. Genetic research can also identify traits beneficial to cultivation such as disease resistance, fruit quality and yield, which can enhance the economic value of *Punica granatum*. Guerrero-Solano et al. (2020) understood the evolutionary process and possible medicinal value of *Punica granatum* by comparing the genetic relationship between *Punica granatum* and their related plant *Punica protopunica*.

This study introduces the latest progress in *Punica granatum* genetic research, analyzes the discovered genetic diversity and how helpful these findings are for improving varieties and protecting *Punica granatum* resources, and by collating the existing research results, explains how important genetic research is in promoting *Punica granatum* cultivation and development. This study will also explore whether the combination of genetic research and traditional breeding methods can more effectively cultivate better *Punica granatum* varieties.

2 Molecular Markers in *Punica granatum*

2.1 Types of molecular markers

In the research of *Punica granatum*, various molecular labeling methods such as simple sequence repeats (SSR) and amplified fragment length polymorphism (AFLP), as well as polymorphism-based markers such as SRAP, TRAP, and ITAP have been used (Mahajan et al., 2018; Youssef et al., 2018; Sinjare and Jubrael, 2020). SSR markers are popular because they can display a lot of different genetic information, have stable and repeatable results, and can detect two alleles simultaneously (Zarei and Sahraroo, 2018; Liu et al., 2020; Patil et al., 2020; Parashuram et al., 2022).

2.2 Applications in genetic studies

Molecular markers can assess the genetic diversity, population structure and genetic relationship among different *Punica granatum* varieties. SSR markers were used to analyze the genetic conditions of *Punica granatum* germplasm resources. The results showed that there were significant differences among these resources, which was beneficial for researchers to find core populations suitable for breeding (Mahajan et al., 2018; Zarei and Sahraroo, 2018; Liu et al., 2020; Patil et al., 2020; Parashuram et al., 2022). Sinjare and Jubrael (2020) demonstrated that AFLP markers were used to study the genetic diversity of *Punica granatum* and discovered many genetic variations. Jeong et al. (2018) found that molecular markers could detect mutations related to anthocyanin synthase, a gene that has a significant impact on the color of *Punica granatum* peels.

2.3 Advantages and limitations

SSR has a high polymorphism and can simultaneously display the information of two alleles, making it suitable for detailed genetic analysis and breeding research (Mahajan et al., 2018; Zarei and Sahraroo, 2018; Parashuram et al., 2022). Sinjare and Jubrael (2020) hold that AFLP can generate many markers with high polymorphism and is suitable for evaluating genetic diversity.

However, in the same year, that is, in 2020, Liu et al. and Patil et al. proposed that before conducting SSR analysis, it is necessary to know a specific DNA sequence used for designing primers, and this process is time-consuming and costly. Sinjare and Jubrael (2020) also demonstrated that AFLP has relatively high technical requirements and requires the use of more complex instruments during analysis. Yan et al. (2019) found that chloroplast DNA sequences can be used to study kinship, but their sequence changes are not significant and are not sufficient for studying genetic diversity (Table 1).

Table 1 Summary of the complete chloroplast genome characteristics of five species in Lythraceae (Adopted from Yan et al., 2019)

Species	*Punica granatum*	*Lagerstromeia indica*	*Sonneratia alba*	*Trapa maximowicizz*	*Heimia myrtifolia*
Genome size	158 638	152 025	153 061	155 577	159 219
LSC size	89 021	84 046	87 226	88 528	88 571
SSC size	18 684	16 914	18 032	18 272	18 821
IR size	25 467	25 623	23 902	24 389	25 914
Number of genes	113	113	107	110	112
Protein-coding genes	79 (6)	79 (7)	79 (6)	77 (5)	78 (7)
tRNA genes	30 (7)	30 (7)	24 (5)	29 (9)	30 (6)
rRNA genes	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)
Number of genes duplicated in IR	17	18	15	18	17
GC content	36.92	37.59	37.29	36.4	36.95
GenBank accession	MK603511	NC_030484	NC_039975	NC_037023	MG921615

3 Genetic Mapping and QTL Analysis

3.1 Construction of genetic maps

High-density genetic maps (HDGMs) maps are like a genetic map and are useful for identifying the locations of genes related to important traits. Wang et al. (2018) established a genetic map containing 3 630 SNP markers using the SAF-Seq technique in the study of peanuts. These markers were distributed across 20 linkage groups, covering a genetic distance of 2 098.14 cM, with an average distance of only 0.58 cM between every two markers. Kulkarni et al. (2020) covered 294.2 cM with 126 SSR markers in the study of rice to analyze the traits related to yield. Guo et al. (2020) established a high-density genetic map containing 10 739 loci through the RIL population of 'Tainong 18 × Linmai 6'.

