"Advancements in Marker-Assisted Breeding for Crop Plants: A Comprehensive Review and Future Directions"

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Abstract

Marker-assisted selection (MAS) is a methodology employed in crop breeding to identify and select desirable traits. This selection process utilizes various markers such as morphological, biochemical, or DNA markers as criteria. Within breeding programs, DNA markers hold significant promise in enhancing the precision and efficiency of trait selection. The integration of Marker-Assisted Selection into traditional breeding programs offers the potential to expedite the improvement of crops. Nonetheless, it is essential to note that implementing Marker-Assisted Selection can be cost-prohibitive, rendering it inaccessible to many countries and breeding initiatives. This comprehensive review will delve into the significance of Marker-Assisted Selection, its methodologies, and its advantages and disadvantages. Additionally, we will elucidate its historical utilization in enhancing a diverse array of crop varieties and its prospective contributions to future breeding programs.

Keywords: Marker assisted selection, DNA markers, marker assisted backcrossing, gene pyramiding, QTL mapping.

1. Introduction

Over the centuries, traditional plant breeding techniques have yielded numerous new crop varieties. However, these conventional methods, while practical, need to be revised to meet the growing global demand for food production shortly. Developing a new crop variety through traditional breeding methods is time-consuming, typically spanning a decade or more. To address

the urgency of food security challenges, we must incorporate molecular technologies, such as Marker-Assisted Selection (MAS), into our breeding strategies, as they offer greater efficiency than conventional approaches (Lema, 2018).

Moreover, the depletion of vital resources like water and soil fertility due to suboptimal agricultural practices has reduced staple crop yields. Consequently, the rapid adoption of novel crop improvement technologies becomes imperative. Plant breeders continually face the formidable task of creating improved crop varieties (Evans *et al*., 1997). Extensive research has been conducted on global crop production prospects for the 21st century, and the outlook is less than promising (Andersen *et al*., 1999). The expanding world population necessitates increased agricultural output, yet some studies indicate a diminishing growth rate in agricultural productivity (Pingali & Heisey, 1999). While conventional plant breeding can achieve gradual progress in yield enhancement, it entails lengthy timelines and multiple crop generations. New technologies, such as biotechnology, are increasingly vital to augment the likelihood of success and accelerate progress (Ortiz, 1998; Ruttan, 1999; Huang *et al*., 2002).

Within the realm of biotechnology, DNA marker technology has emerged as a product of genomics and molecular genetics research. Ideal markers must possess characteristics that render them easily reproducible, polymorphic, cost-effective to detect, and uniformly distributed across the genome (Nadeem *et al*., 2018). These DNA markers represent specific DNA sequences on chromosomes with known locations. They are tightly linked to genes of interest, facilitating the detection of specific genes within genotypes. By employing these DNA markers, the precision and efficiency of trait selection can be significantly enhanced in all breeding programs. These markers encompass various forms, including short sequences surrounding single base-pair changes (single nucleotide polymorphisms or SNPs) and longer sequences like mini and microsatellites (Al-Samarai & Al-Kazaz, 2015).

The construction of linkage maps and the execution of Quantitative Trait Locus (QTL) analysis play pivotal roles in identifying genomic regions associated with specific traits (McCough & Doerge, 1995; Mohan *et al*., 1997). The application of molecular markers has notably contributed to the enhancement of crops such as rice (Mackill *et al*., 1999), wheat (utilizing Single Nucleotide Polymorphisms or SNPs and Diversity Array Technology or DArT for whole genome profiling and background screening) (Gupta *et al*., 2010), barley (Thomas,

2003), oilseeds (Snowdon & Friedt, 2004), horticultural crops (Mehlenbacher, 1995), and pulses (Kelly *et al*., 2003). For instance, Restriction Fragment Length Polymorphism (RFLP) markers have been instrumental in selecting the *Cre1* resistance gene in wheat against cereal cyst nematode (Ogbonnaya *et al*., 2001).

