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RESEARCH PAPER

Recent trends in maize entomology: Integrating host plant resistance, molecular tools for sustainable pest management

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Abstract: Maize (*Zea mays* L.) is a globally significant cereal crop, yet its production is severely constrained by lepidopteran pests, particularly stem borers (*Chilo partellus, Ostrinia nubilalis, Diatraea* spp.), fall armyworm (*Spodoptera frugiperda*), and corn earworm (*Helicoverpa zea*). This review synthesizes recent advances in maize entomology, with a primary focus on host plant resistance mechanisms and their integration into sustainable pest management. Key constitutive resistance mechanisms include antibiosis mediated by biochemical factors such as DIMBOA and maysin, antixenosis through morphological traits like trichome density and husk tightness, and tolerance via plant vigor and root regrowth. The development of multiple borer-resistant (MBR) germplasm at CIMMYT, coupled with marker-assisted selection (MAS) using RFLPs and QTL mapping, has significantly accelerated resistance breeding. Recent breakthroughs include the elucidation of the Cry1Ab dual-pathway mechanism against the Asian corn borer and meta-QTL analyses that have identified stable genomic regions governing insect resistance across diverse genetic backgrounds. Transgenic Bt maize expressing Cry proteins provides effective, season-long control of target pests, but its durability necessitates integrated resistance management strategies. This review underscores the critical role of conventional breeding, biochemical profiling, molecular genetics, and biotechnology in developing durable insect resistance, and advocates for integrated, multi-disciplinary approaches to ensure sustainable maize production.

Keywords: Antibiosis • Antixenosis • Bt maize • Chilo partellus • Cry1Ab • DIMBOA • Host plant resistance • Integrated pest management • Maize • Marker-assisted selection • Maysin • Meta-QTL • Quantitative trait loci (QTL)

Introduction

Maize (*Zea mays* L.) ranks as the third most important cereal crop worldwide, serving as a staple food, animal feed, and industrial raw material. Global maize production has continued to expand, with the crop playing an increasingly vital role in bioethanol production alongside food and feed applications. In developing countries, maize is pivotal for food security, yet average yields remain low (1.6–2.2 t/ha) compared to developed nations (5–6 t/ha) due to multiple constraints, with insect pests being a primary factor (Khan *et al.*, 2015; Alam *et al.*, 2020). Lepidopteran stem borers alone cause annual losses estimated at 200–500 million dollars in the U.S. Corn Belt and up to 80% yield reductions in severe infestation cases in India and Africa (Barry and Darrah, 1991; Sekhon and Kanta, 1997).

Traditional reliance on chemical insecticides has led to environmental contamination, pest resistance, and harm to natural enemies. Consequently, host plant resistance (HPR) has emerged as an economically and ecologically sustainable alternative, forming the cornerstone of

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integrated pest management (IPM) programs. Recent trends in maize entomology emphasize the integration of HPR with biological control agents, cultural practices, and biotechnological innovations to create durable, multi-tiered defense systems against lepidopteran pests. The development of resistant maize varieties not only reduces yield losses but also minimizes insecticide applications, preserves beneficial arthropods, and lowers production costs for resource-limited farmers.

This review aims to: (1) synthesize current knowledge on mechanisms and bases of maize resistance to major lepidopteran pests, including biochemical factors (e.g., DIMBOA, maysin) and morphological traits; (2) evaluate recent advances in conventional breeding, molecular markers, quantitative trait loci (QTL) mapping, and transgenic technologies, including discoveries from 2023–2025; (3) discuss IPM strategies that effectively incorporate HPR as a central component; and (4) highlight the role of molecular diagnostics and genetic tools in strengthening resistance breeding and pest management outcomes.

Major lepidopteran pests of maize

Maize is attacked by a complex of lepidopteran pests worldwide. The European corn borer (*Ostrinia nubilalis*) is predominant in temperate regions, while the spotted stem borer (*Chilo partellus*) dominates in Asia and Africa (Khan *et al.*, 2015; Sekhon and Kanta, 1997). In the Americas, the southwestern corn borer (*Diatraea grandiosella*), sugarcane borer (*D. saccharalis*), fall armyworm (*Spodoptera frugiperda*), and corn earworm (*Helicoverpa zea*) cause significant damage (Williams and Davis, 1997; Wiseman, 1997). These pests attack all growth stages: whorl-stage feeding produces 'dead hearts', while post-anthesis tunneling reduces stalk strength, causes lodging, and directly damages ears. The recent spread of fall armyworm across Africa and Asia since 2016 has intensified the need for durable resistance strategies (Figure 1).

Mechanisms of host plant resistance

Painter (1951) classified resistance into three categories: antixenosis (non-preference), antibiosis, and tolerance. In maize, these mechanisms are mediated by both chemical and physical factors.

