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Review Article

Microsatellite markers for crop improvement: A review

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Abstract
Microsatellites or simple sequence repeats (SSRs) markers are a helpful strategy among the various molecular marker techniques for strengthening molecular breeding programs. These are useful markers for genotyping plant populations with tandem repeats of 2-6 base pair length DNA patterns. The expansion of various molecular markers and advances in sequencing technologies has aided crop improvement. Several articles for research scholars with progressive knowledge of molecular genetics have been published in the last three decades to probe the information regarding molecular markers. This article reviews novel advances regarding molecular markers and their implementations in plant breeding for researchers with no expertise in using molecular markers in plant breeding. A superior comprehension of molecular markers, and a better consciousness of the spectrum of crops that can be grown, has resulted from progress in molecular plant breeding, genetics, genomic selection, and genome rectification. Further-generation sequence technology must enable the production of novel genetic markers for multifaceted and amorphous groups through genotyping-by-sequencing and union mapping. The review also discusses almost all the microsatellite markers and their advantages and disadvantages.

Keywords: Crop improvement, Microsatellite, Marker development, Marker application, Marker-assisted selection (MAS), Polymerase Chain Reaction (PCR)

INTRODUCTION

Microsatellites are small nucleotide sequences of two to seven nucleotides replicated several times. The number of replicates varies depending on the species and is acclimated to detect genetic diversity, paternity, population research, genetic trait characterization, and forensic investigations (Kumar 2018). Litt and Luty were the first to coin the term "microsatellite" (1989). Microsatellites are repeating DNA sequences in both prokaryotic and eukaryotic genomes. (Alam *et al.,,* 2019). The microsatellite marker has a length of one to six base pairs and is repeated 5–50 times. Microsatellites can be found in tens of thousands of places across an organism's genome. Compared to other parts of the genome or DNA, the rate of microsatellite marker mutation is extremely high (McDew-White *et al.* 2019).

SSRs (simple sequence repeats), STRs (short tandem repeats), SSLPs (simple sequence length polymorphism), and VNTRs (variable number of tandem repeats) are a type of repeated DNA sequence found in entire organisms (Vieira *et al.*, 2016). Because of their high allelic variation, codominant mode of inheritance, and automated investigation, microsatellites are an excellent tool for a variety of procedures, including gene genotyping, mapping, and positional cloning. They are present in the genomes of all living things (Cuevas and Vermerris, 2022). The three majorities important kinds of microsatellite sequence-comprising markers in use today are: (1) SSR (simple sequence repeats) is derived by amplification regions among inversely headed closely spaced microsatellites in a PCR reaction with primers complementary to flanking regions; 2) ISSR (inter-simple sequence repeats) is dependent on amplification of sites among conversely oriented intimately spaced microsatellites; and (3) SAMPL (Selective amplification of microsatellite polymorphic loci) is based on AFLP (Amplified fragment-length polymorphism) approach. The microsatellite sequence complements the starters for the second amplification. For plants, the essentiality of the three markers mentioned above for a variety of applications has been thoroughly cited (Rakoczy-Trojanowska and Bolibok 2004).

Sugarcane, a significant cash crop, cultivars (*Saccharum* hybrids spp., 2n = 110-130) are interspecific, extremely polyploid and aneuploid hybrid descendants' clones having the genomes of a few Saccharum progenitor clones' sizes ranging from 7.5 to 10 Gb (Kumar et al. 2012; Singh *et al.,* 2012). Sugarcane molecular breeding has been limited by the genome's high heterozygosity and complexity, which presents hurdles not encountered in other key crops. As a result, sugarcane molecular breeding has progressed slowly. Nonetheless, other DNA markers, such as the 5S rRNA intergenic transcribed spacer, have been employed by multiple groups to evaluate various sources of sugarcane germplasm (ITS) (Pan *et al.,* 2000; Singh et al 2015; Sanghera et al 2016; Marwal et al 2020), restriction fragment length polymorphism (RFLP) (Grivet *et al.,* 1996; Jannoo *et al.,* 1999; Atheeswaran *et al.*, 2023), random amplified polymorphic DNA (RAPD) (Nair *et al.,* 2002; Pan *et al.,* 2004; Singh *et al.*, 2017), amplified fragment length polymorphism (AFLP) (Lima *et al.,* 2002; Aitken *et al.,* 2005; Debibakas *et al.*, 2014; Zang *et al.*, 2022), simple sequence repeats (SSR) (Pan *et al.,* 2003; Pan 2006; Singh *et al.*, 2020), target area amplification polymorphism (TRAP) (Alwala *et al.,* 2006; Khidr *et al.*, 2020), conserved-intron scanning marker (CISP) (Suhail *et al.,* 2011; Chandra *et al.,* 2013) and single nucleotide polymorphism (SNP) (Cordeiro *et al.,* 2006; Devarumath *et al.,* 2013; Wu *et al.*, 2022). Sugarcane breeders have discovered certain cultivar-specific, species-specific, and trait-specific DNA markers that will assist them in accelerating the breeding process (Pan *et al.,* 2001; Selvi *et al.,* 2006; Oliveira *et al.,* 2009; Chandra *et al.,* 2014; Meena *et al.*, 2022).

