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Insights into Mechanisms of Maize Resistance to Major Pests

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Abstract Maize is a critical staple crop, providing food security and supporting economies worldwide. However, the crop faces persistent threats from various pests, leading to significant yield losses and environmental damage. This study explores the mechanisms of maize resistance to major pests, encompassing conventional breeding strategies, biochemical defenses, genetic and molecular tools, and anatomical traits. A case study on Bt maize highlights its role as a breakthrough in pest resistance, delving into its development, mechanisms of action, and socioeconomic impacts. Additionally, integrative approaches combining genetic, agronomic, and biological practices are discussed to enhance pest resistance. Challenges such as resistance evolution, regulatory hurdles, and the need for sustainable solutions are examined. The findings underscore the necessity of continuous innovation in breeding techniques and integrative pest management to ensure long-term maize productivity and sustainability.

Keywords Maize pest resistance; Bt maize; Genetic breeding; Integrative pest management; Sustainable agriculture

1 Introduction

Maize (*Zea mays* L.) is one of the most significant staple crops globally, serving as a primary source of food, feed, and biofuel. It is the largest staple crop produced worldwide, playing a crucial role in ensuring global food security (Yang et al., 2017; López-Castillo et al., 2018). Maize's versatility and high yield potential make it indispensable for both human consumption and livestock feed, contributing significantly to the agricultural economy (Lange et al., 2014; Liu et al., 2023; Cai et al., 2024).

Despite its importance, maize cultivation faces substantial challenges from various pests. Major insect pests such as the maize weevil (*Sitophilus zeamais*), the large grain borer (*Prostephanus truncatus*), the European corn borer (*Ostrinia nubilalis*), and the fall armyworm (*Spodoptera frugiperda*) cause significant damage to maize crops (López-Castillo et al., 2018; Franeta et al., 2019; Warburton et al., 2023). These pests can devastate entire crops, leading to considerable yield losses and affecting the quality of the harvested grain (García-Lara and Bergvinson, 2014; Liu et al., 2023). The continuous threat from these pests necessitates effective pest management strategies to sustain maize production (Karjagi et al., 2017; Gassmann, 2021).

Pest infestations in maize have profound economic and ecological implications. Economically, pest damage can lead to losses of up to 40% of total production, particularly in developing countries where smallholders may lack access to effective pest control measures (García-Lara and Bergvinson, 2014; López-Castillo et al., 2018). This not only affects food availability but also impacts the livelihoods of farmers who depend on maize as a primary income source. Ecologically, the use of chemical insecticides to manage pests can lead to environmental degradation and the development of pest resistance, further complicating pest management efforts (Ngom et al., 2020; Gassmann, 2021). Sustainable pest management practices, including the development of pest-resistant maize varieties, are essential to mitigate these impacts (Lange et al., 2014; Karjagi et al., 2017).

This study attempts to gain insights into the mechanisms of maize resistance to major pests, discuss the genetic, biochemical, and physiological bases of resistance, and provide an overview of the development of maize varieties that can withstand pest attacks without compromising yield and quality. This study will explore the current status and advances in maize pest resistance, discuss the role of specific genes and pathways in conferring resistance, and provide an overview of the potential for integrating these findings into breeding programs to enhance maize resilience against pests. Ultimately, the goal is to explore sustainable solutions for pest management in maize cultivation, discuss ensuring food security, and provide an overview of economic stability for farmers worldwide.

2 Major Pests Affecting Maize

2.1 Overview of key pests: biology, lifecycle, and impact on maize yield

Maize is significantly affected by several major pests, including the maize weevil (*Sitophilus zeamais*), the large grain borer (*Prostephanus truncatus*), the fall armyworm (*Spodoptera frugiperda*), the European corn borer (*Ostrinia nubilalis*), and the corn leaf aphid (*Rhopalosiphum maidis*). The maize weevil primarily affects stored maize, causing up to 40% loss in total production, particularly in developing countries. Its lifecycle includes egg, larval, pupal, and adult stages, with larvae feeding inside the grain, making early detection challenging. Similarly, the large grain borer also targets stored maize, causing significant postharvest losses as larvae burrow into the grains, inflicting extensive damage (López-Castillo et al., 2018; Block et al., 2019; Nuambote-Yobila et al., 2023).

The fall armyworm, native to the Americas, has recently spread to Africa and Asia, becoming a severe threat to maize production. With a rapid lifecycle and multiple generations per year, its larvae feed voraciously on maize leaves, stems, and ears, leading to substantial yield losses. The European corn borer is prevalent in Europe and North America, with larvae boring into maize stalks and ears, disrupting nutrient flow and causing economically significant yield reductions. The corn leaf aphid feeds on the sap of maize plants, weakening them and transmitting plant viruses. With multiple generations per year, aphid infestations can lead to severe yield losses, further challenging maize production (Franeta et al. 2019; Wang et al., 2023).

2.2 Regional variations in pest prevalence and severity

The prevalence and severity of maize pests vary significantly across regions due to climatic conditions, agricultural practices, and pest management strategies. In developing countries, such as those in Sub-Saharan Africa, the maize weevil and large grain borer are particularly problematic due to inadequate storage facilities and limited access to pest control measures, resulting in significant postharvest losses and food security challenges (López-Castillo et al., 2018; Nuambote-Yobila et al., 2023). In the Americas, the fall armyworm has long been a major pest, and its recent spread to Africa and Asia has intensified its global impact on maize production. In Europe and North America, the European corn borer poses significant threats, with its impact varying based on local environmental conditions and pest management practices, highlighting the importance of effective monitoring and control measures. The corn leaf aphid, a globally distributed pest, causes damage influenced by regional climatic conditions and natural predator populations, underscoring the need for effective integrated pest management (IPM) strategies to control its spread and minimize yield losses (Franeta et al. 2019).

