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### Applications of molecular markers in onion (*Allium cepa* L.) improvement - A review

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#### ABSTRACT

Molecular markers have emerged as indispensable tools in onion improvement, facilitating precise assessment of genetic diversity, trait mapping, and marker-assisted selection. Their application has accelerated the development of cultivars with desirable characteristics, including enhanced bulb quality, disease resistance, and stress tolerance. Molecular breeding has revolutionized onion improvement by providing reliable, environment-independent methods for germplasm characterization, genetic diversity analysis, and the construction of high-density genetic maps for gene tagging and selection. These markers are extensively employed in DNA fingerprinting for varietal identification, breeding line validation, and plant variety protection. They also play a crucial role in identifying and transferring resistance genes against biotic and abiotic stresses. Onion breeding has particularly benefited from marker-assisted improvement of traits such as male sterility, earliness, bulb color, yield, total soluble solids, and bolting resistance. Recent advancements have enabled the mapping of genes controlling bulbing and flowering, as well as loci associated with disease resistance and hybrid development. Overall, molecular marker technologies have greatly enhanced the efficiency of onion breeding, supporting the rapid development of elite, high-performing cultivars.

#### Introduction

Onion (*Allium cepa* L.), a diploid species ( $2n = 2x = 16$ ) of the family Alliaceae, is one of the most extensively cultivated and consumed vegetables worldwide (Mohamed & Tawfik, 2025). Renowned for its culinary versatility, medicinal value, and pharmacological significance, onion ranks among the top five vegetable crops worldwide in both production and economic importance. Onion ranks as the second most important vegetable crop in India,

cultivated over 17.40 lakh ha with an annual production of 30.21 million tons; however, its productivity (17.36 t/ha) remains below the global average (FAOSTAT, 2023). Believed to have originated in Central Asia, with the Mediterranean region serving as a secondary center of diversity (Gupta *et al.*, 2024a), onion cultivation sustains millions of smallholder farmers and contributes substantially to export earnings in many developing nations (Ahmed & Sallam, 2020). Onions are rich in bioactive constituents such as flavonoids, sulfur-

containing compounds, and antioxidants that impart anti-inflammatory, antimicrobial, and anti-carcinogenic properties (Sagar *et al.*, 2022). In addition to their nutritional and health benefits, onions play a vital role in ensuring year-round food availability and enhancing dietary diversity across regions. However, productivity and quality are severely affected by biotic stresses including stemphylium blight (*Stemphylium vesicarium*), purple blotch (*Alternaria porri*), Fusarium basal rot (*Fusarium oxysporum* f. sp. *cepae*), and insect pests like thrips (*Thrips tabaci*) (Cramer, 2000; Gill *et al.*, 2015; Khar *et al.*, 2022a; Gupta *et al.*, 2024a; Gupta *et al.*, 2025). Additionally, abiotic challenges such as drought, salinity, and temperature extremes intensified by climate change further contribute to yield instability (Ratnarajah & Gnanachelvam, 2021). Postharvest issues, including sprouting and bulb decay, also cause considerable storage and market losses (Muhie, 2022).

While conventional breeding has improved onion performance, its progress is hindered by the crop's biennial growth cycle, cross-pollinated nature, and large genome (~16.4 Gb), all of which slow genetic gain (Havey, 2018). Moreover, complex inheritance patterns and strong genotype  $\times$  environment interactions limit the efficiency of selection (Khosa *et al.*, 2016). Modern molecular tools such as marker-assisted selection (MAS), quantitative trait loci (QTL) mapping, and genome-wide association studies (GWAS) now provide more precise and rapid means to identify genes controlling disease resistance, bulb quality, and stress tolerance (Sharma *et al.*, 2024). Integrating these molecular approaches with conventional breeding offers a robust pathway towards accelerating genetic improvement and achieving sustainable onion productivity.

