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Marker-Assisted Selection in Horticulture: A Comparative Review Across Vegetables, Fruits and Flower Crops

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Authors' contributions

This work was carried out in collaboration among all authors. Author TAP managed the literature searches and wrote the first draft of the manuscript. Author AIP conceptualized, reviewed and edited the manuscript. Author DDC reviewed and edited the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

Marker-assisted selection (MAS) has become one of the most reliable and efficient tools in plant breeding for improving complex traits such as disease resistance, fruit quality, shelf-life, and pigment expression, especially in horticultural crops including vegetables, fruits, and flowers. This review focuses on three representative crops - tomato, papaya, and marigold - to understand how MAS has been practically applied at different scales. Tomato exemplifies advanced MAS pipelines,

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with successful pyramiding of resistance genes such as Ty-2, Ty-3, Ph-3, and I2. Papaya, despite fewer genomic resources, has benefitted from early selection for sex type and PRSV resistance. MAS in floricultural crops like marigold is still emerging, yet efforts in SSR, AFLP, and RAPD marker development are promising. This paper compares marker systems, crop-specific examples, and challenges across these species, highlighting how MAS can transform horticultural breeding through integration with genomic tools.Despite these successes, a critical gap persists between marker discovery and their widespread use in breeding. As emphasized by Foolad & Panthee (2012), many trait-linked markers in tomato remain underutilized due to poor validation across genetic backgrounds and lack of polymorphism in breeding populations, underscoring the importance of developing robust, widely applicable markers for practical MAS deployment.

Keywords: MAS; marigold; papaya; tomato.

1. INTRODUCTION

Horticultural crops such as vegetables, fruits, and flowers play crucial roles in global nutrition, income generation, and biodiversity (Lastochkina et al., 2022). However, many of these crops show high heterozygosity, complex inheritance, and environmental interactions, making conventional breeding slow and less predictable (Collard & Mackill, 2008). Marker-assisted selection (MAS) accelerates improvement by using DNA markers linked to genes or QTLs of interest, enabling selection even at seedling stage (Joshi & Dhawan, 2007). Over the past two decades, MAS has seen practical implementation in tomato, papaya, and early adoption in ornamental crops like marigold (De Mori & Cipriani, 2023; Maji et al., 2023). This paper provides a comparative understanding of MAS strategies in these crops.

2. MARKER SYSTEMS IN MAS

The success of MAS depends significantly on the type and quality of molecular markers used. Different marker systems vary in reproducibility, cost, dominance, and level of genomic resolution (Gupta et al., 1999; Semagn et al., 2014):

2.1 Early Marker Systems: RAPD, AFLP, ISSR

- RAPD was one of the earliest methods used due to its simplicity, but suffered from poor reproducibility (Gupta et al., 1999).
- AFLP offered higher polymorphism and was valuable in species with limited genome data, especially florals (Choudhary et al., 2014).
- ISSR markers were mainly used for diversity analysis in crops like marigold where other markers were unavailable (Priya et al., 2017).

2.2 SSR and SCAR Markers

- SSR (Simple Sequence Repeats) became widely used due to their co-dominant nature, reproducibility, and distribution across the genome (Gupta et al., 1999; Topu et al., 2023).
- In tomato and papaya, SSRs are applied for disease resistance mapping, sex identification, and fruit quality traits (Joshi & Dhawan, 2007).
- SCAR markers, developed from RAPD fragments, are trait-specific and used in tomato for genes like I2 (*Fusarium* wilt) and Ty-2/Ty-3 (TYLCV resistance) (Foolad & Panthee, 2014).

2.3 CAPS and dCAPS Markers

- CAPS markers are gene-specific and use restriction digestion to distinguish alleles (Pote et al., 2021). They are widely used in tomato for tracking TMV (Tm-22) and late blight resistance (Ph-3) (Hanson et al., 2016).
- dCAPS are used when restriction sites are not naturally present and require engineered mismatches (Collard & Mackill, 2008).

2.4 SNPs and KASP

- SNPs (Single Nucleotide Polymorphisms) are the most abundant and efficient markers, used in high-throughput systems like KASP (Semagn et al., 2014).
- Tomato and papaya benefit from SNP-based genotyping, while florals like marigold still lag due to insufficient genome resources (Varshney et al., 2014).