2.3 Emerging threats due to climate change and agricultural practices

Climate change and evolving agricultural practices are driving the emergence and spread of new pest threats to maize. Rising temperatures and changing precipitation patterns create favorable conditions for pests such as the fall armyworm and European corn borer, leading to increased pest pressure and expanded geographical ranges (Block et al., 2019; Nuambote-Yobila et al., 2023). Intensive monoculture practices and excessive use of chemical pesticides exacerbate the problem by promoting pest resistance and secondary pest outbreaks. To address these challenges, sustainable agricultural practices, including crop rotation, biological control, and the development of pest-resistant maize varieties, are essential. Biotechnological advances, such as the identification of resistance genes and the use of quantitative trait loci (QTL) mapping, are enabling the development of maize varieties with enhanced resistance to multiple pests, including the corn leaf aphid and fall armyworm. Understanding the biology, lifecycle, and regional prevalence of major maize pests, along with the impact of climate change, is critical for designing effective pest management strategies. These combined approaches are pivotal for improving maize resilience and ensuring global food security (Figure 1) (Karjagi et al., 2017; Liu et al., 2023; Niu et al., 2023).

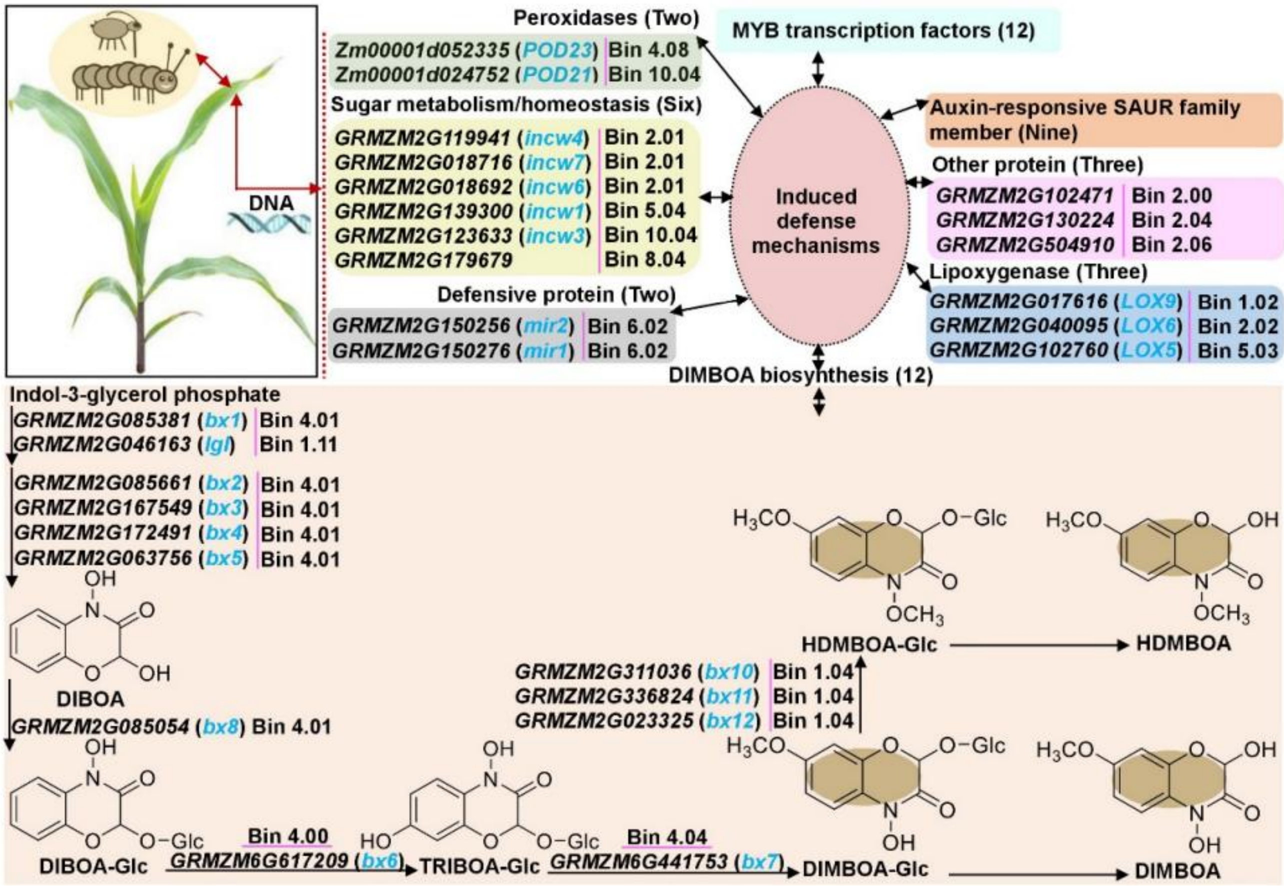

Figure 1 Molecular defense mechanisms underlying resistance to multiple insect pests of Asian corn borer (ACB) and corn leaf aphid (CLA) in maize (Adopted from Liu et al., 2023)