SSR is a potent PCR-based marker created for a specific organism because of its widespread distribution over the whole genome, high polymorphism, and dependability (Platten *et al.* 2019). Molecular breeding scientists have successfully developed sugarcane SSRs, The International Sugarcane Microsatellite Consortium (ISMC) established 221 genomic-SSRs (Cordeiro *et al.,* 2000; Qi *et al.*, 2022), 402 EST-derived SSRs made over da Silva (2001), 837 EST-SSRs since SUCEST by Souza's group (Pinto *et al.,* 2004; Pinto *et al.,* 2006; Parida *et al.,* 2008; Marconi *et al.*, 2011). Paternity testing (Tew and Pan 2010), genetic diversity assessment (Devarumath *et al.,* 2012; Santos *et al.,* 2012; Sharma *et al.,* 2014), genetic linkage map building (Oliveira *et al.,* 2007; Liu *et al.,* 2016), germplasm evaluation, and variety identity testing have all used sugarcane SSR markers (Pan 2006; Liu *et al.,* 2011; Medeiros *et al.*, 2020). Furthermore, because of improved precision and detection power, SSR technology paired utilising a fluorescence detection system and capillary electrophoresis performs improved in genotyping analysis (Liu *et al.,* 2011). This detection technique was recently used to analyse Microsatellite (SSR) marker segregation in sugarcane polyploids (Pan *et al.,* 2014; Lu *et al.,* 2015). As it is known, molecular markers are most suitable compared to other markers, which are also mentioned in Table 1.

Classification of microsatellites

Microsatellites are characterised according to their sizes, the repeating unit, and their location's genome (Marwal and Gaur 2020). Based on the number of nucleotides per repetition unit, microsatellites are categorised as single, double, triple, tetra, penta, or hexa nu-

Table 1. Difference between morphological, cytological, biochemical and molecular markers

Feature	Morphological markers	Cytological markers	Biochemical markers	Molecular markers
Explanation	Morphological markers are evidence of phenotypically distinct features, such as flower colour, form, and size; type of plant development, inflorescences, or root system; pigmentation; or habit.	Cytological markers are markers which are associated with changes in chromosome no., their banding patterns, size, shape, order, and position.	Isozymes, or biochemical markers, are multi-molecular versions of enzymes that are implied by different genes but perform the similar tasks.	Plant breeders can now pick individual plants based on pattern of their markers (genotype) instead of observable features, thanks to molecular marker technology (phenotype). Marker assisted breeding (MAB) or selection is the name for this method (MAS) (Hasan *et al*. 2021).
Advantage	Morphological markers are very easy to use and do not require any special equipment. They don't necessitate any advanced biochemical or molecular techniques. Breeders have effectively employed such markers in breeding programmes for a variety	Readily available and requires small equipments	Genetic diversity, gene flow, population structure and subdivision have all been effectively detected using biochemical markers (Mateu-Andres and De Paco 2005). They are codominant, simply usable, and inexpensive.	The molecular markers offer several advantages over the other genetic markers. These include – abundance, co-dominance, phenotypic neutrality, absence of epistasis, developmental stage, tissue and environment independent expression (Govindaraj *et al.,* 2015).
Disadvantage	The following are the main drawbacks: They are limited in number, are influenced by different phases of plant growth, and are also affected by several abiotic/ ecological factors (Eagles *et al.,* 2001). Humans have effectively exploited many morphological markers to examine dissimilarity for application in plant breeding since ancient times (Karaköy *et al.,* 2014).	Limited in number; they exhibit less polymorphism, and need experts to handle the equipments	They are less numerous, detect smaller variability, and are impacted by means of several extraction procedures, plant growth stages, and plant tissues (Mondini *et al.,* 2009).	Besides the use of such markers, the time and expenses involved in doing genetic analysis is further constrained by the presence of observable polymorphism in some crops (Das *et al.,* 2019). Very broad crossings have been used to construct high-density maps, but the degree of polymorphism in ordinary breeding populations, especially in self-pollinated crops, is significantly lower.

cleotide repeats (Table 2). To classify microsatellites based on nucleotide order inside repeat motifs, Weber (1990) used the terms perfect, imperfect, and compound, whereas Wang *et al.,* (2009) used the terms simple perfect, simple imperfect, compound perfect, and compound imperfect. Imperfect repeats are perfect repeats infrequently interrupted by non-repeat sequences, whereas tandem arrays of one repeat motif are known as perfect repetitions. Compound microsatellites feature two basic repeat patterns that can be combined in a variety of ways. Table 2 shows that Jarne and Lagoda (1996) created the terms pure and interrupted to denote perfect and flawed repeats, respectively.

