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Unveiling Plant Genetic Diversity: A Review of DNA Marker Techniques

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ABSTRACT
DNA markers are essential tools for exploring genetic diversity and understanding population structure within plant species. These markers provide valuable insights into plant adaptation to environmental challenges and aid in uncovering genetic variations associated with traits of economic importance. A diverse array of marker techniques exists, including arbitrarily amplified DNA-based markers (e.g., RAPD, AFLP, SSR), targeted fingerprinting-based markers (e.g., TRAP, CoRAP, ESTP), transposable element-dependent markers (e.g., SSAP, ISAP, IRAP), DNA sequencing-based markers (e.g., SNP, GBS-SNPs, RAD-Seq), markers based on restriction enzymes, specifically restriction endonucleases (e.g., CAPS), and hybridization-based markers (e.g., RFLP). Each marker type possesses distinct advantages and limitations, making it suitable for specific research objectives and experimental designs. The optimal marker selection depends on several factors, such as the degree of polymorphism, reproducibility, cost-effectiveness, as well as access to genomic resources for the organism of interest. By integrating multiple marker systems with cutting-edge sequencing technologies, researchers can obtain a comprehensive genome-wide perspective of genetic diversity. This comprehensive approach enhances our understanding and enables the development of strategies for conserving rapidly diminishing plant genetic resources.

Keywords: DNA markers, Genetic diversity, Genomic resources, Plant adaptation, Population structure

1. Introduction

Genetic diversity in plants forms the foundation of sustainable agriculture and biodiversity preservation (Thuillet et al. 2022). It provides the raw material for crop improvement, playing a vital role in maintaining food security in an ever-changing world. Understanding the genetic diversity, both within and among plant species, is crucial for developing resilient crop varieties, protecting endangered species, and uncovering the mechanism of evolution (Ali et al. 2023). Traditionally, phenotypic traits were used to assess genetic diversity; however, these often provide limited information, particularly for polygenic and low-heritability traits. DNA markers have revolutionized plant genetic studies, providing powerful tools to investigate genetic diversity at the DNA level (Hasan et al. 2021).

These DNA markers providing insights often hidden by phenotypic traits (Amiteye 2021a). By analyzing these markers, scientists can estimate genetic distances, identify unique genotypes, and reconstruct evolutionary relationships. This is important for understanding the processes shaping genetic diversity, such as gene flow, and natural selection. Molecular markers also have practical applications in fields like conservation biology, where they assist in identifying populations that should be prioritize for protection, and in plant breeding, where they facilitate the selection of superior individuals (Yuanyuan Li 2020).

The DNA markers comprises PCR-based markers, which have revolutionized the fields of molecular biology and genetics. This powerful technique uses the natural process of DNA replication to amplify specific DNA sequences, enabling researchers to study even small amounts of genetic material. In the context of plant genetic studies, PCR-based markers are vital for exploring genetic diversity, population structure, and evolutionary relationships (El-Esawi et al. 2023).

Additionally, hybridization-based markers utilize the principle of complementary base pairing between DNA strands to detect genetic diversity (Kumar et al. 2021). These techniques involve the use of probes, which are short, single-stranded DNA sequences designed to hybridize with specific target genomic sequence. Analyzing the hybridization patterns facilitates identification of polymorphisms and assessment of genetic diversity in genomes of different individuals (Singh & Singh 2015). Restriction Fragment Length Polymorphism (RFLP) is a classic example of a hybridization-based marker, where restriction enzymes are used to produce DNA fragments that are separated by gel electrophoresis and hybridized with specific probes (Williams 1989). This review aims to provide a comprehensive overview of molecular marker

techniques, including their principles, strengths, limitations, and applications in genetic diversity, crop improvement, conservation genetics, and evolutionary biology.

2. Types of DNA markers

Plant DNA markers are specific DNA sequences that exhibit variation among individuals. These variations, or polymorphisms, can be used to identify and track different versions of genes or DNA segments within a population. DNA markers act as signposts on the genetic map, allowing scientists to locate and study genes associated with traits like disease resistance, yield quantity and quality. Understanding the genetic makeup of plants enables developing more efficient breeding strategies, improve crop varieties, and gain deeper insights into plant evolution and biodiversity. Broadly, DNA markers can be classified into two major groups: PCR-based and hybridization-based markers (Figure 1).