Image caption: The synergy and antagonism of 49 candidate genes within 19 hot genetic loci formed the complex maize multiple insect pest-induced defense mechanisms, as well as DIMBOA biosynthesis pathway network (Adopted from Liu et al., 2023)

3 Mechanisms of Pest Resistance in Maize

3.1 Conventional breeding approaches

Conventional breeding approaches have been instrumental in developing maize varieties resistant to various pests. These methods involve selecting and cross-breeding plants that exhibit natural resistance traits. For instance, modern breeding programs have successfully developed insect-resistant maize varieties that reduce postharvest pest losses, particularly against pests like the maize weevil and the large grain borer (López-Castillo et al., 2018). Additionally, field experiments have identified specific inbred lines that show resistance to pests such as the Asian corn borer, highlighting the potential of conventional breeding in managing pest resistance (Guo et al., 2022).

3.2 Biochemical mechanisms of resistance

Biochemical mechanisms play a crucial role in maize resistance to pests. One significant biochemical compound is DIMBOA, a benzoxazinoid that has been associated with resistance to multiple insect pests, including the Asian corn borer and corn leaf aphids (Figure 2) (Niu et al., 2023). The accumulation of defense metabolites like lignin and DIMBOA, regulated by genes such as ZmBGLU17, enhances maize resistance to both pathogens and insect pests without compromising yield (Liu et al., 2023). Furthermore, the presence of high levels of benzoxazinoids in resistant maize lines has been linked to their ability to withstand pest attacks more effectively (Guo et al., 2022).

3.3 Genetic and molecular mechanisms

Genetic and molecular mechanisms underpin many of the resistance traits observed in maize. Genome-wide association studies (GWAS) have identified numerous quantitative trait loci (QTLs) and candidate genes associated with resistance to pests like the fall armyworm and maize weevil (Badji et al., 2020). For example, the gene ZmBGLU17 has been shown to confer resistance to both pathogens and insect pests through the regulation of defense metabolites (Liu et al., 2023). Additionally, QTL mapping has revealed specific regions on maize chromosomes that are linked to resistance traits, providing valuable targets for resistance breeding programs (Wang et al., 2023).