Chemical bases

The hydroxamic acid DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) is a key antibiotic factor against first-

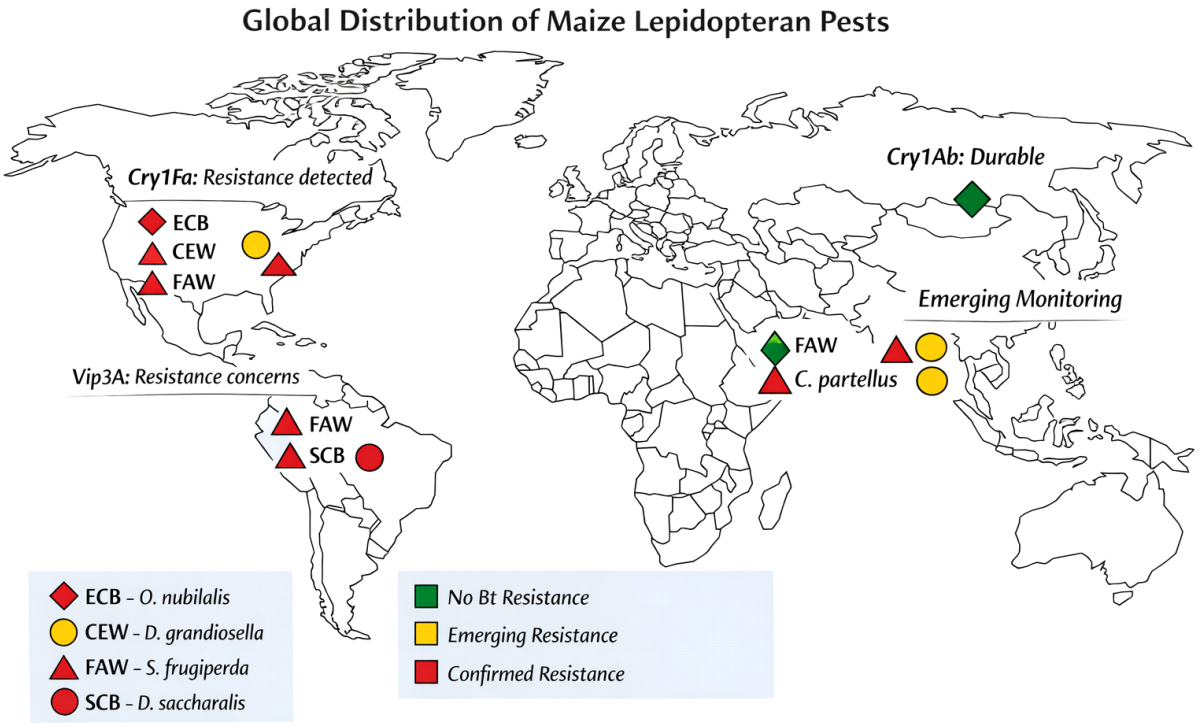


Figure 1. Global distribution of major maize lepidopteran pests with resistance status to Bt proteins

generation *O. nubilalis* and *C. partellus*. Tseng (1997) indicated significant negative correlations between MBOA concentration and larval survival (r = -0.88 to -0.78) across five leaf stages. In silks, the flavone glycoside maysin inhibits *H. zea* and *S. frugiperda* larval growth, with concentrations >0.2% fresh weight reducing larval weight by >50% (Wiseman, 1997; Snook *et al.*, 1997).

Physical bases

Leaf toughness, increased fiber content, cell wall phenolic acids (ferulic and p-coumaric acids), and diferulic acid cross-linking contribute to resistance by reducing nutrient accessibility and increasing mechanical strength (Bergvinson *et al.*, 1997). Recent research has identified candidate genes associated with stalk lodging resistance, with meta-QTL analyses revealing 67 MQTLs linked to cell wall strenthening through lignin biosynthesis pathways. Trichome density on leaf surfaces deters oviposition in *C. partellus* (Kumar, 1997).

Breeding and genetic advances

Conventional breeding has successfully developed multiple borer-resistant (MBR) populations, primarily derived from Antigua germplasm at CIMMYT (Smith *et al.*, 1997). Recurrent selection for S1 progenies has yielded significant genetic gains. For example, selection for resistance to *D. grandiosella* reduced stalk tunneling from 22 cm to 6.7 cm over six cycles (Barry and Darrah, 1997) (Figure 2).

Molecular markers have revolutionized resistance breeding. Khairallah *et al.* (1997) mapped quantitative trait loci (QTL) for SWCB and SCB resistance on chromosomes 1, 3, 5, 7, and 9, explaining 33–52% of phenotypic variance. Recent meta-QTL analyses have substantially advanced this field: a 2025 study integrating 254 QTLs from 21 studies identified 21 stable MQTLs for abiotic stress tolerance and starch content, achieving a 73.4% reduction in confidence interval compared to initial QTLs. Similarly, Fang *et al.* (2025) integrated 889 lodging-related QTLs to identify 67 MQTLs, of which 67% were validated by GWAS. Marker-assisted selection (MAS) allows rapid introgression of resistance alleles without time-consuming field screening (Benson, 1997).