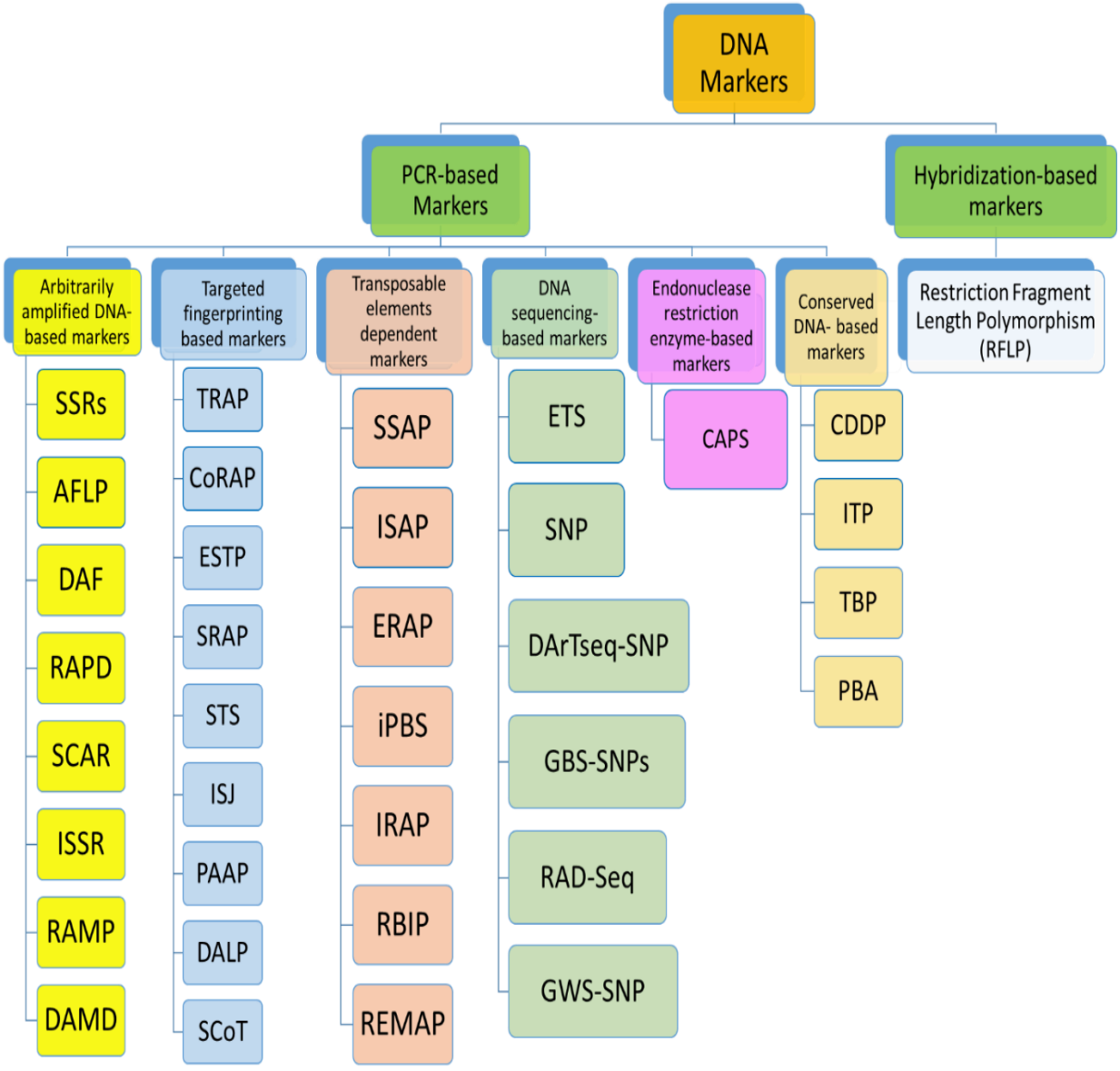


Figure 1- Classification of DNA markers

2.1. Hybridization-based markers

2.1.1. Restriction Fragment Length Polymorphism (RFLP)

RFLP, a hybridization-based DNA fingerprinting technique, utilizes restriction enzymes to generate DNA fragments. These fragments are subsequently hybridized with specific radiolabeled probes to identify and map target DNA sequences, revealing genetic variations among individuals or populations. This technique detects variations between genomes, such as point mutations, insertions, deletions, translocations, inversions, and duplications, by producing DNA fragments of different sizes (Mondini et al. 2009). RFLPs offer several advantages, such as locus specificity, high reproducibility, and

co-dominant inheritance, enabling seamless data exchange between research institutions. However, their practical application is hindered by several limitations, including the requirement for substantial amounts of high-quality DNA, the need for costly radiolabeled probes that necessitate prior sequence knowledge, and the cumbersome Southern blotting technique (Mir et al. 2013). RFLPs have been extensively used in genome mapping for selecting desirable genes, analyzing polygenic traits, and determining genetic relationships and diversity among crop plants. (Bobowski et al. 1999) generated a molecular method to identify buried woody plant parts (roots, rhizomes) using PCR and Fingerprinting. This technique helps understand how these parts contribute to forest regrowth after disturbances. While successful in identifying 15 species, it might have limitations with untested species. Additionally, (Brunner et al. 2001) developed a DNA-based method to identify tree fine roots, which are important for soil health studies. Using the *trnL* intron and specific enzymes, they created a key to identify 30 Alpine tree species. Field testing showed the method's accuracy in mapping root distribution, providing a valuable tool for ecological research.

2.2. PCR-based markers

2.2.1. Arbitrarily amplified DNA-based markers

2.2.1.1. Random amplified polymorphic DNA (RAPD)

RAPD markers, a popular first-generation DNA marker technique, rely on amplifying random DNA fragments using short, arbitrary primers. These amplified fragments are then analyzed through electrophoresis to detect polymorphisms. RAPD is simple, rapid, and cost-effective, making ideal for the assessment genetic diversity in plants.

Researchers have successfully employed RAPD markers for various applications, including identifying superior varieties (Bibi et al. 2015), detecting mutants and assessing genetic diversity (Al-Khayri et al. 2022), and characterizing plant species (Zhang et al. 2010). Their widespread use in plant research has contributed to understanding plant variability, population structures, and facilitating crop improvement and conservation efforts. Heinze et al. (1996) assessed the RAPD assay's utility in Norway spruce genetics, focusing on protocol optimization and reliability. Results confirmed RAPD's efficiency in generating numerous genetic markers, revealing genetic variation within clones and seed populations. Rigorous testing, including Mendelian segregation analysis, validated the assay's applicability for diverse genetic studies in Norway spruce, highlighting its potential for rapid genetic screening.

Despite their advantages, RAPD markers have limitations. These include the use of short primers, which can result in lower levels of polymorphism and non-reproducible PCR amplification products due to their susceptibility to minor variations in experimental conditions. Furthermore, the dominant inheritance patterns associated with RAPD markers can complicate their application in precise marker-assisted selection programs and comprehensive diversity analyses (Ben-Ari & Lavi 2012).

2.2.1.2. DNA amplified fingerprinting (DAF)

DAF is a powerful technique for assessing genetic diversity in plants. By utilizing short, arbitrary oligonucleotide primers, DAF amplifies specific DNA fragments and generating unique banding patterns that can distinguish between individuals and populations (Weising et al. 1994; Waldron et al. 2002; Weising et al. 2005). The key differences between DAF and RAPD lie in the primer length and the gel used for fragment separation. RAPD typically uses longer primers (around 10 nucleotides) and the amplified fragments are usually resolved on agarose gels. In contrast, DAF employs much shorter primers (typically 5-8 nucleotides) and requires the higher resolution of polyacrylamide gels (PAGE) for separating the often smaller and more numerous amplification products. Consequently, DAF often generates more complex banding patterns, potentially offering a higher level of polymorphism detection in some applications. This technique has been used to study genetic relationships , identify cultivars, detect genetic diversity between and within plant species (Caetano-Anollés & Bassam 1993), and assess the genetic variation of germplasm collections (Sharma et al. 2023). DAF is particularly valuable for species with complex genomes or limited genomic information, as it does not require prior sequence knowledge. Despite DAF need careful optimization, it's highly reproducible and automatable. Its flexibility, especially with pre-amplification template digestion to highlight polymorphisms, makes it useful for various genetic studies, from taxonomic classification to gene mapping, offering a powerful tool for dissecting genetic relationships and identifying specific genomic markers (Caetano-Anollés & Gresshoff 1994).

