Central Asian Journal of Plant Science Innovation **1**(4): 192–200 (2021)

REVIEW PAPER

Application of molecular markers in plant sciences; An overview

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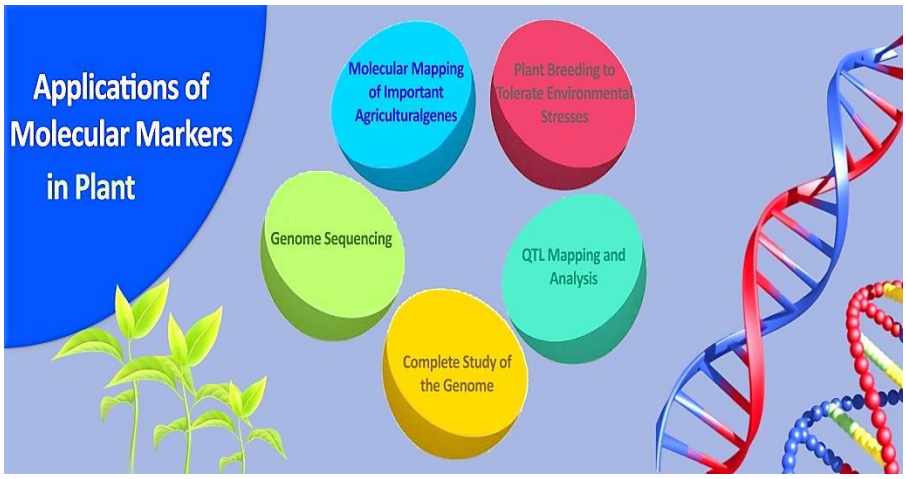
Highlights

- Recent advances in molecular biology have led to the use of DNA markers.
- Molecular markers are not affected by plant growth conditions and stages and do not change due to environmental conditions, and with greater accuracy, speed and sensitivity, they reveal a large number of distinct differences between genotypes at the DNA level.
- While DNA marker technology cannot replace plant breeding, it certainly increases the effort of breeders by providing new tools.

Graphical Abstract



Article Info

Receive Date: 10 November 2021
Revise Date: 15 December 2021
Accept Date: 20 December 2021
Available online: 25 December 2021

Keywords:
Marker-Assisted Selection (MAS)
Plant science
Phylogenetic relationships
Quantitative Trait Location (QTL)

Abstract

Recent advances in cellular and molecular genetics have raised new hopes among breeders, including the development of a variety of molecular markers. There are several types of markers, including morphological, molecular, and cytological markers. Molecular markers are one of the most powerful tools for studying genetic diversity. They are used in the study of phylogenetic relationships, selection of superior plants, and the study of similarities or differences between different specimens. Molecular markers are also used in germplasm management and marker-assisted selection (MAS) to increase the efficiency of germplasm breeding. Among molecular markers, DNA-based markers are of particular importance because of the limitations of morphological and isozyme markers. DNA markers are valuable tools in plant sciences. These markers do not have the problems of morphological markers and allow efficient comparisons to distinguish between very similar organisms. These markers are commonly used to assess genetic variation in agronomic germplasm, analyse population structure, localise quantitative traits (QTL), or linkage mapping for gene mapping. The increasing development of new and specific types of markers demonstrates their importance for understanding genomic diversity and diversity between similar species as well as between different plant species. In this review, we will discuss the types of markers, their advantages and disadvantages, and their applications in plant science.

10.22034/CAJPSI.2021.04.02

E-ISSN: 2783-1310

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1. Introduction

Molecular markers are a useful and accurate tool that the methods based on their use as a complement to traditional and classical methods have a significant role in accelerating breeding programs, increasing accuracy and saving labor and costs (Jiang, 2013). The advent of polymerase chain reactions (PCR) technique and molecular markers in the early 1980s and their gradual evolution with the development of new advanced tools and equipment led to the introduction of the concepts of genomics, bioinformatics and proteomics into molecular biology in the mid-1990s. The combination of these achievements coincided with the end of the twentieth century with the completion of genome research projects on several organisms, including humans, Arabidopsis, and rice (Li et al., 2006). In the 1950s, molecular markers visible by electrophoresis of proteins revolutionized. Some of the differences in DNA sequences appear as proteins of different sizes that can be recorded and studied by different biochemical methods. These markers are also called biochemical markers (Mobasheri et al., 2017).This marker shows polymorphism at the protein level.

