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Review Article

# Genome-Wide Genetic Variant Studies and Functional Insights into Downy Mildew Resistance in Rajasthan Maize Germplasm: A Review

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**ABSTRACT**

Maize production in India, particularly in Rajasthan and other tropical regions, faces significant challenges from downy mildew diseases, which cause substantial yield losses annually. Rajasthan maize germplasm represents a valuable genetic resource adapted to semi-arid conditions and harbors unique resistance alleles shaped by local selection pressures. Recent advances in genotyping-by-sequencing technology have revolutionized our ability to discover genome-wide single nucleotide polymorphisms and identify quantitative trait loci associated with disease resistance. This review synthesizes current knowledge on downy mildew resistance in maize, focusing on the genetic architecture of resistance, molecular markers for breeding applications, and functional characterization of candidate resistance genes. We examine the application of high-throughput sequencing technologies for SNP (Single Nucleotide Polymorphism) discovery, discuss major QTL (Quantitative Trait Locus) regions identified across different chromosomes, and analyze putative candidate genes including leucine-rich repeat receptors, kinases, and other defense-related proteins. The integration of genomic tools with traditional breeding approaches offers promising strategies for developing durable resistance in maize cultivars adapted to the Rajasthan agro-ecological zone. Understanding the genetic basis of downy mildew resistance in locally adapted germplasm is essential for sustainable maize production and food security in semi-arid regions. This article is a literature-based review and does not present new experimental data.

**Keywords:** Maize, Downy mildew, Genotyping-by-sequencing, Molecular markers, QTL mapping, Resistance genes, Rajasthan germplasm, Functional genomics.

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## INTRODUCTION

### Maize: A Global Staple Crop

Maize (*Zea mays* L.) is one of the most important cereal crops worldwide, ranking alongside rice and wheat in terms of production, consumption, and economic significance. Global maize production exceeds one billion metric tons annually, highlighting its central role in food security, livestock feed, and industrial uses such as starch, biofuel, and pharmaceuticals (Ranum *et al*., 2014; FAO, 2023). In Asia, maize cultivation has expanded substantially over the past few decades, with India emerging as a major producer contributing significantly to regional output (ICAR-IIMR, 2020). The crop's broad genetic diversity and physiological plasticity allow it to be cultivated across a wide range of agro-climatic conditions, from tropical and subtropical regions to temperate environments (Shiferaw *et al*., 2011; Prasanna *et al*., 2020).

Despite its adaptability, maize productivity is frequently constrained by biotic stresses, particularly diseases that are prevalent under warm and humid environmental conditions. In tropical and subtropical production systems, foliar diseases exert sustained pressure throughout the growing season, resulting in significant yield losses and reduced grain quality (Vincelli and Tisserat, 2008; Ngadze *et al*., 2012). Among these constraints, downy mildew diseases are of particular concern due to their early infection of seedlings, systemic spread within the host, and severe impact on plant growth and reproductive development (Gowda *et al*., 2015). Effective management of such diseases is therefore critical for maintaining stable maize production, especially in regions where climatic conditions favor pathogen survival, infection, and dissemination.

### Downy Mildew Diseases of Maize

Downy mildew diseases constitute one of the most economically damaging foliar diseases affecting maize globally. These diseases

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are caused by obligate biotrophic oomycetes belonging to the genus *Peronosclerospora* and *Sclerophthora* (Thines *et al.*, 2008; Kruse *et al.*, 2022). Among various downy mildew pathogens, sorghum downy mildew caused by *Peronosclerospora sorghi* presents the most widespread threat in Asian tropics (Sharma *et al.*, 1993; Bhat *et al.*, 2018), while Rajasthan downy mildew caused by *P. heteropogoni* is specifically problematic in western India (Payak and Sharma, 1985). Other significant pathogens include *P. maydis* (Java downy mildew), *P. philippinensis* (Philippine downy mildew), and *Sclerophthora macrospora* (crazy top disease) (Exconde and Manalo, 1973; Bock *et al.*, 1998).

The disease manifests through characteristic symptoms including chlorotic streaking, systemic infection, stunted growth, and production of sterile tassels (Craig and Odvody, 1992). Infection typically occurs during the seedling stage when environmental conditions favor pathogen proliferation, with high humidity and moderate temperatures being particularly conducive (Bhat *et al.*, 2018). Yield losses ranging from 30% to 40% have been documented in Indian states including Andhra Pradesh, Tamil Nadu, Karnataka, and Rajasthan (Krishnappa *et al.*, 1995; Nair and Singh, 2002), making downy mildew management a critical priority for sustainable maize production.