Table 1- Comparison of molecular markers used in genetic analysis

Feature	*Hybridization-based markers (RFLP)*	*Arbitrarily Amplified DNA-based Markers*	*Targeted Fingerprinting Based Markers*	*Transposable Elements Dependent Markers*	*DNA Sequencing-Based Markers*	*Endonuclease Restriction Enzyme-Based Markers*	*Conserved DNA-Based Markers*
Principle	DNA digestion with restriction enzymes, Southern blotting, hybridization with labeled probes	PCR amplification using arbitrary primers	PCR amplification using primers designed for specific, often known, regions	PCR amplification using primers targeting sequences related to transposable elements	Direct sequencing of DNA fragments	PCR amplification followed by restriction enzyme digestion	PCR amplification using primers designed for conserved DNA regions
Genome Coverage	Low to Medium (depends on probe and enzyme)	High (distributed randomly)	Medium to High (depends on target regions)	Medium (biased towards TE locations)	High (can be genome-wide or targeted)	Low to Medium (depends on primer and enzyme)	Low to Medium (focused on specific conserved regions)
Polymorphism Detection	Restriction site variation, fragment length variation	Fragment length variation, presence/absence of bands	Fragment length variation, presence/absence of bands	Fragment length variation, insertion site polymorphism	Single nucleotide variations (SNPs), indels, structural variations	Presence/absence of restriction sites within amplicons	Sequence variation within conserved regions, intron size variation
Reproducibility	High (if protocols are strictly followed)	Low to Medium (sensitive to PCR conditions)	Medium to High (more reliable primers)	Medium (depends on TE distribution and primer design)	Very High (direct sequencing)	High (defined restriction sites)	Medium to High (designed for specific regions)
Dominance	Codominant (can distinguish heterozygotes)	Dominant (cannot easily distinguish heterozygotes)	Dominant (typically)	Dominant (typically)	Codominant (SNPs) or dominant (presence/ absence)	Codominant (can distinguish heterozygotes)	Codominant (can distinguish heterozygotes)
Abundance in Genome	Moderate	High	Medium to High	Medium	Very High (especially SNPs)	Moderate	Low to Medium
Cost	High (labor-intensive, requires radioactive/non-radioactive labeling)	Low to Medium (simple PCR)	Medium (primer design can add cost)	Medium (primer design can add cost)	High (sequencing costs)	Low to Medium (simple PCR and digestion)	Medium (primer design can add cost)
Technical Difficulty	Medium to High (Southern blotting, hybridization)	Low to Medium (PCR optimization is crucial)	Medium (primer design and optimization)	Medium (primer design and understanding TE distribution)	Medium to High (library preparation, bioinformatics)	Low to Medium (PCR and digestion)	Medium (primer design and optimization)
Information Content	Medium (fewer loci typically analyzed)	Low to Medium (dominant markers, band scoring can be complex)	Medium to High (more specific targeting)	Medium (can reveal information about genome organization)	High to Very High (sequence-level data)	Medium (presence/absenc e of specific restriction sites)	Medium (variation within functional regions)
Key Advantages	Codominant inheritance, relatively reliable if well-optimized	Simple and quick to perform, no prior sequence knowledge needed for some types (RAPD, DAF)	More reproducible than arbitrary markers, targets specific regions of interest	Can reveal information about genome evolution and TE dynamics	Highest potential for detecting polymorphism, allows for direct sequence analysis	Simple and quick to perform, can be converted to co-dominant markers (CAPS)	Targets potentially functional or conserved regions, can be informative for phylogenetic studies
Key Disadvantages	Labor-intensive, requires large amounts of high-quality DNA, lower throughput	Low reproducibility, dominant markers, difficulty in band homology assessment, limited information per locus	Can still be dominant markers, requires prior sequence information for primer design	Can be complex to interpret, polymorphism may not always be evenly distributed	High cost, requires specialized equipment and bioinformatics expertise, large datasets to manage	Polymorphism is limited to restriction sites within amplicons	May not be highly polymorphic, requires prior sequence information for primer design

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Note: This table provides a general comparison. Specific markers within each sub-category may have variations in their characteristics. For example, SSRs, while falling under arbitrarily amplified DNA-based markers, are often codominant and highly reproducible compared to RAPDs. Similarly, within sequencing-based markers, the cost and information content can vary depending on the sequencing depth and strategy.

2.2.1.3. Amplified fragment length polymorphism (AFLP)

AFLP is a powerful molecular technique that relies heavily on the selective digestion of genomic DNA with restriction enzymes and is used in studying the genetic diversity of plants. It has various advantages, including the ability to detect DNA polymorphisms without prior sequence information and its superior reproducibility, sensitivity, and high level of polymorphism compared to earlier techniques like RAPD and RFLP (Brugmans et al. 2003). These characteristics have made AFLP a valuable tool for various molecular genetic investigations, such as assessing genetic diversity, uncovering genetic relationships, and informing conservation strategies (Roberto et al. 2021). Numerous studies, including those on citrus (Wang et al. 2022), and various other plant species, have demonstrated the effectiveness of AFLP markers. However, AFLP has some limitations, such as the complexity of interpreting banding patterns, its dominant characteristic, and the possibility of co-migrating bands, which can complicate data analysis and limit the resolution of genetic relationships (Poczai et al. 2013b).

2.2.1.4. Sequence characterized amplified region (SCAR)

SCAR is a molecular marker derived from RAPD markers. Unlike RAPD markers, which rely on short, random primers and can be less reproducible, SCAR markers focus on specific DNA sequences within RAPD fragments (Khan et al. 2017). This is achieved by identifying a target RAPD fragment, cloning and sequencing it, designing specific primers based on the sequence information, and using these primers in PCR to amplify the target fragment. SCAR markers offer advantages such as high specificity, reproducibility, sensitivity, and versatility (Kiran et al. 2010) making them valuable tools in various fields like plant breeding (Zhang & Panthee 2021), genetics, and molecular ecology for identifying and tracking genetic traits, studying genetic diversity, and understanding relationships between organisms (Randig et al. 2002). Shen et al. (2011) developed six specific SCAR markers from RAPD data, enabling precise differentiation of 20 clones, including those from the same origin. This novel application of SCAR markers provides a rapid and reliable method for clone identification, significantly enhancing breeding efficiency in *Cunninghamia lanceolate*.