Chloroplast and mitochondrial microsatellites

Most microsatellites (SSRs) are found in nuclear genomes, although they can also be found in mitochondrial and chloroplast genomes. Due to gene content conservation, pretty much entirely uniparental inheritance, and very low recombination rates, the utilization of comprehensive chloroplast genomes in investigations of plant biodiversity has brought a major improvement over conventional techniques, reducing the complexities of incomplete lineage sorting encountered among nuclear markers (Singh *et al.,* 2014; de Abreu *et al.,* 2018; Magdy *et al.,* 2019; Zhou *et al.,* 2021). Like the nucleus and mitochondria, the chloroplast regulates vital and specialised cellular functions, namely photo-

Table 2. Classifying Microsatellites on a different basis

Classification of Microsatellite markers	
(A) Based on the nucleotides arrangement in repeat motifs	Pure or perfect or simple perfect (CA)n Simple imperfect (AAC)n ACT (AAC)n + 1 Compound or simple compound (CA)n (GA)n
(B) Based on the nucleotides number per repeat (Wang *et al.*, 2009)	Mononucleotide (A)n Dinucleotide (CA)n Trinucleotide (CGT)n Tetranucleotide (CAGA)n Pentanucleotide (AAATT)n Hexanucleotide (CTTTAA)n (n = number of variables)
(C) Based on SSRs location in the genome (Wang *et al.*, 2009)	Nuclear (nuSSRs) Chloroplastic (cpSSRs) Mitochondrial (mtSSRs)

synthesis, with coding genes exclusive to this cellular compartment (Christensen 2020). Organelle genomes date back to roughly one billion years ago, when endosymbiotic cyanobacteria (chloroplast) and alphaproteobacteria (mitochondria) were incorporated into proto-eukaryotic host cells (Allen 2015; Smith and Keeling 2015). The variety of organelle genomes currently discovered in eukaryotic lineages is the consequence of the continual reshaping of organelle genomes throughout evolutionary history (Sloan and Wu 2014). Some functional genes or DNA segments in the genomes of organelles have either been transferred to the host nuclear genome or completely lost throughout this complex co-evolutionary process (Sloan *et al.,* 2018; Hill *et al.,* 2019).There is continual molecular crosstalk among cellular compartments in the sequence of coordinated cellular signalling and gene expression because of numerous gene transfers from organelles to the nucleus (Adams *et al.,* 2002; Wu *et al.,* 2017; Choi *et al.,* 2020). For *Miscanthus, Saccharum*, and related grasses, chloroplast SSRs (cpSSRs) markers loci including both microsatellites (cpSSRs) and single nucleotide polymorphisms (SNPs) have been found (de Cesare *et al.,* 2010)

Plant mitochondrial genomes (mtDNA) are more complex than animal mitochondrial genomes (Singh *et al.,* 2014a; Kozik *et al.,* 2019). Because of its complexity and high repetitive content, the sugarcane mitochondrial genome has proven difficult to study. Several unsuccessful attempts have been made to extract the genome from whole-genome shotgun sequencing (Thirugnanasambandam *et al.,* 2018). Plant mtDNA is differentiated by molecular heterogeneity, which is exhibited as different sizes and relative abundances of circular chromosomes (Morley and Nielsen 2017). Because of the fast rate of sequence reorganisation in mitochondrial genomes, they are rarely used for phylogenetic research in plants (Cui *et al.*, 2021). However, in some cases, mitochondrial haplotype diversity linked to sequence rearrangement was found valuable in identifying populations (Sperisen *et al.,* 2001).

In various agricultural crops, many forms of DNA molecular markers have been produced and efficaciously used in genetics and breeding. The sections that follow provide some basic information about molecular markers and how they are detected. Table 3 compares the most essential aspects of commonly employed molecular markers.

Gene-targeted and Functional Markers (GTMs and FMs)

A molecular marker can be made from polymorphic stretch of DNA and labelled with a variable-length primer. Nevertheless, a simple recombination can nullify the efficacy of such neutral markers in many circumstances, restricting the usage of randomly amplified DNA markers (Rafalski and Tingey 1993). Non-targeted amplicons, in other words, can be observed in either the transcribed or non-transcribed areas of the genome, and they were created with no awareness of their purpose. The expansion of targeted markers resulting from polymorphism locations within the variety of genes that influence phenotypic traits has been aided by genetic development programs that focus on structural and functional aspects in numerous plant species (Andersen and Lübberstedt 2003). Because not all gene-targeted markers (GTMs) are involved in phenotypic trait variation and thus may not become functional, it is important to distinguish between GTMs and functional markers (FMs). Untranslated sections of expressed sequence tags can likewise be tagged with gene-targeted markers (Arnholdt-Schmitt 2005; Varshney *et al.,* 2007). According to Andersen and Lübberstedt (2003), polymorphic sequences are used to create functional markers, which are more likely to participate in phenotypic trait variation. The marker systems listed in Table 4 are all (gene)-targeted markers having the potential to become effective in this intangible setting. This kind of marker system has recently been commercially produced.

