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Review

Plant Genetic Diversity Studies: Insights from DNA Marker Analyses

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Abstract: The plant adaptation response to a changing environment depends on the genetic diversity level it possesses. Genetic diversity and a thorough understanding of population indices are pivotal for decoding plant adaptation to dynamic environmental stressors. The development of polymerase chain reaction (PCR)-based molecular markers enables comprehensive population analyses and the precise detection of individuals and groups with unique genetic variations. Various molecular markers have been employed to assess genetic diversity, examine population structure, and delineate cluster patterns within and among populations. DNA markers revolutionize plant diversity studies by allowing detailed analyses of genetic variations, including economically significant trait-influencing genes. Despite their simplicity, they offer high reproducibility, ensuring accurate estimations of plant variation. Integrating multiple marker systems with advanced high-throughput sequencing techniques is poised to enhance the understanding and management of depleting plant genetic resources by providing a comprehensive picture of diversity at the genome-wide level. This review explores diverse molecular markers, elucidating their advantages and limitations, and highlights their impact on evaluating the genetic diversity and population structure of plants.

Keywords: genetic diversity; DNA marker; dominant markers; polymorphism; population structure; germplasm; conservation

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1. Introduction

Molecular markers have been widely used for plant genetic diversity and population genetics studies, essential for breeding and crop improvement, conservation, protection, introduction, and reintroduction of endangered and valuable plants [1–3]. They also enable the identification of new plant varieties and detect genetic changes from the known ones, providing valuable insights into the existing genetic variations within and between plant populations [4]. Genetic diversity is vital for adapting and adjusting plants to environmental changes [5]. The responses of plants and their adaptive abilities to climatic change depend on their genetic diversity levels [6]. Molecular markers offer essential insights into the variation in plant genetic composition and population structures, thereby playing vital roles in optimizing plant utilization and ensuring effective management [7]. They also assist in quickly identifying the wild relatives of cultivated plants, thereby providing the possibility of improving crop varieties with increased resistance to diseases

and environmental stress [8]. With the recent increase in the understanding of plant genome sequences and the varied molecular roles of plant genes, the field of plant molecular genetics has been revolutionized, increasing its efficacy in the application of plant genetic variety study and breeding programs [9].

The morphological characters and cytological and ethnological parameters traditionally employed to estimate genetic diversity levels are not reliable and effective, as only a small part of the plant genome is represented by these traits, and they are easily affected by environmental factors [10]. They provide an incomplete picture of the complex genetic structure variation within and between species, genera, and plant groups [11]. Enhancements in biochemistry and molecular biology have led to the development of more powerful biochemical and molecular markers, overcoming the inherent limitations of traditional weak markers [12]. The novel invention of polymerase chain reaction (PCR) by Kary Mullis in 1983 has dramatically simplified plant genetic variation analyses by developing sophisticated DNA markers with high reproducibility [13]. Biochemical isozyme and DNA markers have been employed to determine genetic diversity, population structures, and phylogenetic relationships, identify cultivars, and construct genetic linkage maps in several plant species [14–16]. However, DNA markers are more effective and favorable than isozymes due to their abundance, dominant and co-dominant inheritances, and involvement of both express and non-express sequences specific to their gene locus [17]. They are also less dependent on environmental factors and can provide more detailed information about the underlying genomic variation in an organism. Recently, plant diversity studies with single marker types have not been considered complete without applying other markers [18]. The cumulative application of multiple markers imparts more accurate and reliable genetic diversity information, population structure, and cluster determination than using a single marker type [19,20]. The genetic variability within various plants has been effectively assessed by employing a combination of diverse markers [4,21,22]. The recent advancements in DNA sequencing techniques have further bolstered the efficacy of DNA markers in diversity studies, genome mapping, and crop improvement [23]. The present review aims to provide a comprehensive overview of different DNA markers, their advantages, limitations, and applications in genetic diversity, cluster resolution, and population structure studies of plants.

2. DNA Markers

DNA markers are fragments of DNA that reveal variation among organisms [24,25]. They may even be used to detect polymorphisms between different genotypes within a population based on the divergence in a particular DNA sequence [26,27]. DNA marker development may be based on either the coding or non-coding regions of the genes, and this may or may not necessitate prior sequence information [9]. Researchers continue to strive to establish more reliable and accurate markers such as AFLP, ISSR, SCoT, iPBS, DArT, ITS, SNP, and others, which are more efficient for estimating diversity than morphological and biochemical markers [28]. However, an ideal DNA marker should possess properties such as high polymorphism, dominant or co-dominant inheritance, frequent occurrence, independence from environmental and developmental conditions, high reproducibility, easy accessibility, and fast and cost-effective assays [10,17,29]. DNA markers may broadly be classified as hybridization- and PCR-based markers (Figure 1).

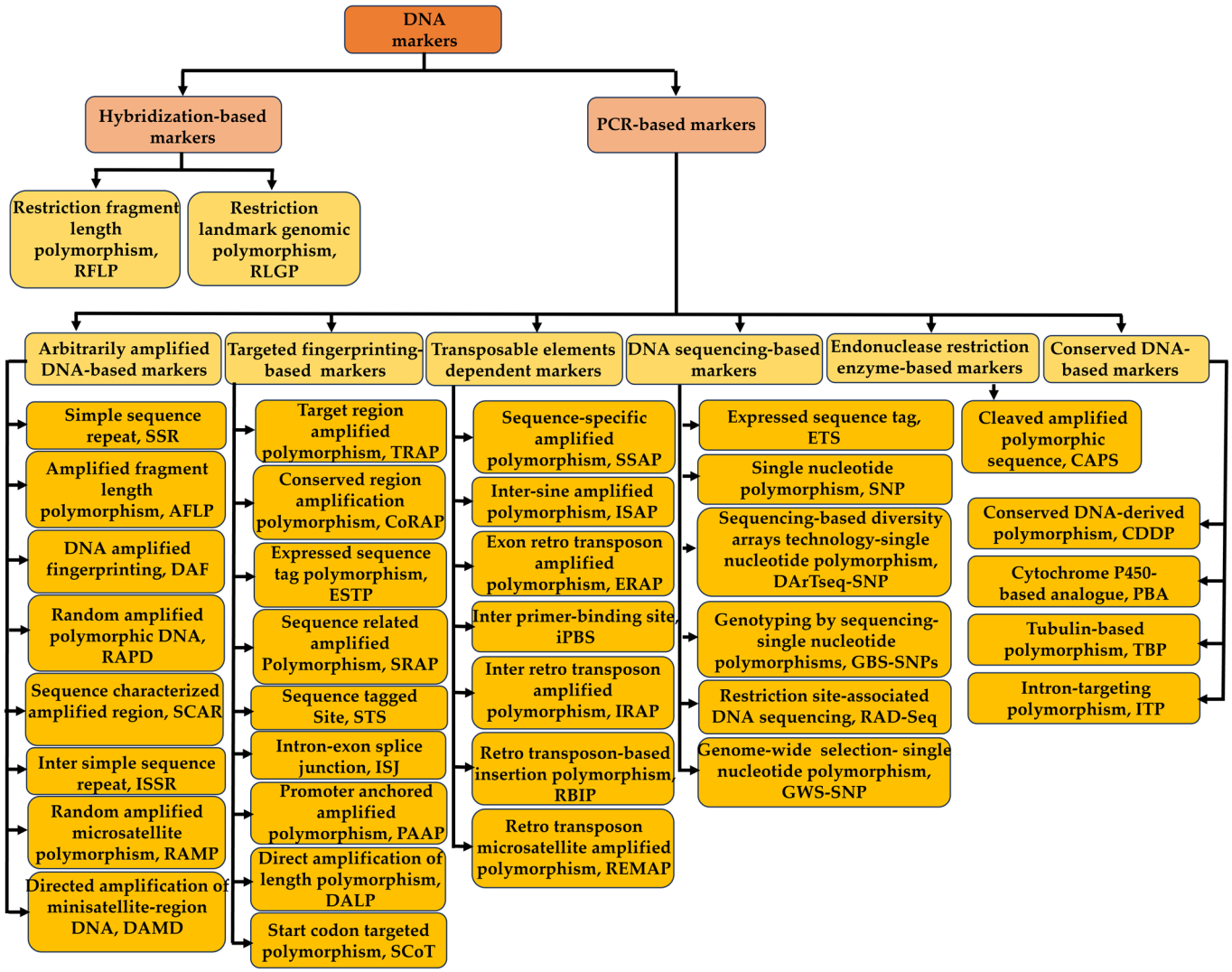

Figure 1. The broad classification of DNA markers.

3. Application of Markers for Genetic Diversity and Population Structure Studies

The enormous utility of molecular markers in plant research is excellent. After their development, these markers can be used for DNA fingerprinting, genotype characterization, the construction of genetic linkage maps, quantitative trait locus (QTL) mapping, genetic homogeneity testing, and population and genetic diversity studies [30,31]. Earlier, a single marker system was employed to evaluate plant genetic variation. However, multiple markers have been recommended to obtain more reliable, accurate, and comprehensive information about the diversity level, genetic population structure, and cluster resolution of the investigated plant species [32–35]. The combined utilization of different marker systems ensures the validation of the results from plant genetic investigations derived from the analysis of each marker system [4]. The following flowchart depicts the basic steps of gel-based molecular markers explicitly designed for plant genetic diversity studies (Figure 2).