This review provides essential insights and a comprehensive understanding of emerging biotechnological interventions employing markers. The rice crop is an illustrative example of recent Marker-Assisted Selection (MAS) advances. Using these DNA markers in plant breeding programs to identify and select desired traits is known as Marker-Assisted Selection (MAS). This powerful tool significantly enhances the quality of breeding programs while expediting crop improvement timelines.

Marker assisted selection

Marker-Assisted Selection (MAS) represents a valuable mechanism for identifying preferred candidates within a breeding program, leveraging DNA marker patterns as criteria instead of or in conjunction with traditional trait assessments. By relying on MAS, breeding programs can significantly enhance the precision and efficiency with which they pinpoint desirable traits within crops. However, it is essential to exercise caution, as MAS is only sometimes advantageous; its implementation can be financially burdensome. Therefore, a judicious assessment of the benefits of MAS, relative to conventional breeding methodologies, must be conducted, considering the available funding for the specific breeding program.

2. Marker

DNA markers consist of specific DNA sequences on chromosomes with precisely known positions. These markers exhibit variations and have the capacity to identify the presence or absence of polymorphism within breeding populations. There are two primary categories of markers: dominant and co-dominant. Dominant markers cannot distinguish between heterozygotes and homozygotes, whereas co-dominant markers can differentiate between these two genetic states *(see Figure 1)*. Various types of markers have been developed for application in molecular breeding strategies. Notably, while effective, Restriction Fragment Length Polymorphism (RFLP) markers are characterized by prolonged processing times and a higher demand for DNA quantities.

Consequently, Simple Sequence Repeat (SSR) markers have largely supplanted RFLP markers. SSR markers are highly dependable, polymorphic, and exhibit co-dominant traits, allowing for concurrently using multiple markers through multiplexing techniques. Another category of markers gaining considerable prominence in recent years is Single Nucleotide Polymorphisms (SNPs). SNPs have become the marker of choice in numerous plant breeding programs (Gupta *et al*., 2001). Their utility extends to association mapping, genetic diversity analysis, and the construction of high-resolution genetic maps (Rafalski, 2002a).

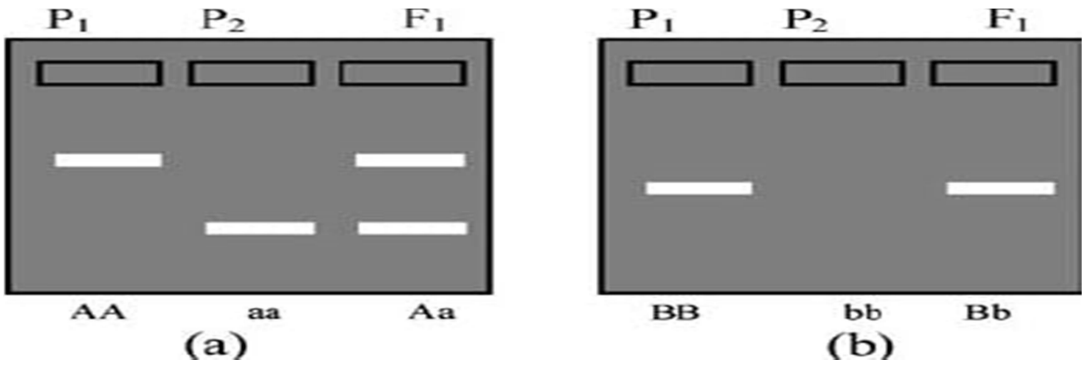

Figure 1: a) Co-dominant marker. b) Dominant marker.

3. Uses of DNA Markers in Marker-Assisted Selection (MAS)

4.1. Reliability:

The reliability of DNA markers hinges on their tight linkage to the target gene of interest. The greater physical distance between a marker and the gene can increase the likelihood of inaccurate results. Flanking markers on both sides of the gene of interest is advisable to mitigate this. This strategy substantially enhances the precision of marker selection for desirable traits (see Figure 1).