3.2 Identification of quantitative trait loci (QTL)

QTL mapping can identify the gene regions related to certain traits. Wang et al. (2018) used QTL plotting to identify 62 QTLs related to 14 yield-related traits, which were distributed on 12 chromosomes. They also found that the traits of peanut seeds and pods occurred in the same region. Kulkarni et al. (2020) identified 22 QTLs related to traits such as total rice yield, panicle weight, and plant height, and some of them also showed obvious

intergene interactions. Zhao and Su (2019) detected 33 QTLs related to the seven yield traits of corn and found several stable QTLs on chromosomes 2, 5, 7 and 9. Mekonnen et al. (2021) used three different populations and discovered 105 QTLs related to agronomic traits and yield of sorghum, which were integrated into 25 meta QTLs.

3.3 Applications in breeding programs

Researchers can introduce some good traits into newly cultivated varieties through MAS. Kulkarni et al. (2020) found that some of the main QTLs identified in rice are beneficial for breeding excellent hybrid rice varieties. Guo et al. (2020) focused on stable QTL related to protein and starch content in wheat to conduct more detailed localization and identify candidate genes, thereby improving the quality of terminal products such as flour. Zhao and Su (2019) analyzed the differences in gene expression within the QTL region, predicted the candidate genes affecting the size and weight of corn kernels, and provided a clear direction for future molecular breeding.

4 Genomic Studies and Sequencing

4.1 Genome sequencing projects

Singh et al. (2021) conducted a comprehensive chloroplast genome analysis of 16 *Punica granatum* genotypes. Through large-scale sequencing and assembly, they discovered differences in the size and structure of chloroplast genomes among these genotypes. Usha et al. (2022) conducted high-quality genomic assembly of the important diploid *Punica granatum* variety "Bhagwa" in India, providing detailed information on the genomic characteristics of *Punica granatum* and identifying 30 803 protein-coding genes, demonstrating its potential in gene function research and breeding. In 2019, Yan et al. analyzed the complete chloroplast genomes of three *Punica granatum* varieties and found that the genetic content and structure of these varieties changed little in the Lythaceae family.

4.2 Identification of key genes

Chen et al. (2023) utilized the data from whole-genome sequencing to identify the U-box gene families that play a key role in the ubiquitination process of plants, discovered 56 U-box genes, determined their positions on chromosomes, analyzed their evolutionary relationships, and studied their expression under abiotic stress conditions. Patil et al. (2020) conducted computational analysis using the draft genome of the *Punica granatum* variety "Dabenzi", developed a large number of SSR markers, and discovered 173 633 SSR markers that are very useful in genetic research and breeding. Chang et al. (2019) identified a region-specific 4-O-glycosyltransferase related to gallic acid metabolism using CRISPR/Cas9 technology, indicating that genome editing holds great potential in the study of *Punica granatum* functional genes.

4.3 Comparative genomics

Yan et al. (2019) compared the chloroplast genomes of *Punica granatum* and other plants in the Lythaceae family and found that their genetic contents and structures were very similar, and the sequence differences among different *Punica granatum* varieties were not significant. Lu et al. (2023) compared the mitochondrial genomes of *Punica granatum* and their closely related plants, identified homologous fragments between them, and through phylogenetic analysis, found that the genetic relationship between *Punica granatum* and *Lagerstroemia indica* was very close. Chen et al. (2022) analyzed the complete chloroplast genome of wild *Punica granatum* in Tibet, providing useful information for *Punica granatum* breeding research and the classification of Lythylaceae plants.