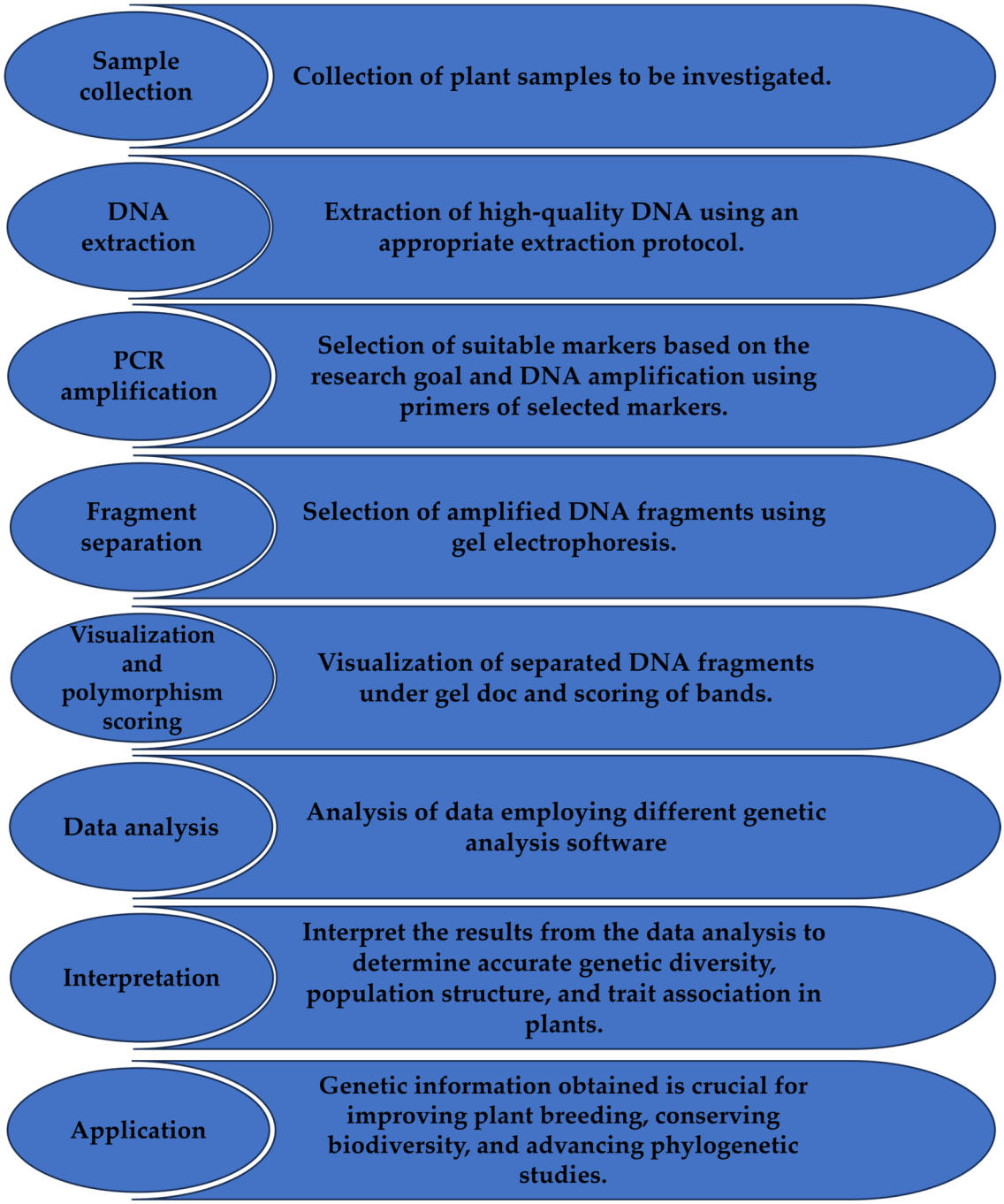

Figure 2. Schematic representation of the utilization of gel-based DNA markers for genetic diversity studies in plants.

3.1. Utilisation of Single Molecular Marker Systems

Exploring plant genetic diversity is crucial for understanding their evolutionary history, adaptation, and potential for future breeding programs. Among the various approaches to ascertain genetic diversity and population structure is using a single marker system, which involves the utilization of only specific molecular markers.

3.1.1. Random Amplification of Polymorphic DNA (RAPD)

RAPDs are popular first-generation DNA markers based on the amplification of random DNA fragments in different loci of a DNA template with short, arbitrary primers and detect polymorphisms through amplified DNA fragments analyses after electrophore-

sis [36]. They are simple, quick, and cost-effective and have proven effective for evaluating genetic variations in both wild and domesticated plants [37]. Bibi [38] used seven selected RAPD primers out of fifteen to detect the best linseed variety, generating precise polymorphic bands. Dhakshanamoorthy [39] also utilized 20 polymorphic RAPD primers to identify mutants in *Jatropha curcas* treated with gamma rays and ethyl methane sulphonate (EMS). Fu [40] demonstrated their usefulness by resolving the genetic relationships among populations of the rare, endemic species of *Changium smyrnioides* through a genetic diversity evaluation. Zhang [41] applied 14 RAPD primers, generating 98 polymorphic bands to genetically characterize *Coptis omeiensis*. RAPD markers have been widely employed in elucidating plant variability and interconnections, deciphering population genetic structures, advancing crop development, and supporting conservation initiatives [42,43]. However, the markers have limitations arising from a short primer length, lower polymorphism levels and non-reproducible PCR outcomes, and the dominant mode of inheritance, rendering them less reliable and unsuitable for marker-assisted selection (MAS) and accurate diversity studies [44].

3.1.2. Restriction Fragment Length Polymorphism (RFLP)

The RFLP is a hybridization-based marker that employs restriction enzymes for DNA fragment generation and subsequent hybridization to target fragments using specific radio-labeled probes. The marker detects differences between individual genomes due to point mutation, insertion/deletion, translocation, inversion, and duplication by generating different-sized DNA fragments through restriction digestion [45,46]. RFLPs are locus-specific markers showing high reproducibility and reliability with co-dominant inheritance and offering easy data exchange between laboratories [47]. However, the main shortcomings of the markers include the necessity of a substantial amount of high-quality DNA, costly radioactive probes with prior sequence knowledge for their development, and the requirement for long and tedious Southern blotting techniques [10]. RFLPs have been used widely in genome mapping to select desirable genes, analyze polygenic characters, and determine genetic relationships and diversity between crop plants [48,49]. Chang [50] applied RFLP markers to design a linkage map for the nuclear genome of *Arabidopsis thaliana*, associating it with clones of the unknown gene function exhibiting the mutant phenotype and vice versa. Benchimol [51] demonstrated the effectiveness of RFLPs in assessing genetic diversity and allocating the genotypes from tropical maize populations into heterotic groups. However, they could not determine the line crosses from genetically diverse heterotic groups. The markers also proved to be efficient in revealing the differences among wild wheat relatives from regions separated by natural barriers [52]. The RFLP method has also been employed to construct genome maps for tomatoes, potatoes, and chili peppers [53,54].

3.1.3. Amplified Fragment Length Polymorphism (AFLP)

The AFLP markers developed by Vos [55] have been used widely for genetic diversity studies of closely related plant species. Applying the markers does not require an introductory sequence, making them a powerful tool for detecting polymorphisms at the DNA level [56]. AFLPs have shown higher reproducibility and sensitivity than RAPD and RFLP markers [24]. They have emerged as the markers of preference for several investigations due to the non-necessity of previous sequence information, greater abundance, and genome-wide, high polymorphism flexibility when used for molecular assays, with the potential for automation [57]. Al-Nadabi [58] identified six distinct citrus cultivars out of thirty-three by employing an AFLP fingerprint, providing phylogenetic information on citrus cultivars and their diversity in Oman. AFLPs revealed high genetic diversity between 26 different populations of *Eupatorium adenophorum* from China, suggesting the plant diversification rate was dependent on the invasion time and the geographical location [59]. Murariu [60] employed AFLP markers to assess wide genetic diversity in 60 maize landrace accessions from Romania, offering the potential for incorporation into

the breeding programs. Bhattacharrya [61] highlighted the utility of AFLP markers in estimating diversity for effective conservation strategies, as demonstrated in *Dendrobium thyrsiflorum*, which exhibited high antioxidant activity without prior genetic information on linkage maps and QTL. AFLP markers provided efficient information on genome coverage, genetic variation, and phylogenetic relationships in the *Origanum* and *Thymus* species [62].