4.2. DNA Quantity and Quality:

Many MAS methodologies necessitate substantial quantities of high-quality DNA, which can sometimes pose challenges. Acquiring the requisite quality and quantity of DNA demands costly chemicals and machinery, potentially escalating the overall procedural costs. Moreover, it

can extend the time required for DNA acquisition. It is essential to consider both the time involved in the technical procedures and the simplicity of the process.

4.3. Polymorphism:

The selected markers should exhibit high polymorphism within all the breeding materials employed. They must be capable of distinguishing between different genotypes, particularly within the core breeding material. These markers should possess co-dominant characteristics, enabling discrimination between heterozygotes and homozygotes.

4.4. Cost:

The markers and the associated technical procedures should be cost-effective and user-friendly for implementation in diverse breeding programs. Simple sequence repeats (SSRs) or microsatellites are frequently favoured markers in various cereal crops (Gupta *et al*., 1999; Gupta & Varshney, 2000). These markers inherit co-dominance, exhibit high polymorphism, possess exceptional reproducibility, and are relatively straightforward and economical to employ compared to other marker types. However, they necessitate poly-acrylamide gel electrophoresis and offer information for a single locus per PCR reaction. These limitations can be circumvented in numerous cases by selecting SSR markers with substantial size disparities easily detectable in agarose gels or by multiplexing multiple markers in a single reaction. Multiplexing refers to the simultaneous amplification of multiple loci within a single PCR reaction, accompanied by the utilization of numerous markers on a single agarose gel to interpret outcomes.

Nonetheless, developing these SSR markers demands a consistent investment of financial resources and time. For several minor crop species, an adequate number of SSR markers suitable for high-density mapping still needs to be made available. Other marker types, such as Sequence Tagged Sites (STS) and Single Nucleotide Polymorphisms (SNPs), derived from specific DNA sequences of tightly linked markers (e.g., RFLPs), are also valuable tools for MAS (Shan *et al*., 1999; Sharp *et al*., 2001).

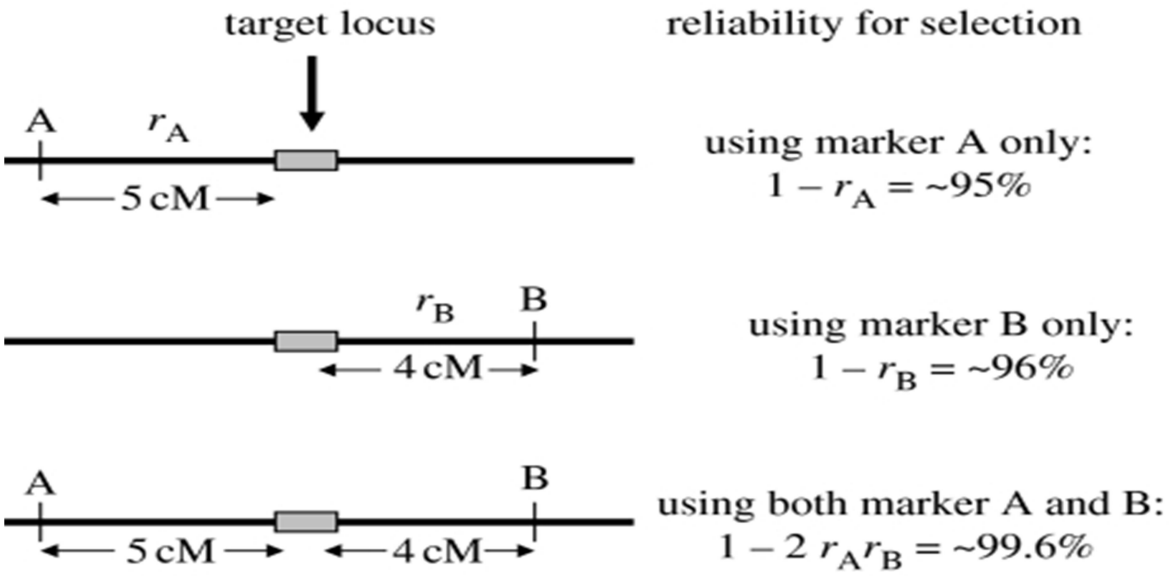

Figure 2: Reliability of Selection Using Single and Flanking Markers (Adapted from Tanksley, 1983). The figure illustrates the reliability of selection when employing single markers versus flanking markers, and it is based on the concept of recombination frequencies. In this context, the recombination frequency between the target gene and marker A is 5 centimorgans (cM), signifying a 5% chance of recombination occurring between marker A and the target gene in the progeny. Similarly, the recombination frequency between marker B and the target gene is 4 cM, indicating a 4% chance of recombination between marker B and the target gene in the progeny.