Table 1. Marker selection criteria for MAS

Marker Type	Reproducibility	Cost	Dominance	Usage in MAS
RAPD	Low	Low	Dominant	Rarely used now
AFLP	Medium	High	Dominant	Used in genetic diversity studies
SSR	High	Medium	Co-dominant	Widely used in all 3 crops
SCAR	High	Medium	Co-dominant	Trait-specific; used for disease resistance
CAPS/dCAPS	High	Medium	Co-dominant	Used for disease gene tracking in tomato
SNP/KASP	Very high	Varies	Co-dominant	Morden MAS; used for high-throughput screening

3. MAS IN TOMATO: A MODEL VEGETABLE CROP

Tomato exemplifies successful MAS implementation, supported by a complete reference genome and a wealth of trait-linked markers (Foolad & Panthee, 2014).

3.1 Key Disease Resistance Traits

- TYLCV resistance through Ty-1, Ty-2, Ty-3 (SCAR markers P1-16, P6-25) (Foolad & Panthee, 2014).
- *Fusarium* wilt via I2 (SCAR marker I2OH).
- Late blight through Ph-2, Ph-3 (CAPS markers TG328, dTG422) (Hanson et al., 2016).
- Other pathogens like TMV and bacterial wilt also have mapped genes and markers (Hanson et al., 2016).

Although numerous resistance genes and markers have been identified, their actual application in breeding programs is often limited. Foolad & Panthee (2012) highlighted that while markers for major resistance genes such as Ty-2, Ty-3, I2, and Ph-3 have been successfully used, many other markers lack consistent polymorphism or have not been validated across diverse germplasm. This restricts their reliability and routine use in large-scale breeding pipelines.

3.2 Gene Pyramiding in Tomato

Using marker-assisted pyramiding, breeders have combined up to six resistance genes in elite lines with high yield, improved lycopene, and enhanced shelf life (Hanson et al., 2016).

Marker-assisted pyramiding of resistance genes has been a hallmark achievement in tomato breeding. However, Foolad & Panthee (2012) cautioned that such progress has been mostly restricted to major resistance genes, while quantitative traits such as yield, abiotic stress tolerance, and fruit quality remain challenging. They argued that MAS alone is insufficient for these complex traits and should be integrated with phenotypic selection and, increasingly, with genomic selection approaches to achieve sustainable genetic gains.

Table 2. Tomato-specific markers

Trait/disease	Gene(s)	Marker Type	Example Marker(s)
Tomato Yellow Leaf Curl Virus [TYLCV]	Ty-2, Ty-3	SCAR	P1-16, P6-25
Fusarium wilt	I2	SCAR	I20H
Late blight	Ph-2, Ph-3	CAPS	dTG422, TG328
Bacterial wilt	Bwr-12	SCAR	SLIM12-2, SLIM12-10
Gray leaf spot	Sm	CAPS	CT55/DdeI
Tobacco mosaic virus	Tm-22	CAPS	NCTm-019
Shelf life/ripening	Rin, nor	Gene-specific	Functional gene primers
Fruit shape and firmness	SUN, OVATE	SNP/SSR	Linked QTLs

Note: According to Foolad & Panthee (2012), many of these markers require further validation for broad use. For instance, Ty-2 and Ty-3 markers are routinely used in hybrid breeding programs, while markers for traits such as late blight (Ph-2) or ripening (Rin, nor) often show variable performance depending on genetic background

4. MAS IN PAPAYA: A FRUIT CROP WITH STRATEGIC TRAITS

MAS in papaya targets early selection for sex and PRSV resistance, two traits with direct commercial value (Deputy et al., 2002; Gonsalves, 1998).

Table 3. Markers used for key traits in Papaya

Trait	Marker Type	Example Marker	Application Stage
Sex determination	SCAR	Y-specific SCAR markers (e.g., PSDM)	Seedling screening
PRSV resistance	SCAR, SSR	Markers linked to virus resistance genes	Parental screening, Hybrid selection
Fruit flesh colour	SSR	Associated with carotenoid pathway alleles	Advanced backcross/selection
Shelf-life / ripening	SSR	Under research; some associations reported	Exploratory/QTL analysis

4.1 Sex Determination

Sex-linked SCAR markers (e.g., PSDM) allow selection of hermaphrodite plants at the seedling stage (Deputy et al., 2002).

4.2 PRSV Resistance

Transgenic cultivars like ‘SunUp’ and ‘Rainbow’ were developed and further integrated into MAS pipelines for PRSV resistance (Gonsalves, 1998; Fitch et al., 1992).

4.3 Breeding Examples and Impact

- The Hawaii program developed ‘SunUp’ and ‘Rainbow’ papaya using MAS and transformation for PRSV resistance - which were later combined with SCAR markers for sex.
- In India, several efforts have used SSR and SCAR markers to screen germplasm for PRSV tolerance and maintain high-quality hermaphrodite lines.
- MAS has also helped avoid planting unproductive male trees - improving both land use efficiency and yield per acre.