Furthermore, their application yielded insights into eco-geographic factors and genetic differentiation patterns influencing the variation and population structure of *Elymus tangutorum* in Western China [63]. AFLP markers were also instrumental in the genetic restoration and conservation efforts for *Panicum turgidum* in Saudi Arabia [64], identifying the optimal niche for *Rhodiola rosea* at an altitude of 3150–3250 m [65] and facilitating effective germplasm conservation of *Rhododendron concinnum* [66]. Despite numerous advantages, AFLP markers have limitations, including challenges in interpreting banding profiles, their dominant nature, and the potential occurrence of co-migrating bands during homology identification [67].

3.1.4. CAAT Box-Derived Polymorphism (CBDP)

CBDPs utilize the nucleotide sequence of the CAAT box of plant promoters, characterized by a consensus GGCCAATCT sequence, and play a vital role in transcription [68]. The marker is valuable for cultivar identification, distinguishing indigenous from introduced varieties, marker-assisted selection, and construction of linkage maps [69]. Moreover, CBDPs are easy to develop and provide reproducible profiles. The marker can be applied singly or combined with other markers to accurately determine population structure and specify the genetic relationships among plant species [70,71]. The efficiency of the markers was demonstrated in analyzing the genetic diversity of wheat and lentil germplasms [72,73]. CBDP markers also exhibited tremendous potential for the effective genetic diversity evaluation of the *Salvia* species, which is necessary for crop improvement programs involving hybridization and QTL mapping [74]. They unveiled a high level of genetic variation in Iranian Aegilops, providing vital information for potential valuable genes for wheat breeding programs [75]. However, these markers are also associated with limitations, as the reproducibility of the assay depends on the DNA sample quality and the PCR conditions used [68]. Additionally, the transferability of CBDP markers across species can be limited [74]. Furthermore, the CBDP markers have relatively low discriminatory power, making them less suitable for complex genetic relationship studies in some plant species [72].

3.1.5. Sequence-Related Amplified Polymorphism (SRAP)

SRAP markers are a valuable tool in molecular genetics research, amplifying coding regions of DNA using primers that target open reading frames [76]. These markers have demonstrated high variability and robustness, comparable to the commonly used AFLP markers, with the added benefit of being less technically demanding [77]. A significant advantage of using an SRAP marker is that one SRAP primer can combine with an unlimited number of other primers [78]. SRAP markers have primarily been used in agronomic and horticultural research, including developing quantitative trait loci in advanced hybrids and assessing genetic diversity in extensive germplasm collections [79]. Additionally, they were utilized to better understand the genetic diversity, molecular characteristics, and population structure of prairie grass (*Bromus catharticus*) and Bermuda grass (*Cynodon dactylon*) [80,81]. The investigation of gene flow between populations using SRAP markers provided valuable insights into the conservation and breeding efforts of Simao pine and *Coloneaster shantungensis* [82,83].

Furthermore, the high discriminatory power and ability to amplify gene-rich regions of the genome have made SRAP markers a promising tool for genetic mapping studies aimed at marker-assisted introgression in sugarcane [84]. They have also been applied in *Morus macroura* genetic differentiation studies, where primer E was found to distinguish between male and female PCR bands [85]. Although SRAP markers have been predominantly used

in the investigation of plant genetic diversity, their applications in taxonomic studies could be influenced by anthropogenic or different types of selection pressures [77].

3.1.6. Start Codon-Targeted Polymorphism (SCoT)

SCoT markers are based on short, conserved regions flanking the ATG start codon in plant genes [86]. They are more reproducible and effective than arbitrary RAPD and ISSR markers in assessing the diversity and population structures of many plant varieties [19]. In the bottle gourd germplasm, 20 SCoT markers produced 161 amplicons and generated 82.61% polymorphisms, demonstrating the efficacy of SCoT markers in identifying and characterizing genetic diversity [87]. They have been applied to identify and analyze the genetic diversity of mango cultivars, enhancing breeding strategies and facilitating germplasm management [88]. Furthermore, they were utilized to identify inter-varietal distinctions among eight cereal grass varieties [89]. SCoT markers have also been instrumental in investigating the genetic foundation of *Elymus sibiricus* and *Boehmeria nivea*, which are cross-pollinated heterozygous species [90,91]. The markers were also deployed to differentiate selected Glycine max cultivars and to study rose genotypes' genetic backgrounds [92,93]. The detection of induced allelic variations within *Fusarium* yellow tolerant/resistant lines of ginger was also performed using SCoT markers [94]. SCoT markers are rarely used directly for species identification, though they have been prominently employed for genetic diversity and population structure studies of several plants [95].

3.1.7. Cleaved Amplified Polymorphism Sequence (CAPS)

The CAPS, also known as PCR-restriction fragment length polymorphism (PCR-RFLP) markers, are designed by first performing the PCR amplification of DNA fragments generated via restriction enzyme digestion using specific primers, and the resulting products are separated using an agarose gel [96]. They present several advantages, including the co-dominance of alleles, the ability to utilize a small amount of template DNA, locus specificity, and high reproducibility. Unlike RFLP markers, CAPS markers eliminate the need for technically demanding procedures such as Southern blot hybridization and radioactive detection [97]. However, the size of amplified fragments and the need for sequence data for designing the marker are significant shortcomings of the marker [98].

CAPS markers are primarily applied in gene mapping investigations [97] and serve as a valuable tool for detecting SNPs within watermelon genomes [99] and for the identification of distinct Glycyrrhiza glabra genotypes [100]. These markers have been harnessed to differentiate fiber quality in two cultivated cotton varieties, *Gossypium hirsutum* and *G. barbadense*. This distinction facilitates marker-assisted selection initiatives, aiding in incorporating phytochrome and/or HY5 genes between these species [99]. CAPS markers have also been used for genetic diversity and population structure analyses and to manage emerging button mushroom genetic resources [101].

3.1.8. Inter-Primer Binding Site (iPBS)

The iPBS marker system has emerged as a robust DNA fingerprinting technique that operates effectively without requiring sequence information. This system has become the favored universal marker for discerning genetic distinctions within and between various eukaryotic organisms, spanning both intra-specific and inter-specific levels [102,103]. iPBS was described by Kalendar [104] as a universal DNA labeling method used in plants based on the primer binding site for the reverse transcription enzyme of the LTR retrotransposon. This marker system has been successfully applied for genetic diversity investigations related to breeding and conserving rare and economic plants like *Allium ledebourianum*, *Juglans regia*, and cotton germplasm [105–107]. Similarly, iPBS markers have identified an extensive diversity of scarlet eggplant, forming the genetic base resource of a specific breeding program in African indigenous vegetables [108]. The first-ever safflower (*Carthamus tinctorius*) plant-breeding parents were successfully determined using iPBS markers [109]. These markers exhibit genome-inherent plasticity, enabling them to uncover

variations within Turkish okra germplasm [110] effectively. Furthermore, iPBS markers have been employed to distinguish well-defined genetic relationships among various tree peony germplasm, accurately classifying the varieties [111]. The markers have also been utilized for the DNA fingerprinting of natural hybrids that share morphological similarities with their parents, determination of phylogenies, and taxonomic discrimination in species belonging to Fagaceae [112].

3.1.9. Simple Sequence Repeats (SSRs)

SSRs, also known as microsatellites, are DNA markers based on short tandem repeated motifs, the number of which varies at a specific locus [113]. SSR markers offer several advantages over other marker systems. Firstly, they are highly reproducible, making them valuable for genetic analysis. Additionally, ultra-pure DNA templates are not required for their use. Secondly, SSR markers are highly polymorphic, allowing for the detection of allelic variations even among closely related varieties [10]. Thirdly, SSR polymorphisms are co-dominant, allowing for the easy interpretation of results. Finally, SSR markers are abundant and well-distributed throughout eukaryotic genomes [114]. They have been successfully used in various genetic applications, such as evaluating the genetic diversity and relationships among *Chrysanthemum morifolium* cultivars [115], mutation detection in pineapple [116], cultivar and germplasm selection and differentiation, genetic improvements, population structure determination and marker-assisted selection breeding of new varieties [117,118]. SSR markers have also been applied for the genotype identification of Tunisian citrus species [119], linkage mapping for *Curculigo latifolia*, *Chrysanthemum indicum*, and *Capsicum frutescens* [120–123], and genetic diversity evaluation of *Lathyrus species* and *Lactuca indica* [124,125]. Bhardwaj et al. [126] analyzed the genetic diversity of 353 *Solanum tuberosum* accessions using 25 SSR markers and found a high level of allelic polymorphisms among the accessions. However, SSR marker development is complex and costly, requiring sequence information to design primer sets for a specific species. Alternative approaches, such as next-generation sequencing, EST libraries, and enriched genome library searches, have been designed to substantially increase the production of SSR loci [127].

3.1.10. Inter-Retrotransposon Amplified Polymorphism (IRAP)

IRAP markers are retrotransposon-based markers that identify the insertion sequence between two retrotransposons with outward-facing long terminal repeats (LTRs) [128]. Retrotransposons are abundant in plant genomes and occur irreversibly in high copy numbers, making them particularly useful for phylogenetic and gene mapping studies [129]. IRAP markers were applied to determine the genetic diversity of 29 citrus genotypes and confirm Pommelo and Mandarin as true citrus species [130]. Additionally, they have been widely used to differentiate among hybrids and assess inter-species variations in different plants [131]. The first species-specific LTR retrotransposons cloned from five rare relic species of drugs plants, namely *Adenophora lilifolia*, *Adonis sibirica*, *Adonis vernalis*, *Digitalis grandiflora*, and *Paeonia anomala*, revealed the genetic diversity among the six populations of *A. vernalis* [132].