Recent developments in molecular biology have expanded the possibilities for genetics and plant breeding

Table 3. Comparison between major molecular marker characteristics (Nadeem *et al.* 2017; Amiteye 2021)

Marker	DNA Re-quire (µg)	PCR based	Inheritance	Locus specificity	Level of polymorphism	Reproducibility	Automation	Utility for genetic mapping	Marker index
RFLP	5-50	No	Codominant	Yes	Low-Medium	High	Low	Species specific	Low
RAPD	0.01-0.1	Yes	Dominant	No	Medium-High	Low	Moderate	Cross specific	Medium
AFLP	0.5–1.0	Yes	Dominant	No	High	Medium	Moderate	Cross specific	High
SSRs	0.05-0.12	Yes	Codominant	Yes	High	High	High	Species specific	Medium
SSLP	0.05-0.12	Yes	Codominant	Yes	High	High	High	Species specific	Medium
ISSR	≥0.05	Yes	Dominant	No	High	Medium-High	High	Species specific	Medium
TRAP	0.05	Yes	Codominant	Yes	High	High	Medium	Species specific	Medium
SCAR	0.02	Yes	Codominant	Yes	High	High	Medium	Species specific	Medium
CISP	0.02-0.05	Yes	Codominant	Yes	Moderate	High	High	Cross specific	High
SNPs	0.05	Yes	Codominant	Yes	High	High	High	Species specific	Medium
CpSSR	0.02	Yes	Codominant	Yes	Low	High	High	Cross specific	High
SAMPL	0.5–1.0	Yes	Codominant	Yes	High	High	Moderate	Cross specific	High
SRAP	0.02	Yes	Dominant	No	Medium-High	Low	Medium	Species specific	Medium
SSCP	0.01	Yes	Codominant	Yes	High	Medium-High	Can’t auto-mated	Cross specific	Medium
CAPS	0.01	Yes	Codominant	Yes	High	High	Medium	Species specific	Medium
SNP	0.05	Yes	Codominant	Yes	Extremely High	High	High	Species specific	Medium
DarT	0.05-0.1	No	Dominant	Yes	High	High	High	Species specific	High
EST	0.02-0.05	Yes	Dominant	Yes	High	High	High	Cross specific	Medium
STS	0.01-0.02	Yes	Codominant	Yes	High	High	High	Species specific	Medium
RAMP	0.02	Yes	Codominant	Yes	High	High	High	Species specific	Medium
ScoT	0.02	Yes	Dominant	Low	High	Medium	High	Species specific	High
CoRAP	0.02-0.05	Yes	Codominant	Medium	High	Medium	Medium	Species specific	Medium

Table 4. Working concept of marker systems along with their groups

Group	Marker	Working principle	Reference
Conserved DNA and gene family-based markers (CDMs)	Conserved DNA - Derived Polymorphism (CDDP)	Short universal or degenerate primers are used to detect length polymorphism and develop conserved genes that produce protein sequences with retained amino acid composition. Primer combinations can also be employed.	Poczai *et al.,* (2013); El Dessoky *et al.,* (2020); Igwe *et al.,* (2021)
	P450-based Analogue (PBA) Markers	Variations in the random distribution of cytochrome (cyt) P450 sequences repeated with all-purpose primers that link the heme- or CYP-binding sites in plants are used to evaluate polymorphism. Polymorphism is identified by randomly examining the distribution of gene family members.	Poczai *et al.,* (2013); Ravi *et al.,* (2020);
	Tubulin-Based Polymorphism (TBP)	Single degenerate primer pairs anneal and amplify intervening introns from distinct tubulin isotypes by complementing conserved regions of the -tubulin exons.	Poczai *et al.,* (2013); Braglia *et al.,* (2020); Braglia *et al.,* (2023)
	Intron - Targeting Polymorphism (ITP)	Exon flanking primers amplify intron regions of interest, exposing polymorphism.	Weining and Langridge (1991); Amiteye (2021)
Transposable element - based markers (TEMs)	Inter-Retrotransposon Amplified Polymorphism (IRAP)	Primers that annealed to LTR motifs were used to amplify internal sequences between two retrotransposon repeats.	Kalendar *et al.,* (1999); Cheraghi *et al.,* (2018);
	Retrotransposon Microsatellite Amplification Polymorphisms (REMAP)	Polymorphism is detected by using a LTR specific and an ISSR primer.	Kalendar *et al.,* (1999); Cheraghi *et al.,* (2018);
	Intron Sequence Amplified Polymorphism (ISAP)	To amplify nearby genomic areas, primers designed in various places within SINE elements are utilised.	Seibt *et al.,* (2012); Seibt *et al.,* (2016)
	Inter-primer Binding Site (iPBS)	Primers anneal to the PBS regions of LTR retrotransposons that are orientated head-to-head. LTR segments and intervening genomic regions are present in the amplified products.	Kalendar *et al.,* (2010); Aydın *et al.,* (2020);
	Sequence-Specific Amplified Polymorphism (SSAP)	Restriction enzymes are used to breakdown DNA. LTR and adapter specific primers comprising specific nucleotides are utilised for amplification once adapters are ligated to restriction sites.	Waugh *et al.,* (1997); Roy *et al.,* (2021)
Resistance-gene based Markers (RGMs)	Resistance Gene Analog Polymorphism (RGAP)	By using primer pairs that match conserved R-gene sections or degenerate-specific primers, analogue fingerprints depending on resistance genes can be produced.	Leister *et al.,* (1996); Amiteye (2021)
	Nucleotide Binding Site (NBS) Profiling	Following the ligation of adapters, genomic DNA is digested with restriction enzymes. With adapter specific and R-gene specific primers, specific fingerprints are obtained from resistance gene regions.	Van der Linden *et al.,* (2004)
	Intron Length Polymorphism (ILP)	PCR primers intended to attach exons adjoining target introns were used to detect it.	Badoni *et al.,* (2016); Cai *et al.,* (2017); Li *et al.,* (2022);
RNA-based markers (RBMs)	Inter Small RNA Polymorphism (iSNAP)	A complementary primer for short RNAs and a primer analogous to flanking regions are employed to develop polymorphism profiles.	Gui *et al.,* (2011); Poczai *et al.,* (2013); Amiteye (2021)
	cDNA-Amplified Fragment Length Polymorphism (cDNA-AFLP)	For an AFLP analysis, cDNA is the starting pool, with many alterations available for fine-tuning.	Bachem *et al.,* (1996); Amiteye (2021)
	cDNA-Restriction Fragment Length Polymorphism (cDNA-RFLP)	RFLP probes are used that are having typically short, single- or low-copy genomic DNA or cDNA clones.	Bryan *et al.,* (1999); Singh *et al.,* (2008)
	Expressed Sequence Tag-derived Simple Sequence Repeat Markers (EST-SSR)	SSRs are discovered and primers for genetic microsatellites are created by using *in silico* mining of EST databases.	Kantety *et al.,* (2002); Amiteye (2021)