2.2.1.5. Inter simple sequence repeat (ISSR)

ISSR markers are based on the presence of microsatellite sequences, which are short tandem repeats of DNA, scattered throughout the genome. ISSR primers, with a core microsatellite motif and typically 16-25 base pairs in length, amplify DNA fragments situated between two microsatellite repeats. This technique is relatively simple and cost-effective compared to other molecular markers. It has found widespread application in diverse fields, such as plant breeding (Al-Khayri et al. 2023), studying of genetic diversity in different plant species such as Kalanchoe (Al-Khayri et al. 2022), date palm (Abdelghaffar et al. 2023). ISSR markers are especially valuable for species with limited genomic data, as they do not necessitate prior sequence knowledge. However, they can be less reproducible than other marker systems, and their interpretation can be complex due to the potential for multiple bands to be amplified from a single primer. Aga et al. (2005) used ISSR markers to assess genetic diversity in Ethiopian forest coffee trees, revealing a high degree of differentiation between populations, suggesting limited gene flow within them. Geographic clustering was observed, but some population mixing indicated human and animal-mediated seed dispersal. Despite lower polymorphism compared to RAPD, ISSR proved useful for characterizing *Coffea arabica* populations, providing crucial data for effective *in situ* conservation planning.

*2.2.1.6. Random amplified microsatellite polymorphism (RAMP***)**

RAMP is a PCR-based molecular marker technique that combines the principles of SSR and RAPD markers. It utilizes a single primer containing a core microsatellite motif and a random sequence to amplify DNA fragments. This approach offers a balance between the specificity of SSR markers and the simplicity of RAPD markers. RAMP has been used in various plant species, including *Prunus*, to assess genetic diversity (Rasouli et al. 2015), construct genetic maps (Rasouli et al. 2015), and identify genotypes (Prasad et al. 2000). While RAMP is a powerful tool, it is less reproducible than other molecular markers and may require optimization for specific species.

2.2.1.7. Directed amplification of minisatellite-region DNA (DAMD)

DAMD molecular markers technique is mainly used to generate DNA fingerprints. It targets minisatellite regions, which are highly variable sequences of DNA composed of short tandem repeats. DAMD involves using a single primer that is complementary to the core sequence of the minisatellite and can bind to multiple sites in the genome, amplifying a complex pattern of DNA fragments. The resulting DNA fingerprint can be used in DNA fingerprinting and genome identification (Zhou et al. 1997), differentiate strains, and study genetic diversity (Saleh 2019b). Also, DAMD is valuable for constructing a database to identify cell lines by comparing them to reference profiles, distinguishing similar lines from various sources, and monitoring cell cultures over time. Saleh (2019a) explored genetic diversity in *Ficus sycomorus* using DAMD markers, uncovering significant polymorphism and identifying distinct subspecies groupings. While revealing unique markers for some genotypes, the study suggests that DAMD, though effective, requires

validation with more precise molecular tools to solidify the observed genetic relationships and fully characterize *F. sycomorus* diversity. Additionally, Jena & Chand (2025) utilized DAMD markers to analyze the genetic diversity of Indian mangoes, effectively identifying unique genotypes and exploring population structure. The study revealed significant genetic variation, particularly within East Indian populations, and demonstrated the association of specific DAMD markers with key fruit traits. These findings offer valuable insights for mango breeding programs, enabling marker-assisted selection and the identification of elite parental genotypes for genetic improvement.

2.2.2. Targeted fingerprinting based markers

2.2.2.1. Target region amplified polymorphism (TRAP)

Target region amplified polymorphism (TRAP) markers, developed by (Hu & Vick 2003), have found diverse applications in plant research, particularly for genotyping and assessing genetic diversity related to specific genes or genomic regions of interest. For instance, TRAP markers have been employed to evaluate genetic variability in sweet sorghum germplasm based on lignin and sucrose metabolism genes (Khidr et al. 2020), and to identify markers linked to drought tolerance-related traits like chlorophyll content and leaf senescence in wheat (Saleh et al. 2014). These examples highlight the utility of TRAP markers in dissecting genetic variation associated with important agronomic traits in various plant species.

2.2.2.2. Conserved region amplification polymorphism (CoRAP)

CoRAP is a molecular marker technique that utilizes conserved DNA regions to amplify polymorphic DNA fragments. By designing primers to anneal to both conserved and polymorphic regions, CoRAP ensures specificity and allows for the detection of genetic variation (Fabriki-Ourang & Yousefi-Azarkhanian 2018) and plant genotyping (Wang et al. 2009). This technique offers several advantages, including high specificity, versatility, informativeness, and reproducibility. CoRAP has profound applications in various fields, such as plant breeding, genetics, and evolutionary biology, making it an important tool for studying genetic diversity, mapping genes, and understanding evolutionary relationships (Wang et al. 2009).

2.2.2.3. Expressed sequence tag polymorphism (ESTP)

ESTP is a molecular marker technique that utilizes expressed sequence tags (ESTs) to identify genetic variations. ESTs are short DNA sequences derived from mRNA, representing transcribed regions of the genome. Comparing EST sequences from different individuals or populations enables identifying polymorphisms, such as single nucleotide polymorphisms (SNPs), insertions, or deletions. ESTP markers offer several advantages, including their direct link to functional genes, high transferability across different species, and the potential for developing functional markers. They have been successfully utilized in different fields, such as plant breeding, genetics, and evolutionary biology, to study genetic diversity, map genes, and identify genes associated with specific traits (Pelgas et al. 2004). ESTPs can be utilized as orthologous markers for comparative mapping between species. Additionally, they can be employed to map genes with known functions or to identify candidate genes associated with important traits in loblolly pine (Temesgen et al. 2001). Temesgen et al. (2001) focused on developing and mapping ESTP markers in loblolly pine, utilizing cDNA sequences to generate primers for PCR. Polymorphisms were detected through various methods, with DGGE showing superior sensitivity. The successful mapping of 56 ESTPs onto the pine's genetic map provides valuable tools for comparative genomics, functional gene analysis, and identifying genes linked to important traits, enhancing loblolly pine genetic research and breeding.

2.2.2.4. Sequence-related amplified polymorphism (SRAP)

SRAP markers, valuable tools in molecular genetics research, amplify coding regions of DNA by targeting open reading frames with specifically designed primers. These markers offer advantages including high variability, robustness, and ease of use. A key benefit is their versatility, as one primer can combine with many others. This flexibility has led to their widespread use in agriculture, horticulture, and conservation genetics. SRAP markers have been crucial in developing quantitative trait loci (Saeidnia et al. 2021), assessing genetic diversity (Essa et al. 2023), understanding population structure (Mohamed et al. 2024), and investigating gene flow in various plant species (Song et al. 2021a). Thakor et al. (2019) employed SRAP markers to analyze genetic diversity in Gujarat teak populations, essential for conservation. The markers successfully distinguished teak genotypes into seven groups, revealing significant genetic variation. High polymorphism and diverse similarity coefficients confirmed SRAP's effectiveness in characterizing teak germplasm, providing crucial data for sustainable forest management and breeding initiatives.

2.2.2.5. Sequence tagged site (STS)

STSs are short DNA sequences that have a single occurrence in the genome and known location and base sequence.