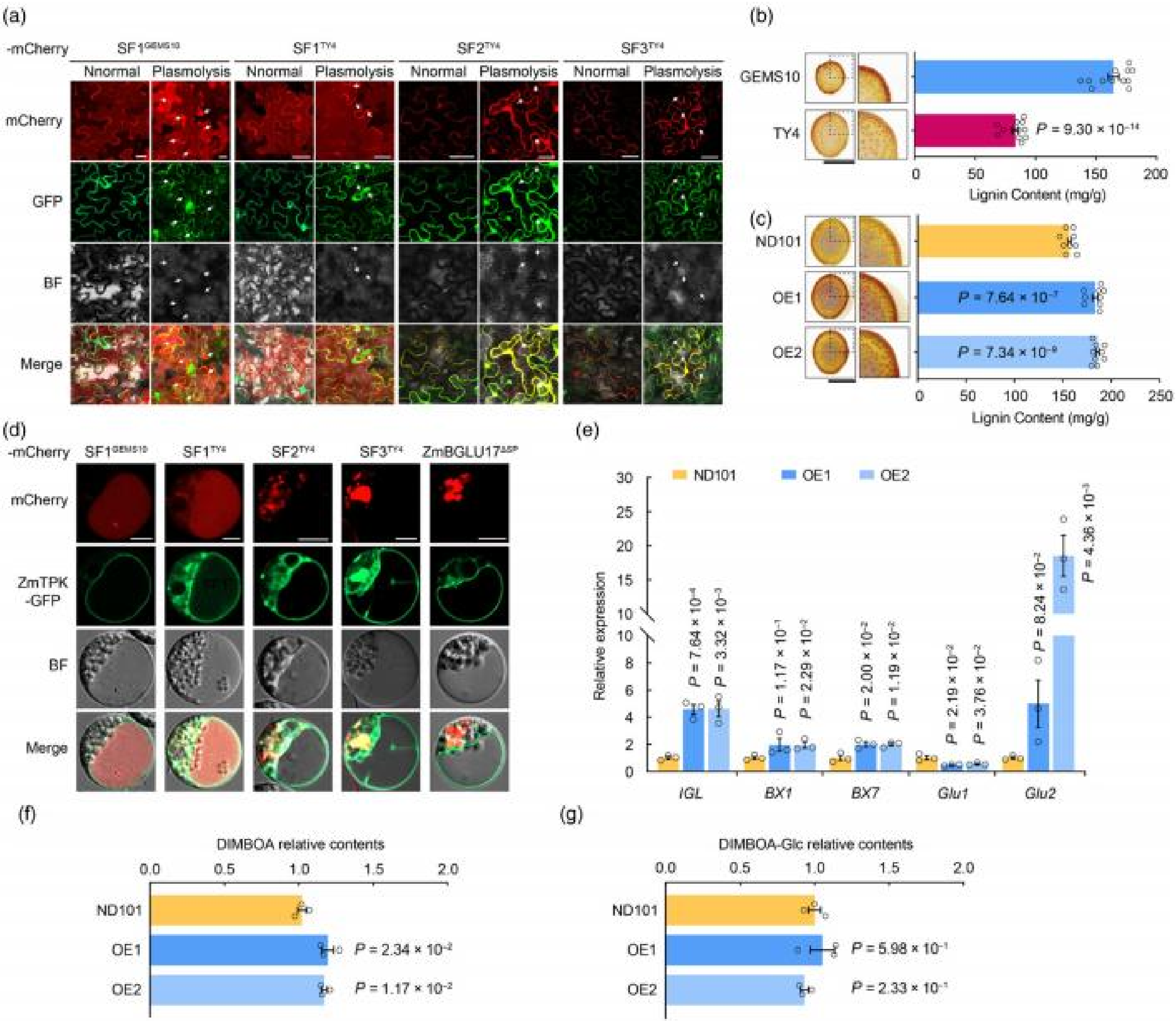

Figure 2 Apoplastic and vacuolar localized ZmBGLU17 contributes to the accumulation of both lignin and DIMBOA in maize (Adopted from Liu et al., 2023)

3.4 Anatomical and morphological traits

Anatomical and morphological traits also contribute to maize resistance against pests. Certain maize inbred lines exhibit physical traits that enhance their resistance to root herbivores like the western corn rootworm. For instance, the inbred line Mp708 shows increased resistance to cutting in nodal roots and stable root growth during insect infestation, along with high levels of jasmonic acid and specific defense-related proteins (Castano-Duque et al., 2017). These traits, combined with the constitutive and induced expression of herbivore-defense genes, form a multi-trait phenotype that provides robust resistance to pests.

Maize resistance to major pests is achieved through a combination of conventional breeding approaches, biochemical mechanisms, genetic and molecular mechanisms, and anatomical and morphological traits. Conventional breeding has led to the development of resistant varieties, while biochemical compounds like DIMBOA play a significant role in pest resistance. Genetic studies have identified key loci and genes involved in resistance, and specific anatomical traits enhance the plant's ability to withstand pest attacks. Together, these mechanisms provide a comprehensive strategy for managing pest resistance in maize.

4 Case Study: Bt Maize-A Milestone in Genetic Resistance

4.1 Development and adoption of Bt maize varieties

Bt maize varieties were first introduced in the 1990s as a revolutionary approach to pest management in agriculture. These genetically engineered crops express insecticidal proteins derived from the bacterium *Bacillus thuringiensis* (Bt), which protect the plants from insect damage. The first Bt maize in Brazil, containing the MON 810 event that expresses the Cry1Ab protein, was launched in 2008 and provided commercial levels of control against the fall armyworm (FAW), *Spodoptera frugiperda*, despite the Cry1Ab dose not being high against this pest (Omoto et al., 2016). In the United States, Bt maize has been used since 2003 to manage the western corn rootworm, *Diabrotica virgifera virgifera*, a major pest of maize. The adoption of Bt maize has been widespread due to its effectiveness in reducing pest damage and associated yield losses, as well as its environmental benefits, such as reduced insecticide use (Arends et al., 2021; Gassmann et al., 2021).

4.2 Mechanisms of action: cry proteins and pest targeting

Bt maize varieties work by expressing Cry proteins, which are toxic to specific insect pests. These proteins bind to receptors in the gut cells of the target insects, causing cell lysis and eventually leading to the insect's death. Different Cry proteins target different pests; for example, Cry1Ab targets lepidopteran pests like the European corn borer, while Cry3Bb1 targets coleopteran pests like the western corn rootworm (Gassmann, 2021; Álvarez-Alfageme et al., 2021). In Brazil, Bt maize expressing Cry1F, Cry1A.105, Cry2Ab2, and Vip3Aa20 proteins has been effective in managing FAW, providing near 100% protection from kernel-feeding damage (Moscardini et al., 2020). However, resistance to these proteins can develop, as seen with the Cry1F resistance in FAW populations in Brazil, which also showed cross-resistance to Cry1A.105 and Cry1Ab (Bernardi et al., 2015).

4.3 Field performance and resistance management strategies

The field performance of Bt maize has generally been positive, with significant reductions in pest damage and increased yields. For instance, MON 810 maize in Brazil showed significantly less damage from FAW compared to non-Bt maize, although resistance monitoring from 2010 to 2015 indicated a reduction in Cry1Ab susceptibility over time (Omoto et al., 2016). In the US, resistance to Cry3Bb1 in western corn rootworm populations has been documented, necessitating diversified management strategies such as crop rotation and the use of soil-applied insecticides (Gassmann, 2021). Effective resistance management strategies include planting refuges of non-Bt maize to maintain a population of susceptible pests, monitoring for resistance, and using pyramided Bt maize varieties that express multiple Cry proteins to delay resistance development (Saikai et al., 2020; Álvarez-Alfageme et al., 2021).

4.4 Socioeconomic and environmental impact of Bt maize adoption

The adoption of Bt maize has had significant socioeconomic and environmental impacts. Economically, Bt maize has led to reduced yield losses and lower pest management costs, benefiting farmers. For example, in Argentina, the adoption of Bt maize has been part of a multi-institutional approach to manage resistance, ensuring sustainable and profitable maize production with yields above the average (Signorini et al., 2018). Environmentally, Bt maize has contributed to reduced insecticide use, which lowers the risk of off-target effects and environmental contamination (Arends et al., 2021). However, the development of resistance in pest populations can diminish these benefits, highlighting the need for effective resistance management strategies to sustain the long-term advantages of Bt maize (Saikai et al., 2020; Gassmann, 2021; Orozco-Restrepo et al., 2024).