Many variations of retrotransposon-based markers are in existence, which include the sequence-specific amplified polymorphism (S-SAP), retrotransposon-microsatellite amplified polymorphism (REMAP), and retrotransposon-based insertional polymorphism (RBIP). S-SAP constitutes a multiplex marker system explicitly designed to detect variations in DNA flanking retrotransposon insertion sites [133]. In contrast, REMAP employs a single primer system grounded in the LTR target sequence and a simple sequence repeat motif to amplify regions exhibiting polymorphisms [128]. RBIP, on the other hand, operates as a co-dominant marker system utilizing PCR primers designed from the retrotransposon and flanking DNA to examine the insertional polymorphisms related to individual retrotransposons [134]. The primary historical limitation associated with retrotransposon-based marker systems has been the necessity for sequence data [129].

3.1.11. Conserved DNA-Derived Polymorphism (CDDP)

CDDP markers have been derived from extensively characterized plant genes responsive to biotic and abiotic stresses and developmental processes [135]. This approach results in the creation of functional markers that are directly associated with particular plant phenotypes. The markers produced detectable length polymorphisms with conserved DNA regions that share the same priming site but differ in genomic distribution [136]. Investigations of plants employing CDDP markers have revealed that genetic diversity is influenced by geographical distances and the level of gene exchange among groups and sexes of plants under different environmental conditions [137]. These markers have been successfully applied in evaluating genetic diversity in various plant species, aiding in genetic rescue, in situ and ex situ conservation efforts, and cultivar identification [67,138]. CDDP markers have many advantages, including convenience, lower cost, and rich polymorphisms, which can be utilized to produce targeted trait markers [24].

3.1.12. Diversity Array Technique (DArT)

The DArT was developed as a sequence-independent, hybridization-based marker performed on a microarray platform to capture the allelic diversity inherent to the target organism [139]. They offer the advantage of concurrently assessing numerous polymorphisms based on restriction sites across genotypes without necessitating the availability of DNA sequence information or site-specific oligonucleotides [140]. The polymorphism observed through DArT markers primarily arises from validated restriction site variations, a characteristic substantiated through investigations involving the model plant *Arabidopsis thaliana* [140].

They have become promising markers in genomic discovery, comparative mapping, directed breeding of superior oat varieties, and generating consensus maps of rye and oat [141]. Sánchez-Sevilla [142] showed that a comprehensive set of 603 DArT markers was highly efficient for classifying 62 strawberry cultivars based on historical, geographical, and pedigree-based cues. DArT markers have also demonstrated robustness among different mapping plant populations, allowing for map alignment [143]. In addition, they have proven highly efficient and cost-effective for genetic mapping in apples, providing moderate genome coverage [144]. DArT markers also have the potential to provide comprehensive genetic diversity analysis, whole-genome profiling, and high-density mapping of complex traits essential for marker-assisted breeding. Consequently, molecular analyses using DArT markers have significantly improved various crop species [145].

However, applying DArT markers in plant research poses significant technical challenges, characterized by intricate and time-consuming procedures requiring trained personnel. Moreover, this microarray-based technique demands substantial investments in physical energy, costs, and access to advanced laboratory facilities. These factors collectively constrain the widespread utilization of DArT markers in plant diversity studies [10].

3.1.13. Internal Transcribed Spacer (ITS)

ITS markers are indispensable for accurate species identification and play a pivotal role in DNA barcoding, focusing on the spacer DNA located within repetitive ribosomal RNA gene sequences [146]. The nuclear ribosomal DNA ITS region exhibits significant divergence across species while maintaining a higher level of conservation within a specific species, making them the preferred genetic markers for species-level identification [147]. Eukaryotic ITS regions possess several advantageous attributes, including their compact size, highly conserved flanking sequences, and ease of detection, even when working with limited DNA quantities due to the abundance of rRNA gene clusters [148].

Furthermore, they exhibit substantial variation, even among closely related species, and undergo rapid concerted evolution driven by unequal crossing over and gene conversion [149]. ITS1 has been successfully used to distinguish medicinal herbs, such as *Amomum villosum* (*Zingiberaceae*), and to differentiate *Boerhavia diffusa* (*Punarnava*) from *Boerhavia erecta* [150,151]. ITS1 has also been exploited for the reliable authentication of medicinal

plants, detecting adulterants and substitutes of *Gmelina arborea* (Gambhari) [152]. Combining the ITS rDNA marker and cytogenetic analysis has helped resolve many taxonomic riddles, including citrus species and subspecies [153]. The main concern with this marker is its weak discrimination power for lower taxa and lack of species resolution, so carefully selecting the ITS marker is of utmost importance to avoid negative results [154].

3.1.14. Directed Amplification of Minisatellite DNA (DAMD)

DAMD markers were elucidated by Heath [155] and have found varied applications in plant diversity research in *Cucumis sativus* [156], *Capsicum* [157], and more recently, in citrus [158] and *Musa cavendishii* [159]. Numerous DAMD primers have been successfully harnessed to assess genetic diversity among distinct plant genotypes, as evidenced by the works of Ince and Karaca [160], Jain [161], and Saleh [162]. The DAMD markers have the advantages of not requiring prior sequence information, inheriting through Mendelian fashion, and behaving as dominant markers, although they may have limitations in reproducibility and the non-homology of generated fragments [155].

A concise overview, including examples, of applying a single marker system in genetic diversity studies of some plant species is illustrated in Table 1.

3.2. Utilization of Combined Molecular Markers

Using a single marker system in plant genetic diversity studies has limitations, necessitating the adoption of a multi-marker approach [19]. These arise because the conclusions drawn from analyzing a specific marker type can be effectively supported and validated by the findings derived from another marker. The simultaneous use of multiple markers can yield more precise outcomes with enhanced reliability and accuracy, thereby aiding in developing effective plant conservation strategies and improving crop varieties [6].

3.2.1. Cumulative Applications of Dominant Markers

Goswami [163] utilized RAPD and SCoT markers to investigate genetic variation in *Lasiurus sindicus*, revealing high percentages of polymorphic bands from both markers. The study emphasized substantial within-population genetic variation (90%) compared to among-population variation (10%) and provided valuable insights into the plant's genetic diversity and potential for conservation and enhancement. Hromadova [164] assessed the effectiveness of 10 RAPD and 10 SCoT markers in detecting genetic diversity among 33 common bean genotypes. The SCoT markers (MI = 7.474, DI = 2.265) proved more effective than the RAPD ones (MI = 5.323, DDI = 1.612) with higher diversity detection index (DDI) and marker index (MI) values. Dendrograms and PCoA plots from both markers confirmed the distinct separation of bean genotypes, with the SCoT markers outperforming the RAPD markers in detecting genetic diversity.

Mansoory [165] employed ISSR and SCoT markers to evaluate the genetic diversity of 57 Diospyros genotypes from Iran. A cluster analysis grouped the genotypes into four clusters, with *D. kaki* in groups one and two, *D. lotus* in group three, and *D. virginiana* in group four. Combining both markers enhanced genotype separation, indicating Iran's rich Diospyros germplasm and the utility of multiple markers for accurate diversity assessment. Alzahrani [166] examined genetic divergence in sixteen *Medicago sativa* (Alfalfa) cultivars (twelve from Saudi Arabia and four from Egypt) using ISSR and SCoT markers. ISSR generated 163 bands (60% polymorphism), while SCoT produced 150 bands (77% polymorphism), with the cultivars clustering into two populations in the dendrogram, aiding alfalfa breeding for drought tolerance and high yield. SCoT and IRAP markers have also proven helpful for assessing inter- and intra-specific genetic diversity in Diospyros germplasms for genotype identification and the adoption of effective conservation efforts [167]. Bhattacharyya [168] deployed ISSR and DAMD markers cumulatively to accurately assess the genetic relationships among distinct *Dendrobium nobile* germplasms. Khodaee [169] studied the genetic diversity of 48 *Aegilops triuncialis* accessions in Iran using SCoT, CBDP, and ISSR markers. A total of 359 DNA fragments were generated, with ISSR showing the highest

diversity (PIC = 0.3, MI, Rp) among the multiple markers applied. Genetic diversity was greater in the Alborz population, with the UPGMA classification of accessions aligned with the geographical distribution. Combined markers offer more significant insights for future wheat breeding programs.