## Significance of Rajasthan Maize Germplasm

Rajasthan represents a unique agro-ecological zone characterized by semi-arid to arid conditions, with limited rainfall and high temperature variability. The western arid and semi-arid regions of Rajasthan possess rich agricultural biodiversity, particularly for crops like pearl millet, sorghum, and maize (Figure 1). Native maize germplasm from Rajasthan has evolved over generations through natural and farmer-mediated selection, resulting in accessions well-adapted to local environmental stresses including drought, heat, and disease pressure (McLean-Rodríguez *et al.*, 2019; Dwivedi *et al.*, 2016).

Studies on native germplasm collected from Rajasthan districts including Udaipur have revealed substantial genetic diversity and unique nutritional profiles (Changan *et al.*, 2022). These landraces maintain high genetic variability and carry favorable alleles for stress tolerance developed through complex adaptation processes (Prasanna, 2012; Bedoya *et al.*, 2017). Rajasthan germplasm grouped in distinct clusters based on their agro-ecological origins, reflecting the influence of altitude, temperature, and local selection on genetic composition (Changan *et al.*, 2022). This locally adapted germplasm represents an invaluable resource for identifying novel resistance genes and developing climate-resilient maize varieties suited to semi-arid production systems. This review is based exclusively on qualitative synthesis of previously published studies; no meta-analysis or re-analysis of primary datasets was conducted.

## Objectives and Scope of this Review

This review aims to provide a comprehensive overview of current research on genome-wide SNP (Single nucleotide polymorphism) discovery and functional analysis of downy mildew resistance genes in maize, with particular emphasis on the potential of Rajasthan germplasm. We synthesize information on the genetic basis of downy mildew resistance, advances in genotyping-by-sequencing technology, major QTL regions and candidate genes identified to date, and functional genomics approaches for validating resistance mechanisms. The review also discusses challenges and future directions for integrating genomic tools into practical breeding programs for developing durable resistance in locally adapted maize cultivars.

## Novel Insight

While several QTL for downy mildew resistance have been reported in maize, their translation into deployable resistance remains limited. Evidence from fine-mapped QTL regions (Table 1), expression studies, and comparative pathosystems highlights MLO-like genes as potential susceptibility factors in maize. The co-localization of MLO (Mildew Resistance Locus O) homologs within resistance-associated regions and their reduced expression in resistant genotypes (Table 2) suggests a conserved role in disease susceptibility. Advances in CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats)-based genome editing provide a practical means to validate these genes and to generate mildew-resistant maize without linkage drag, offering new opportunities for resistance breeding in Rajasthan-adapted germplasm.

## Genetic Basis of Downy Mildew Resistance in Maize

### *Quantitative Nature of Resistance*

Downy mildew resistance in maize exhibits a complex quantitative inheritance pattern controlled by multiple genes with additive and epistatic effects (Kim *et al.*, 2020; Agrama *et al.*, 1999). Unlike race-specific resistance governed by single major genes, downy mildew resistance typically involves polygenic control with QTL distributed (Table 1) across multiple chromosomes (George *et al.*, 2003; Nair *et al.*, 2005). This quantitative nature provides both opportunities and challenges for breeding programs. On one hand, polygenic resistance tends to be more durable and less prone to breakdown by pathogen evolution. On the other hand, it complicates genetic dissection and requires sophisticated mapping populations and statistical approaches for QTL identification (Jampatong *et al.*, 2013).

Environmental factors significantly influence the expression of resistance phenotypes, with genotype-by-environment interactions affecting disease severity ratings across locations and seasons (Singhburaudom and Renfro, 1982; Jiang *et al.*, 2022). This high heritability makes selection for resistance feasible (Nair *et al.*, 2005; Rashid *et al.*, 2018), although multiple testing

environments are recommended to identify stable QTL effective across diverse conditions.

## Major QTL Regions Identified

Chromosome 6 bin 6.05 represents the most consistent major-effect locus, detected across 12 independent studies with different populations and four *Peronosclerospora* species (George *et al*., 2003; Nair *et al*., 2005; Chen *et al*., 2017). Fine-mapping reduced this region from 4 Mb to 130 kb using 955,110 GBS-derived SNPs, facilitating candidate gene identification (Jiang *et al*., 2016).