### Onion genomics and molecular markers

Molecular markers have become indispensable tools in onion research, facilitating germplasm characterization, genetic diversity analysis, cultivar identification, phylogenetic studies, genome mapping, and gene tagging (Yang *et al.*, 2015). Commonly employed marker systems include restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), inter-simple sequence repeats (ISSR), simple sequence repeats (SSR or microsatellites), amplified fragment length polymorphism (AFLP), sequence-characterized amplified regions (SCAR), sequence-related amplified polymorphism (SRAP), cleaved amplified polymorphic sequences (CAPS), and single nucleotide polymorphisms (SNPs) (Semagn *et al.*, 2006; Chinnappareddy *et al.*, 2013).

Onion possesses an exceptionally large genome (~16.4 Gb), composed predominantly (>95%) of repetitive elements, particularly long terminal repeat (LTR) retrotransposons (Pearce *et al.*, 1996; Kelly & Leitch, 2011). This high level of repetitiveness complicates accurate genome assembly, leading molecular breeding efforts to depend largely on linkage maps and marker-based approaches. The first molecular marker study in onion was conducted by De Vries *et al.* (1992), yet genomic resources for the crop remain less developed compared to many other species. While related crops such as garlic (16.2 Gb) and asparagus (1.1 Gb) have complete genome assemblies, onion comparative genomics remains limited due to reduced synteny (Harkess *et al.*, 2017; Sun *et al.*, 2020).

Recent technological advances, including RNA sequencing (RNA-seq), QTL mapping, and specialized databases like the Onion Genomic Resource (OGR), have enhanced gene discovery related to bulb development, stress tolerance, and male sterility (Shukla *et al.*, 2016; Sharma *et al.*, 2024). High-quality genome assemblies represent a major milestone: a 12.77 Gb chromosomal-level assembly comprising 65,730 annotated genes (Finkers *et al.*, 2021) and a 14.9 Gb assembly predicting 540,925 genes, of which 47,066 are supported by RNA-seq data (Cho *et al.*, 2025). These genomic resources are poised to accelerate functional genomics research and advance molecular breeding in onion.

### Varietal identification and genetic diversity in onion

Molecular markers are widely used for onion varietal identification and diversity analysis due to their reproducibility and stability. Several marker systems, including RFLP, RAPD, AFLP, SSR, ISSR, SRAP, SNPs, and intron length polymorphic (ILPs), have been employed with varying levels of efficiency (Table 1).

RAPD markers have differentiated onion cultivars into distinct genetic clusters, though often showing weak correlation with phenotype (Tanikawa *et al.*, 2002; Sangeeta *et al.*, 2006). RAPD and ISSR analyses further grouped cultivars into major clusters, while SRAP markers revealed higher breeding utility (Sudha *et al.*, 2019; Mansour *et al.*, 2020). SSR markers have proven particularly effective, enabling fine-scale discrimination within accessions (McCallum *et al.*, 2008; Gupta *et al.*, 2020). Studies using EST-SSR and genomic SSRs reported high polymorphism, unique alleles, and strong genetic differentiation across accessions, useful for seed purity testing and breeding (Anandhan *et al.*, 2014;

Hanci & Gokce 2016; Lyngkhai *et al.*, 2021). SNP-based approaches, derived from next generation sequencing (NGS) and ddRAD-seq, have provided reliable cultivar authentication and insights into domestication (Khar *et al.*, 2011; Lee *et al.*, 2018; Villano *et al.*, 2019).

More recently, ILP markers have been used for the genetic grouping of onion genotypes, assisting in the selection of parental lines for breeding (Khade *et al.*,

2022; Gupta *et al.*, 2024b). SSR-based studies continue to reveal moderate diversity and additive gene action, supporting hybrid development strategies (Raj *et al.*, 2022). Additionally, analysis of the *atp6* gene highlighted phylogenetic clustering of *A. cepa* and *A. sativum*, with implications for male sterility restoration (Gowd *et al.*, 2023). Overall, molecular markers particularly SSRs and SNPs have greatly enhanced onion diversity analysis, varietal identification, and breeding efficiency.