The development and adoption of Bt maize varieties have revolutionized pest management in agriculture, providing significant economic and environmental benefits. The mechanisms of action of Cry proteins and their effectiveness in targeting specific pests have been well-documented, although resistance development remains a challenge. Field performance has generally been positive, but effective resistance management strategies are crucial to maintaining the benefits of Bt maize. The socioeconomic and environmental impacts of Bt maize adoption underscore its importance in modern agriculture, while also highlighting the need for ongoing resistance management efforts.

5 Integrative Approaches to Pest Resistance

5.1 Combining genetic and agronomic practices

Combining genetic and agronomic practices is a pivotal strategy in enhancing maize resistance to pests. Modern breeding programs have focused on developing insect-resistant maize varieties through the identification and incorporation of resistance genes. For instance, the use of quantitative trait loci (QTL) mapping has been instrumental in identifying genetic regions associated with resistance to pests like the corn leaf aphid and fall armyworm (Figure 3) (Badji et al., 2020; Wang et al., 2023). Additionally, integrating these genetic advancements with agronomic practices such as crop rotation, intercropping, and optimized planting schedules can significantly reduce pest incidence and improve overall crop resilience (Viana et al., 2022; Al-Kahtani et al., 2023). The combination of these practices not only enhances pest resistance but also supports sustainable agricultural systems by reducing reliance on chemical pesticides.

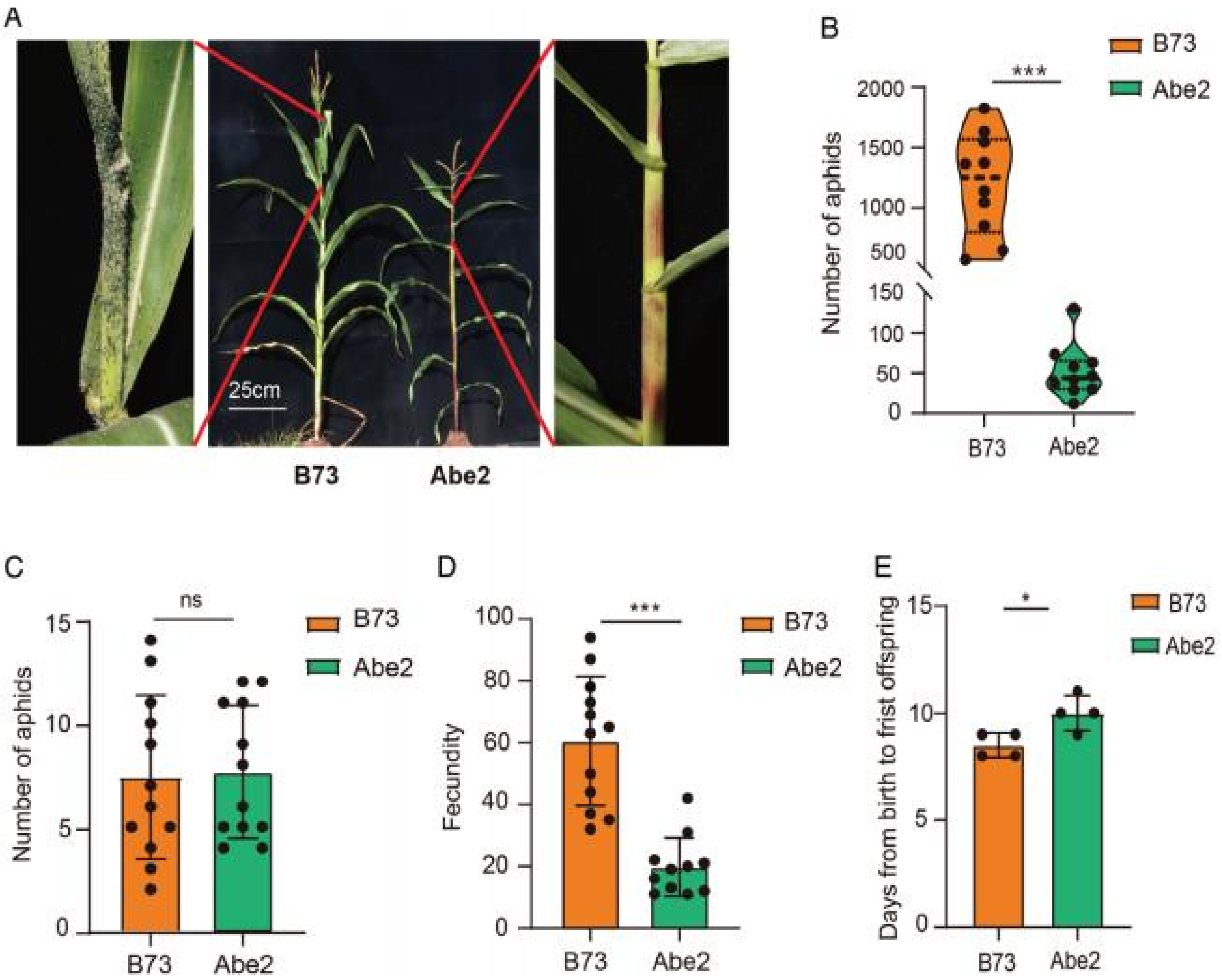

Figure 3 Maize lines B73 and Abe2 show differential resistance to *R. maidis* (Adopted from Wang et al., 2023)