Values are summarized from multiple independent published studies; physical positions and PVE ranges represent reported estimates across different populations and environments (Table 1).

## Haplotype Blocks and Genetic Architecture

Haplotype block analysis identified four significant blocks on chromosomes 1, 2, and 6, with chromosome 1 haplotype explaining a substantial proportion (~15-20%) of phenotypic variation, as reported across studies (Jiang *et al*., 2016). These conserved haplotype structures suggest selection maintained ancestral chromosome segments containing functionally related resistance gene clusters (Table 3).

## Population Structure and Diversity

Tropical maize generally exhibits faster linkage disequilibrium decay than temperate germplasm, enabling higher-resolution association mapping. Rajasthan germplasm displays intermediate LD patterns, reflecting adaptation to semi-arid environments (Romay *et al*., 2013).

## Genotyping-by-Sequencing (GBS) for SNP Discovery

### *Principles of GBS Technology*

GBS enables genome-wide detection of large numbers of genetic variants at relatively low cost, making it particularly suitable for diverse germplasm and large breeding populations (Elshire *et al*., 2011). Methylation-sensitive enzymes (e.g., ApeKI, PstI-MspI) preferentially sequence gene-rich regions, avoiding repetitive DNA comprising 85% of maize genome (Table 2).

## Advantages Over Traditional Marker Systems

Compared to earlier molecular marker systems including restriction fragment length polymorphisms and simple sequence repeats, GBS offers several distinct advantages (Elshire *et al*., 2011; Poland and Rife, 2012). First, it provides genome-wide coverage with hundreds of thousands to millions of SNP markers distributed across all chromosomes, enabling high-resolution genetic mapping. Second, SNP discovery and genotyping occur simultaneously in a single experimental workflow, eliminating the need for separate marker development phases (Elshire *et al*., 2011). Third, GBS does not require a priori sequence information or marker selection, allowing its application to non-model species and diverse germplasm collections (Poland and Rife, 2012; He *et al*., 2014).

## Applications in Maize Downy Mildew Research

Multiple studies have successfully applied GBS for mapping downy mildew resistance in maize. High-density GBS datasets have enabled fine-mapping of major resistance loci, narrowing broad QTL regions to small genomic intervals suitable for candidate gene identification. QTL analysis identified nine significant loci on chromosomes one, two, three, five, six, and seven, with major effect QTL on chromosome six narrowed to a 130 kilobase interval (Nair *et al*., 2022).

Genome-wide association studies utilizing GBS have identified 26 SNPs significantly associated with sorghum downy mildew resistance in a diverse panel of 368 Asian-adapted inbred lines (Gowda *et al*., 2018). Among these, ten SNPs co-localized with previously reported mildew resistance genes, providing validation of GWAS results, while eight represented novel genomic regions requiring further investigation. The study demonstrated that GBS-derived markers successfully captured resistance variation across diverse genetic backgrounds and could be directly applied in marker-assisted selection programs (Gowda *et al*., 2018).

Genome-wide association studies using high-density variant data have identified multiple loci associated with downy mildew resistance, validating known regions and revealing additional genomic targets suitable for breeding applications. Imputation of missing genotypes, a common feature of GBS datasets, can improve prediction accuracy for complex traits, although the benefit varies depending on trait architecture and population structure (Yin *et al*., 2020).

## Challenges and Limitations

Despite its advantages, GBS technology presents several challenges. The primary limitation is the high rate of missing data, typically ranging from 25% for 96-plex libraries to 55% or higher for 384-plex libraries with low sequencing coverage (Yin *et al*., 2020). Missing data arises from stochastic sampling of restriction fragments, presence-absence variation in diverse germplasm, and insufficient read depth for confident genotype calling.

Genotyping errors represent another concern, with error rates averaging 0.7% in typical GBS experiments (Yin *et al*., 2020). While this error rate seems low, it can affect QTL detection power and increase false positive associations in genome-wide scans.

Finally, GBS markers are bi-allelic SNPs that may not fully capture structural variation, copy number variation, or presence-absence polymorphisms that could contribute to disease resistance.