However, the likelihood of a double crossover event, involving both markers A and B, is substantially lower than that of a single marker (approximately 0.4%). Consequently, when flanking markers are employed for the target gene, the reliability and precision of the selection process experience a remarkable enhancement. This insight is adapted from the formulas outlined by Liu (1998).

5. Marker-Assisted Selection in Plant Breeding Approaches

5.1. Marker-Assisted Backcrossing

Backcrossing has been a fundamental crop breeding technique for crop improvement for over a century. The parent used in backcrossing often possesses numerous desirable traits but lacks one or a few specific attributes (Allard, 1999). This method is employed when an elite cultivar requires augmentation with crucial characteristics or specific traits that must be

introduced into an elite cultivar. The elite cultivar is the recurrent parent, while the donor parent is the genotype contributing to the desired traits. Both parents are hybridized, and progeny inheriting the desired donor parent genes are selected. Subsequently, these progenies undergo multiple rounds of backcrossing with the recurrent parent until the complete genome of the recurrent parent is recovered.

The concept of backcrossing was initially introduced by Stoskopf *et al*. in 1922. The efficacy of this approach primarily relies on the precision of the selection process. Here, Marker-Assisted Selection is pivotal in facilitating accurate and efficient trait selection. Marker-Assisted Backcrossing (MAB) has three levels (Holland, 2004; *see Figure 3*).

In the first level, tightly linked markers are employed to select the gene of interest or a Quantitative Trait Locus (QTL), termed "foreground selection" (Hospital and Charcoss *et al*., 1997). This proves highly advantageous for identifying traits that require labour-intensive field screening techniques. It enables the selection of traits that are only observable during the reproductive stages of the crop at the seedling phase. Furthermore, it aids in identifying recessive alleles, which are challenging to detect using conventional methods due to their masked expression by dominant alleles.

The second level, referred to as "recombinant selection," involves choosing progeny carrying the gene of interest. The primary objective of recombinant selection is to prevent the inheritance of donor genes or chromosomal fragments linked to the target gene. This step is critical because reducing the number of linked donor fragments related to the target gene is more challenging than decreasing unlinked donor fragments. Numerous backcrosses are necessary to minimize the linked donor fragment's size, and the presence of linked donor chromosomal fragments can negatively impact the crop's performance, known as "linkage drag" (Hospital, 2005; see Figure 3). Traditional breeding procedures often result in large donor chromosomal segments even after multiple backcrosses (e.g., more than 10), which can contribute to substantial linkage drag (Ribaut & Hoisington, 1998; Salina *et al*., 2003). Using flanking markers on both sides of the gene of interest during selection, along with a minimum of two backcross generations, can significantly alleviate linkage drag (Frisch *et al*., 1999b).