Breakthrough in Bt technology

A landmark study published in PNAS (April 2025) by researchers at Nanjing Agricultural University and the University of Arizona revealed that Cry1Ab kills pests through two distinct pathways, one requiring ABCC2 receptor and another requiring both cadherin and ABCC3.

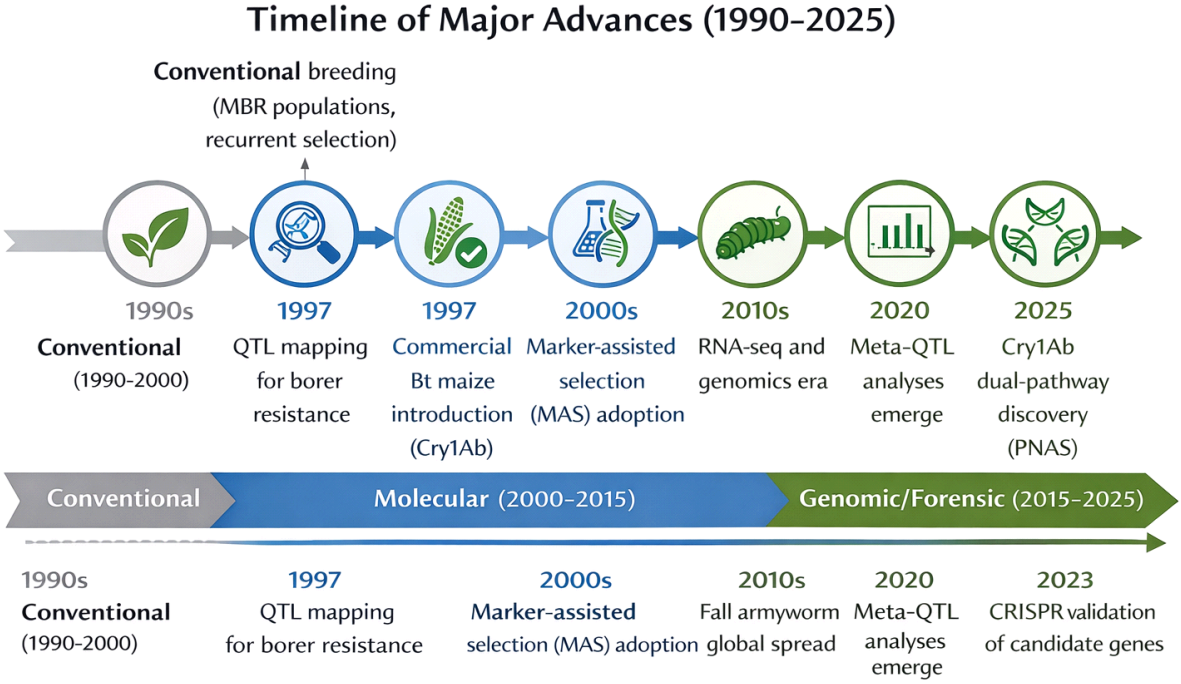


Figure 2: Timeline of major advances in maize entomology (1990-2025) showing conventional breeding, molecular markers, Bt maize, meta-QTL, CRISPR validation, and dual-pathway discovery.

This dual-pathway mechanism fundamentally explains why Cry1Ab has remained effective for over 21 years, while Cry1Fa-resistant European corn borer populations emerged after just 12 years. In contrast, Cry1Fa relies on a single pathway (ABCC2 only), making resistance development more likely. This discovery positions Cry1Ab as a 'natural pyramid' gene, giving critical insights for sustainable Bt maize deployment.

Transgenic Bt maize expressing CryIA(b) protein provides near-complete control of ECB, with tunneling reduced from 59 cm to <2 cm under heavy infestation (Estruch *et al.*, 1997; Sagers *et al.*, 1997). However, resistance management strategies including refuge requirements and gene pyramiding are essential to delay pest adaptation (Maredia, 1997).

Integrated pest management (IPM)

IPM combines HPR with biological control (e.g., Trichogramma egg parasitoids, ladybirds), cultural practices (crop rotation, residue destruction), and judicious insecticide use. The EU-funded IPMWORKS initiative (2020-2025) has demonstrated that holistic IPM is cost-effective and can achieve a 50% reduction in pesticide use without compromising food security. Farmer-led networks across Europe have successfully adopted biological controls including parasitic wasps and beneficial fungi. Bayer's Marana Innovation Center similarly employs ladybug releases as a core biological control strategy within their IPM framework. The USDA defines IPM as 'a sustainable situation to managing pests by combining biological, cultural, physical, and chemical tools in a way that minimizes economic, and environmental risks'.