Image caption: (A) Phenotype of B73 and Abe2 in the field upon aphid infestation. Scale bar=25 cm. (B) Quantitative comparison of aphid number on B73 and Abe2 (n=10). (C) Results of aphid preference tests comparing B73 and Abe2 (n=12). (D) Fecundity of aphids on B73 and Abe2 (n=12). (E) Number of days from birth to first offspring for aphids on B73 and Abe2 (n=4). Data are means ±SD; significant differences were determined using Student's t-test and are indicated with asterisks (*P<0.05, ***P<0.001; ns, not significant) (Adopted from Wang et al., 2023)

5.2 Role of biological control agents in resistance systems

Biological control agents play a crucial role in integrated pest management (IPM) systems by naturally regulating pest populations. The use of natural enemies, such as parasitoids and predators, can effectively control pest species like the maize weevil and the large grain borer, which are significant postharvest pests (López-Castillo et al., 2018). Moreover, the integration of biological control agents with resistant maize varieties can create a synergistic effect, enhancing the overall effectiveness of pest management strategies. For example, resistant maize lines can reduce pest populations to levels that are more manageable by natural enemies, thereby improving the sustainability and efficiency of biological control methods (Yang et al., 2017; Nuambote-Yobila et al., 2023).

5.3 Synergistic effects of pest-resistant maize with sustainable farming practices

The deployment of pest-resistant maize varieties in conjunction with sustainable farming practices can lead to significant improvements in pest management and crop productivity. Sustainable practices such as conservation tillage, organic amendments, and the use of cover crops can enhance soil health and biodiversity, creating an environment that supports the effectiveness of resistant maize varieties (López-Malvar et al., 2021; Guo et al., 2022). For instance, the presence of beneficial soil microorganisms and improved soil structure can enhance the expression of resistance traits in maize, leading to better pest suppression and higher yields. Additionally, these practices can reduce the environmental impact of maize cultivation by minimizing the need for chemical inputs and promoting ecological balance.

Integrative approaches to pest resistance in maize, including the combination of genetic and agronomic practices, the role of biological control agents, and the synergistic effects of resistant varieties with sustainable farming practices, offer a comprehensive strategy for managing major pests. These methods not only enhance pest resistance but also contribute to sustainable agricultural systems, ensuring long-term productivity and environmental health.

6 Challenges and Future Directions

6.1 Evolution of pest resistance and overcoming resistance breakdown

The evolution of pest resistance to control measures, such as Bt maize, poses a significant challenge. For instance, the western corn rootworm has developed resistance to multiple Bt traits, which has diminished the effectiveness of these genetically engineered crops (Gassmann, 2021). Factors contributing to this resistance include non-recessive inheritance, minimal fitness costs, and continuous maize cultivation. To delay resistance, diversified management strategies, including crop rotation and the use of non-Bt maize refuges, are recommended.

6.2 Balancing pest resistance with other agronomic traits

Achieving a balance between pest resistance and other agronomic traits, such as yield, is crucial. Studies have shown that resistance to pests like the Mediterranean corn borer can sometimes negatively impact yield and other agronomic traits. However, certain genetic loci have been identified that can improve both yield and resistance simultaneously, suggesting that it is possible to breed maize varieties that do not compromise on yield while enhancing pest resistance (Jiménez-Galindo et al., 2017; Jiménez-Galindo et al., 2019). Additionally, the integration of defensive chemicals like benzoxazinoids has been shown to enhance resistance without affecting growth (Guo et al., 2022).

6.3 Implications of biotechnology regulations and public perception

The adoption of biotechnological solutions, such as genetically modified (GM) crops, is often hindered by regulatory frameworks and public perception. The development and deployment of GM maize varieties resistant to pests like the Asian corn borer and western corn rootworm are subject to stringent regulations, which can delay their availability to farmers (Gassmann, 2021). Public perception also plays a critical role, as acceptance of GM crops varies widely across different regions. Effective communication and education about the benefits and safety of GM crops are essential to gain public trust and regulatory approval.

6.4 Opportunities for next-generation molecular tools and precision breeding

Next-generation molecular tools and precision breeding offer promising opportunities to enhance maize resistance to pests. Techniques such as genome-wide association studies (GWAS) and quantitative trait loci (QTL) mapping have identified numerous genetic loci associated with resistance to multiple pests (Jiménez-Galindo et al., 2017; Badji et al., 2020; Niu et al., 2023). These tools enable the precise identification and manipulation of genes responsible for resistance, facilitating the development of maize varieties with improved pest resistance and agronomic traits. Additionally, the use of CRISPR/Cas9 and other gene-editing technologies can accelerate the breeding process and introduce specific resistance traits without the drawbacks of traditional breeding methods (Liu et al., 2023).

The future of maize resistance to major pests lies in addressing the evolution of pest resistance, balancing resistance with agronomic traits, navigating biotechnology regulations, and leveraging next-generation molecular tools. By integrating these strategies, it is possible to develop sustainable and effective solutions to protect maize crops from pest damage while maintaining high yields and meeting regulatory and public acceptance.

7 Concluding Remarks

Research on maize resistance to major pests has revealed several critical mechanisms. The identification of quantitative trait loci (QTL) and specific genes, such as ZmBGLU17, has been pivotal in understanding resistance to pathogens and pests like the Asian corn borer and Pythium aphanidermatum, without compromising yield. Studies have also highlighted the role of biochemical compounds like DIMBOA in conferring resistance to multiple pests, including the Asian corn borer and corn leaf aphids. Additionally, the integration of QTL mapping with multiomics profiling has identified candidate genes involved in the hypersensitive response and jasmonic acid pathway, which are crucial for aphid resistance. Furthermore, native genetic resistance mechanisms, such as non-preference and antibiosis, have been identified in tropical maize inbred lines against the fall armyworm.