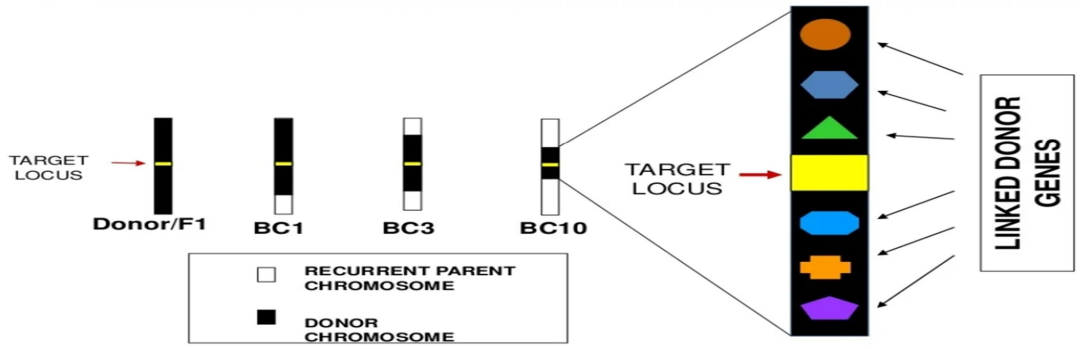

Figure 3: Large number of donor genes that are linked to the target locus negatively affects the performance of the recurrent parent. It is called as linkage drag.

5.2. Level Three of Marker-Assisted Backcrossing:

5.2.1. Background Selection

The third level of Marker-Assisted Backcrossing (MAB) involves the selection of backcross progeny with a higher proportion of the Recurrent Parent (RP) genome, commonly referred to as "Background Selection." In MAB, this objective is achieved by employing as many markers as possible that are not closely linked to the gene of interest. In the existing literature, background selection encompasses the utilization of tightly linked flanking markers positioned on both sides of the target gene for recombinant selection and the incorporation of multiple markers that are not linked to the target gene to expedite the recovery of the RP genome (Hospital and Charcoss *et al*., 1997; Frisch *et al*., 1999). These background markers, distinct from the target gene, play a pivotal role in selecting and retrieving the RP genome. Their inclusion significantly expedites the process of RP recovery. With conventional backcrossing, a minimum of six backcross generations is typically required to fully recover the RP genome, with many donor chromosomal fragments remaining linked to the target gene. By integrating numerous markers that are not linked to the target gene, it becomes feasible to achieve RP recovery as early as the BC_4, BC_3, or even BC_2 generation (Visscher *et al*., 1996; Hospital and Charcoss *et al*., 1997; Frisch *et al*., 1999). This approach results in substantial time savings, reducing the requirement for approximately four backcross generations (see Figure 4).

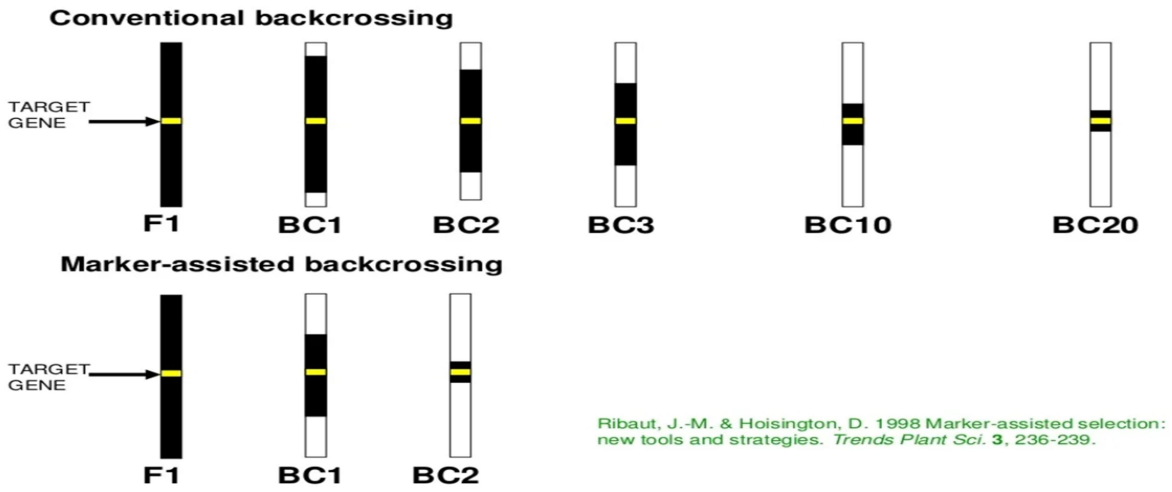

Figure 4: By using marker assisted backcrossing we can reduce donor chromosomal fragment that is linked to the target gene very quickly and it reduces the time of many BC generations.