Khan *et al.* (2015) reported that IPM treatments reduced *C. partellus* infestation from 12.92% to 2.32% and increased yield from 6.23 to 8.64 t/ha compared to untreated controls. Synergistic interactions exist between HPR and natural enemies: FAW larvae on resistant maize are more susceptible to parasitism by *Cotesia marginiventris* (Wiseman, 1997).

Materials and methods

Literature search strategy

A systematic literature search was conducted to identify peer-reviewed articles, symposium proceedings, and original research reports relevant to maize resistance against lepidopteran pests. The following electronic databases were searched: PubMed, Scopus, Web of Science, Google Scholar, and CAB Abstracts. The search period spanned from January 1994 to December 2025 to encompass foundational studies as well as recent advances. The search strings combined keywords related to maize (*Zea mays*), insect pests (stem borers, fall armyworm, corn earworm), resistance mechanisms (host plant resistance, antibiosis, antixenosis, tolerance), biochemical factors (DIMBOA, maysin), molecular genetics (QTL, marker-assisted selection, meta-QTL, CRISPR), and transgenic technologies (Bt maize, Cry proteins). Boolean operators (AND, OR) were used to refine the searches. Additional articles were identified through manual screening of reference lists of relevant reviews and key primary studies.

Inclusion and exclusion criteria

Studies were included if they met the following criteria: (1) original research or comprehensive reviews published in English in peer-reviewed journals or recognized conference proceedings; (2) investigations focused on maize resistance mechanisms against major lepidopteran pests (*Chilo partellus, Ostrinia nubilalis, Diatraea* spp., *Spodoptera frugiperda, Helicoverpa zea*); (3) studies reporting quantitative data on biochemical resistance factors (e.g., DIMBOA, maysin) or morphological traits (trichomes, husk tightness); (4) molecular mapping studies identifying QTLs or markers associated with insect resistance; (5) field trials evaluating transgenic Bt maize performance and efficacy; and (6) IPM validation experiments incorporating host plant resistance as a component. Studies were excluded if they: (1) focused solely on non-lepidopteran pests; (2) did not include original experimental data or rigorous statistical analysis; (3) were published in non-peer-reviewed outlets or predatory journals; or (4) were not available in full text.

Screening and data extraction

The screening process was conducted in two stages. In the first stage, titles and abstracts were independently reviewed by two authors to eliminate clearly irrelevant records. In the second stage, full texts of potentially eligible articles were assessed against the inclusion criteria.

Disagreements were resolved through discussion or consultation with a third reviewer. From the final set of included studies, data were extracted using a standardized form covering: (1) pest species and experimental conditions; (2) resistance mechanisms investigated (antibiosis, antixenosis, tolerance); (3) biochemical and morphological traits quantified; (4) molecular markers, QTL positions, and genomic tools employed; (5) transgenic event details and efficacy outcomes; (6) IPM strategies and comparative treatment designs; and (7) yield responses and agronomic performance.

Thematic integration and synthesis

Extracted data were organized thematically into four major categories: (i) conventional host plant resistance mechanisms (biochemical, morphological, and tolerance-based); (ii) molecular genetics and breeding approaches (QTL mapping, marker-assisted selection, meta-QTL, genomic selection, and CRISPR-based studies); (iii) transgenic Bt maize and resistance management; and (iv) IPM frameworks integrating HPR with biological control and cultural practices. Findings were synthesized narratively, with quantitative data summarized in tabular form where appropriate. Meta-QTL results from multiple independent studies were compiled to identify consensus genomic regions associated with stable resistance across diverse genetic backgrounds and environments.

Results and Discussion

Host plant resistance mechanisms against lepidopteran pests

Host plant resistance in maize encompasses a diverse array of constitutive and induced mechanisms that operate through antibiosis, antixenosis, and tolerance. Table 1 provides a comprehensive summary of the major resistance factors reported against key lepidopteran pests.

DIMBOA-mediated resistance: A broad-spectrum defensive metabolite

DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) and its glucoside derivative are among the most extensively studied resistance factors in maize. The negative correlations between MBOA concentration and both leaf feeding (r = -0.82 to -0.86) and larval survival (r = -0.78 to -0.88) confirm DIMBOA as a major resistance factor for early-whorl feeding in stem borers (Tseng, 1997). However, the significance of DIMBOA extends far beyond stem borer resistance.

DIMBOA functions as a broad-spectrum defensive compound active against multiple arthropod pests. Niemeyer (1988) demonstrated its toxicity against cereal aphids (*Rhopalosiphum padi*, *Sitobion avenae*), leafhoppers (*Cicadulina* spp.), and several lepidopteran species including fall armyworm (*S. frugiperda*) and European corn borer (*O. nubilalis*). The compound acts through multiple mechanisms: (i) protein denaturation and enzyme inhibition in the insect midgut; (ii) feeding deterrence at sublethal concentrations; and (iii) reduced digestibility of plant proteins through complex formation. Importantly, DIMBOA concentrations are highest in young, rapidly growing tissues (up to 2-3 mmol/kg fresh weight) and decline with plant age, which explains the greater susceptibility of older plants to late-season pests. This ontogenetic pattern has significant implications for breeding programs, as efforts to extend DIMBOA expression into later growth stages could provide season-long protection.