These unique sequences can be amplified with PCR using specific primers, making them valuable tools for genetic and physical mapping of genomes (Qiao et al. 2021). STSs serve as landmarks on the genetic map, aiding in the localization of genes and understanding the organization of chromosomes (Yu et al. 2021). They are particularly useful in constructing high-resolution genetic maps, identifying disease genes, and tracking genetic variation within populations (Huebner et al. 2021). Perry & Bousquet (1998) focused on developing STS markers in black spruce, uncovering various polymorphisms including codominant and dominant length variations, and null alleles. PCR and gel electrophoresis revealed these markers, which showed Mendelian inheritance. The codominant markers exhibited significant length differences, often due to repeats in noncoding regions. These markers, with an average heterozygosity of 0.26, provide valuable tools for genetic studies, including diversity assessment and linkage mapping, in black spruce.

2.2.2.6. Intron-exon splice junction (ISJ)

ISJs are the boundaries between exons and introns within a gene. These junctions play a crucial role in the process of RNA splicing. The sequences at ISJs are highly conserved and contain specific motifs that are recognized by the splicing machinery. Variations in these sequences can lead to splicing errors, resulting in altered protein products and potentially causing genetic diseases. Therefore, ISJs are important targets for studying genetic diversity and species relationships (Warlarphih et al. 2022). ISJs markers have proven useful in various plant genetic studies. For instance, in rice (*Oryza sativa*), ISJ markers were effectively used for DNA fingerprinting, varietal identification, and assessing genetic diversity among different genotypes (Ramadan et al. 2017). Similarly, in barley (*Hordeum vulgare*), ISJ markers, combined with morphological traits, helped distinguish between two-rowed and six-rowed as well as hulless and hulled genotypes and assess overall genetic diversity (Drikvand et al. 2012). Furthermore, ISJ markers have been employed to study genetic relationships within the *Malva* genus (Celka et al. 2010) and to evaluate genetic variation in endangered species like *Pulsatilla patens*, sometimes complementing data obtained from other markers like SSRs (Bilska & Szczecińska 2016). These examples highlight the versatility of ISJ markers in plant research for diversity analysis, identification, and phylogenetic studies.

2.2.2.7. Promoter anchored amplified polymorphism (PAAP)

PAAP is a molecular marker technique focused on analyzing the regulatory regions of plant genomes. It combines the principles of RAPD and conserved core promoter sequences. A degenerate promoter primer, based on conserved core promoter sequences, is used in combination with a RAPD primer to amplify DNA fragments. This approach allows for the identification of polymorphisms within promoter regions, which can influence gene expression and contribute to phenotypic variation. PAAP marker has been effectively applied in various plant species to study genetic diversity and population structure analysis (Ma et al. 2022), map genes (Amiteye 2021b), and identify markers related to specific characters, particularly those related to gene regulation and expression (Ma et al. 2022).

2.2.2.8. Direct amplification of length polymorphism (DALP)

DALP is a molecular marker technique that combines the advantages of Arbitrarily Primed PCR (AP-PCR) and sequencing-based polymorphism detection (Desmarais et al. 1998). It involves using specifically designed primer pairs that generate a specific multi-banded pattern. The amplified fragments can then be directly sequenced, allowing for the identification and characterization of DNA polymorphisms. DALP offers high resolution and ability to directly analyze genetic variation, making it a valuable tool for various applications in genetics and molecular biology (Chandra et al. 2024).

2.2.2.9. Start codon-targeted Polymorphism (SCoT)

SCoT markers offer a more efficient and reliable method compared to the arbitrary RAPD and ISSR markers for analyzing population structure and genetic diversity in diverse plant species. It is designed from conserved sequences flanking the ATG start codon in plant genes. For instance, SCoT markers have been successfully used to characterize genetic diversity in faba bean genotypes (Essa et al. 2023), identify and analyze Daylily somaclone variants (Shalan et al. 2023), differentiate bread wheat genotypes (Ezzat et al. 2024), investigate the genetic basis of cross-pollinated species like *Elymus sibiricus* and *Boehmeria nivea* (Zhang et al. 2015a). While SCoT markers may not be the primary method for species identification, they have proven to be a good resource for investigating genetic variation and population dynamics across a wide range of plant species. Chhajer et al. (2017) explored the genetic diversity of the endangered *Tecomella undulata* in India using SCoT markers. The study revealed substantial genetic variation among 108 accessions from 21 populations, leading to their classification into five distinct clusters. High genetic differentiation, likely due to cross-pollination, was observed. This work provides valuable genetic information for conservation efforts of this important tree species. Furthermore, Orman et al. (2025) examined Turkish chestnut genetic diversity using SCoT markers, revealing clear population differentiation based on geographic origin. The markers effectively distinguished genotypes, with most genetic variation occurring between individuals rather than within

populations. The study highlighted the utility of SCoT markers for phylogenetic analyses in *Castanea sativa*, demonstrating their ability to capture genetic relationships influenced by geographic distance.

2.2.2.10. Simple sequence repeats (SSRs)

SSR markers, also known as microsatellites are DNA markers characterized by short tandem repeats of 1-6 base pairs at specific genomic loci. The variation in the number of these repeats within a population provides the basis for their use in genetic analysis (Zhao et al. 2023). They offer several advantages over other markers, including high reproducibility, lack of requirement for ultra-pure DNA, high polymorphism, co-dominant inheritance, and abundance in eukaryotic genomes (Garg et al. 2024). The functional enrichment analysis conducted by (Song et al. 2021b) revealed that SSR-containing genes were significantly associated with transcription factor families, notably Myb_DNA-bind_4, AP2, and FAF, indicating potential roles for SSRs in regulating plant development and abiotic stress responses. Furthermore, the observed variation in functional term enrichment across species, particularly the high enrichment in *Citrus sinensis*, underscores species-specific adaptations and evolutionary divergence, suggesting that SSRs contribute to the unique biological characteristics of each tree species. A previous study implied that AP2 family genes play important roles in fruit growth and development in peach (Zhang et al. 2012). Chen et al. (2020) explored the genetic diversity of a selected *Liquidambar formosana* population, revealing unexpectedly high diversity compared to natural populations. Using EST-SSR markers, the study found significant levels of heterozygosity and polymorphism, suggesting that even after selection, the "plus" trees retain a rich genetic pool. This diversity, coupled with the known heterosis in *Liquidambar* hybrids, positions this selected population as a valuable resource for future breeding programs, aiming to enhance production potential and adaptation strategies in *Liquidambar* species.