5.2.2. Gene Pyramiding in Plant Breeding

Gene pyramiding incorporates multiple favourable genes into a single genotype to create a plant with a combination of desirable traits. While this can be achieved through traditional breeding methods, the identification and screening of plants possessing multiple genes using conventional techniques can be exceptionally challenging. For instance, traditional methods such as destructive bioassays may prove impractical when screening for disease resistance or specific characteristics. In such situations, DNA markers assume great significance in the selection process. These markers are non-destructive; enabling early-stage selection based on a single DNA sample, with phenotyping conducted subsequently using the genotype information obtained.

The most prevalent application of gene pyramiding involves amalgamating multiple disease-resistance genes within a single genotype. This approach is driven by pathogens often evolving to overcome resistance conferred by a single gene, leading to new pathogen races and the subsequent breakdown of resistance. A more stable and enduring resistance can be achieved

by pyramiding various disease-resistance genes. Numerous documented instances support the efficacy of combining different disease-resistance genes in providing long-lasting protection against specific pathogen races (Kloppers & Pretorius, 1997; Shanti *et al*., 2001; Singh *et al*., 2001).

Traditionally, pyramiding multiple resistance genes has been challenging because they often yield the same observable phenotype. As a result, progeny testing becomes essential to identify plants carrying multiple genes. However, using linked DNA markers, it is relatively straightforward to determine the presence or incorporation of multiple resistance genes within a plant. The concept of quantitative resistance involves the combination of multiple genes that confer resistance to the same pathogen. As described by Castro *et al*. (2003), this form of resistance provides the plant with heightened protection against a specific pathogen. It acts as an "insurance policy" if qualitative resistance, which relies on a single gene, proves inadequate.

5.3. Marker assisted selection in early generations:

Markers can be employed at various stages within a plant breeding program, and their utilization in the early generations can reduce population sizes. Integrating Marker-Assisted Selection (MAS) offers the advantage of potentially replacing extensive field trials. It enables the precise identification and removal of undesired plants or genotypes, allowing the retention of only those possessing the sought-after traits. Particularly in the early generations, such as F_2 and F3, MAS can eliminate approximately 70% of undesired genotypes. This holds significant importance since plant breeders typically contend with many plants during these early stages. Managing such a large population of plants can prove highly challenging. However, through early-generation selection facilitated by MAS, the plant population can be substantially reduced, allowing breeders to focus their efforts on fewer plants exhibiting the desired traits.

5.4. Combined marker assisted selection:

There are situations where both Marker-Assisted Selection (MAS) and phenotypic screening approaches can be effectively combined to enhance the efficiency of the screening process. The term "combined MAS," as coined by Moreau *et al*. (2004), represents an approach that surpasses the efficacy of either phenotypic screening or MAS used in isolation. This combined approach proves particularly advantageous when dealing with many Quantitative Trait

Loci (QTLs). It becomes more efficient when the population is substantial and the trait's heritability is low. For instance, Bohn *et al*. (2001) investigated the application of MAS to improve pest resistance in tropical maize. They found that relying solely on MAS for pest-resistance gene screening is less effective than traditional screening methods. However, when both MAS and traditional screening procedures are employed simultaneously, the screening process's efficiency is significantly enhanced. In the case of a major QTL associated with *Fusarium* head blight resistance in wheat's 3BS chromosome, a combination of MAS and conventional screening demonstrated greater effectiveness (Zhou *et al*., 2003).

In practical MAS applications, phenotypic selection at various stages remains a common practice. It is essential to employ phenotypic selection alongside MAS to validate MAS results and select genes with unknown map locations. Unless markers flanking the QTL are utilized, recombination between the marker and the QTL is typically limited, as observed in only a few instances (Sanchez *et al*., 2000; Sharp *et al*., 2001). In other words, DNA markers may not consistently yield precise results and may not always predict the phenotype accurately. Nonetheless, MAS can be instrumental in selecting a subset of plants within a breeding program, thus reducing the number of plants requiring phenotypic evaluation. Its utility is particularly evident when the cost of MAS is lower than that of conventional screening, as is the case when screening for quality traits, a concept referred to as 'tandem selection' (Han *et al*., 1997).