The biosynthesis of DIMBOA is regulated by the *Bx* gene cluster, and recent genomic studies have identified key regulatory elements controlling its temporal and spatial expression. The identification of allelic variation in *Bx* genes has opened avenues for marker-assisted selection to enhance constitutive and induced DIMBOA levels in elite germplasm (Dutartre *et al.*, 2021).

Genetic gains from recurrent selection

Recurrent selection has proven highly effective in accumulating favorable alleles for insect resistance. Barry and Darrah (1997) reported that six cycles of recurrent selection reduced stalk tunneling from 22.0 cm to 6.7 cm in the PR-Mo2 population, representing a 69.5% reduction in damage. Similarly, selection for fall armyworm resistance in PopG reduced leaf damage ratings by 0.16 units per cycle (Welcker *et al.*, 1997). These gains demonstrate that additive genetic variance is exploitable through S1 family selection. More recent breeding efforts at CIMMYT have developed multiple borer-resistant (MBR) germplasm with combined resistance to stem borers and fall armyworm, which are

Table 1. Comprehensive Summary of Maize Resistance Mechanisms Against Lepidopteran Pests

Mechanism	Category	Chemical/Physical Factor	Target Pest(s)	Efficacy Indicator	References
Antibiosis	Biochemical	DIMBOA/MBOA	*O. nubilalis*, *C. partellus*, *S. frugiperda*, aphids, leafhoppers	r = -0.85 (leaf damage); broad-spectrum activity	Tseng (1997); Niemeyer (1988)
Antibiosis	Biochemical	Maysin (C-glycosyl flavone)	*H. zea*, *S. frugiperda*	50% growth reduction at 0.2% silk concentration	Wiseman (1997); Snook *et al.* (1997)
Antibiosis	Biochemical	Chlorogenic acid	*O. nubilalis*, *S. frugiperda*	Larval growth inhibition; synergistic with DIMBOA	Nicol *et al.* (1997)
Antibiosis	Biochemical	Cell wall phenolics (ferulic acid, p-coumaric acid)	*O. nubilalis*, stem borers	$R^2 = 0.78$ for leaf damage; reduced digestibility	Bergvinson *et al.* (1997)
Antibiosis	Biochemical	Peroxidase and polyphenol oxidase	*O. nubilalis*, *S. frugiperda*	Oxidative cross-linking; reduced nutrient availability	Dowd and Vega (1996)
Antixenosis	Morphological	Leaf trichomes (density and length)	*C. partellus*, *S. frugiperda*	2× fewer eggs on hairy leaves; reduced oviposition	Kumar (1997)
Antixenosis	Morphological	Husk tightness and extension	*H. zea*, *S. frugiperda*	Reduced ear entry; >70% protection in tight-husk genotypes	Barry and Darrah (1991)
Antixenosis	Morphological	Silks and cuticular lipids	*S. frugiperda*, *H. zea*	Reduced larval settling and feeding initiation	Wiseman (1997); Smith (1989)
Antixenosis	Morphological	Leaf toughness and rind penetrometer resistance	Stem borers (*Diatraea* spp.)	Reduced boring success; stalk lodging resistance	Bergvinson *et al.* (1997)
Tolerance	Physiological	Root regrowth capacity	*Diabrotica* spp., stem borers	50% less yield loss despite infestation	Moellenbeck *et al.* (1997)
Tolerance	Physiological	Vigor and compensatory growth	Generalist pests	Maintenance of yield under moderate infestation	Smith (1989)
Induced	Biochemical	Jasmonic acid and salicylic acid pathways	*S. frugiperda*, *O. nubilalis*	Upregulation of proteinase inhibitors; volatile emission	Turlings *et al.* (1990); Kessler and Baldwin (2002)
Induced	Biochemical	Herbivore-induced plant volatiles (HIPVs)	Multiple lepidopteran pests	Attraction of natural enemies (parasitoids)	Turlings *et al.* (1990); Degenhardt *et al.* (2009)
Induced	Biochemical	Systemic acquired resistance	*O. nubilalis*	Priming of defense responses upon repeated infestation	Morris *et al.* (2005)

now being deployed in African and Asian breeding programs.

QTL mapping, Meta-QTL, and marker-assisted selection

Khairallah *et al.* (1997) identified QTLs for Southwestern corn borer resistance on chromosomes 1, 3, 5, 7, and 9 in two F_2 populations. Notably, QTLs on chromosomes 1 and 5 were common to both SWCB and sugarcane borer resistance, indicating shared genetic components. Additive effects were predominantly from resistant parents, but dominance effects also contributed (d/a ratios ranging from 0.5 to 2.0). These findings support the feasibility of marker-assisted selection for pyramiding multiple resistance alleles.