Continuous research and innovation are essential to address the evolving challenges posed by maize pests. The rapid adaptation of pests like the western corn rootworm to Bt maize underscores the need for diversified pest management strategies and the development of new transgenic traits. Advances in genome-wide association studies and multiomics approaches have provided deeper insights into the genetic basis of pest resistance, which are crucial for breeding programs. Moreover, understanding the synergistic effects of combined stressors, such as flooding and pest infestation, can lead to the development of maize varieties with enhanced resilience.

The study of maize resistance to major pests has advanced significantly, uncovering key genetic and biochemical mechanisms. Researchers are focusing on integrating multiomics data to reveal complex genetic networks involved in pest resistance, prioritizing the identification of candidate genes and their functional validation to develop robust pest-resistant maize varieties. Breeders are utilizing identified resistant inbred lines and QTLs in breeding programs to create new maize varieties with enhanced resistance to multiple pests, emphasizing the incorporation of native genetic resistance traits, such as those found in CML71, for sustainable pest management. Policymakers play a critical role by supporting funding for research on pest resistance mechanisms and the development of innovative pest management strategies, while promoting policies that encourage integrated pest management practices and the adoption of resistant maize varieties to reduce reliance on chemical insecticides. Continued research, innovation, and collaboration among researchers, breeders, and policymakers are essential to address evolving pest challenges and ensure global food security.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Al-Kahtani S., Kamara M., Taha E., El-Wakeil N., AlJabr A., and Mousa K., 2023, Combining ability and inheritance nature of agronomic traits and resistance to pink stem (*Sesamia cretica*) and purple-lined (*Chilo agamemnon*) borers in Maize, Plants, 12(5): 1105. https://doi.org/10.3390/plants12051105

Álvarez-Alfageme F., Devos Y., Camargo A., Arpaia S., and Messéan A., 2021, Managing resistance evolution to transgenic Bt maize in corn borers in Spain, Critical Reviews in Biotechnology, 42: 201-219. https://doi.org/10.1080/07388551.2021.1931018

Arends B., Reisig D., Gundry S., Huseth A., Reay-Jones F., Greene J., and Kennedy, G., 2021, Effectiveness of the natural resistance management refuge for Bt-cotton is dominated by local abundance of soybean and maize, Scientific Reports, 11(1): 17601.
https://doi.org/10.1038/s41598-021-97123-8

Badji A., Kwemoi D., Machida L., Okii D., Mwila N., Agbahoungba S., Kumi F., Ibanda A., Bararyenya A., Solemanegy M., Odong T., Wassw P., Otim M., Asea G., Ochwo-Ssemakula M., Talwana H., Kyamanywa S., and Rubaihayo P., 2020, Genetic basis of maize resistance to multiple insect pests: integrated genome-wide comparative mapping and candidate gene prioritization, Genes, 11(6): 689.
https://doi.org/10.3390/genes11060689

Bernardi D., Salmeron E., Horikoshi R., Bernardi O., Dourado P., Carvalho R., Martinelli S., Head G., and Omoto C., 2015, Cross-resistance between cry1 proteins in fall armyworm (*Spodoptera frugiperda*) may affect the durability of current pyramided Bt maize hybrids in Brazil, PLoS One, 10(10): e0140130.
https://doi.org/10.1371/journal.pone.0140130

Block A., Hunter C., Sattler S., Rering C., McDonald S., Basset G., and Christensen S., 2019, Fighting on two fronts: elevated insect resistance in flooded maize, Plant, Cell and Environment, 43(1): 223-234.
https://doi.org/10.1111/pce.13642

Cai Y.F., Chen B., Hou J.F., Zhao F.C., Wang G.Y., and Cai R.X., 2024, Genetic structure and diversity in Zea genus: implications for conservation and breeding, Maize Genomics and Genetics, 15(2): 70-79.
https://doi.org/10.5376/mgg.2024.15.0008

Castano-Duque L., Loades K., Tooker J., Brown K., Williams P., and Luthe D., 2017, A maize inbred exhibits resistance against western corn rootwoorm *Diabrotica virgifera virgifera*, Journal of Chemical Ecology, 43: 1109-1123.
https://doi.org/10.1007/s10886-017-0904-2

Franeta F., Mikić S., Milovac Ž., Mitrović B., Inđić D., and Vuković S., 2019, Maize defence mechanisms against the European corn borer *Ostrinia nubilalis* Hübner (Lepidoptera: Crambidae), International Journal of Pest Management, 65: 23-32.
https://doi.org/10.1080/09670874.2018.1454629

García-Lara S., and Bergvinson D., 2014, Phytochemical and nutraceutical changes during recurrent selection for storage pest resistance in tropical maize, Crop Science, 54: 2423-2432.
https://doi.org/10.2135/CROPSCI2014.03.0223

Gassmann A., 2021, Resistance to bt maize by western corn rootworm: effects of pest biology the pest-crop interaction and the agricultural landscape on resistance, Insects, 12(2): 136.
https://doi.org/10.3390/insects12020136