2.2.3. Transposable elements dependent markers

2.2.3.1. Sequence-specific amplified polymorphism (SSAP)

SSAP is a molecular marker technique that utilizes transposable elements (TEs) as anchors to detect polymorphisms in the flanking genomic regions. In SSAP, one primer is designed to anneal to a specific sequence within the TE, while the other primer is random. This combination allows for the amplification of DNA fragments that vary in length due to differences in the flanking regions. SSAP markers are highly polymorphic and can be used to assess genetic diversity (Biswas et al. 2011), construct genetic maps, and identify genes associated with specific traits (Syed et al. 2006). They are particularly useful for studying species with limited genomic information, as they do not require prior sequence data. (Campos-Rivero et al. 2017) assessed SSAP and SSR markers for guava breeding, aiming to enable early selection for desired fruit traits. SSAP markers showed high polymorphism and effectively clustered varieties based on fruit characteristics, indicating potential linkage to fruit trait genes. Specific SSR markers also correlated with key fruit qualities. Both marker types proved valuable for marker-assisted selection, facilitating efficient identification of superior guava genotypes for breeding programs.

2.2.3.2. Inter-sine amplified polymorphism (ISAP)

ISAP is a molecular marker technique that utilizes Short Interspersed Nuclear Elements (SINEs) to generate genotype-specific fingerprints. SINEs are repetitive DNA sequences that are distributed across the genome. In ISAP, primers are designed to target the conserved regions of SINEs, allowing for the amplification of DNA fragments located between two SINE elements (Wenke et al. 2015). The resulting amplified fragments can vary in length due to polymorphisms in the intervening sequences, generating unique banding patterns. Due to their high polymorphism, reproducibility, and cost-effectiveness, ISAP markers are well-suited for various applications in plant breeding and genetics, including genotype differentiation and progeny tracing in poplar trees (Reiche et al. 2021). They have been successfully used to assess genetic diversity, construct genetic maps, and identify markers linked to specific traits (Tomlekova et al. 2023).

2.2.3.3. Exon retro transposon amplified polymorphism (ERAP)

ERAP is a molecular marker technique that utilizes the combination of gene-specific primers and retrotransposon-specific primers to amplify DNA fragments. This approach takes advantage of the fact that retrotransposons can insert themselves near or within genes. By designing one primer to target a specific gene region and another primer to target a retrotransposon element, ERAP can amplify polymorphic DNA fragments that vary in size due to differences in the distance between the gene and the retrotransposon. ERAP markers offer several advantages, including high specificity, reproducibility, and the ability to directly link genetic markers to functional genes. They have been used in several plant species to study genetic diversity, gene mapping, and identify markers associated with traits of interest (Pfaff & Kahl 2003). ERAP markers are particularly useful for identifying polymorphisms in gene-rich regions and for studying the impact of retrotransposon insertions on gene expression and function.

2.2.3.4. Inter-primer binding site (iPBS)

The iPBS molecular markers are reliable tools for DNA fingerprinting, circumventing the requirement for prior sequence information. Owing to its broad applicability and high discriminatory power, iPBS molecular marker has emerged as a preferred universal marker for assessing genetic differentiation between and within diverse eukaryotes, encompassing intra-specific to inter-specific levels (An et al. 2021). As described by Ouyang et al. (2021), iPBS is a universal DNA labeling method that targets the primer binding site of LTR retrotransposons. This system has been used in numerous genetic diversity studies, particularly in agriculture and conservation (Borna et al. 2017). It has been powerful in examining genetic diversity in crops like *Allium ledebourianum*, *Juglans regia*, and cotton, scarlet eggplant and safflower (Kalendar et al. 2010; Shimira et al. 2021; Başak et al. 2022; Baran et al. 2023).

2.2.3.5. Inter-retrotransposon amplified polymorphism (IRAP)

IRAP markers, derived from retrotransposons, exploit the insertion sequences between outward-facing LTRs to identify genetic
variations. Given their abundance and irreversible nature in plant genomes, retrotransposons are valuable tools for phylogenetic and genetic mapping studies. IRAP markers have been successfully utilized to assess genetic diversity in citrus genotypes and differentiate among plant hybrids and species (El zayat et al. 2021). Additionally, they have been used to explore genetic diversity within rare plant species like *Adonis vernalis* (Boronnikova & Kalendar 2010). Various retrotransposon-based marker systems, including SSAP, REMAP, and RBIP, have been developed to further enhance genetic analysis. While these markers offer significant advantages, a historical limitation has been the requirement for prior sequence information. Fan et al. (2014) developed IRAP markers from masson pine LTR retrotransposons to assess genetic diversity, showing clear, polymorphic bands. However, stress tests revealed no retrotransposon activation over two months, suggesting either specific stress requirements or limitations in the study's timeframe.

2.2.3.6. Retro transposon-based insertion polymorphism (RBIP)

RBIP is a molecular marker technique that utilizes the presence or absence of retrotransposon insertions in the genome to detect genetic variation (Meng et al. 2021). Retrotransposons are mobile genetic elements that can insert themselves into various locations within the genome (Arvas et al. 2023). By designing primers that target both the retrotransposon sequence and the flanking genomic regions, RBIP can amplify DNA fragments that vary in length depending on the presence or absence of the retrotransposon insertion (Meng et al. 2021). This technique has been effectively applied to diverse plant species for exploring genetic diversity, constructing genetic maps, and identifying genes linked to specific traits (Meng et al. 2021). RBIP markers offer several advantages, including high specificity, reproducibility, and the ability to detect large-scale structural variations in the genome.

2.2.3.7. Retro transposon microsatellite amplified polymorphism (REMAP)

REMAP is a molecular marker technique that combines between retrotransposon and microsatellite sequences to detect genetic diversity (Leśniowska-Nowak et al. 2021). Retrotransposons are mobile genetic elements that can insert themselves into various genomic locations. Microsatellites, on the other hand, are short, repetitive DNA sequences. In REMAP, one primer is designed to anneal to a conserved region of a retrotransposon, while the other primer targets a microsatellite sequence located within or near the retrotransposon. This combination allows for the amplification of DNA fragments that vary in length due to differences in the number of repeats in the microsatellite region or the presence of additional retrotransposon insertions. REMAP allow researchers to pinpoint genetic polymorphisms that distinguish between different species and also reveal variations within a single species or among cultivated varieties (Cheraghi et al. 2018). (Pakhrou et al. 2020) used SRAP and REMAP markers to analyze genetic diversity in *Argania spinosa*, finding high polymorphism but significant variation between populations. Two genetic groups were identified, and outlier loci suggested adaptation through selection. These findings are crucial for conservation efforts.