**Table 1.** Applications of molecular markers in onion crop improvement

Markers	Applications
RFLP	Genetic diversity analysis, comparative mapping and synteny analysis, genetic mapping, hybrid confirmation
RAPD	Hybrid confirmation, genetic diversity analysis, bulk segregant analysis
SSR	DNA fingerprinting and genetic identity test, gene mapping, genetic diversity analysis, comparative mapping and synteny analysis, hybrid confirmation, MAS
ISSR	DNA fingerprinting and genetic identity test, genetic diversity analysis, hybrid confirmation
SNP	Genetic diversity analysis, genetic mapping, hybrid confirmation, MAS, genomic selection
AFLP	DNA fingerprinting, studying diversity and germplasm characterization

### Genetic linkage mapping and QTL identification in onion

Genetic linkage maps are critical for marker-trait associations and marker-assisted selection (MAS). In onion, mapping has been constrained by its large (~16 Gb) genome and biennial nature (Jo *et al.*, 2017). Nevertheless, molecular markers have enabled the construction of saturated maps and the identification of QTLs for key traits.

Early work mapped ESTs using CAPs in the ‘Brigham Yellow Globe’ × ‘Ailsa Craig’ population, showing that SSCP/duplex analysis is a cost-effective approach for gene mapping (McCallum *et al.*, 2001). Initial linkage maps for *A. fistulosum* were developed using AFLP, SSR, and CAPS markers, covering 775-947 cM (Takayoshi *et al.*, 2005), while SSR-based maps from F<sub>2</sub> populations identified 17 linkage groups, later aligned with *A. cepa* chromosomes using alien addition lines (Tsukazaki *et al.*, 2008).

Trait mapping has revealed markers linked to purple blotch resistance (Chand *et al.*, 2018), QTLs for pungency associated with *SiR* and *ATPS* on chromosome 3 (McCallum *et al.*, 2007), and genomic regions controlling flower stalk height and heterosis (Li *et al.*, 2023). The latter study generated the most detailed map to date, comprising 10,584 SLAF markers across eight linkage groups (928.32 cM, 0.09 cM spacing), validated by localizing the male fertility (*Ms*) locus. Beyond trait mapping, genome-wide analyses have identified transcription factor families such as 24 GATA genes, implicated in development,

hormone regulation, and stress tolerance (Bose *et al.*, 2025). These advances highlight the increasing resolution of onion maps and their growing utility in functional genomics and breeding applications.

### Molecular markers in onion trait improvement

Molecular markers have significantly advanced onion breeding by enabling precise improvement of complex traits. Bulb color, determined by flavonoids such as anthocyanins, is controlled by major loci (I, C, G, L, L<sub>2</sub>, R) and genes like *DFR* and *ANS*, with functional markers aiding selection (Kim *et al.*, 2005; Kim *et al.*, 2009a). A major QTL on chromosome 7 near *DFR* explains ~88% of anthocyanin variation (Choi *et al.*, 2020). Regulatory factors, including *AcB2* (C locus) and *AcMYB1*, as well as allelic variations in *ANS* and novel genes such as *AcLAC12*, further shape pigmentation (Zhang *et al.*, 2018; Kim *et al.*, 2017; Han *et al.*, 2023).