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Targeted Fingerprinting markers (TFMs)	Penta-primer Amplification Refractory Mutation System (PARMS)	SNP genotyping via fluorescent imaging. Allele-specific primer pairs, universal fluorescent primer pairs, and reverse shared primer pairs are used to amplify SNP locations.	Zhang *et al.,* (2019); Lu *et al.,*, (2020); Gao *et al.,* (2021)
	Direct Amplification of Length Polymorphisms (DALP)	To generate fingerprints, the typical M13 sequencing primer was combined with a forward primer made up of the 40 USP core and 3' selected nucleotides.	Ha *et al.,* (2001); Poczai *et al.,* (2013)
	Promoter Anchored Amplified Polymorphism (PAAP)	There are sections of short PCR primers that occur prior to plant promoter regions that are faulty. Polymorphism is then detected using these.	Pang *et al.,* (2008); Mokate *et al.,* (2017)
	Sequence-Related Amplified Polymorphism (SRAP)	A random 5' filter, an AATT or CCGG core sequence, and three variable nucleotides at the 3' end are all features of primers. Mismatches at a lower temperature can be used to create a starting pool for further amplification at a higher temperature in the first step of amplification.	Li and Quiros (2001); Amiteye (2021)
	Target Region Amplification Polymorphism (TRAP)	A random SRAP primer and a predetermined primer analogous to ESTs are combined to create polymorphic profiling.	Junior *et al.,* (2020); Khidr *et al.,* (2020)
	Conserved Region Amplification Polymorphism (CoRAP)	ESTs are used to make arbitrary primers that are then coupled with a fixed primer using the CACGC plant intron associated sequence core.	Fabriki and Azarkhanian (2018)
	Start Codon Targeted (SCoT) Polymorphism	Random primers with ATG start codons are utilised to create polymorphic fragments from the genome. Primer can be used on its own or in conjunction with several other products.	Thakur *et al.,* (2021); Rai (2023)

research. Genotype selection has become a significant method in the buildout of resistant plant types (Varshney *et al.,* 2021). Molecular markers that can detect genetic differences at the DNA sequence level have outperformed morphological, chromosomal, and protein markers. They are more efficient than other genetic markers due to their special genetic characteristics (Jiang 2013). They are plentiful and broadly spread across the genome. Compared to phenotypic markers, DNA-based markers have various advantages, including being highly inherited, relatively easy to assess, and unaffected by environmental influences (Li *et al.,* 2020).

Around the past three decades, several molecular marker techniques have developed and been applied in a variety of systems all over the world. Only a few of these approaches, such as RFLPs, RAPDs, AFLPs, ISSRs, SSRs, and SNPs, have gained comprehensive recognition. The detection and deployment of molecular markers have reached ultrahigh- a recent uprising in DNA sequencing technology has increased throughput levels. Microsatellites, SNPs, and genotyping by sequencing (GBS) substantially satisfy most user requirements, albeit the preference of marker will be contingent on the desired purpose. Furthermore, contemporary transcriptomic and functional markers and other high throughput techniques will lead to high-density genetic map creation, QTL identification, breeding, and conservation strategies in the future (Gali *et al.,* 2019). Table 5 summarises several marker technologies and their findings, as well as a comparison of their distinguishing characteristics.