5 Functional Genomics and Gene Expression

5.1 Transcriptome analysis

Fu et al. (2021) conducted a combined analysis of the metabolome and transcriptome of *Punica granatum* seeds throughout the entire process from pre-germination to post-germination, and found that the expression of 6 984 genes changed significantly. Through weighted gene co-expression network analysis (WGCNA), the gene modules related to different germination stages were identified. At the beginning of seed soaking, some key genes involved in RNA transmission and glycolysis were discovered. At the stage when germination truly began, more genes related to metabolic processes were found. Chang et al. (2019) discovered 11 increased expression UDP-dependent glycosyltransferases (UGTs) genes in *Punica granatum* plants edited with CRISPR/Cas9

technology through transcriptome and real-time qPCR analysis, indicating that transcriptome analysis is very useful in the study of *Punica granatum* functional genes.

5.2 Gene function studies

The application of CRISPR/Cas9 technology enables scientists to have a clearer understanding of the gene functions in certain key metabolic pathways. In 2019, Chang et al. double-edited the two genes *PgUGT84A23* and *PgUGT84A24* in the hairy roots of *Punica granatum* and found that this would lead to the accumulation of 3-O- and 4-O-glucosides of gallic acid in a special way, indicating that these two genes have overlapping functions in the synthesis of β -gluconic acid. Chang et al. (2019) also discovered the *PgUGT72BD1* gene that specifically acts on the glycosyltransferase at the 4-O- site of gallic acid, demonstrating the potential of CRISPR/Cas9 in the study of Punica granatum gene function and metabolic improvement. The recent research by Chen et al. (2023) found that the U-box gene family in *Punica granatum* has different functional manifestations when facing abiotic stress, indicating that these genes may be crucial in adapting to the environment.

5.3 Regulation of gene expression

The regulatory process of gene expression in *Punica granatum* is rather complex. Chen et al. (2023) found that the U-box genes in *Punica granatum* would be activated when exposed to abiotic stress, indicating that they play a certain role in the process of plants coping with stress. Yan et al. (2019) analyzed the chloroplast genomes of different *Punica granatum* varieties and found that their gene structures were very conformed, with 11 genes in a positive selection state, most of which were related to photosynthesis or the genetic system, indicating that the gene regulation mode of *Punica granatum* is closely related to their ability to adapt to the environment. Patil et al. (2020) developed a large number of SSR markers using whole-genome information, which are beneficial for studying gene expression regulation and genetic diversity, and can also be used for marker-assisted selection in breeding.

6 Trait Improvement in *Punica granatum*

6.1 Traits of interest

6.1.1 Disease resistance

Bacterial blight caused by the bacteria *Xanthomonas axonopodis* pv. punicae can lead to a significant reduction in *Punica granatum* yield (Singh et al., 2020). Singh et al. (2020) found by comparing the transcriptomes of different varieties that the significant increase in the expression of some genes related to defense mechanisms in disease-resistant varieties provided a basis for the breeding of new disease-resistant varieties. Peerajade et al. (2020) demonstrated that *Punica granatum* have a high heritability and improvement potential for resistance to this disease, indicating that this trait can be enhanced through selective breeding.

6.1.2 Fruit quality

The quality traits of fruits such as fruit weight, aril weight, and the amount of juice will affect consumers' preferences and market sales. Khadivi et al. (2018) and Peerajade et al. (2020) both found that different *Punica granatum* varieties have significant differences in these aspects, indicating that there is a lot of room for improvement. Peerajade et al. (2020) also held that traits such as fruit weight and phenol content have relatively high heritability and show significant genetic progression, supporting the possibility of improving fruit quality through genetic means. Jeong et al. (2018) identified genetic markers related to fruit color and anthocyanin content, which is very beneficial for the breeding of *Punica granatum* varieties with good appearance and high nutritional value.

6.1.3 Environmental adaptability

Environmental adaptability is a key factor for *Punica granatum* to be smoothly cultivated in different climates. Peerajade et al. found in their genetic research in 2020 that the mutual influence between genotype and environment can affect traits such as plant growth, fruit length and fruit peel thickness. It is crucial to select varieties that perform well in specific environments. Zarei and Sahraroo (2018), as well as Liu et al. (2020), discovered rich genetic diversity from *Punica granatum* germplasm resources collected in different regions,

indicating that *Punica granatum* varieties with stronger adaptability may be cultivated through selection and breeding.