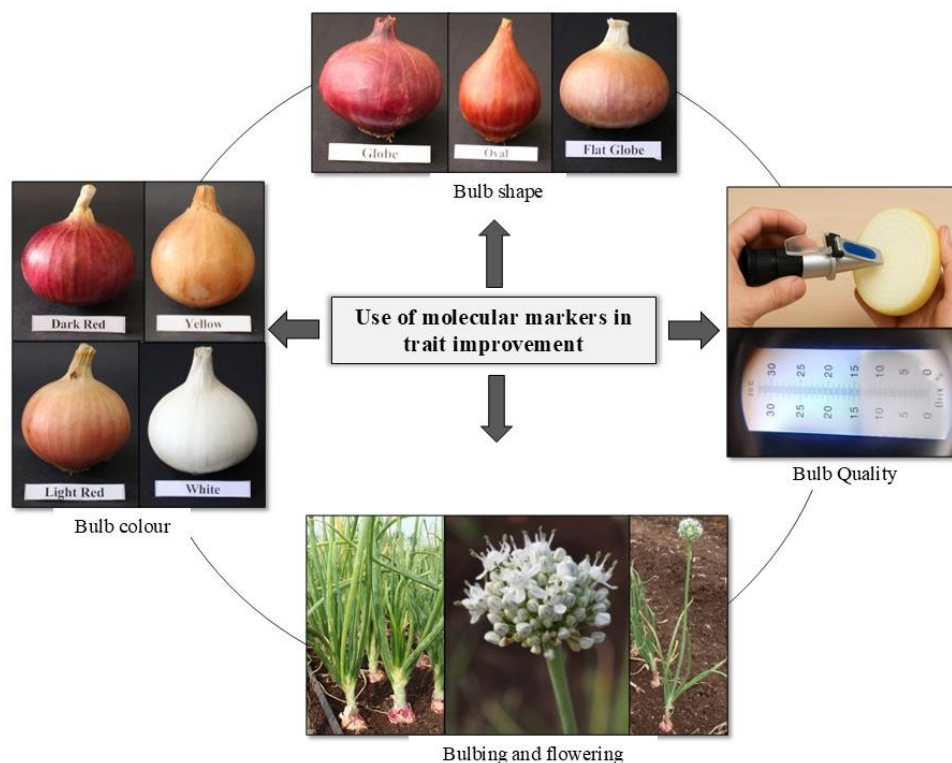
For yield traits, SNPs linked to bulb weight have been identified, with machine learning achieving >80% prediction accuracy, while bulb shape variation is largely explained by PC1 (height-to-diameter ratio) and a QTL on chromosome 5 (Sekine *et al.*, 2023; Choi *et al.*, 2024). Bulb quality traits such as soluble solids, sugars, fructans, and pungency have also been mapped using SSRs, ILPs, and NGS tools. QTLs for sugar metabolism and sulfur-related genes (*SiR*, *ATPS*) regulate sweetness and pungency (McCallum *et al.*, 2007; Havey *et al.*, 2004), while *LFS* on chromosome 5 is a key determinant of lachrymatory

factor (Masamura *et al.*, 2012). High-TSS genotypes identified using SSRs and ILPs support breeding for processing quality (Singh *et al.*, 2021; Mahajan *et al.*, 2025).

Bolting in onion is characterized by high photosynthesis, low respiration, and carbohydrate accumulation, which induces flowering hormones such as vernalin or florigen, promoting flower bud formation and shortening the bulb's life cycle (Gupta

*et al.*, 2015). Bulbing and flowering responses, regulated by photoperiod and vernalization, are controlled by *FT* homologs (*AcFT1*, *AcFT4*, *AcFT2*), with QTLs associated with bolting and bulbing traits (Lee *et al.*, 2013; Mareidiya, 2020; Havey, 2024).

Collectively, structural, regulatory, and QTL-based markers for bulb color, yield, quality, bulbing, and flowering constitute a powerful toolkit for accelerating onion breeding programs (Fig. 1).



**Fig. 1.** Use of molecular markers in onion trait improvement

### Molecular markers for male sterility and hybrid breeding in onion

Male sterility plays a crucial role in hybrid seed production in onion, and the use of molecular markers has significantly advanced the detection of different cytoplasmic types and identification of maintainer lines (Table 2). Early investigations differentiated normal (N) and sterile (S, T) cytoplasm through PCR-based and cytoplasm-specific markers (Havey, 1995; Engelke *et al.*, 2003). The subsequent discovery of the chimeric mitochondrial gene *orf725* present in CMS-S and CMS-T lines but absent in N cytoplasm facilitated the development of reliable PCR markers for cytoplasm classification (Kim *et al.*, 2009b).

Markers linked to the nuclear *Ms* locus are equally important for detecting maintainer genotypes. RAPD, CAPS and SSR-derived markers such as *jnurf13*, *jnurf05* and *ACms.1100* showed close linkage with *Ms* (Bang *et al.*, 2013; Park *et al.*, 2013; Kim & Kim 2015), allowing early identification of maintainers

and elimination of fertile contaminants. However, marker reliability varies across germplasm, highlighting the need for additional validation (Khar & Saini 2016).