2.2.4. DNA sequencing-based markers

2.2.4.1. Expressed sequence tag (ETS)

ESTs are short DNA sequences derived from mRNA, providing insights into gene expression, discovery, and genome annotation. By identifying transcribed regions, comparing sequences to known proteins, annotating genomes, comparing gene expression across species, and developing genetic markers, ESTs have significantly advanced our understanding of gene function and genome organization (Kerry et al. 2022). As sequencing technologies progress, ESTs continue to be a valuable tool in genomic research. Liu et al. (2023) utilized ETS to assess the effectiveness of *ex-situ* conservation strategies, they developed ETS markers derived from transcriptome genes of *A. nanus*. Wang et al. (2010) created a cDNA library from birch cambium, identifying 1,540 unique genes. 50 of these are linked to wood formation, with expression peaking in spring and late summer, indicating key periods for cell wall development.

2.2.4.2. Single nucleotide polymorphism (SNP)

SNP is the most prevalent kind of genetic diversity among plant genotypes, it represents a diversity in a single DNA base at a specific genomic location. SNPs can be found within or between genes, or in non-coding gene regions. A comprehensive SNP analysis was undertaken on 137 tea germplasm resources collected from Wuyi Mountain and the surrounding regions to evaluate population structure, genetic diversity, and genetic distances (Liu et al. 2022). SNPs are amenable to high-throughput automation, facilitating rapid and efficient genotyping of numerous castor bean (*Ricinus communis*) genotypes (Foster et al. 2010). (Zhang & Zhang 2005) advocates for SNP-based association studies in forest trees, leveraging rapid LD decay to link specific alleles to complex traits. It outlines SNP discovery and application for breeding, highlighting its potential to enhance quantitative trait analysis in forestry. Also, SNPs serve as powerful molecular markers in plant genetics, enabling high-resolution genetic analyses. For instance, in rice (*Oryza sativa*), SNPs have been extensively used for constructing high-density genetic maps, facilitating the identification of quantitative trait loci (QTLs) associated with grain yield and quality (McCouch et al. 2010). Furthermore, in wheat (*Triticum aestivum*), SNP markers have been instrumental in marker-assisted selection (MAS) for disease resistance genes, such as the *Lr34/Yr18/Pm38* locus conferring resistance to multiple rust and mildew diseases (Mammadov et al. 2012). These examples highlight the utility of SNPs in dissecting complex traits and accelerating breeding programs for crop improvement.

Genotyping by sequencing- single nucleotide polymorphisms (GBS-SNPs) is a robust method for SNP discovery and genotyping. It involves digesting genomic DNA with restriction enzymes to simplify the genome, followed by sequencing the resulting fragments. SNP identification is achieved by comparing these fragment sequences across individuals. GBS is a popular choice due to its high throughput, cost-effectiveness, and capacity to identify novel SNPs, making it applicable in fields like plant breeding, population genetics, and evolutionary biology. GBS-SNPs were utilized to predict the accuracy of various quantitative traits in 19 tropical maize populations evaluated in multi-environment trials (Zhang et al. 2015b). Also, GBS-SNPs were utilized in an association mapping study to investigate the genetic basis of CIGS resistance in maize, with resistance measured by relative germination rate (RGR) (Cao et al. 2024). Hamon et al. (2017) provided a comprehensive *Coffea* phylogeny using advanced sequencing techniques, resolving previous uncertainties. It suggests Africa or Asia as the origin of coffee, with independent radiations across continents. The research also explores caffeine evolution, linking high caffeine content to specific African environments and indicating potential convergent evolution in Madagascar.

2.2.4.3. Sequencing-based diversity arrays technology-single nucleotide polymorphism, DArTseq-SNP

DArTseq-SNP is a technology used for high-throughput SNP genotyping and uses the power of sequencing to identify SNPs. It involves a complexity reduction step where specific DNA fragments are selected for sequencing, followed by bioinformatics analysis to identify SNPs. This efficient and cost-effective approach is well-suited for large-scale genetic studies. DArTseq-SNP markers have found broad application in assessing genetic diversity across a range of plant species (Gelaw et al. 2023), map genes (Ren et al. 2015), and identify markers associated with traits of interest (Odesola et al. 2023).

2.2.4.4. Restriction site-associated DNA sequencing (RAD-Seq)

RAD sequencing is a powerful technique for discovering and genotyping genetic variations, particularly SNPs. It involves digesting genomic DNA with restriction enzymes, ligating barcodes and adapters, selecting fragments within a specific size range, sequencing the fragments, and analyzing the data to identify SNPs and other genetic variations. RAD-seq offers high-throughput, reduced genome complexity, discovery of novel markers, applications in population genetics, and ability to construct high-density genetic maps. This technique has become useful in various fields, including genetic diversity (Probowati et al. 2023), evolutionary genomics (Andrews et al. 2016), and plant breeding (He et al. 2023). Wang et al. (2024) used genetic sequencing to explore the diversity of Sichuan tea, focusing on compounds affecting taste and nutritional value (FAAs and TPs). It identified genes linked to these compounds, revealing two distinct tea populations and offering insights for breeding improved tea varieties.

2.2.4.5. Genome-wide selection-single nucleotide polymorphism (GWS-SNP)

GWS-SNPs is a powerful technique that uses the genetic information encoded in SNPs across the entire genome to predict and improve traits of interest in plants. By analyzing the genetic variation at millions of SNPs, GWS can identify individuals with superior genetic feature, leading to more efficient and accurate selection. This approach has revolutionized breeding programs, enabling faster genetic gain and the development of improved varieties with desired traits such as increased yield, disease resistance, and improved quality. GWS-SNPs have become a cornerstone of modern breeding strategies, offering significant potential for enhancing agricultural productivity and addressing global food security challenges. This technique also holds significant promise for plant breeding. Previous studies

demonstrated its effectiveness in improving various crops; maize (Bernardo & Yu 2007), oil palm (Wong & Bernardo 2008), barley (Zhong et al. 2009).

2.2.5. Endonuclease restriction enzyme-based markers

2.2.5.1. Cleaved amplified polymorphism sequence (CAPS)

CAPS markers utilize PCR to amplify DNA fragments that have been previously digested with restriction enzymes. The resulting amplified fragments are then subjected to agarose gel electrophoresis to visualize and differentiate between different DNA sequences based on the presence or absence of restriction sites (Shavrukov, 2016). These markers exhibit several advantages, such as co-dominance, suitability for small DNA samples, locus specificity, and high reproducibility. However, limitations include the size of amplified fragments and the requirement for prior sequence information for marker development. CAPS markers are predominantly used for gene mapping purposes, SNP detection in various species like watermelon and *Glycyrrhiza glabra*, and differentiating cotton varieties to facilitate marker-assisted selection (Liu et al. 2016; Jo et al. 2018). They are also valuable tools for genetic diversity and population structure analyses, as demonstrated in button mushroom genetic resource management (Kushanov et al. 2016). MCCLEARY et al. (2009) conducted a genetic test to identify these hybrids by their maternal lineage. This test helps researchers study how the invasive Japanese walnut is impacting native butternut populations.