6.2 Molecular breeding techniques

6.2.1 Marker-assisted selection (MAS)

MAS is mainly used in *Punica granatum* breeding to improve important traits such as disease resistance and fruit quality. The application of SSR markers in genetic diversity analysis provides strong support for MAS in *Punica granatum* (Zarei and Sahraroo, 2018; Liu et al., 2020). These molecular markers enable breeders to select plants with ideal traits more quickly and accurately, saving a significant amount of time and resources required for traditional breeding (Holland and Bar-Ya'akov, 2018).

6.2.2 Genomic selection (GS)

GS predicts the breeding value of each plant through genome-wide marker data. Tiwari et al. (2022) hold that GS has been extensively studied in crops such as tomatoes, and its application in *Punica granatum* should also be promising, with the potential to accelerate the breeding process and enhance the efficiency of genetic improvement. The development of high-throughput sequencing technology and bioinformatics tools has made it possible to apply GS in *Punica granatum* breeding, which is useful for improving complex traits more quickly (Tiwari et al., 2022).

6.2.3 CRISPR/Cas9 and gene editing

CRISPR/Cas9 and other gene editing technologies have provided *Punica granatum* with new methods for precise gene improvement. Chang et al. (2019) demonstrated that CRISPR/Cas9 is highly effective in regulating the synthesis of important metabolites such as hydrolyzable tannins, and can also be used to precisely knockout or insert specific genes, helping to cultivate *Punica granatum* varieties with stronger disease resistance, higher fruit quality, and better environmental adaptability.

6.3 Field trials and validation

Researchers will evaluate the agronomic traits of the selected varieties in the field during field trials. The combination of molecular breeding data and field trial results can provide a more comprehensive understanding of the genetic basis of these important traits and better guide future breeding work (Figure 1) (Holland and Bar-Ya'akov, 2018; Khadivi et al., 2018; Peerajade et al., 2020). Good field trials can ensure that newly bred *Punica granatum* varieties meet the expected standards and are suitable for large-scale commercial cultivation.

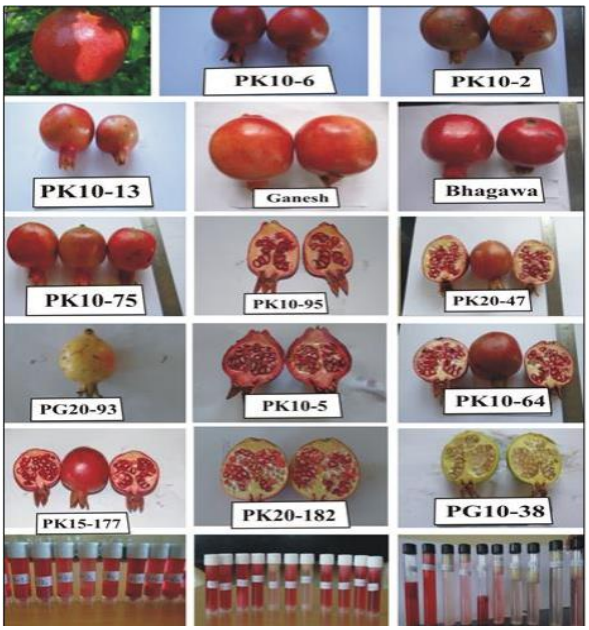

Figure 1 Variability in fruit, aril and juice colour in *Punica granatum* genotypes (Adopted from Peerajade et al., 2020)

7 Genetic Diversity and Conservation

7.1 Assessment of genetic diversity

Aziz et al. (2020) analyzed 48 wild *Punica granatum* samples from the Azad Jammu and Kashmir region of Pakistan using 41 SSR markers and found significant genetic differences among the samples. On average, 7.39 alleles were detected for each marker, the average polymorphism information content (PIC) was 0.54, and the genetic distance between genotypes ranged from 0.27 to 0.74, indicating rich genetic variations. Zarei and Sahraroo (2018) studied 50 samples using 16 SSR markers and found that the average expected heterozygosity was 0.33, while the actual observed heterozygosity was 0.48. They also detected multiple specific alleles, indicating that the genetic diversity of *Punica granatum* in Fars Province, Iran, is relatively high. Mahajan et al. (2018) analyzed 20 *Punica granatum* varieties using 17 SSR markers and discovered 29 alleles, with an average of 1.71 at each locus, indicating significant genetic differences between cultivated and wild varieties.