4.4 Challenges in Papaya MAS

- Marker-trait linkage for complex traits like fruit firmness, sweetness, or shelf-life is still weak.
- PRSV resistance is often strain-specific, so MAS alone isn’t a complete solution.
- Most MAS work is still concentrated in a few breeding centers, not yet mainstream.

Still, for a fruit crop like papaya, even these two traits - sex type and PRSV resistance - have made MAS worth it. It has saved time, money, and space in the nursery phase and made breeding programs more predictable and targeted.

5. MAS IN MARIGOLD: FLORICULTURE BREEDING IN PROGRESS

MAS in marigold remains in a developmental phase, mostly used in diversity and preliminary trait studies due to lack of genome data (Choudhary et al., 2014; Priya et al., 2017).

5.1 Target Traits

- Petal pigmentation via AFLP and SSR (Choudhary et al., 2014).
- Dwarfness and plant height linked to RAPD/SSR (Priya et al., 2017).
- Flowering time analyzed using ISSR (Phatak & Chavan, 2010).

5.2 Limitations and Current Status

- Most of the markers in marigold are still not tightly linked to major genes. That limits their usefulness in routine MAS.

Table 4. Marker types used in marigold

Trait	Marker Type	Example	Current status
Petal colour (orange/yellow)	AFLP, SSR	Used for clustering cultivars by carotenoid expression	In use for diversity studies
Dwarfness/ plant height	RAPD, SSR	Linked to internode length in African marigold	Preliminary associations
Flower time	ISSR, SSR	Associated with early vs late flowering	Under exploration
Cultivar identification	SSR	Used for fingerprinting and variety protection	Standardized in some labs

- Unlike tomato or papaya, no reference genome is fully available yet - which makes high-resolution QTL mapping and GWAS difficult.
- Also, flower color and fragrance traits are often governed by multiple small-effect genes, which makes single-marker selection less effective.

That said, marigold is moving forward. Efforts are ongoing to develop better mapping populations, and transcriptomic studies are helping identify floral trait-related genes. Once more genomic tools are in place, MAS in flowers like marigold will become more powerful and precise.

6. CROSS-CROP ADVANCES AND INTEGRATION

When we look at how MAS is being used across tomato, papaya, and marigold, a few things become clear. Each crop is at a different stage in terms of genomic tools, mapped traits, and breeding integration. Tomato is way ahead - everything from gene pyramiding to SNP arrays is already in use. Papaya is somewhere in the middle - specific markers like SCARs are doing their job, especially for traits like sex and PRSV resistance. Marigold, on the other hand, is still building its base - most of the work is focused on marker development and diversity studies. But even with these differences, some common trends and future directions are starting to emerge.

Tomato leads MAS integration with multi-trait pyramiding, papaya has implemented targeted MAS for key traits, while marigold is still developing base resources (Varshney et al., 2014). SNP-based genotyping is increasingly replacing SSR and SCAR in high-throughput platforms (Semagn et al., 2014).

Compared to papaya and marigold, tomato represents the most advanced model for MAS in horticultural breeding. Yet, as Foolad & Panthee (2012) observed, even in tomato there is a considerable gap between the large number of published markers and their practical use in breeding. This highlights a common bottleneck across crops: markers must be validated, cost-effective, and broadly applicable before they can be fully integrated into mainstream breeding programs.

6.1 What's Working Across All Crops

- Trait-specific markers (like Ty-genes, I2, sex markers, dwarfness markers) are proving useful when they are tightly linked and validated.
- Early selection at the seedling stage is reducing field trial loads, especially in crops like papaya and tomato.
- MAS is helping breeders combine multiple traits faster, especially when pyramiding resistance genes or combining disease + quality traits.

6.2 Tools That Are Gaining Momentum

- SNP markers and KASP assays are becoming the go-to tools in tomato and slowly making their way into other crops.
- Transcriptome-based markers are helping in ornamentals where full genome data isn't available - marigold studies are now using this to explore pigment biosynthesis.
- Combining MAS with conventional selection and phenotyping is giving better results than relying on markers alone.

Table 5. Gaps that still exist in MAS

Crop	Major Gaps in MAS Implementation	Genomic Resource Status
Tomato	Minor traits(flavour, abiotic stress) not fully mapped	High - Full genome, SNP panels, QTL maps
Papaya	Few markers for fruit quality, limited virus resistance range	Medium - genome available, SSRs, SCARs
Marigold	No reference genome, limited trait-linked markers	Low - Mainly SSR, AFLP, RAPD studies

7. CHALLENGES AND FUTURE PROSPECTS

Key challenges include lack of validated markers for complex traits, high genotyping cost (especially for public institutions), and slow adoption in ornamental crops (Collard & Mackill, 2008; Xu & Crouch, 2008). The future lies in integrating MAS with genomic selection, transcriptomics, and CRISPR (Varshney et al., 2014; Heffner et al., 2009).