Comparative advantages and disadvantages of microsatellite markers

For most large-scale plant breeding operations, molecular markers are excessively expensive. As a result, MAS techniques are now being applied for a wider range of applications. Since they are passed down as codominant markers in a Mendelian manner, microsatellites make good genetic markers. Additionally, microsatellites have become a preferred genetic marker in plant breeding programs considering their extreme polymorphism, abundance, and widespread dispersion across the genome (Wright and Bentzen 1994; Morgante *et al.,* 2002). However, adopting microsatellite-based approaches has several limitations, including relatively high developmental expenses and some methodological problems during the production of supplemented libraries and species-specific primers (Miah *et al.,* 2013). Table 6 lists the pros and downsides of the most often used markers.

Conclusion

With the introduction of microsatellite markers, it is now conceivable to make straight implications regarding genetic diversity and evolutionary relationships between organisms at the DNA level, without the mysterious effects of environmental aspects or erroneous pedigree record processing. Microsatellite markers are also commonly employed in MAS programmes to generate

Table 5. Discoveries of some important genetic markers

Marker type	Concept	Firstly reported by
Morphological	As a scientific discipline, morphological characterization was originated by Goethe in 1790.	Donald (2001)
Isozymes	Hunter and Markert (1957) well-defined isozymes as various versions of the same enzyme that have equal roles and exist in a similar individual. Isozymes are enzyme variations produced by distinct genes that reflect different loci.	Hunter and Markert (1957)
Minisatellites (VNTR)	Wyman and White were the first to describe the utility of polymorphic minisatellites (also identified as VNTRs for variable numbers of tandem repeats).	Wyman and White (1980)
RFLP	The RFLP technique was invented by Botstein *et al.* (1980). DNA fragments are cleaved with a restriction enzyme, segregated by size on an agarose gel, blotted onto a membrane, hybridised, and subjected to a tagged probe in genotyping technology.	Botstein *et al.* (1980)
RAPD	Random amplified polymorphic DNA markers (RAPDs), a PCR-based unique class of molecular markers, proved to be an exciting choice for varietal documentation almost immediately.	Welsh and Mc Clelland (1990); Williams *et al.* (1990)
AFLP	Amplified fragment length polymorphism (AFLP), is a PCR-based fingerprinting technique that builds and compares unique fingerprints for genomes of interest via selective amplification of a subset of digested DNA fragments.	Vos *et al.* (1995)
SSRs	Litt and Luty (1989) and Edwards *et al.,* (1991) discovered and developed SSRs in humans, and Akkaya *et al.* (1992) applied them to plants for the first time. Specific primers surrounding a simple repeat of 1–5 nucleotides are used to PCR amplify specific loci for genotyping.	Litt and Luty (1989); Edwards *et al.* (1991); Akkaya *et al.* (1992)
SSLP	SSLPs (microsatellites) were used to cluster different continental populations.	Rosenberg *et al.* (2002)
ISSR	In 1994, the first research using ISSR markers was published. Without prior sequence knowledge, the ISSR marker system reveals polymorphisms from inter-microsatellite DNA regions.	Zietkiewicz *et al.* (1994)
SCAR	A SCAR marker is a genomic DNA fragment identified by PCR amplification at a single genetically defined locus using a set of particular oligonucleotide primers.	Paran and Michelmore (1993)
CISP	Conserved-intron scanning primers (CISPs), an alternate codominant marker technique, anneal to the exon boundary and use the higher evolutionary restraints for sequence conservation on exons than introns to intensify sequence changes within the highly variable spanning intron. CISPs can give a significant number of pan-grass tools that can be used to link genomics research in numerous orphan crops that are important nutritionally and economically but lack sufficient sequence info to blossom knowledge in botanical models and better-studied crops.	Feltus *et al.* (2006)
SNPs	SNPa (single-nucleotide polymorphism arrays) were initially used in 1998 to investigate the linkage between a disease locus and a chromosomal region forgenotype–phenotype relationship.	Wang *et al.* (1998)
CpSSR	Powell *et al.* (1995) were the first to establish CpSSRs as genetic markers, emphasising their high polymorphism and codominant inheritance, making them appealing genetic markers when combined with just a few loci required to distinguish unique genotypes.	Powell *et al.* (1995)
SAMPL	The selective Amplification of Microsatellite Polymorphic Loci (SAMPL) technique was primarily used in bread wheat to explore genetic variability, genotype identification, and gene tagging.	Roy *et al.* (2002)
EST	Adams and colleagues created the term EST and started an initiative to do more systematic sequencing in 1991.	Adams *et al.* (1991)
SRAP	A sequence-related amplified polymorphism (SRAP) was created by Li and Quiros (2001), is a molecular technique for detecting genetic variation in the open reading frames (ORFs) of plant and comparable species genomes.	Li and Quiros (2001)
TRAP	Targeted Region Amplified Polymorphism (TRAP) is similar to SRAP along with PCR parameters used but is grounded on prior sequence information.	Hu and Vick (2003)
SSCP	Single-strand conformation polymorphism (SSCP) analysis is a less expensive approach for sleuthing polymorphisms within a DNA sequence. SSCP is a fast way to detect small sequence deviations in DNA amplified by polymerase chain reaction. SSCP has been frequently utilised to discover mutations in oncogenes, tumour suppressor genes, and genes accountable for hereditary disorders since it was initially published in 1989.	Orita *et al.,* (1989)