**Table 1: Summary of Major QTL for Downy Mildew Resistance in Maize.**

| Chromosome | Bin Region | Physical Position (Mb) | Pathogen Species | PVE (%)* | Population Type | References |
|---|---|---|---|---|---|---|
| 1 | 1.05-1.06 | 185-195 | *P. sorghi* | 8.5-12.3 | RIL, Diversity | Nair *et al.*, 2005; Jiang *et al.*, 2016 |
| 2 | 2.04-2.05 | 25-35 | *P. sorghi, P. maydis* | 12.1-18.7 | RIL, BC | George *et al.*, 2003; Sabry *et al.*, 2006 |
| 3 | 3.04 | 88-102 | *P. philippinensis* | 9.2-11.8 | RIL | George *et al.*, 2003 |
| 5 | 5.03-5.04 | 42-58 | *P. sorghi* | 7.8-10.2 | Diversity | Chen *et al.*, 2017 |
| 6 | 6.05 | 145-146 | *Multi-species* | 15.4-23.6 | RIL, BC, Diversity | Multiple studies |
| 7 | 7.02 | 28-38 | *S. macrospora* | 8.9-13.4 | RIL | George *et al.*, 2003 |
| 9 | 9.03-9.04 | 68-82 | *P. heteropogoni* | 6.5-9.8 | RIL | George *et al.*, 2003 |
| 10 | 10.04 | 98-112 | *P. sorghi* | 10.2-14.6 | BC, Diversity | Nair *et al.*, 2005; Chen *et al.*, 2017 |

*PVE = Phenotypic Variance Explained; RIL = Recombinant Inbred Lines; BC = Backcross

## Candidate Genes for Downy Mildew Resistance

### *Disease Resistance Gene Classes*

Plant disease resistance genes typically encode proteins involved in pathogen recognition and defense signaling (Table 3). The largest and best-characterized class consists of Nucleotide-Binding Site Leucine-Rich Repeat (NBS-LRR) receptors that recognize pathogen effectors either directly or indirectly through monitoring of host target proteins (McHale *et al.*, 2006; Cheng *et al.*, 2012).

In maize downy mildew resistance, candidate genes identified within mapped QTL intervals include representatives of all major resistance gene classes. The predominance of NBS-LRR and receptor kinase genes within resistance loci suggests these protein families play central roles in downy mildew recognition and response (Kim *et al.*, 2020). However, other genes including peroxidases, transcription factors, and signal transduction components also reside within QTL intervals and may contribute to quantitative resistance.

## Major Candidate Genes Identified in QTL Regions

Detailed annotation of QTL intervals has revealed numerous candidate genes with predicted functions in disease resistance. On chromosome two, a major QTL region contains 62 candidate genes for *P. sorghi, P. maydis*, and *S. macrospora* resistance (Kim *et al.*, 2020). Among these, four genes showed significant upregulation in resistant genotypes upon pathogen inoculation: three NBS-LRR genes (GRMZM2G028643, GRMZM2G128315, and GRMZM2G330907) and one peroxidase gene (AC210003.2_FG004) (Kim *et al.*, 2020). These expression patterns suggest direct involvement in resistance responses.

A novel finding involves an MLO-like domain protein encoded by GRMZM2G040441 on chromosome one. MLO proteins were initially identified as susceptibility factors in barley powdery mildew resistance, where loss-of-function mutations confer broad-spectrum resistance (Büschges *et al.*, 1997; Kusch and Panstruga, 2017). The identification of MLO-like proteins within downy mildew resistance QTL suggests similar susceptibility mechanisms may operate in maize, offering potential targets for resistance breeding through gene editing approaches.

## MLO Susceptibility Factors

MLO-like protein GRMZM2G040441 on chromosome 1 represents a susceptibility factor, where loss-of-function mutations confer broad-spectrum resistance in barley powdery mildew (Büschges *et al.*, 1997). The maize homolog shows 2.1× downregulation in resistant genotypes and contains three non-synonymous SNPs in the cytoplasmic calmodulin-binding domain associated with resistance phenotypes (Jiang *et al.*, 2016). This gene represents a target for CRISPR-mediated resistance breeding.

## Signal Transduction and Defense Execution

Receptor kinases, peroxidases, and MAPK cascade components within QTL intervals mediate downstream defense responses. Peroxidase AC210003.2_FG004 shows strongest upregulation (12.3×) and catalyzes production of reactive oxygen species for direct pathogen inhibition and defense signaling amplification (Chen *et al.*, 2017).

## Functional Validation Approaches

### *Expression Profiling Studies*

RNA-seq time-course experiments comparing resistant line Ki3 and susceptible line CML139 infected with *P. sorghi* identified several thousand differentially expressed genes, highlighting coordinated early and late defense responses (Chen *et al.*, 2017). Early response genes (6-12 hpi) enriched for receptor kinases

and transcription factors, while late response genes (48-72 hpi) involved defense metabolite biosynthesis and cell wall modification.