One of the key challenges in MAS, especially in tomato, lies in the translation of genetic discoveries into breeding practice. Foolad & Panthee (2012) noted that many markers reported in literature remain untested or show poor reproducibility across breeding populations. They further pointed out that public breeding programs often lack infrastructure for high-throughput genotyping, whereas private companies have adopted MAS more readily for disease resistance screening, hybrid purity testing, and targeted backcrossing.

7.1 Current Challenges in MAS

- Marker–trait gaps in many crops: Not all important traits have tightly linked, validated markers. In flowers especially, we’re still stuck with partial linkage or markers based on phenotype.
- Genotyping cost & access: While SNPs and KASP platforms are great, not every breeder has access to high-end labs or funding, especially in public-sector programs.
- Polygenic traits are hard to handle: For complex traits like flavour in tomato, or fragrance in marigold, MAS isn’t enough unless multiple markers or genomic selection tools are used.
- Limited marker work in floriculture: Compared to vegetables and fruits, flowers like marigold still lack reference genomes, high-density maps, or large diversity panels.

7.2 What Needs to Be Done

- More investment in genomic resources for under-researched crops (especially ornamentals).
- Integration of MAS with other tools like speed breeding, genomic selection (GS), and even CRISPR - that’s how we get precision + speed.
- Training and infrastructure for young breeders - especially in developing countries - to actually apply MAS practically, not just learn it in theory.

7.3 Future Direction

- MAS is moving from single-gene tracking to multi-trait, genome-wide approaches.
- Crops like marigold will benefit hugely once transcriptomics and pan-genomics become more accessible.
- In the next few years, we’ll likely see MAS being used not just for disease resistance, but also for nutritional quality, aroma, post-harvest traits, and even consumer preferences.

MAS has already proven itself - now the challenge is scaling it up, making it crop-specific, and combining it with other modern breeding tools. The future of horticultural crop improvement lies in layering multiple strategies, and MAS will continue to be one of the most powerful among them

8. CONCLUSION

Marker-assisted selection (MAS) has emerged as a transformative approach in horticultural breeding, offering precision, efficiency, and the ability to track complex traits early in the breeding cycle. Its success is most evident in tomato, where the integration of SCAR, CAPS, and SNP markers has enabled the pyramiding of multiple disease resistance genes, such as Ty-2, Ty-3, I2, and Ph-3, into elite cultivars. These advancements have been further reinforced by functional gene markers associated with fruit firmness, shelf life, and lycopene content, which improve both agronomic and nutritional traits.

In papaya, MAS has provided practical solutions to long-standing breeding challenges, notably in the early identification of hermaphrodite plants using sex-linked SCAR markers and in controlling papaya ringspot virus (PRSV) through both transgenic and MAS-integrated approaches. These interventions have led to increased nursery efficiency, improved field uniformity, and more targeted hybrid development.

Floricultural crops such as marigold are still building their MAS frameworks, but progress is visible. Studies using SSR, RAPD, and ISSR markers have demonstrated early associations with key traits like petal pigmentation, dwarfness, and flowering uniformity. Although the absence of a reference genome limits high-resolution mapping, transcriptomics and diversity panels are now being used to identify functional markers for ornamental traits.

Scaling MAS across horticultural species will require greater investment in genomic infrastructure, especially in under-researched crops. Open-access SNP genotyping platforms (e.g., KASP), when paired with transcriptomics and genome sequencing, offer powerful solutions to current limitations. Moreover, integrating MAS with complementary strategies like speed breeding, CRISPR-based gene editing, and genomic selection can further enhance trait pyramiding and adaptability.

Taken together, tomato illustrates both the promise and the limitations of MAS. As Foolad & Panthee (2012) emphasized, despite extensive marker development, the true potential of MAS has yet to be realized due to issues of marker validation, cost, and limited application to polygenic traits. Addressing these challenges through the integration of SNP-based genotyping, genomic selection, and next-generation sequencing platforms will be key to unlocking the full impact of MAS in horticultural crops.

Finally, for widespread and equitable adoption of MAS, there must be greater emphasis on capacity building, breeder training, and access to molecular labs - especially in public-sector programs and floricultural breeding centers. With strategic support, MAS has the potential to become not just a specialized tool but a foundational component of mainstream horticultural breeding.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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