Recent advances in insect resistance-related Meta-QTL analysis

A 2024 meta-QTL analysis by Badji *et al.* integrated 128 QTLs from 12 independent mapping studies focused on maize resistance to lepidopteran stem borers and fall

armyworm. The study identified 18 stable meta-QTLs (MQTLs) distributed across all 10 maize chromosomes, with an average confidence interval reduction from 22.7 cM to 4.9 cM (78.4% reduction). Six MQTL hotspots on chromosomes 1, 2, 3, 5, 6, and 9 were identified as "core regions" containing multiple resistance-associated genes. Candidate genes within these MQTL intervals included those involved in cell wall biosynthesis (cellulose synthases, phenylpropanoid pathway genes), proteinase inhibitors, and genes regulating DIMBOA biosynthesis (*Bx* genes). RNA-seq-based expression profiling confirmed that 72 candidate genes within MQTL regions were differentially expressed upon insect infestation, providing robust targets for MAS and genomic selection.

Complementary meta-analyses targeting stalk lodging resistance (Fang *et al.*, 2025) have indirect relevance to insect resistance, as stem borer tunneling is a primary cause of lodging. This study integrated 889 QTLs to identify 67 MQTLs, of which 32 were designated as "core MQTLs." Comparative genomics revealed 40 evolutionarily conserved orthologs with rice lodging resistance genes, and 802 candidate genes were identified with KEGG enrichment implicating galactose degradation II in cell wall reinforcement (Figure 3).

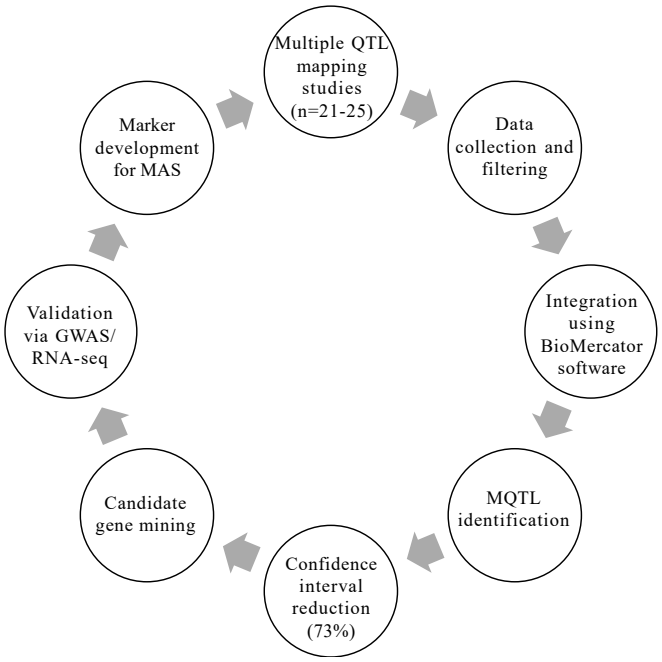


Figure 3. Workflow of Meta-QTL Analysis for Maize Pest and Stress Resistance

Field performance of transgenic Bt maize

i) Global introduction and adoption

Genetically engineered Bt maize expressing insecticidal *Cry* proteins derived from *Bacillus thuringiensis* was first commercially introduced in 1996 in the United States. Since then, adoption has been rapid, with Bt maize planted on over 80% of U.S. corn acreage by 2020 and extensive cultivation in Brazil, Argentina, South Africa, Canada, and the Philippines. Globally, Bt maize is now cultivated on more than 60 million hectares annually, contributing significantly to pest suppression and yield stability.

ii) Efficacy against target pests

Estruch *et al.* (1997) reported that transgenic maize expressing synthetic *CryIA(b)* under tissue-specific promoters (PEPC, pollen-specific) achieved >99% reduction in European corn borer tunneling (0.3 cm vs. 59 cm in controls). Sagers *et al.* (1997) confirmed these results across multiple U.S. locations, with Bt hybrids showing leaf feeding ratings of 1.06 (vs. 3.71 for non-Bt) and stalk tunneling of 0.15 cm (vs. 4.53 cm). Importantly, *CryIA(b)* protein was undetectable in kernels, addressing food safety concerns. Subsequent field trials across multiple countries have consistently demonstrated excellent efficacy against key lepidopteran pests including *O. nubilalis*, *C. partellus*, *S. frugiperda*, and *H. zea*, with damage reductions typically exceeding 95% in single-gene events and near-complete protection in pyramided events.

iii) Resistance evolution and management strategies

The evolution of Bt resistance in target pest populations is the most significant threat to the long-term sustainability of Bt maize. Field-evolved resistance to Cry1Ab maize has been documented in *S. frugiperda* in Puerto Rico (Storer *et al.*, 2010), Brazil, and Argentina, and in *Busseola fusca* in South Africa. To manage resistance, the U.S. Environmental Protection Agency mandates structured refuge strategies, requiring non-Bt refuge areas to sustain susceptible pest populations. The "high-dose/refuge" strategy assumes that resistance alleles are functionally recessive and that rare resistant survivors mating with susceptible individuals will produce susceptible offspring, delaying resistance evolution.