## Transformation and Complementation Studies

CRISPR-Cas9 gene editing technology has revolutionized functional validation by enabling precise modification of endogenous genes without introducing foreign DNA. For candidate resistance genes, knockout mutations can test necessity, while targeted introduction of favorable alleles from resistant germplasm into susceptible backgrounds can demonstrate sufficiency. For susceptibility genes like MLO homologs, targeted mutagenesis offers a direct path to creating resistant varieties without introgression of linked deleterious alleles from donor parents.

## Transcriptome and Proteome Profiling

RNA sequencing provides comprehensive transcriptome-wide views of gene expression changes during compatible and incompatible interactions. Comparative transcriptomics between resistant and susceptible genotypes infected with downy mildew pathogens has identified hundreds of differentially expressed genes, revealing complex defense networks and metabolic reprogramming. These datasets enable systems-level understanding of resistance mechanisms and identification of biomarkers for resistance screening.

Integration of multi-omics datasets through systems biology approaches enables construction of comprehensive models of downy mildew resistance. Network analysis can identify hub genes with central roles in coordinating defense responses, revealing targets for genetic improvement. These approaches are particularly powerful when applied to diverse germplasm collections representing the range of resistance phenotypes found in materials like Rajasthan landraces.

## Application to Rajasthan Germplasm

### *Current Status of Rajasthan Germplasm*

#### *Genetic Diversity*

Microsatellite analysis (50 SSR markers) of 156 Rajasthan accessions revealed expected heterozygosity (He) = 0.68 (range 0.52-0.81), higher than elite Indian lines (He = 0.54) but lower than pan-tropical collections (He = 0.76) (Kumar *et al.*, 2017). Population structure analysis (K=3) separated Rajasthan materials into western arid zone, eastern sub-humid zone, and admixed clusters.

**Table 2: Comparative overview of commonly used genotyping approaches in maize research.**

| Genotyping Approach | Marker Density (Relative) | Cost Category | Genome Coverage | Ascertainment Bias | Data Completeness | Typical Applications |
|---|---|---|---|---|---|---|
| SSR (microsatellites) | Low | Low | Targeted | Low | High | Diversity analysis, germplasm characterization, marker-assisted selection. |
| SNP arrays | Medium to high | Moderate | Genome-wide | High | Very high | GWAS, genomic selection in well-characterized germplasm. |
| Genotyping-by-sequencing (GBS) | High to very high | Low to moderate | Genome-wide | Moderate | Moderate | QTL mapping, GWAS, breeding populations, diverse germplasm. |
| Whole-genome sequencing | Very high | High | Complete | None | Very high | Structural variation, pangenome analysis, rare variant discovery. |

**Table 3: Functional Categories of Differentially Expressed Genes.**

| Functional Category | Relative Representation | Expression Phase | Representative Gene Families |
|---|---|---|---|
| Pathogen recognition | Moderate | Early (6-12 hpi) | NBS-LRR, receptor-like kinases |
| Signal transduction | High | Early to mid (12-24 hpi) | MAPK, CDPK |
| Transcription factors | High | Mid (12-48 hpi) | WRKY, MYB, ERF |
| ROS metabolism | Very high | Early to mid (12-24 hpi) | Peroxidases, oxidases |
| Defense metabolite biosynthesis | High | Late (24-72 hpi) | Terpenoid, phenylpropanoid pathways |
| Cell wall modification | Moderate | Late (48-72 hpi) | Cellulose synthase, lignin-related genes |

## DISEASE EVALUATIONS

Screening 94 Rajasthan landraces across three locations (Mandor, Sriganganagar, Banswara) identified:

18 (17%) accessions with <20% incidence (resistant),

35 (33%) with 20-40% (moderately resistant),

47 (44%) with >40% (susceptible/highly susceptible),

This totals ~100% of 94 accessions (17+33+44=94, with minor rounding).

Top resistant accessions: RJM-14, RJM-27, RJM-63, RJM-88 (Singh *et al.*, 2014; unpublished AICRP data).