Arya [170] explored the genetic diversity of 20 *Morinda tomentosa* genotypes using 131 SCoT, 97 RAPD, and 70 ISSR markers. The SCoT markers exhibited the highest polymorphism (70.23%), Nei's gene diversity (0.20), and geographic clustering, followed by ISSR and RAPD. The efficacy of SCoT and ISSR markers for genetic diversity analysis and geographic patterning of *M. tomentosa* was emphasized, enabling potential strategies for conservation and collection across regions and globally. EL-Mansy [171] also investigated the divergence aspects of six tomato lines (G1, G2, G3, G4, G5, and G6) using RAPD, ISSR, and SCoT markers. The marker analysis highlighted ISSR primers 49A, HB-14, 49A, 49B, and 89B as the most informative, with ISSR providing the highest unique specific markers (six), followed by RAPD (four) and SCoT (three). The cluster analysis showed the grouping of G1, G2, and G3 together and separated other lines. Apana [6] conducted an investigation into the genetic diversity and population structure of *Clerodendrum serratum* utilizing diverse molecular markers, including CBDP, iPBS, ISSR, and SCoT. The findings revealed that SCoT markers exhibited more efficacy in detecting polymorphisms and distinguishing genotypes than the remaining markers in the study. The multiple marker analysis revealed moderate gene flow and low genetic differentiation among the populations, with no significant correlation between the geographic and genetic distances. Three genetic clusters were determined using individual markers, while five genetic groups with high admixture were observed using pooled marker data, aiding in the conservation and management of *C. serratum*. The combined use of 15 ISSR, 11 SCoT, and 10 iPBS primers by Amom [4] in the genetic diversity and population structure study of endemic *Dendrocalamus manipureanus* showed significant genetic differentiation among the populations due to low gene flow, as indicated by the G_{ST} (0.684) and Nm (0.230) values. The BARRIER analysis identified nine genetic barriers, suggesting hindrances to gene flow. The findings from the cumulative analyses hold significant implications for effectively managing and enhancing the genetic characteristics of indigenous bamboo.

Tahir [20] applied ISSR, CDDP, and SCoT markers to explore genetic diversity in 59 barley accessions, generating 391 bands (255 ISSR, 35 CDDP, and 101 SCoT). SCoT displayed superior allelic diversity assessment with gene diversity averages at 0.77 (ISSR), 0.67 (CDDP), and 0.81 (SCoT), and the PIC recorded at 0.74 (ISSR), 0.63 (CDDP), and 0.80 (SCoT). Barley was grouped into two main clusters, with 15%, 9%, and 14% variability among the populations. Tiwari [172] utilized two sets of markers for the analysis of genetic diversity in 39 *Andrographis paniculata* specimens. They employed gene-targeted markers, specifically twenty-two SCoT and nineteen CBDP primers, alongside arbitrary amplified markers comprising eighteen RAPD and five ISSR primers. Notably, gene-targeted markers yielded more amplified amplicons, with 132 and 97 for SCoT and CBDP, respectively, compared to 124 and 32 for the RAPD and ISSR markers. Furthermore, it was observed that the polymorphic information content (PIC) values ranged from 0.09 to 0.48, with an average value of 0.34 and 0.41 per primer for the SCoT and CBDP markers, respectively. The resolving power ranged from 2.36 to 10.54, averaging 1.39 to 13.15 per primer for the SCoT and CBDP markers, respectively. Both the PIC and resolving power exhibited high values in the gene-targeted markers, whereas for the RAPD and ISSR markers, the PIC values extended from 0.32 to 0.45, and the resolving power ranged from 2.13 to 10.03. These findings underscore the clear applicability and reliability of gene-targeted markers for assessing genetic diversity in *A. paniculata*.

Table 1. Plant genetic diversity studies using a single marker system.

	Molecular Markers	Applications	Plants Investigated	References
AFLP	Amplified fragment length polymorphism: uses restriction enzymes and primers specific to genomic DNA to amplify DNA fragments of different sizes.	Detects genetic variation within and among populations, linkage mapping, discrimination of cultivars, and association analyses.	*Tectona grandis*; *Brassica oleracea*; *Glehnia littoralis*; *Solanum tuberosum*; *Daucus carota*	[173–177]
ISSR	Inter-simple sequence repeat: uses primers specific to inter-microsatellite regions to amplify DNA fragments of different sizes.	Evaluates genetic variation within and among populations, linkage mapping, and association analyses.	*Lepidium sativum*; *Balanites aegyptiaca*; *Prunus armeniaca*; *Vigra unguiculata*; *Camellia yuhsienensis*; *Clitaria ternatea*	[178–183]
RAPD	Random amplified polymorphic DNA: uses arbitrary primers to amplify DNA fragments of different sizes.	Detects genetic variation within and among populations and genetic similarity.	*Carica papaya*; *Coffee canephora*; *Allium sativum*; *Dendrobium species*; *Nigella sativa*	[184–188]
SSR	Simple sequence repeat: uses primers specific to microsatellite regions to amplify DNA fragments of different sizes.	Ascertains genetic variation within and among populations, linkage mapping, association analyses, and plant breeding.	*Solanum tuberosum*; *Cajanus cajan*; *Vicia amoena*; *Allium sativum*; *Curcuma longa*	[119,126,189–191]
RFLP	Restriction fragment length polymorphism: uses restriction enzymes to cut DNA at specific sites, and the resulting fragments are separated via gel electrophoresis.	Detects genetic variation within and among populations and DNA fingerprinting.	*Oryza sativa*; *Fragaria* x *Ananassa*; *Brassica juncea*	[192–194]
DArT	Diversity array technology: a high-throughput marker technology that uses a combination of restriction enzymes and a microarray platform.	Determines genetic variation within and among populations and marker-assisted selection.	*Lesquerella species*; *Glycine max*; *Vigna unguiculata*; *Camellia sinensis*	[195–198]
SCAR	Sequence-characterized amplified region: uses primers specific to a known DNA sequence to amplify a fragment of a specific size.	Detects specific genes or alleles in a population and marker-assisted selection.	*Calanthe species*; *Poa pratensis*; *Dendrobium officinale*; *Musa species*; *Moringa oleifera*	[199–203]
CAPS	Cleaved amplified polymorphic sequence: uses restriction enzymes and primers specific to a known DNA sequence to amplify a fragment of a specific size.	Detects specific genes or alleles in a population, identification of cultivars, and marker-assisted selection.	*Glycyrrhiza species*; *Lathyrus sativum*; *Citrullus lanatus*; *Zingiber officinale*; *Capsicum annum*	[100,204–207]
IRAP	Inter retrotransposon amplified polymorphism: uses primers specific to transposable elements to amplify DNA fragments of different sizes.	Evaluates genetic variation within and among populations.	*Sorghum bicolor*; *Piper nigrum*; *Hordeum vulgare*; *Pinus sylvestris*; *Sakura species*	[208–212]
CDDP	Conserved DNA-derived polymorphism: uses a single primer constructed with a conserved area of functional genes.	Ascertains genetic variation within and among populations.	*Salix taishanensis*; *Pistacia vera*; *Musa species*; *Arachis hypogaea*; *Amomum tsao-kosaleh*	[138,213–216]

Table 1. *Cont.*

	Molecular Markers	Applications	Plants Investigated	References
DAMD	Directed amplification of minisatellite-region DNA: uses a single primer specific to inter-microsatellite regions.	Assesses genetic variation within and among populations.	*Capsicum*; *Origanum syriacum*; *Salvia officinalis*; *Ficus sycomorus*	[157,217–219]
SRAP	Sequence-related amplified polymorphism: uses arbitrary forward and reverse primer combinations targeting ORFs to amplify a coding region.	Detects genetic variation within and among populations, mapping and tagging genes, germplasm identification, and sex determination.	*Cuminum cyminum*; *Pinus yunnanensis*; *Lavandula angustifolia*; *Aspergillus flavus*; *Zea mays*	[220–224]
SCoT	Start codon-targeted polymorphism: uses a short-conserved region flanking the start codon, producing highly reproducible amplification of targeted DNA fragments of different sizes.	Detects genetic variation within and among populations, determines population structures, identifies cultivars, QTL mapping, and DNA fingerprinting.	*Ardisia crenata*; *Avena nuda*; *Scutellaria baicalensis*; *Trigonella species*; *Triticum aestivum*; *Crataegus monogyna*	[225–230]
ITS2	Internal transcribed spacer 2: a segment of the internal transcribed spacer (ITS) region, utilized as an alternative for species differentiation, involves the spacer DNA located within the tandem repeats separating the small and large subunits of ribosomal RNA (rRNA). ITS primers are designed to amplify the gene sequence containing the fastest-evolving region of the rRNA gene, resulting in fragments of varying sizes for differentiating species.	Evaluates genetic variation within and among populations, intraspecific variation, species identification, authentication of plant variety, and detection of adulterants.	*Dendrobium species*; *Physalis species*; *Astragalus species*;	[231–233]
iPBS	Inter-primer binding site: uses the primer binding site for the reverse transcription enzyme of the LTR retrotransposon. No prior sequence information to amplify DNA fragments of different sizes, a preferred universal marker system.	Detects genetic differentiation at both the intra-specific and inter-specific levels, marker-assisted selection, and breeding.	*Abelmoschus esculentus*; *Alfalfa*; *Phaseolus vulgaris*; *Triticum species*; *Brassica species*; *Castanea sativa*	[234–239]
CBDP	CAAT-box derived polymorphism: Uses the CAAT box consensus sequence of the plant promoter upstream of the start codon to amplify DNA fragments of different sizes.	Detects genetic diversity among and within species/populations, cultivar identification, linkage map construction, and marker-assisted selection.	*Triticum durum*; *Salvia species*; *Lens culinaris*	[73,74,240]
STS	Sequence-tagged site: Short DNA sequences of known locations that are easily detectable using PCR and serve as landmarks in the physical map of the genome.	Variation analysis, gene expression, genome mapping, and gene silencing.	*Cenchrus species*; *Triticum aestivum*; *Oryza sativa*; *Agropyron cristatum*; *Secale cereale*; *Thinopyrum intermedium*	[241–246]