More recent strategies involve pyramiding (stacking) multiple *Bt* genes with different modes of action in a single event. SmartStax® (Cry1A.105, Cry2Ab2, Cry1F) and Genuity® VT Double Pro® (Cry1A.105, Cry2Ab2) represent commercial pyramided products with improved resistance management potential. The molecular discoveries regarding receptor specificity (discussed in Section 4.6) have provided a mechanistic foundation for optimizing gene pyramids.

iv) Yield benefits and economic impact

Meta-analyses of Bt maize field trials indicate average yield increases of 5-15% under moderate pest pressure and up to 30-50% under severe infestation. In developing countries where pest pressure is high and insecticide access is limited, Bt maize offers particularly significant benefits, with yield gains of 20-40% reported in Kenya, South Africa, and the Philippines. Economic analyses show that Bt maize reduces insecticide applications by 3-5 sprays per season and increases net returns by $30-80 per hectare, with even higher benefits in tropical environments.

Breakthrough discoveries in Bt mode of action

A paradigm-shifting study published in PNAS (April 2025) by Wang *et al.* elucidated the molecular basis for differential resistance risk between *Cry1Ab* and *Cry1Fa*. Using CRISPR-Cas9 gene editing, the researchers created six Asian corn borer (*O. furnacalis*) knockout lines targeting three gut receptors: ABCC2, ABCC3, and cadherin.

The discovery that Cry1Ab functions as a "natural pyramid" with two redundant lethal pathways explains its exceptional durability. In contrast, Cry1Fa's reliance on a single receptor (ABCC2) means that mutations disrupting ABCC2 alone confer resistance. This finding has profound implications for resistance management: pyramiding Cry1Ab with other *Bt* genes that utilize different receptor combinations will further delay resistance evolution (Figure 4).

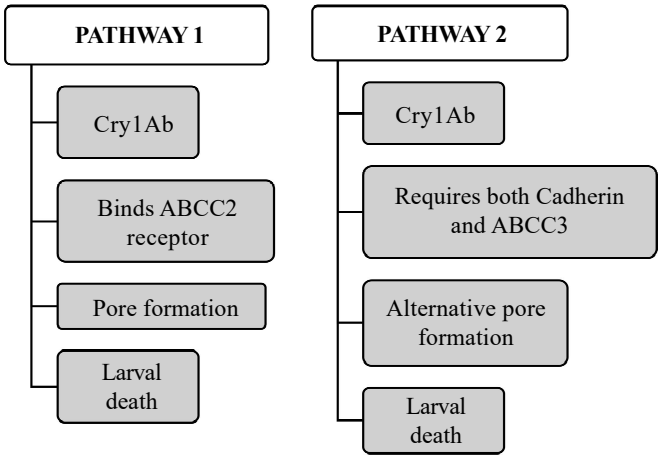


Figure 4. Schematic of Cry1Ab Dual-Pathway Mechanisms

Integration of HPR into IPM frameworks

The practical utility of HPR within IPM frameworks has been validated through numerous field studies. Wiseman (1997) demonstrated that high-level silk resistance (maysin >0.4%) could reduce corn earworm generations from six to four and surviving larvae from 1.6 million to 168 per season—a 10,000-fold reduction in population carryover. Subsequent studies have validated these findings in field settings, with resistant silks reducing larval establishment by 60-80% and significantly reducing the need for insecticide applications during the silking period.

Khan *et al.* (2015) demonstrated that an IPM package combining cultural (intercropping, trap crops), mechanical (removal of crop residues), biological (*Trichogramma* release), and host plant resistance components reduced *C. partellus* infestation from 12.92% to 2.32% and increased yield from 6.23 to 8.64 t/ha (38.7% increase) over two years. These results highlight the synergistic effects of combining HPR with other IPM tactics.

Contemporary IPM approaches have evolved to include landscape-level considerations. The EU IPMWORKS project (2020-2025) demonstrated that farmer-led IPM networks achieve pesticide reductions of up to 50% without yield penalties. Key success factors included peer-to-peer learning, hub coaches, and economic incentives that frame IPM as an opportunity rather than

Key findings

Bt Protein	Receptor Requirement	Resistance Risk	Field Durability
Cry1Ab	ABCC2 OR (Cadherin + ABCC3) - Two pathways	Low	>21 years effective
Cry1Fa	ABCC2 only - Single pathway	High	Resistance reported after 12 years

a constraint. These principles are increasingly being adapted to maize-based systems in developing countries.