Population studies have revealed high frequencies of S cytoplasm in Indian germplasm (Saini *et al.*, 2015), while authentic T cytoplasm remains rare in commercial programs (Havey & Kim 2021). Gupta *et al.* (2016) identified two naturally occurring male-sterile lines from red onions (RGP-4-Sel and Arka Kalyan), and Khar *et al.* (2022) reported five S-cytoplasm sterile plants out of eight in Arka Kalyan. However, these lines still need full characterization to clarify their S or T cytoplasmic status. Khar *et al.* (2022b) identified T cytoplasm in Indian accessions for the first time, expanding resources for hybrid development.

Chloroplast and mitochondrial polymorphism analyses (Von *et al.*, 2013), together with nuclear-cytoplasmic gene expression studies (Yuan *et al.*, 2018), have provided deeper insights into the

mechanisms of cytoplasmic male sterility (CMS). Structural rearrangements in mitochondrial genomes that generate novel ORFs are key contributors to CMS diversity (Hanson & Bentolila, 2004). The advent of PCR-based assays has enabled rapid and precise identification of sterile (A), maintainer (B), and restorer (R) lines, significantly shortening breeding cycles from years to months compared with traditional progeny testing (Satoh *et al.*, 1993; Havey,

2000). Moreover, the utilization of alternative CMS sources from *A. galanthum* and *A. roylei* has expanded the genetic base available for hybrid onion breeding (Havey, 1999; Vu *et al.*, 2011).

Overall, CMS- and *Ms*-linked markers have transformed onion hybrid breeding, ensuring efficient line development, genetic purity, and improved hybrid seed productivity.

**Table 2.** Molecular markers linked to male sterility and fertility restoration in onion

Cytoplasm/ <i>MS</i> locus trait	Marker/ gene	References
CMS-S	AcMSH1, 5'cob, orfA501, orf725, orfA501	Mainkar <i>et al.</i> , 2023; Saini <i>et al.</i> , 2015; Abbasi, 2023
CMS-S & CMS-T	Orf725	Kim <i>et al.</i> , 2009b
N Cytoplasm	IGS insertion marker orfA501, orf725	Abbasi, 2023
Cytoplasm - T	accD & MKFR	Khar <i>et al.</i> , 2022b
<i>Ms</i> locus (fertility restoration)	jnurfl3 & jnurfl610, jnurfl2 & jnurfl3	Kim & Kim 2015; Kim, 2014
<i>Ms</i> locus	AcPMS1 & AcSKP1	Khar <i>et al.</i> , 2022b; Kim <i>et al.</i> , 2015; Huo <i>et al.</i> , 2015

### Molecular markers in biotic stress management

A significant yield gap is attributed to foliar, root, and bulb diseases that impair plant health and postharvest storability (Cramer, 2000). Consequently, breeding for disease resistance has become a major priority, with molecular markers emerging as valuable tools for tagging resistance genes and enabling marker-assisted selection (MAS) (Ashkani *et al.*, 2015). Although progress in onion remains relatively modest (Scholten *et al.*, 2007), recent advances underscore the growing potential of molecular approaches.

For purple blotch (*Alternaria porri*), mapping populations derived from 'Arka Kalyan' × 'Agrifound Rose' identified the SSR marker *AcSSR7* and STS marker *ApR-450* linked to *ApR1*, facilitating MAS (Chand *et al.*, 2018). In the case of downy mildew (*Peronospora destructor*), the *DMR1* marker was associated with an *A. roylei*-derived resistance fragment, enabling marker-assisted backcrossing (Kim *et al.*, 2016). Similarly, for gray mold (*Botrytis* spp.), RAPD-derived *SCAR-OPANI* and *SNP-3 HRM* markers were developed to screen resistant genotypes (Kim *et al.*, 2021). Transcriptomic analyses further revealed stronger defense-related gene expression in *A. cepa* genotypes resistant to *A. porri*, while *Allium hookeri* exhibited resistance to *Thrips tabaci* through elevated lectin activity, which reduced pest damage and survival (Khandagale *et al.*, 2022).