Amom [19] applied four markers (RAPD, ISSR, iPBS, and SCoT) to analyze 50 genotypes of native bamboo in North-East India. Forty primers of four marker systems generated varying polymorphic bands, with SCoT being the most informative and discriminatory. The Mantel test revealed a highly positive correlation between the markers, ranging from 0.60 (SCoT and RAPD) to 0.83 (iPBS and ISSR), indicating their effectiveness. The genetic clustering of bamboo genotypes is based on DNA markers aligned with their geographical origins. The multiple markers analysis produced precise genetic relationship determination among the native bamboo. Gene-targeted markers like SCoT and CBDP, used in conjunction with other molecular markers such as DAMD, CDDP, and IRAPs, have significantly contributed to the analysis of genetic relationships, gene mapping, conservation, breeding, and conservation of many medicinal and food crops [247,248].

3.2.2. Cumulative Application of Dominant and Co-Dominant Markers

Using both dominant and co-dominant markers in plant genetic diversity studies offers several advantages, as these markers provide good genome coverage and more accurate genetic data [249]. Additionally, they compensate for each other's limitations. The studies conducted on Maize [250], *Shorea curtisii* [251], and *Stenotaphrum secundatum* [252] using AFLP and SSR markers facilitated the identification of quantitative trait loci (QTL) on specific chromosome regions. Applying AFLP and SSR markers has also been instrumental in explaining the high phenotypic variance observed between rice varieties [253]. Basu [254] assessed genetic diversity in jute cultivars (*Corchorus olitorius* and *C. capsularis*) using SSR and AFLP markers. The study revealed high variation between the two jute species, indicating distant maternal and possible different origins. However, some prominent Indian cultivars were closely related to wild accessions with unique genotypes from India and Kenyan accessions.

The genetic relatedness of 82 walnut genotypes from the Himalayan region was examined using 13 SSR and 20 RAPD primers [255]. High genetic diversity was evident within populations, with SSR primers displaying one to five alleles per locus and RAPD primers showing two to six alleles. Polymorphic loci were at 100%, and the average similarity was 49% (12% to 79%). The dendrogram analysis using these two markers revealed four subclusters, significantly affecting walnut breeding and conservation strategies. Zargar [256] employed 15 RAPD and 23 SSR markers to assess diversity among 51 common bean genotypes exhibiting high polymorphism, generating 171 polymorphic RAPD and 268 SSR bands. SSRs demonstrated a greater PIC value (0.300) and resolving power (5.241) than RAPDs, while RAPDs had a higher marker index (2.69). Hierarchical clustering accurately grouped genotypes based on cultivation area, and STRUCTURE analysis revealed three subpopulations aligned with distance-based groupings, indicating significant genetic diversity. Dar [257] explored genetic diversity among 47 sesame accessions using 22 RAPD and 18 SSR primers, with RAPD primers yielding 191 polymorphic bands while SSR primers produced only polymorphic fragments. SSRs exhibited higher polymorphic information content (0.194), while RAPDs showed a greater marker index (1.426) and resolving power (4.012). The genetic information derived from the cumulative application of markers emphasized their potential applications in DNA fingerprinting, germplasm conservation, and crop enhancement for *Sesamum indicum*.

Nascimento [258] observed high polymorphisms (95% for SSR and 75.8% for ISSR) while assessing the genetic diversity of 53 *Dioscorea trifida* accessions using eight SSR and sixteen ISSR markers. The dendrogram analysis of both markers showed the accessions clustering into three main groups, with the Bayesian and principal coordinate analyses supporting the grouping. While high variation was observed within groups (66.5% for SSR and 60.6% for SSR), the genetic and geographic distances showed slight correlations ($r = 0.08$, $p = 0.0007$ for SSR; $r = 0.16$, $p = 0.0002$ for ISSR). Hammami [259] demonstrated significant differences among populations (67%) but lower variation within populations (24%) in wild Brachypodium using SSR and ISSR markers. SSR and ISSR analyses revealed higher polymorphic fragments in *B. hybridum* than in *B. distachyon* with species-specific

clustering. The principal component analysis linked genetic traits, climate, and geography, separating the two species. Ramzan [260] investigated the genetic diversity in twenty-one Tamarix samples using ten ISSR and six SSR primers, with significant polymorphisms (88.5% for ISSR and 80.28% for SSR) and high mean PIC values of 0.34 (ISSR) and 0.35 (SSR). The genetic variability among ecotypes was high, with dissimilarity indexes ranging from 0.00 to 0.77, and the Kalurkot and Bhakkar specimens showed the highest dissimilarity. Nazir [261] showed that using SSR markers in a study on 63 buckwheat genotypes, including local variants from India's northwestern Himalayas, produced effective polymorphisms. ISSRs exhibited higher resolving power (4.38) than SSRs (1.42), while SSRs showed a greater average PIC value (0.43) than ISSRs (0.36). Geographical clustering using the two marker systems was accurate, and the STRUCTURE analysis unveiled substantial genetic diversity within the population, benefiting buckwheat breeding and conservation endeavors. Papaioannou [262] examined the genetic diversity of 27 garlic accessions using SSR and ISSR markers, revealing 26 distinct alleles for SSR and 84 for ISSR. SSR markers exhibited a higher redundancy level than ISSRs, potentially indicating duplicated accessions. An AMOVA highlighted that most molecular diversity originated from within-accession differences while clustering analyses using UPGMA, STRUCTURE, and PCoA based on SSRs showed consistent results.

The comparative analysis of gene diversity using dominant DArT and co-dominant SSR and SNP markers in *Lolium perenne* revealed that the DArT marker exhibited the highest consistency and reproducibility [263]. Additionally, genome SSR and CAPS markers were proven effective in identifying suitable candidates for breeding salt-tolerant rice (*Oryza sativa* L.) and locating high sodium transport-associated genes for mapping [264]. Shahnazari [265] employed SSR and CAPS-SSR markers to genetically fingerprint 13 sweet orange cultivars using SSR markers, which enabled hybrid prediction in orange cultivars, showing high diversity among sweet orange trees. The cultivars exhibited high genetic variability (with an average polymorphism of 98.46%), with Behshahr and Jadeh Ghadim 2 genotypes showing the highest and lowest genetic diversity values. Additionally, K-means clustering divided the cultivars into two main groups, while genetic similarity suggested potential cases of homonymy or synonymy. The applications of combined markers in the genetic diversity studies of different plants are briefly described in Table 2.

Table 2. Genetic diversity studies in plants using multiple marker systems.

Marker Combination	Marker Types	Number of Marker Systems	Plant Species	References
SCoT + ISSR	Dominant	Two	*Dendrobium crysotoxum* (SCoT = nine primers; ISSR = twenty primers; genetic diversity within population: ISSR = 86%; SCoT = 74% and between population: ISSR = 14%, SCoT = 26%) *Diospyros* species (ISSR = seven primers; SCoT = ten primers; average PIC: ISSR = 0.30, SCoT = 0.36; average marker index (MI): ISSR = 1.81; SCoT = 1.79) *Cucurbita pepo* (seven SCoT primers produced forty-nine polymorphic bands and six ISSR primers generated forty-two bands)	[33,165,266]
CBDP + SCoT	Dominant	Two	*Bauhinia racemose* (out of 25 CBDP primers, 21 produced 97 scorable bands, and for SCoT, 18 out of 36 primers produced 88 scorable bands) *Triticum aestivum, Aegilops cylindrical,* and *A. crassa* (CBDP = 15 primers; SCoT = 15 primers; PIC for SCoT: 0.31–0.39, CBDP: 0.28–0.36; cluster analysis: all samples were grouped based on their genomic constitution)	[267,268]
SCoT + ISSR + RAPD	Dominant	Three	*Kalanchoe* genotype (ScoT, ISSR, and RAPD = 10 primers each; polymorphism percentage: SCoT = 57%; ISSR = 15%, RAPD = 60.25%) *Lathyrus* species (SCoT = eight primers; ISSR = eight primers; RAPD = six primers; polymorphism: SCoT = 96%; ISSR = 96.81%; RAPD = 94.2%)	[269,270]
SSR + AFLP	Co-dominant and dominant	Two	*Jatropha curcas* (seven AFLP primer combinations produced seventy amplified polymorphic loci; thirty SSR primers were used, out of which seventeen were amplified in an appropriate size range) *Pyrus pyrifolia* (SSR; AFLP = 10 primers each; average PIC for SSR = 0.7585; polymorphism percentage for AFLP = 86.46%; genetic diversity: rich and highly representative)	[271,272]
ISSR + DAMD	Dominant	Two	*Rosa* species (ISSR = ten primers; DAMD = eight primers; genetic variation within population = 86%, between populations = 14%)	[273]
DArT + SNP	Dominant and co-dominant	Two	*Manihot esculenta* (DArT = 10,521 markers; SNP = 10,808 markers; average PIC for DArT = 0.36; SNP = 0.28) *Glycine max* (DArT = 16,116 markers; SNP = 19,505 markers; genetic variance: DArT = 98%; SNP = 97%)	[274,275]
DArT + SNP + SSR	Dominant and co-ominant	Three	*Lolium perenne* (DArT = 1384 markers; SNP = 182 markers; SSR = 48 markers; Genetic diversity: DArT = 0.26; SNP = 0.32; SSR = 0.45)	[263]