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CAPS	To display RFLP, the CAPS test employs restriction endonuclease digestion of amplified DNA fragments.	Akopyanz *et al.,* (1992); Konieczny and Ausubel (1993)
DarT	DArT was first described in 2001 and has a number of benefits over other standard primer-based approaches, including the capacity to analyze vast amounts of different samples from a little quantity of original DNA.	Jaccoud *et al.* (2001)
STS	A brief (200–500 bp) PCR-amplified sequence known as a Sequence-Tagged Site (STS) can be amplified, recognised during the occurrence of all genomic sequences, and its positioning in the genome can be determined.	Olson *et al.* (1989)
RAMP	RAMPs (random amplified microsatellite polymorphisms) were named after the combination of microsatellites and RAPDs into a new method for detecting and mapping codominant polymorphisms lacking cloning and sequencing to overcome the limitations of these two methods (SSR & RAPD) and to distinguish them from specific microsatellites with unique primers.	Wu *et al.* (1994)
ScoT	After being introduced by Collard and Mackill (2009), the gene-targeted potential marker known as Start Codon Targeted Polymorphism (SCoT), focuses on the conserved region flanking the translation initiation start codon (ATG) of plant genes, quickly acquired prominence.	Collard and Mackill (2009)
CoRAP	Conserved region amplification polymorphism (CoRAP), a new PCR-based molecular marker technology, is grounded on the employment of a fixed and arbitrary primer.	Wang *et al.* (2008)
IRAP	Because of its simple methodology, the IRAP technique has been employed in a number of investigations of plant genetic diversity. Inter-retrotransposon amplified polymorphism is produced by PCR amplification of genomic DNA segments that fall between two retrotransposon insertion sites (IRAP).	Kalendar *et al.* (1999)
REMAP	Amplification of segments between a retrotransposon insertion site and a microsatellite position produces retrotransposon-microsatellite amplified polymorphism (REMAP).	Kalendar *et al.* (1999)

Table 6. Advantages and disadvantages of some potential genetic markers

Marker type	Advantages	Disadvantages	References
Morphological	Easy to use Cheaper Visually characterized	Low polymorphism Environment dependent Affected by plant growth stages Allowing dominance to mask the underlying genetics	Eagles *et al.* (2001)
Isozymes	There is no requirement for a specific instrument. Easy to use Codominant	Low polymorphism Environment dependent	Mondini *et al.* (2009)
Minisatellites (VNTR)	Highly polymorphic Multiallelic markers High reproducibility Low cost Numerous multiallelic loci	Numerous informative bands per response Band profiles cannot be explained on the basis of loci and alleles Plant fingerprints with low resolution	Nakamura *et al.* (1987); Lindblom and Holmlund (1988); Jones *et al.* (2009); Kumar *et al.* (2009)
RFLP	A simple and precise molecular method for population profiling and characterization Codominant No need of prior sequence information	Time taking High quantity of pure DNA needed Expensive Radiolabeled probes required Laborious and expensive Limited polymorphism Not amenable for automation	Martya *et al.* (2012); Nadeem *et al.* (2017)
RAPD	Simplicity of the technique For genetic analysis, only a small amount of target DNA is required Possibility of automatization Polymorphic	Dominant Extremely purified DNA is required Low reproducibility Not locus-specific	Madhumati (2014)

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AFLP	Generate vast numbers of marker pieces quickly for any organism, even if you do not know the genome's sequence. Reliable It can be easily multiplexed High reproducibility Additionally informative	Dominant marker A large quantity of highly purified and pure DNA is required	Paun and Schönswetter (2012)
SSRs	Codominant Easily automated Genomic abundance high Highly reproducible Highly polymorphic Multiple alleles Abstemiously genome coverage No radioactive labelling	Not well-assessable Can not be suitable across species Sequence data is needed High developmental price Occurrence of more null alleles and homoplasy	Kalia *et al.* (2011)
SSLP	All the necessary equipment for the assay is readily available Many researchers and technicians can routinely conduct it without the need for particular training that is required for SNP-based techniques	The strain background may limit its utility for a specific research aim if it is mutated under a specific strain background. Backcrossing is required to introduce the mutation into a desired strain background in this case.	Gurumurthy *et al.* (2015)
ISSR	Highly polymorphic Simple and easy to use Prior sequence information is not required	Dominant Low reproducibility Pure DNA is needed The fragments differ in size	Ng and Tan (2015)
SCAR	Quick and simple to utilize High replication rate and locus-specificity Only little amounts of template DNA are required They have been applied in gene mapping and marker-assisted selection studies and are locus specific	The necessity for sequence data to construct PCR primers is one of the main disadvantages	Yuskianti and Shiraishi (2010)
CISP	Co-dominant Helps in effective exploration of poorly described genomes for polymorphism and noncoding sequence conservation on a genome-wide or candidate gene basis, as well as anchor points for comparative genomics over a variety of species used for species-level and inter-species mapping that have few or no molecular markers available	Occasionally, despite per nucleotide DNA sequence variance, rigid intron size limitations were applied	Zeid *et al.* (2010); Chandra *et al.* (2013); LaMantia *et al.* (2018)
SNPs	Many platforms have a high level of polymorphism and reproducibility Fewer platforms are subject to homoplasy Convenient, rapid, and highly-throughput analysis Most of the platforms are cost-effective because many data points are formed	Target genome sequence is necessary. Certain platforms also need for sequence data for the species being studied Dedicated qualified personnel and specialised software are also needed The high cost of equipment is one of the main drawbacks	Lejman *et al.,* (2020)