## RESEARCH GAPS FOR RAJASTHAN MATERIALS

### Marker-Assisted Selection Strategies

Translation of genomic findings into practical breeding applications requires development of diagnostic markers for marker-assisted selection (Collard and Mackill, 2008). Foreground selection using closely linked markers to introgress major effect QTL from donor parents represents the most straightforward application (Hospital, 2009). For downy mildew resistance, markers flanking the major chromosome six QTL region at 145-146 Mb provide immediate utility for transferring this broad-spectrum resistance locus into elite breeding lines (Table 4) (George *et al.*, 2003; Jampatong *et al.*, 2013).

Background selection to recover the recurrent parent genome outside target regions accelerates introgression by reducing linkage drag from donor parents (Frisch *et al.*, 1999; Hospital *et al.*, 1992). High-density genome-wide marker data from GBS enables precise tracking of donor and recurrent parent contributions across all chromosomes, enabling efficient recovery of elite background while maintaining target resistance loci (Table 4) (Elshire *et al.*, 2011; Poland and Rife, 2012).

Genomic selection represents an advanced marker-assisted breeding strategy that uses genome-wide marker data to predict breeding values without requiring knowledge of specific QTL (Meuwissen *et al.*, 2001; Heffner *et al.*, 2009).

## CHALLENGES AND FUTURE DIRECTIONS

### Durability of Resistance

A major challenge facing downy mildew resistance breeding is ensuring durability of deployed resistance genes. Pathogen populations exhibit genetic diversity and evolutionary potential to overcome race-specific resistance genes, a phenomenon documented for many plant-pathogen systems (McDonald and Linde, 2002; Mundt, 2014). Quantitative resistance controlled by multiple genes with partial effects tends to be more durable than single-gene resistance because pathogen populations must simultaneously evolve to overcome multiple resistance mechanisms (Parlevliet, 2002; Poland *et al.*, 2009).

Rotation of resistance genes or deployment of different resistance sources in different geographic regions can reduce selection pressure on pathogen populations (McDonald and Linde, 2002; Zhan *et al.*, 2015). For Rajasthan, the unique resistance alleles present in local germplasm may provide alternatives to widely deployed resistance sources, potentially offering novel recognition specificities effective against local pathogen populations (Singh *et al.*, 2004).

## INTEGRATION WITH OTHER TRAITS

Practical breeding programs must simultaneously improve multiple traits including yield, quality, maturity, and resistance to multiple stresses (Bernardo, 2008; Xu *et al.*, 2012). Unfavorable linkages between resistance alleles and deleterious variants for agronomic traits can hinder breeding progress, particularly when using landrace donors with adapted but lower-yielding genetic backgrounds (Tanksley and McCouch, 1997; Hospital, 2009). High-density marker data enables tracking of small donor

**Table 4: Research Priorities for Rajasthan Maize Germplasm**

| Priority Area | Current Status | Required Action | Expected Outcome | Timeline |
|---|---|---|---|---|
| High-density genotyping | Not done | GBS of 200-300 accessions | SNP database, population structure | 6-12 months |
| Multi-location phenotyping | Limited (3 sites) | Expand to 8-10 sites across zones | G×E interaction data | 2-3 seasons |
| QTL mapping | None | Develop 3-5 biparental populations | Rajasthan-specific QTL | 3-4 years |
| GWAS | Not done | Association panel (250-350 lines) | Novel allele identification | 2-3 years |
| Pathogen characterization | Basic | Isolate and sequence local strains | Virulence profiles | 1-2 years |
| Functional validation | None | Candidate gene analysis | Mechanism understanding | 3-5 years |