2.2.6. Conserved DNA- based markers

2.2.6.1. Conserved DNA-Derived polymorphism (CDDP)

CDDP markers are derived from characterized plant genes known to play roles in diverse biological processes, such as stress response and development. This strategy generates functional markers directly linked to specific plant traits. These markers display detectable length variations within conserved DNA sequences. These conserved regions share common primer binding sites but exhibit differences in their genomic distribution. Studies employing CDDP markers in plant systems have demonstrated that genetic diversity is influenced by geographical factors, gene flow between populations and sexes, and environmental conditions (Bidyananda et al. 2024). The effectiveness of these markers in evaluating genetic diversity across diverse plant species has been demonstrated (Igwe et al. 2021). These markers are valuable tools for genetic rescue, supporting both *in situ* and *ex situ* conservation, as well as cultivar identification. CDDP markers offer advantages including ease of use, cost-effectiveness, and high polymorphism, which allows for the development of markers targeting specific traits (Collard & Mackill 2009). Wang et al. (2020) analyzed the genetics of endangered *Elaeagnus macrophylla* plants on islands and coasts. It found low genetic diversity but high population differences, with genetics tied to island location, not just distance. This suggests unique island populations needing specific conservation efforts.

2.2.6.2. Intron-targeting polymorphism (ITP)

ITP is a molecular marker technique focuses on the variation within introns, the non-coding regions of genes. Introns are known to evolve at a relatively neutral rate, making them a useful source of genetic variation. ITP involves designing primers that target conserved regions flanking the introns, allowing for the amplification of polymorphic DNA fragments (Choi et al. 2004). These fragments can then be analyzed to identify variations in size or sequence, which can be employed to assess genetic diversity, construct genetic maps, and identify genes associated with specific traits. ITP offers several advantages, including high specificity, reproducibility, and the ability to target specific genes or genomic regions. It has been utilized in various plant species to study genetic diversity and map genes (Choi et al. 2004). For example, ITP markers have been successfully applied in studies of genetic diversity and population structure in crops such as tea (*Camellia sinensis*), banana (*Musa spp*.), longan (*Dimocarpus longan Lour*.), and cultivated peanut (*Arachis hypogaea* L.) (Xiong et al. 2013; Shen et al. 2024).

2.2.6.3. Tubulin-based polymorphism (TBP)

TBP is a molecular marker technique that exploits the variation in intron lengths within the highly conserved β-tubulin gene. By targeting conserved regions and amplifying polymorphic intron regions, TBP generates unique DNA fingerprints for different individuals or populations (Bardini et al. 2004). This technique offers high specificity, reproducibility, and versatility, making it suitable for various plant species. TBP has been successfully applied to assess genetic relationships, identify unique genotypes, and develop molecular markers for breeding programs (Braglia et al. 2020). Bardini et al. (2004) revealed that TBP a new genetic marker that uses variations in the plant β-tubulin gene. It's a fast, easy way to identify genetic differences in plants, shown to work well in various species, without needing prior genome knowledge. It's especially useful for studying genetic diversity in diverse plant varieties.

2.2.6.4. Cytochrome P450- based analogue (PBA)

Cytochrome P450-Based Analog (PBA) markers are a type of molecular marker that utilizes conserved regions of cytochrome P450 genes to amplify polymorphic DNA fragments (Poczai et al. 2013a). Cytochrome P450 genes encode a large family of enzymes involved in various metabolic processes, including drug metabolism and detoxification. By targeting conserved regions within these genes, PBA markers can be used to identify genetic variation across different individuals or populations. PBA markers offer several advantages, including high specificity, reproducibility, and the ability to target functional genes. They have been successfully applied in various plant species to study genetic diversity, map genes, and identify markers associated with traits of interest (Putri et al. 2020).

3. Bioinformatics tools for DNA marker data analysis

Bioinformatics tools are essential for analyzing DNA marker data, encompassing a range of software for various purposes (Gibas & Jambeck 2001). Tools like FastQC (Alexander et al. 2009), Trimmomatic (Bolger et al. 2014), and PGDSpider (Lischer & Excoffier 2012) handle data preprocessing and format conversion, ensuring data quality and compatibility. Marker-specific analysis includes GATK (Van der Auwera et al. 2013) and SAMtools (Li et al. 2009) for SNP analysis, which are crucial for identifying genetic variations; Tandem Repeats Finder (Benson 1999) for SSR analysis, important for studying population structure and evolution; and specialized software for AFLPs (Vos et al. 1995), often analyzed with general statistical software or custom scripts). For population genetics, tools like Arlequin (Excoffier & Lischer 2010), STRUCTURE (Pritchard et al. 2000) are used to infer population structure, analyze genetic diversity, and understand evolutionary relationships. MEGA (Kumar et al. 2018) and PHYLIP (Felsenstein 1989) handle phylogenetic analysis, constructing evolutionary trees. PLINK (Purcell et al. 2007) and TASSEL (Bradbury et al. 2007) are valuable for statistical analysis, genome-wide association studies (GWAS), and data visualization. These tools enable researchers to efficiently process, analyze, and interpret DNA marker data, driving discoveries in genetics, breeding, and conservation.

4. Conclusions

Concluding, DNA markers are vital for understanding plant genetic diversity and population structure, revealing adaptation and trait associations. Researchers face a choice among marker types: arbitrarily amplified (RAPDs, AFLPs) are cost-effective but less reproducible and locus-specific; targeted (SSRs, ITPs) are more reliable and often co-dominant but require prior sequence data; sequencing-based SNPs offer genome-wide coverage but are pricier; restriction enzyme-based (RFLPs) are locus-specific but low-throughput; and hybridization-based (VNTRs) are highly polymorphic but technically demanding. Selecting markers involves balancing polymorphism levels, locus specificity, cost, resource availability, and study scale. Combining genome-wide SNPs with locus-specific, co-dominant markers like SSRs or ITPs, along with advanced sequencing, provides a robust and increasingly feasible approach for comprehensive genetic analysis crucial for plant conservation and sustainable use.

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