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CpSSR	Higher polymorphism levels Population genetic studies and genotyping are very simple. Only few loci are needed to identify unique genotypes Effectual transferability amongst closely or vaguely related plant species Widespread application in the estimate of genetic diversity	Absence of variation in some species or the persistence of genetic diversity that is fairly limited Lacking general primers The outcomes of size homoplasy, heteroplasmy, and interspecific hybridization-mediated cytoplasmic introgression	Amiteye (2021)
SAMPL	High multiplexing codominant markers extensive polymorphism	Some blurred banding Stutter bands are formed	Amiteye (2021)
EST	Codominant Highly reproducible, robust and reliable High degree of sequence conservation Transportable across the pedigree and species Enable a transfer of linkage information between species	The development of markers is restricted to species for whom a sequencing database is already available	Cato *et al.,* (2001); Dhingani *et al.,* (2015)
SRAP	Simplicity High throughput Numerous codominant markers High reproducibility Targets coding sequences Detects many loci without prior sequence knowledge PCR products are sequenced immediately	Detects codominant and dominant markers, which can lead to complexity Null alleles detected directly	Uzun *et al.* (2009); Poczai et a. (2013)
TRAP	It is s easy to use and provides a lot of information. Creates a large number of markers by utilising current public EST databases Uses markers targeted to a specific gene	For primer creation, cDNA or EST sequence information is required	Poczai *et al.,* (2013)
SSCP	Allelic codominance Only a small amount of template DNA is necessary Ability to detect mutations (small deletions, insertions, and substitutions) in DNA fragments at a variety of locations with high sensitivity	The requirement for sequence data in order to construct PCR primers The need for exceedingly uniform electrophoretic settings to obtain precise outcomes Also, some mutations may go hidden, making the nonappearance of mutation impossible to confirm	Hayashi (1992); Kakavas (2021)
CAPS	Primarily used in gene mapping studies It involves PCR, which entails only a small amount of template DNA Allelic codominance Highly reproducible Unaffected by DNA methylation Radioactive probe not required	Due to the smaller size of the amplified fragments (300-1800 bp), CAPS polymorphisms are harder to locate than RFLP polymorphisms. Furthermore, sequence data is necessary to create PCR primers.	Matuszczak *et al.* (2020)
DArT	Cost-effective High throughput Highly polymorphic No prior sequence knowledge is required Reproducibility is high Analyse a huge number of different samples from a small amount of starting DNA	Dominant marker High developmental cost	Nadeem *et al.* (2017)

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STS	Assists in the compilation of counting maps Enormously reproducible No radioactive labelling Filters can be used multiple times Moderate genome coverage	Requires sequence information Mutation detection is impossible beyond the target regions Time-consuming Cloning and probe characterisation is necessary	Miah *et al.,* (2013)
RAMP	Less expensive Reflect a high rate of polymorphism Have a large no of copies in the genome	Interpreting mixtures is more challenging Repeatability can be impacted.	Salazar *et al.,* (2014); Rasouli *et al.,* (2015); Nadeem *et al.* (2017)
ScoT	Primers are usually repeatable, albeit annealing temperature and primer duration are not the only factors to consider	They are dominant markers, but during amplification, multiple co-dominant markers are also formed, which might add to the complexity.	Gorji *et al.* (2012)
CoRAP	Rapid and efficient Codominant Highly reproducible Polymorphic	For primer creation, cDNA or EST sequence information is required.	Poczai *et al*. (2013)
IRAP and REMAP	Distinguish amongst genotypes or species Analyse population variability They are very simple to evaluate Low cost	Dominant marker	Chadha and Gopalakrishna (2005); Biswas *et al.*(2010); Kalendar *et al.* (2011)
Retrotransposons	Simple and easy to use There is no necessity to know what comes next in the sequence. Highly reproducible	Dominant marker	Kalendar *et al.* (2011); Roy *et al*. (2015)

cultivars resistant to specific diseases for a long time. Microsatellite-based markers have become increasingly common in recent years. Microsatellites have been discovered to be highly polymorphic, genome-specific, numerous, and codominant, making them useful genetic markers in plant breeding. Molecular markers, on the other hand, should not be used in place of other agro-morphological or biochemical markers; instead, they should be used in conjunction with other genomics and plant breeding techniques to understand better the diversity in available germplasm and how that diversity can be best utilized to expand agricultural production for sustainable food security.

Conflict of interest

The authors declare that they have no conflict of interest.

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