Numerous reports have been published comparing the efficiency of molecular markers for estimating plant genetic parameters in genetic diversity studies (Etminan et al., 2016). Most research has been done on different plant genomes and various breeding programs (Hilscher et al., 2017). Molecular markers may vary according to important characteristics, such as genomic abundance, level of polymorphism detected, locus specificity, reproducibility, technical requirements, and financial investment (Table 1). No molecular marker is superior to other markers for a wide range of applications. The most appropriate molecular marker depends on the specific application, the probable level of polymorphism, the availability of sufficient technical facilities and knowledge, time constraints and financial constraints.

Table 1. Characteristics of some widely used molecular markers (Agarwal et al, 2008).

	Abundance	Reproducibility	Degree of polymorphism	Locus specificity	Technical requirement	Quantity of DNA required	Major application
RFLP	High	High	Medium	Yes	High	High	Physical mapping
RAPD	High	Low	Medium	No	Low	Low	Gene tagging
SSR	Medium	Medium	Medium	No	Medium	Low	Genetic diversity
SSCP	Low	Medium	Low	Yes	Medium	Low	SNP mapping
CAPS	Low	High	Low	Yes	High	Low	Allelic diversity
SCAR	High	High	Medium	Yes	Medium	Low	Gene tagging and physical mapping
AFLP	High	High	Medium	No	Medium	Medium	Gene tagging

2. Genetic markers

Any trait that differs between individuals is due to differences in the DNA sequence of their chromosomes. Even traits that are expressed differently under environmental conditions reflect differences in DNA sequences. These differences can be used as genetic markers (Callahan et al., 2017). These differences may be expressed in different ways. In general, for a trait to be used as a genetic marker, it must show a polymorphism between two individuals and be inherited. Therefore, genetic markers are divided into different types, including morphological markers, cytological markers and molecular markers (Nadeem et al., 2018).

2.1. Morphological markers

Morphological markers are the result of visible mutations in plant morphology. Morphological traits are mainly expressed by a gene that can be used as genetic markers. These markers include a wide range of genes controlling phenotypic traits and are among the first markers used to assess diversity within and between populations that have been used since the location of genes on the chromosome and are still relevant today.

Although these markers are easier to evaluate than other markers, they also have disadvantages that limit their use (Sepahvand et al., 2021). These markers have a dominant inheritance and have epistatic and pleiotropic effects, are affected by environmental conditions and growth stage, have little abundance and diversity, and are difficult to observe and record in perennials.

2.2. Molecular markers

Molecular markers have provided powerful tools for assessing the genetic diversity of plant genotypes and plant breeding (Nadeem et al., 2018). They have many applications in the study of genetic diversity, fingerprinting, cultivar identification, phylogenetic analysis, and the careful selection of suitable parents to produce strong hybrids. The types of molecular marker techniques vary depending on the application, performance requirements, sensitivity, and accuracy. These markers are divided into two groups: Biochemical Markers and DNA markers (Agarwal et al., 2008; Chukwu et al., 2019). Characteristics of an ideal molecular marker for studying phylogenetic relationships:

1- Have Mendelian inheritance.
2- The polymorphism rate should be high: it should be polymorphic because it is polymorphic that is measured for genetic diversity studies.
3- Codominant inheritance: determination of homozygous and heterozygous states of organisms.
4- Selective neutral behaviors.
5- High reproducibility.
6- It should have high dispersion and frequency in the genome.
7- Its expression should be independent of the environment.
8- It should be low cost, fast and easy.

None of the molecular markers have all of these properties together (Dong et al., 2018). Some are used in breeding because of their codominant nature, and some are used in genetic diversity studies because of their high polymorphism (Dong et al., 2018). Therefore, a researcher chooses her desired marker according to her goals and possibilities (Merritt et al., 2015).

2.2.1. Biochemical markers

In the 1950s, molecular markers visible by electrophoresis of proteins revolutionized. Codominant inheritance, low cost, easy analysis and high reproducibility are some of the advantages of these markers. These markers are divided into two categories (Elghamery et al., 2021).

2.2.1.1. Isozyme markers

The most common type of biochemical marker is isozymes, which show different forms of an enzyme. Isozymes are encoded by different genes, each gene can have different alleles at one locus, so changing the alleles of one locus may cause the protein to change slightly (Metakovsky et al., 2018).Such changes in the subgroup of isozymes are called allozymes (Leht and Jaaska, 2019). Isozymes have been widely used in the study of genetic diversity and crop classification. Disadvantages of these markers include the limitation of recordable genetic diversity, low frequency, and complexity of electrophoresis phenotypes (Ni et al., 2018).

2.2.1.2. Seed storage proteins

These proteins include glutenin and gliadin in wheat and hordein in barley (Moehs et al., 2019; Daly et al., 2020). Storage proteins are highly polymorphic and very stable (Akasha et al., 2016). Environmental factors have very little effect on their presence in seeds. The use of electrophoresis patterns of seed proteins is an excellent criterion for the identification of populations and varieties individually and with other markers (Hamouda, 2019).