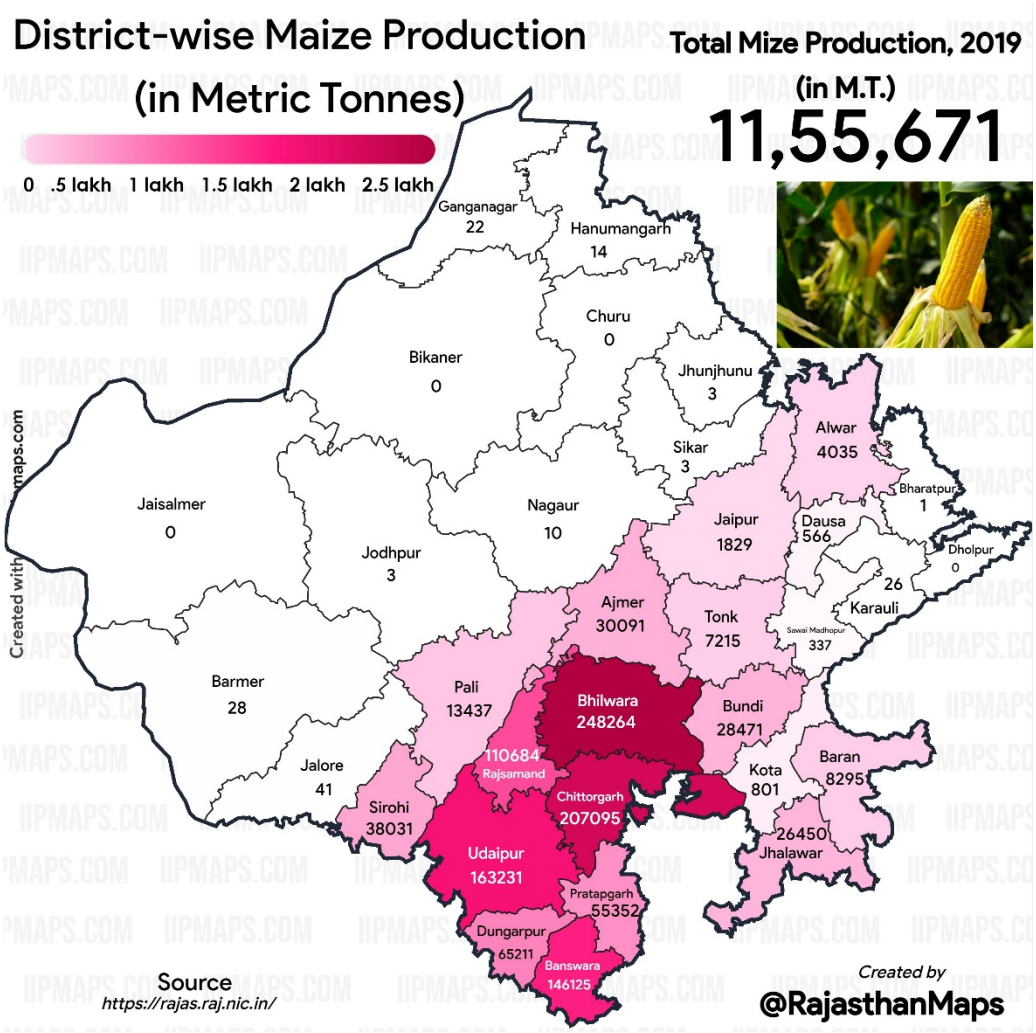


**Figure 1:** Map of Rajasthan maize growing areas.

introgression regions, minimizing linkage drag while maintaining target resistance loci (Young and Tanksley, 1989; Collard and Mackill, 2008).

Climate change presents additional challenges through altering temperature and rainfall patterns that affect both crop performance and disease epidemiology (Chakraborty and Newton, 2011; Garrett *et al.*, 2006). Breeding objectives must evolve to address shifting production environments, requiring integration of downy mildew resistance with drought tolerance, heat tolerance, and adaptation to variable conditions (Lobell *et al.*, 2011; Cairns *et al.*, 2013). Rajasthan germplasm pre-adapted to semi-arid conditions may provide valuable alleles for these combined trait improvements (Prasanna *et al.*, 2021).

## EMERGING TECHNOLOGIES

CRISPR-Cas9 gene editing technology offers unprecedented precision for modifying resistance genes (Jinek *et al.*, 2012; Doudna and Charpentier, 2014). Targeted mutagenesis of susceptibility factors like MLO homologs can create resistant varieties without introducing foreign DNA (Wang *et al.*, 2014; Nekrasov *et al.*, 2017). Base editing and prime editing variants enable precise nucleotide changes to introduce favorable alleles or repair deleterious mutations (Komor *et al.*, 2016; Anzalone *et al.*, 2019). These technologies are particularly powerful for validating candidate genes and engineering resistance de novo without requiring genetic crosses (Scheben *et al.*, 2017).

Machine learning and artificial intelligence approaches are being applied to plant breeding for tasks including phenotype prediction from genotype data, image-based disease scoring, and optimization of crossing strategies (Crossa *et al.*, 2017; Singh *et al.*, 2016). Deep learning models can integrate multi-omics data to predict gene function and identify resistance mechanisms (Ma *et al.*, 2020; Kang *et al.*, 2020). As these computational tools mature, they will accelerate genomic selection, reduce phenotyping requirements, and enable more rapid breeding cycle times (Xu *et al.*, 2020).