In traditional breeding programs, mapping QTLs for relevant traits can indirectly benefit the breeding process. Many complex traits are controlled by one or a few critical QTLs in numerous instances. For example, downy mildew resistance in pearl millet was influenced by genes of significant importance (Jones *et al*., 1995), and rice tolerance to submergence was shaped by the primary QTL Sub1, which has proven invaluable in the breeding process (Mackill *et al*., 2006).

6. Plants improved through marker assisted selection

Table 1. Examples of marker assisted backcross in cereals.

Species	Trait	Gene	Reference

Barley	Barley yellow dwarf virus	*Yd2*	Jefferies *et al*., (2003)
Barley	Leaf rust	*Rphq6*	Van Berloo *et al*., (2001)
Barley	stripe rust	*QTLs on 4H and 5H*	Toojinda *et al*., (1998)
Barley	yield	*QTLs on 2HL and 3HL*	Schmierer *et al*., (2004)
Maize	corn borer resistance	*QTLs on chromosomes 7, 9 and 10*	Willcox *et al*., (2002)
Rice	bacterial blight	*Xa21*	Chen *et al*., (2000)
Rice	bacterial blight	*Xa21*	Chen *et al*., (2001)
Rice	bacterial blight	*xa5, xa13 and Xa21*	Sanchez *et al*., (2000)
Rice	bacterial blight	*xa5, xa13 and Xa21*	Singh *et al*., (2001)
Rice	bacterial blight+ quality	*Xa13, Xa21*	Joseph *et al*., (2004)
Rice	blast	*Pi1*	Liu *et al*., (2003)
Rice	deep root	*QTLs on chromosomes 1, 2, 7 and 9*	Shen *et al*., (2001)
Rice	quality	*Waxy*	Zhou *et al*., (2003a)
Rice	root traits and aroma	*Genes on chromosomes 2, 7, 8, 9 and 11*	Steele *et al*., (2006)
Rice	Submergencetolerance resistance and quality	*Subchr9 QTL, Xa21, Bph and blast QTLs and quality loci*	Toojinda *et al*., (2005)
Wheat	Powdery mildew	*22 Pm genes*	Zhou *et al*., (2005)

Source: B. C. Y. Collard & D. J. Mackill Marker-assisted selection in plant breeding

Table 2 examples for gene pyramiding in cereals.

Species	traits	Genes from parent1	Genes from parent 2	Selection stage	Reference
Barley	barley yellow mosaic virus	*rym1*	*rym5*	F2	Okada et al., (2004)
Barley	barley yellow mosaic virus	*rym4,*	*rym4, rym9,*	F1–derived	Werner et al.,

		rym9, rym11	*rym11*	doubled haploids	(2005)
Barley	stripe rust	*RspxRspx*	*QTLs 4,7QTL 5*	F1–derived doubled haploids	Castro et al., (2003)
Rice	bacterial blight	*xa5, xa13*	*Xa4, Xa21*	F2	Huang et al., (1997)
Rice	bacterial blight, yellow stem borer, sheath blight	*Xa21, Bt*	*RC7 chitinase gene, But*	F2	Datta et al., (2002)
Rice	blast disease	*Pi1, Piz–5*	*Pi1, Pita*	F2	Hittalmani et al., (2000)
Rice	brown plant hopper	*Bph1*	*Bph2*	F4	Sharma et al., (2004)
Rice	insect resistance and bacterial blight	*Xa21*	*Bt*	F2	Jiang et al., (2004)
Wheat	powdery mildew	*Pm2*	*Pm4a*	F2	Liu et al., (2000)

Source: B. C. Y. Collard & D. J. Mackill Marker assisted selection in plant breeding

7. Reasons for the Limited Impact of Marker-Assisted Selection (MAS)

7.1. Development Stage: The application of DNA markers initially developed in the late 1980s, faced limitations regarding user-friendliness until the advent of more accessible markers such as SSRs in the 1990s. The number of available markers has substantially increased in the last decade, but MAS is still evolving. It is anticipated that the adoption of MAS will continue to grow significantly.