2.2.2. DNA markers

Among the various methods available for estimating genetic diversity among plant species, DNA molecular markers are a powerful tool for assessing genetic diversity and relationships. At present, the best way to study biodiversity and genetics in species, breeds, populations, lines and strains of vertebrates and invertebrates and plants is to study DNA molecular markers (Coates et al., 2018). Nuclear, chloroplast, or mitochondrial DNA can be used to study polymorphism. Molecular markers DNA are the most abundant and easiest molecular markers and can be used in any organism (Nadeem et al., 2018). DNA-based markers examine differences through direct DNA analysis. These markers have made it possible to create physical and genetic maps in living organisms as well as to identify genes that control qualitative and quantitative traits. There is a difference between these markers in terms of characteristics such as degree of polymorphism, dominance and codominant, chromosome distribution, and reproducibility. These markers are divided into two categories: These markers are divided into two categories: PCR-based markers and hybridization-based markers.

2.2.2.1. PCR-based markers

The development that played the most important role in the development and evolution of DNA markers was the invention and introduction of the polymerase chain reaction. The polymerase chain reaction is a method in which DNA replication is performed in vitro by the basic elements of the DNA replication process. Polymerase chain reaction methods are widely used today to study the genetic diversity of different plant cultivars due to their ease, low cost, speed and lack of need for radioactive probes. These markers are used as a powerful tool to identify polymorphisms and study diversity and genetic relationships in plants (Amom and Nongdam, 2017). The most important PCR-based markers are RAPD, SSR, ISSR and AFLP (Grover and Sharma, 2016).

2.2.2.2. hybridization-based markers

These DNA markers are produced without the use of a polymerase chain reaction. Different types of these markers include RFLP, RLGS and VNTR markers (Adhikari et al., 2017). At the head of this group of markers is the restriction fragment length polymorphism (RFLP) (Landry et al., 1987). To help you choose the right marker, a summary of the main features of marker technologies is given in Table 2.

3. Applications of molecular markers

3.1. Molecular mapping of important agricultural genes

In the past, genetic linkage mapping using morphological markers was not possible in most crops due to the lack of sufficient molecular markers (Cai et al., 2015). Mapping required a lot of manpower, years of time and different mapping populations. These maps carried a small number of markers and therefore could not be used to effectively map target genes (Bassil et al., 2015). With access to a large number of molecular markers, such as AFLP, RAPD, RFLP, and microsatellites, complete mapping of plant genomes became a reality. Molecular genome maps have been created in almost all crops. Most of these maps are based on RFLP markers (Nadeem et al., 2018).The current mapping works mainly include PCR-based markers such as AFLP, STMS, RAPD, CAPS, SCAR, and STS (Kumawat et al., 2020). Among crops, the rice genome map is the most complete (Du et al., 2017). Access to molecular markers and complete linkage maps has made it possible to map the genes responsible for quantitative as well as qualitative traits (Allen, 2020).

3.2. Genome Sequencing

In the past, sequencing the large genome of eukaryotes like plants was difficult (Husnik and McCutcheon, 2018). Genome sequencing required the initial preparation of the studied genome sample, its division into very small fragments, and then the implementation of a series of sequencing, imaging and visualization operations, and finally the assembly of sequenced fragments and data analysis (Goodwin et al., 2016). For this purpose, it is

necessary to identify standard points as markers on DNA for sequencing so that the results of sequencing the fragments can be put together based on them. Today, PCR-based techniques for detecting DNA polymorphism along with the Sanger method and the development of various new generation sequencing (NGS) methods have made it easy for breeders to sequence thousands or millions of sequences simultaneously. Also, complete the sequencing of the studied genes and prepare standard genetic maps of higher plants (Nadeem et al., 2018).

Table 2. Advantages and disadvantages of some widely used markers.