7.2 Conservation strategies

Zarei and Sahraroo (2018) identified some specific alleles and classified different genotypes based on geographical locations, indicating that unique genetic materials in some regions require focused protection. In vitro protection is also an effective method. Parashuram et al. (2022) systematically maintained genetic diversity by analyzing the morphological, biochemical and molecular characteristics of 40 samples and dividing them into 8 groups. Liu et al. (2020) utilized SSR markers to select 42 samples with strong representativeness from 218 *Punica granatum* genotypes and established a core germplasm bank, which could retain most of the genetic information without preserving all the samples. Aziz et al. (2020) indicated that in-situ conservation in regions rich in genetic diversity such as Azad Jammu and Kashmir is an important means to protect wild *Punica granatum* and their natural environment.

7.3 Utilization of genetic resources

Patil et al. (2020) argued that SSR markers discovered in genome-wide studies are useful for mark-assisted selection and QTL localization. The genetic diversity data collected from different regions can be used to introduce new traits and improve existing varieties (Zarei and Sahraroo, 2018). Parashuram et al. (2022) demonstrated that the combination of morphological, biochemical and molecular data can ensure that different characteristics are taken into account during breeding. Phylogenetic analysis of *Punica granatum* populations also revealed significant genetic differences and kinship among samples from different regions, providing strong support for the breeding of new *Punica granatum* varieties with better characteristics (Youssef et al., 2018; Sevindik and Efe, 2021).

8 Challenges and Future Directions

8.1 Current limitations in genetic studies

The chloroplast genome diversity of *Punica granatum* is relatively low, and its role in studying genetic diversity becomes limited (Yan et al., 2019). Although SSR markers have been developed, they are still in the early stage as a whole. Many markers have not been deeply studied and widely used (Liu et al., 2020; Patil et al., 2020). The complexity of the genetic structure of *Punica granatum* themselves makes genetic analysis and breeding work more difficult (Patil et al., 2021). At present, there are relatively few cases that combine morphological, biochemical and molecular data for comprehensive research. Such integrated analysis remains a difficulty point (Parashuram et al., 2022).

8.2 Technological advances and opportunities

Chang et al. (2019) hold that the application of CRISPR/Cas9 gene editing technology has opened a new door for the functional gene research of *Punica granatum*, making it more accurate to modify genes and discover new functional genes. The development of high-throughput sequencing technology and bioinformatics analysis tools enables researchers to better identify SSR markers on a genome-wide scale and improve the research accuracy of genetic diversity (Youssef et al., 2018; Patil et al., 2020). The complete sequencing of the chloroplast genome of *Punica granatum* also provides important clues for studying its phylogenetic relationship in the Lythaceae family,

which is beneficial for understanding its evolutionary characteristics and seeking new genetic markers (Yan et al., 2019). Trainin et al. (2021) found that multi-omics integration could help to gain a more comprehensive understanding of the genetic mechanism of *Punica granatum* and how to improve their traits.

8.3 Future research priorities

It is necessary to develop more molecular markers with rich types and large amounts of information, further improve the genetic map and enhance the efficiency of MAS (Patil et al., 2020; 2021) Actively apply advanced gene editing technologies such as CRISPR/Cas9 to study the functions of key genes related to important traits (Trainin et al., 2021). The combined study of morphological, biochemical and molecular data can help to understand the diversity of *Punica granatum* more comprehensively and evaluate its application value in breeding (Parashuram et al., 2022). Saeed et al. (2018) and Rizzo et al. (2023) demonstrated that the potential of *Punica granatum* as functional foods can be further explored, which will open up new directions for their development in medicinal and nutritional aspects.

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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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