Resistance to Fusarium basal rot was identified in short-day varieties 'Saba' and 'Saba-HS,' characterized by upregulation of *Lectin*, *LOX*, and *Osmotin* genes (Poursakhi *et al.*, 2024). ITS sequencing and PCR-based diagnostics have also aided the detection of onion twister disease (Patil *et al.*, 2016). Pathogenicity assays revealed that *Colletotrichum gloeosporioides* induces twisting symptoms, whereas *Fusarium acutatum* causes neck elongation; co-infection along with GA<sub>3</sub> application intensifies symptom expression, offering insights for molecular marker based resistance breeding (Dutta *et al.*, 2024).

In addition, gut microbiome profiling of *Thrips tabaci* populations from various Indian regions revealed diverse bacterial communities showing strong geographic variation, indicating potential for identifying microbial or host-associated molecular markers relevant to pest resistance (Gawande *et al.*, 2019). Despite onion's large genome (~16 Gb) and biennial growth cycle, these studies collectively highlight the expanding role of molecular tools in developing cultivars with enhanced resistance to diseases and insect pests (Khar *et al.*, 2022a; Finkers *et al.*, 2021).

### Molecular markers in abiotic stress management

Abiotic stresses such as drought, salinity, waterlogging, and heat pose major limitations to

onion productivity. Molecular research has led to the identification of key stress-responsive genes and tolerant germplasm, supporting the development of resilient cultivars through molecular breeding.

For drought tolerance, *NAC* transcription factors (*CepNAC-IV*, *CepNAC-V*) play central roles in regulating stress adaptation (Gokce et al., 2022), while the *I-SST* gene involved in fructan biosynthesis contributes to enhanced drought resilience (Liu et al., 2022). Genotypes U12, U47, U49, and cultivar K52 have shown combined tolerance to both drought and salinity (Mahajan & Gupta, 2023). Salinity tolerance has been linked to aquaporin genes *AcPIP1* and *AcTIP2*, which maintain water transport and osmotic balance under saline conditions (Sanwal et al., 2022; Solouki et al., 2023).

Waterlogging tolerance is mediated by genes associated with anaerobic respiration (*ADH*, *PDC*) and the stress-responsive transcription factor *WRKY22*, which together sustain energy metabolism under oxygen-deficient conditions (Gedam et al., 2023). In response to high-temperature stress, upregulation of heat shock protein (HSP) families (*HSP40*, *HSP60*, *HSP70*, *HSP90*, *HSP101*) and transcriptional regulation by *HSPF1* provide protection against protein denaturation (Galsurker et al., 2018). Collectively, the use of molecular markers for identifying stress-responsive genes is accelerating the breeding of climate-resilient onion varieties capable of withstanding multiple abiotic challenges.

## Conclusion

Molecular markers represent a transformative advancement in onion breeding, offering precise, efficient, and environment-independent tools to unravel complex traits and accelerate genetic improvement. Their applications extend across varietal identification, genetic diversity analysis, trait linkage, QTL mapping, and the characterization of cytoplasmic types for hybrid development. They have proven invaluable in improving traits such as bulb color, shape, TSS, pungency, flowering, and stress tolerance, while also facilitating the identification of male-sterile, maintainer, and restorer lines for hybrid breeding. Unlike conventional morphological markers, DNA-based markers provide reproducible and high-throughput insights, enabling more effective selection strategies. Advances in genomics, bioinformatics, and molecular technologies promise the development of superior onion cultivars with enhanced yield, resilience, and quality. This article underscores the pivotal role of molecular markers in modern onion breeding and highlights their potential to address global challenges in food security, sustainability, and climate adaptation.

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## Author's contributions

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## Conflict of Interest

The authors have no conflict of interest.

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## Data sharing

This article did not generate any supplementary data.

## Informed Consent

All the authors agree with the content of this article.

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