Disadvantages	Advantages	Type of markers
Restriction Fragment Length Polymorphism (RFLP)	-High genomic abundance -Co-dominant markers -Highly reproducible -Can use filters many times -Good genome coverage -Can be used across species -No sequence information -Can be used in plants reliably (well-tested) -Needed for map-based cloning	-Need a large amount of good quality DNA -Laborious (compared to RAPD) -Difficult to automate -Need radioactive labeling -Cloning and characterization of the probe are required
Randomly Amplified Polymorphic DNA (RAPD)	-High genomic abundance -Good genome coverage -No sequence information -Ideal for automation -Less amount of DNA (poor DNA acceptable) -No radioactive labeling -Relatively faster	-No probe or primer information -Dominant markers -Not reproducible -Cannot be used across species -Not very well-tested
Simple Sequence Repeat (SSR)	-High genomic abundance -Highly reproducible -Fairly good genome coverage -High polymorphism -No radioactive labeling -Easy to automate -Multiple alleles	-Cannot be used across species -Need sequence information -Not well-tested
Amplified Fragment Length Polymorphism (AFLP)	-High genomic abundance -High polymorphism -No need for sequence information -Can be used across species -Work with smaller RFLP fragments -Useful in preparing contig maps	-Very tricky due to changes in patterns concerning materials used -Cannot get a consistent map (not reproducible) -Need to have very good primers
Sequence-Tagged Site (STS)	-Useful in preparing contig maps -No radioactive labeling -Fairly good genome coverage -Highly reproducible -Can use filters many times	-Laborious -Cannot detect mutations out of the target sites -Need sequence information -Cloning and characterization of probe are required
ISOZYMES	-Useful for evolutionary studies -Isolation lot easier than of DNA -Can be used across species -No radioactive labeling -No need for sequence information	-Laborious -Limited in polymorphism -Expensive (each system is unique) -Have to know the location of the tissue -Not easily automated

3.3. Complete study of the genome

The project of complete decoding of the plant genome requires the preparation of an accurate genetic map, the determination of the regular accumulation of tens of thousands of DNA fragments containing the genome, and the determination of the exact sequence of the nucleotides that make it up (McGuire et al., 2020). Genome

information including genome modification such as the number of copies and insertions, deletion, inversion and transfer of a large part of the DNA sequence can be obtained through a complete study of the plant genome (McGuire et al., 2020). This information can be used as a guide for using the right materials in the breeding program, determining the characteristics of genotypes, identifying and selecting suitable specimens to intersect with other specimens (König et al., 2020). Based on this, it is also possible to select the appropriate parent lines and plan the necessary intersections to produce hybrid plants (Caballo et al., 2018). Plant genome information can also be used to estimate genetic relationships between breeding sources or populations or lines. With the help of markers, samples can be screened for genetic uniformity or non-uniformity and decisions can be made about their use in breeding programs (Jamali et al., 2019).

3.4. Determination of chromosomes containing the desired gene

Identifying genotypes that are compatible with target environments in which a number of genes work well together is necessary to transfer the characteristics of a genotype to a specific genetic context in a breeding program. With the help of more markers, the location of the marker can be determined with the gene on the chromosome and the above gene can be assigned to a specific chromosome.

3.5. QTL mapping and analysis

There are two different methods, including physical mapping and genetic mapping, for mapping chromosomes (Kuzay et al., 2019). Mapping with genetic correlation analysis is different from mapping with physical methods (Boisset et al., 2018). To map genetic mapping, simply identifiable genes in the form of phenotypic traits should be used to determine the distances between genes using gene continuity analysis (Kirungu et al., 2018). The development of PCR-based methods and DNA markers has made correlation analysis easier and has enabled the preparation and application of correlation maps and QTL mapping in different types of plants (Nadeem et al., 2018).

3.6. Application of molecular markers in plant breeding to tolerate environmental stresses

The use of molecular markers in breeding programs can assist the breeder in locating genes that control traits that are effective in tolerating stress without the need for phenotype determination and minimize field evaluations (Oladosu et al., 2019). Other applications of molecular markers include finding and discovering genetic diversity and the possibility of marker-assisted selection (MAS) under stress conditions (Asadi and Jalilian, 2021; Platten et al., 2019).

4. Conclusion

One of the most important findings in the field of plant breeding over the past few decades has been the recognition of the huge capital of genetic diversity in plants. Genotypic studies are very important to identify similar genotypes in order to preserve, evaluate and use genetic resources, to study the diversity of wild, native or modified germplasm before the start of breeding programs, as well as to identify and differentiate genotypes. In plant breeding, genetic diversity is one of the requirements for plant breeding, which originates from natural evolution and is the most important component in the sustainability of biological systems. Certainly, knowing the content and level of genetic diversity of plant resources of each product is the most important step in estimating breeding goals.

In the traditional method, the evaluation of genetic diversity was based on phenological and morphological characteristics. This method is time-consuming and in it, several traits are affected by environmental changes. Also, due to the interaction of environment and genotype on plant phenotype, this method will not be effective. Among the various methods available for estimating genetic diversity among plant species, DNA molecular markers are a powerful tool for assessing genetic diversity and relationships. Over the last two decades,

significant advances in molecular plant breeding, especially DNA marker technology, have provided new tools to increase the efficiency of breeding methods.

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How to cite this paper:

Mirzaei, S., 2021. Application of molecular markers in plant sciences; An overview. *Cent. Asian J. Plant Sci. Innov.*, **1**(4), 192-200.