Molecular diagnostics and emerging tools

The integration of molecular diagnostics has strengthened HPR breeding and pest management. DNA barcoding enables accurate identification of pest species and biotypes, including cryptic species complexes that differ in host range and insecticide susceptibility. Real-time PCR and LAMP assays are now available for rapid, field-deployable identification of resistance alleles in pest populations. These tools facilitate early detection of Bt resistance and informed decision-making for refuge management and insecticide rotation strategies.

Summary and conclusion

This review has synthesized three decades of progress in maize entomology, with significant advances extending through 2025. The key findings are summarized below.

Host plant resistance mechanisms

Host plant resistance in maize operates through a multi-mechanistic defense system comprising biochemical, morphological, and tolerance-based components. DIMBOA remains the most extensively characterized biochemical factor, conferring broad-spectrum activity against stem borers, fall armyworm, aphids, leafhoppers, and other pests through protein denaturation and feeding deterrence. However, DIMBOA levels decline with plant age, necessitating complementary mechanisms for season-long protection. Morphological traits including leaf trichomes, husk tightness, stem rind hardness, and silk characteristics provide critical antixenosis barriers against pest colonization and feeding. Recent meta-QTL analyses have identified stable genomic regions controlling these resistance traits, with candidate genes involved in cell wall biosynthesis, secondary metabolism, and defense signaling. Conventional breeding via recurrent selection has achieved genetic gains of 5–13% per cycle, demonstrating the exploitable additive genetic variance for resistance traits.

Transgenic Bt maize: performance and resistance management

Transgenic Bt maize, commercially introduced in 1996 and now cultivated on over 60 million hectares globally, provides near-complete control of target lepidopteran pests with yield benefits of 5–50% depending on infestation pressure. The 2025 discovery that Cry1Ab operates through two redundant lethal pathways (ABCC2 OR cadherin+ABCC3) explains its exceptional durability (>21 years without field-evolved resistance in *O. nubilalis*), compared to Cry1Fa which relies on a single receptor and has experienced resistance in *S. frugiperda* within 12 years. Documented cases of field-evolved resistance in *S. frugiperda* (Puerto Rico, Brazil, Argentina) and *Busseola fusca* (South Africa) underscore the necessity of proactive resistance management through structured refuges and pyramiding of *Bt* genes with distinct receptor specificities.

Integration into IPM frameworks

The integration of HPR, Bt maize, biological control, and cultural practices within IPM frameworks yields additive or synergistic benefits. Field validation of maysin-mediated silk resistance demonstrates population-level suppression of corn earworm, while multi-tactic IPM packages combining cultural, mechanical, biological, and host resistance components have achieved 38–50% yield increases and pesticide reductions without yield penalties. Landscape-level IPM approaches and farmer-led networks are emerging as effective models for sustainable pest management.

Recent genomic advances

Recent advances in GWAS, genomic selection, transcriptomics, metabolomics, and CRISPR-Cas9 gene editing have accelerated resistance breeding. Genomic selection models now enable prediction of complex resistance traits with accuracies of 0.4–0.6. CRISPR-Cas9 has enabled functional validation of candidate resistance genes and elucidation of Bt receptor mechanisms, paving the way for targeted enhancement of native resistance traits.

Future research priorities

Based on the findings of this review, the following research priorities are identified:

- Pyramiding of native and transgenic resistance traits to create layered defenses that delay pest adaptation, leveraging insights from Cry1Ab's dual-pathway mechanism.
- Functional validation of MQTL-derived candidate genes using CRISPR-Cas9 to enhance DIMBOA biosynthesis, cell wall reinforcement, and resistance gene regulation.
- Expansion of IPM programs in smallholder farming systems through farmer-led networks, peer-to-peer learning, and economic incentives.
- Exploration of novel resistance sources from wild relatives (*Zea* spp., *Tripsacum* spp.) and underutilized germplasm.
- Climate-resilient insect resistance breeding to maintain efficacy under changing environmental conditions affecting pest dynamics and plant defense expression.
- Development of rapid molecular diagnostics for field-deployable detection of resistance alleles (ABCC2, cadherin mutations) to enable proactive resistance management.
- Integration of genomic selection with high-throughput phenomics to accelerate genetic gains in complex resistance traits.

Concluding remarks

The convergence of conventional breeding, molecular genetics, and advanced genomic tools promises to sustain maize productivity while reducing the environmental footprint of pest control. The elucidation of Cry1Ab's dual-pathway mechanism, the identification of stable MQTLs for insect resistance, and the emergence of CRISPR-based functional genomics collectively provide unprecedented opportunities for developing durable, climate-resilient insect resistance in maize. Sustained investment in multidisciplinary research and participatory IPM programs will be essential to translate these advances into tangible benefits for farmers worldwide.

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