7.2. Reliability and Accuracy of QTL Mapping: The success of MAS heavily relies on the precision of QTL mapping studies. This aspect becomes particularly critical when studying complex traits liSke yield and quality, influenced by numerous genes with modest effects. Factors such as the replication level in phenotypic data collection and the population size can impact the accuracy of QTL mapping. Studies have indicated that small populations (e.g., fewer than 200 plants) may need more ability to detect QTLs effectively, which can affect the reliability of MAS.

7.3. Linkage between Gene and Marker: Tight linkage between markers and target genes is crucial to avoid recombination events between markers and genes. Even when an initial QTL mapping study suggests a strong linkage, the accuracy of such linkage can be uncertain. Marker validation processes are essential to ensure the marker's reliability in predicting phenotypes.

7.4. High Cost of MAS: The cost of MAS can vary significantly compared to conventional screening methods. Factors such as the phenotypic evaluation method, trait heritability, expenses for field and greenhouse trials, and labour costs can all influence the cost-benefit ratio of MAS. Substantial initial capital investments are required for machinery and equipment, with ongoing expenses for maintenance.

8. Future Prospects of MAS

The future of MAS holds promise, as it has already found widespread adoption in numerous plant breeding institutes, generating vast amounts of data from MAS studies and QTL mapping. However, the extent of its adoption will largely depend on funding availability. The past decade has witnessed significant growth in genomics research, identifying many traits and associated genes. These genes can be valuable for "association mapping" and, eventually, MAS. Nevertheless, genomics research can be cost-intensive and may only be feasible for some countries, significantly underdeveloped and many developing nations.

Advanced methods for DNA extraction and high-throughput genotyping platforms have been developed, particularly for SNP and SSR markers in various cereals. To promote the widespread use of MAS, cost-effective markers, increased availability of publicly accessible markers, and user-friendly databases for storing marker and QTL data will be essential. MAS should be an integral part of plant breeding techniques due to its significant potential for crop improvement.

The high costs associated with infrastructure, chemicals, equipment, and markers have limited the widespread use of MAS, primarily in developed countries. To address this issue, international collaboration through organizations like the *Consultative Group of International Agricultural Research* (CGIAR) is crucial to facilitate the rapid dissemination of MAS technology in developing countries. Private industries must come together to support the application of molecular technology, benefiting humanity and global interests alike. International cooperation among research institutes engaged in MAS programs is essential to harness the potential of this technology.

Efforts should be made to make MAS technology accessible to developing countries through collaborations between public and private organizations. Capacity-building programs in

MAS technology, organized by *International organizations like the Food and Agriculture Organization (FAO)* and CGIAR, should be implemented in developing and underdeveloped nations. MAS are a highly efficient tool for crop improvement and breeding programs, capable of reducing the time required for improvement and accelerating variety development. However, it should be viewed as a complementary approach rather than a substitute for conventional breeding methods.

9. Conclusions

Plant breeding has substantially enhanced various crop varieties, with most breeding programs predominantly relying on traditional methods. While progress can be achieved through these conventional approaches, it takes time and effort. Marker-Assisted Selection (MAS) offers the potential to significantly expedite the improvement of diverse crops. MAS can save four or more generations of time in any breeding program by providing precise and reliable results in a relatively short timeframe. This has the potential to bring about a substantial impact on crop enhancement. However, the persistently high cost associated with MAS remains a significant impediment, delaying its integration with traditional techniques in plant breeding programs. To mitigate costs and enhance efficiency, it is essential to develop crop-specific MAS approaches. Recent years have witnessed the development of numerous novel marker technologies, which have considerably reduced the expenses associated with MAS. If these emerging marker technologies successfully facilitate easy access to the required equipment while concurrently reducing the cost of MAS, many developing and underdeveloped countries could incorporate MAS into their conventional breeding programs.

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