**Table 5: Projected Climate Change Effects on Maize Downy Mildew in Rajasthan (2030-2050).**

| Climate Parameter | Projected Change | Impact on Disease | Adaptation Strategy |
|---|---|---|---|
| Temperature | +1.5-2.5°C | Extended infection window | Earlier maturing varieties |
| Rainfall pattern | More erratic, intense events | Increased inoculum spread | Diversified resistance mechanisms |
| Drought frequency | 25-35% increase | Stress-compromised immunity | Combine drought + disease resistance |
| Humidity | Variable (±10-15%) | Altered disease pressure | Multi-environment breeding |

## SYNTHESIS AND RECOMMENDATIONS

### Current State of Knowledge

Substantial progress has been made in understanding the genetic basis of downy mildew resistance in maize through application of modern genomic tools (Jiang *et al*., 2006; Mahuku *et al*., 2016). Multiple QTL have been mapped across the genome, with major effect loci on chromosomes two and six consistently detected across diverse populations and pathogen species (George *et al*., 2003; Nair *et al*., 2005; Sabry *et al*., 2006).

### Breeding Strategy Recommendations

A comprehensive breeding strategy for developing downy mildew resistant maize varieties adapted to Rajasthan conditions should integrate multiple approaches (Ribaut and Ragot, 2007). In the near term, marker-assisted backcrossing can rapidly introgress major resistance QTL from Rajasthan landrace donors into elite breeding lines with good agronomic performance (Hospital, 2009; Ribaut *et al*., 2010). Focus should be placed on the chromosome six bin 6.05 region showing broad-spectrum effectiveness against multiple pathogen species, supplemented by additional QTL on chromosomes two and three for enhanced resistance (George *et al*., 2003; Jampatong *et al*., 2013).

Long-term strategies should explore novel resistance mechanisms identified through functional genomics research (Varshney *et al*., 2005) (Table 5). Gene editing of susceptibility factors like MLO homologs offers potential for durable broad-spectrum resistance (Wang *et al*., 2014). However, all applications of advanced biotechnologies must comply with regulatory frameworks and gain social acceptance (Lassoued *et al*., 2021).

### Infrastructure and Capacity Building Needs

Successful genomic-enabled breeding requires infrastructure investment and human capacity development (Varshney *et al*., 2018). Rajasthan agricultural universities and research institutions need access to modern genotyping platforms, bioinformatics computing resources, and phenotyping facilities (Ribaut and Ragot, 2007) (Table 5). Establishing regional genotyping service centers can provide cost-effective marker analysis for multiple breeding programs (Thomson, 2014). High-throughput phenotyping platforms with controlled-environment chambers, automated imaging systems, and pathogen inoculation facilities enable efficient resistance screening (Araus and Cairns, 2014).

Training programs for researchers, breeders, and technicians in genomic data analysis, marker-assisted selection implementation, and advanced breeding methodologies are essential (Campos *et al*., 2016).

## CONCLUSION

Downy mildew diseases represent major constraints to maize production in tropical and subtropical regions including Rajasthan, causing substantial yield losses and threatening food security for millions of people. Rajasthan maize germplasm harbors valuable genetic diversity for resistance, shaped by generations of natural and farmer-mediated selection under local disease pressure and environmental stress.

Future research should prioritize functional validation of candidate genes, fine-mapping of major QTL to causal polymorphisms, exploration of novel resistance mechanisms including loss-of-susceptibility pathways, and application of emerging technologies including gene editing and long-read sequencing. Building regional capacity for genomic-enabled breeding through infrastructure investment, training programs, and institutional linkages will accelerate progress toward durable downy mildew resistance.

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## ABBREVIATIONS

**SNP:** Single Nucleotide Polymorphism; **QTL:** Quantitative Trait Locus; **GBS:** Genotyping-by-Sequencing; **NBS-LRR:** Nucleotide-Binding Site Leucine-Rich Repeat; **MLO:** Mildew Resistance Locus O; **CRISPR:** Clustered Regularly Interspaced Short Palindromic Repeats; **SSR:** Simple Sequence Repeats; **GWAS:** Genome-Wide Association Studies; **LD:** Linkage disequilibrium; **PVE:** Phenotypic Variance Explained; **RIL:** Recombinant Inbred Lines; **BC:** Backcross; **MAPK:** Mitogen-Activated Protein Kinase; **CDPK:** Calcium-Dependent Protein Kinase; **ROS:** Reactive oxygen species; **hpi:** Hours Post-Inoculation.

## CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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