Table 2. *Cont.*

Marker Combination	Marker Types	Number of Marker Systems	Plant Species	References
SCAR + RAPD	Co-dominant and dominant	Two	*Nicotiana tabacum* (two out of eight SCAR markers; seven out of two hundred RAPD markers efficiently discriminated a large number of Tobacco cultivars)	[276]
CAPS + SSR	Co-dominant	Two	*Oryza sativa* (a set of twenty-eight genome-wide SSR markers; eleven salt-responsive genic SSR markers; eight salt QT-linked SSR markers; CAPS markers: OsHKT1; 5v395) *Citrus sinensis* (a total of five markers; average genetic polymorphism = 98.46%; CAPs-SSR indicated more genetic variability)	[264,265]
CAPS + SSR + SNP	Co-dominant	Three	*Citrullus lanatus* (CAPS = fifteen markers; SSR = six markers; SNP = two markers; mapping confirmation of BSA-seq: yellow skin)	[277]
SSR + ISSR	Co-dominant and dominant	Two	A total of 28 accessions of *Curcubita pepo* were compared utilizing ISSR markers, detecting 90 polymorphic bands. Additionally, SSR markers were proposed to further elucidate infra-specific relationships within *C. pepo*. *Gossypium herbaceum* (SSR = thirteen markers; ISSR = five markers; average coefficient similarity = 0.32; low correlation and high variation)	[278,279]
SCoT + DAMD	Dominant and co-dominant	Two	Mosses (the inaugural genetic diversity study of three moss species incorporated the utilization of SCoT and DAMD markers to enhance the discriminatory power and precision within the species)	[280]
CDDP+ ISSR	Dominant	Two	*Quercus infectoria* (ISSR = twelve primers; CDDP = nine primers; population variance within: ISSR = 92.97%; CDDP = 94.17%)	[281]
ISSR + SRAP	Dominant	Two	*Musa species* (ISSR = eight primers; SRAP = seven primers; polymorphic bands: ISSR = 81.6%; SRAP = 87.7%)	[282]
STS + CAPS	Co-dominant	Two	*Camelia sinensis* (STS = two primers; CAPS = thirty-seven primers; high genetic diversity between the two varieties: *C. sinensis* var. *sinensis* and *C. sinensis* var. *assamica*)	[283]
SCoT + IRAP	Dominant	Three	*Bletilla striata* (SCoT = twenty primers; IRAP = eight primers; polymorphic bands: SCoT = 96.17%; IRAP = 94%)	[284]

4. Drawbacks and Recent Developments in DNA Marker Technology

The applicability of DNA markers is enormous, but they are endowed with many drawbacks that limit their uses in plant research. One of the main disadvantages is the high cost of marker technology, which may require expensive equipment like PCR and DNA sequencers, commercial kits, reagents, etc. [285,286]. The high expenses may restrict access to this technology for a smaller group of researchers with limited funds [23]. Other weaknesses of molecular markers include longer time consumption, especially for large-scale investigations, and potential environmental effects on the results of molecular marker studies due to factors such as temperature, light, moisture, etc. [24]. Specific markers must be selected for certain investigations, as the choice of marker may influence the outcome of the study [287]. Hussain and Nisar [2] also emphasized the significance of selecting suitable markers for plant genetic diversity studies, as some may not work for other species. However, markers specifically designed for a particular species are not readily available and are difficult to establish, as the available reference genomes or markers influence the development of new markers [288]. Many markers cannot represent the entire genome, as they cannot provide complete coverage of the whole plant genome, resulting in an inaccurate evaluation of genetic diversity and relationships. Guo [289] highlighted the importance of combining molecular markers and other techniques to acquire a more comprehensive and accurate picture of genetic variation. Jagtap [290] also stressed the validation of the results of molecular marker analysis with other methods, as they are associated with a high false positive rate. Another drawback of molecular markers is the difficulty in interpreting and analyzing complex data. The interpretation of extensive molecular data requires experts with good knowledge of biology and population genetics [13]. Furthermore, managing and analyzing large datasets generated from high-throughput genotyping by sequencing platforms is a daunting task that involves advanced software and expertise. Using these markers requires technical personnel with specialized skills and knowledge in genetics and molecular biology [9].

Despite several limitations, molecular markers remain vital tools for understanding genetic diversity and the evolution of plant species for the last three decades. However, the necessity to develop more efficient and novel markers for assessing genetic variation, species identification, and molecular systematic studies is becoming increasingly apparent. The advancement of marker technology in recent times has partly addressed some limitations and challenges in using markers in plant research. One significant advancement was the emergence of SNPs, representing a third-generation molecular marker technology succeeding RFLPs and SSRs, among others. SNPs, which determine variation within a single nucleotide of DNA, can be easily detected with recent advancements in genomics [291]. Coined by Eric S. Lander in 1996, SNPs originated from sequence polymorphisms resulting from single nucleotide mutations at specific loci within DNA sequences [292] (Figure 3).

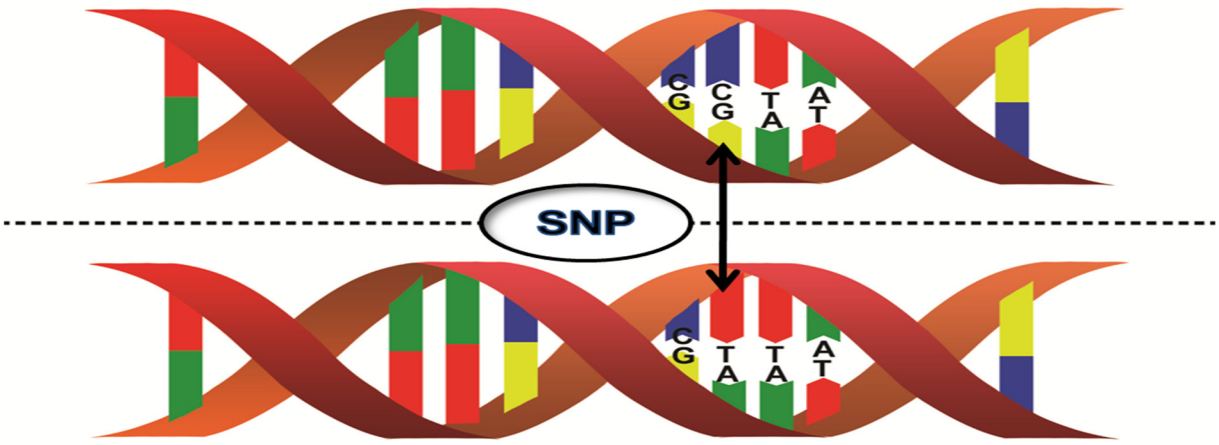

Figure 3. SNPs generated due to single nucleotide mutation (transition mutation).

SNPs have yielded profound insights into genetic diversity, facilitating the elucidation of relationships between distinct varieties and empowering cultivators to enhance crop yields and safeguard germplasm integrity [293]. Notably, SNP markers have effectively delineated *Gossypium hirsutum* from other *Gossypium* species and have further demarcated wild from cultivated *G. hirsutum* [294]. Similarly, they have facilitated discrimination within the notably diverse Ethiopian sorghum population [295]. Employing SNP sequences from nuclear and chloroplast gene regions has proven advantageous in diverse applications, including phylogenetic analysis, evolutionary studies, and inheritance determination [296]. Remarkable genetic diversity within maize inbred lines and heterotic groups has been revealed through SNP genotyping [296]. Furthermore, genome-wide SNPs within various *Camellia sinensis* varieties have been identified through genotyping-by-sequencing [297]. SNPs are preferred over conventional SSR markers as they are economical, reliable, effective, stable, and amenable to automation [298,299]. However, developing SNPs in plants is tough with the unavailability of many sequenced model plants and the possibility of duplication of complex genomes with rich repeat sequences [300].

The rapid progression of next-generation sequencing (NGS) technology, cost reduction, and the development of new bioinformatics pipelines have enabled the discovery of SNPs on a large scale in several plants [300]. Genotyping-by-sequencing (GBS) is a rapid, high-throughput, and affordable NGS-based approach for SNP identification in a combined one-step marker detection and genotyping process without requiring the reference genome [301,302]. A simplified representation of experimental steps involved in GBS technology is shown in Figure 4. SNPs generated through GBS application are extremely helpful for genetic diversity analysis, genome-wide association studies (GWAS), QTL mapping, genomic selection, and breeding improvement without known markers in several non-model plant species prevailing across the globe [303,304]. Tomar [305] used a total of 14,563 high-quality SNPs identified using GBS to genotype and illustrate the population structure and genetic variation within and between subgroups of 141 elite advanced breeding lines of spring wheat from CIMMYT (Mexico). The determination of low heterozygosity between advanced wheat breeding lines within subgroups and the moderate variation among subgroups revealed the possibility of applying the elite wheat breeding lines for further GWAS studies. Diaz [306] utilized the SNPs from GBS to analyze the genetic diversity and population structure of the *Acrocomia* genus, consisting of 172 samples from seven species. The study affirmed the classical taxonomy of the genus, showing specific groups and the genetic differentiation of *A. aculeata*, *A. totai*, *A. intumescens*, and *A. crispa*. Dang [307] also employed 92,719 high-quality SNPs originating from restriction-site-associated DNA sequencing (RADseq/GBS) technology to determine low genetic diversity (HO = 0.249 and HE = 0.208) and population differentiation in *Reaumuria trigyna*.

They also observed the positioning of 353 outlier SNPs in 243 gene coding sequences in the *R. trigyna* transcriptome with potential sites of diversifying selection in the genes related to secondary metabolite synthesis and hormone regulation. The SNPs identified through GBS proved to be highly efficient markers that have been applied for genetic diversity studies of several plants, such as *Cenchrus americanus* [308], maize [309], and *Ipomea batata* [310]. A systematic investigation of 128 maize inbred lines by Dube [311] using 11,450 SNP markers revealed significant genetic diversity ($p < 0.001$) in key phenotypic traits. The mean gene diversity (GD) and polymorphic information content (PIC) were 0.40 and 0.31, indicating substantial variation. The population structure analysis identified three subpopulations consistent with the phylogenetic analysis. These findings from SNP marker analysis highlighted considerable genetic diversity in maize inbred lines, providing a foundation for selecting lines with favorable alleles and suggesting potential applications of marker-assisted selection for key agronomic traits. Haung [312] proposed constructing a broccoli fingerprint using SNPs for cultivar identification, understanding global broccoli diversity, and providing insights for advancing breeding programs. They analyzed 161 broccoli cultivars using 10 selected pairs of SNP primers, generating 78 alleles.

The polymorphic information content (PIC) ranged from 0.64 to 0.90, revealing genetic similarities and distinctions between domestic and foreign cultivars.

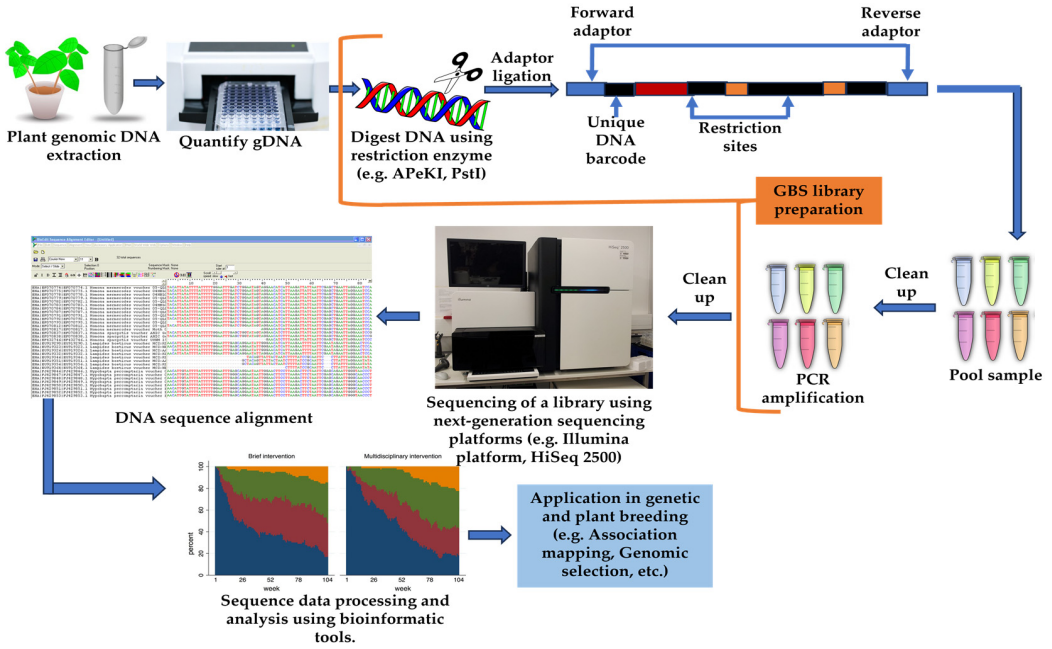

Figure 4. Schematic representation of the steps involved in GBS (genotype-by-sequencing) technology for plant research.

SNP microarrays are another high-throughput genotyping platform that relies on hybridization and fluorescence principles and can genotype thousands to millions of SNPs across the genome in a single experiment [313]. These microarrays are extensively used in plant genetic research due to their efficiency, accuracy, and ability to provide comprehensive insights into the genetic makeup of plant populations [313]. The SNP array is a specialized type of DNA microarray that includes carefully designed probes, each carrying information about specific SNP positions. In the hybridization process, these probes interact with fragmented DNA to determine the distinct alleles of all SNPs present on the array for a specific DNA sample [314]. The exhaustive scrutiny of SNP data yields insights into genetic variations and structural modifications within the genome, allowing for a meticulous characterization of genomic abnormalities [315]. Several SNP arrays have demonstrated successful applications in genotyping diploid plants. Notable examples include the Apple 480 K SNP array, the Maize 600 K SNP array, and the Rice 700 K SNP array [316]. Each array provided a comprehensive platform for genotyping, offering insights into the genetic variations within their respective plant species [317]. Creating and fine-tuning SNP arrays involves a significant investment of time and effort and a notable challenge in this process is the occurrence of ascertainment bias [318]. This bias often arises from non-random polymorphism sampling or limited SNP discovery panels [319]. Various strategies are employed to address and minimize such bias. High-coverage whole-genome sequencing is one approach that aims to provide a more comprehensive and unbiased representation of genetic variation [320]. Additionally, updates to SNP array markers are implemented to incorporate discoveries and enhance the accuracy of genotyping information. Another tactic involves the integration of markers from multiple arrays, offering a more inclusive perspective on genetic diversity [321].

The development of DNA barcode techniques also facilitates plant diversity research by correctly identifying plant samples in a repeatable and reliable manner and determining the consistency of species definition across plant lineages with a measure of genetic variability based on the DNA barcode sequence data [321]. The efficiency of DNA barcodes relies on combining the strengths of molecular genetics, sequencing technologies, and

bioinformatics [321]. Ribulose bisphosphate carboxylase large chain (rbcL) and maturase K (matK) genes are used as core DNA barcodes for seed plants, while the psbA-trnH intergenic spacer (psbA-trnH) and internal transcribed spacer (ITS) sequences are employed as supplementary DNA barcodes [322]. DNA barcode technology is utilized for accurate identification, genetic differentiation, and phylogenetic and species discrimination studies on several plants [323,324]. Enhancements in the field of epigenetics may also play a significant role in diversity study as epigenetic modification, like DNA methylation, can alter gene expression, influencing different adaptation responses of plants to environmental changes [17]. Massicote [325] mentioned the dependence of epigenetic processes on genetic variation. Wang [326] stated that epigenetic variation is the absolute downstream effect of genetic changes, while some considered it an independent phenomenon [327]. The assimilation of marker data with epigenetic information may potentially provide new insights into plant genetic diversity studies. The recent development of many improved bioinformatics tools also enabled the integration of molecular marker data with other sources of genetic information like genomic sequences, making it more efficient in plant genetic diversity analysis [328]. Advancements in molecular genetics, next-generation sequencing technologies, and bioinformatics have accelerated the development of more efficient and advanced molecular markers, which help address the challenges and limitations of using molecular markers in plant research.

5. Conclusions

Various molecular markers have been employed over the past three decades to study varied aspects of genetic diversity, including assessing the gene flow, population structure, and cluster analysis of several plants. The development of more advanced gene-targeted markers through rapid progression in molecular genetics has enabled the generation of high-resolution genetic data to make accurate decisions about appropriate conservation strategies for many important plants. Despite their many useful characteristics, the markers are also associated with several limitations that must be resolved. Developing efficient and cost-effective markers that can offer more precise and complete information on plant diversity level, population genetic structure, and cluster assignment is highly essential. The combination of multiple markers and genomic data generated through high throughput sequencing technologies will immensely help accelerate the understanding of plant genetic structure by providing a more comprehensive picture of diversity at the genome-wide level. With the continuously evolving technology, the prospect of molecular markers in the genetic analysis of plants is promising and bright, offering great potential in expanding our knowledge in properly preserving and utilizing increasingly depleting plant resources.

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