Guo J., Liu S., Jing D., He K., Zhang Y., Li M., Qi J., and Wang Z., 2022, Genotypic variation in field-grown maize eliminates trade-offs between resistance tolerance and growth in response to high pressure from the Asian corn borer, Plant Cell and Environment, 46(10): 3072-3089.
https://doi.org/10.1111/pce.14458

Jiménez-Galindo J., Malvar R., Butrón A., Santiago R., Samayoa L., Caicedo M., and Ordás B., 2019, Mapping of resistance to corn borers in a MAGIC population of maize, BMC Plant Biology, 19: 1-17.
https://doi.org/10.1186/s12870-019-2052-z

Jiménez-Galindo J., Ordás B., Butrón A., Samayoa L., and Malvar R., 2017, QTL mapping for yield and resistance against mediterranean corn borer in Maize, Frontiers in Plant Science, 8: 698.
https://doi.org/10.3389/fpls.2017.00698

Karjagi C., Sekhar J., Lakshmi S., Suby S., Kaur J., Mallikarjuna M., and Kumar P., 2017, Breeding for resistance to insect pests in maize, Breeding Insect Resistant Crops for Sustainable Agriculture, 2017: 201-229.
https://doi.org/10.1007/978-981-10-6056-4_7

Lange E., Balmer D., Mauch-Mani B., and Turlings T., 2014, Insect and pathogen attack and resistance in maize and its wild ancestors the teosintes, New Phytologist, 204: 329-341.
https://doi.org/10.1111/NPH.13005

Liu C., He S., Chen J., Wang M., Li Z., Wei L., Chen Y., Du M., Liu D., Li C., An C., Bhadauria V., Lai J., and Zhu W., 2023, A dual‐subcellular localized β‐glucosidase confers pathogen and insect resistance without a yield penalty in maize, Plant Biotechnology Journal, 22: 1017-1032.
https://doi.org/10.1111/pbi.14242

López-Castillo L., Silva-Fernández S., Winkler R., Bergvinson D., Arnason J., and García-Lara S., 2018, Postharvest insect resistance in maize, Journal of Stored Products Research, 77: 66-76.
https://doi.org/10.1016/J.JSPR.2018.03.004

López-Malvar A., Reséndiz Z., Santiago R., Jiménez-Galindo J., and Malvar R., 2021, Relationships between stalk resistance and corn borers agronomic traits and cell wall hydroxycinnamates in a set of recombinant inbred lines from a maize magic population, Agronomy, 11: 1132.
https://doi.org/10.3390/AGRONOMY11061132

Moscardini V., Marques L., Santos A., Rossetto J., Silva O., Rampazzo P., and Castro B., 2020, Efficacy of *Bacillus thuringiensis* (Bt) maize expressing Cry1F Cry1A.105 Cry2Ab2 and Vip3Aa20 proteins to manage the fall armyworm (Lepidoptera: Noctuidae) in Brazil, Crop Protection, 137: 105269.
https://doi.org/10.1016/j.cropro.2020.105269

Ngom D., Fauconnier M., Malumba P., Dia C., Thiaw C., and Sembene M., 2020, Varietal susceptibility of maize to larger grain borer *Prostephanus truncatus* (Horn) (Coleoptera; Bostrichidae) based on grain physicochemical parameters, PLoS One, 15(4): e0232164. https://doi.org/10.1371/journal.pone.0232164

Niu Y., Zhao X., Chao W., Lu P., Bai X., and Mao T., 2023, Genetic variation DIMBOA accumulation and candidate gene identification in maize multiple insect-resistance, International Journal of Molecular Sciences, 24(3): 2138. https://doi.org/10.3390/ijms24032138

Nuambote-Yobila O., Bruce A., Okuku G., Marangu C., Makumbi D., Beyene Y., Mahungu N., Prasanna B., Marion-Poll F., and Calatayud P., 2023, Assessment of resistance mechanisms to fall Armyworm *Spodoptera frugiperda* in tropical maize inbred lines, Agronomy, 13(1): 203. https://doi.org/10.3390/agronomy13010203

Omoto C., Bernardi O., Salmeron E., Sorgatto R., Dourado P., Crivellari A., Carvalho R., Willse A., Martinelli S., and Head G., 2016, Field-evolved resistance to Cry1Ab maize by *Spodoptera frugiperda* in Brazil, Pest Management Science, 72(9): 1727-36. https://doi.org/10.1002/ps.4201

Orozco-Restrepo S., Santos-Amaya O., Miranda M., S.Tavares C., and Pereira E., (2024)., Fall armyworm (Lepidoptera: Noctuidae): practical resistance of 2 Brazilian populations to Cry1A.105+Cry2Ab and Cry1F Bt Maize, Journal of Economic Entomology, 117: 1095-1105. https://doi.org/10.1093/jee/toae082

Saikai Y., Hurley T., and Mitchell P., 2020, An agent-based model of insect resistance management and mitigation for Bt Maize: A social science perspective, Pest Management Science, 77(1): 273-284. https://doi.org/10.1002/ps.6016

Signorini A., Abratti G., Grimi D., Machado M., Bunge F., Parody B., Ramos L., Cortese P., Vesprini F., Whelan A., Araujo M., Podworny M., Cadile A., and Malacarne M., 2018, Management of field-evolved resistance to bt maize in argentina: a multi-institutional approach, Frontiers in Bioengineering and Biotechnology, 6: 67. https://doi.org/10.3389/fbioe.2018.00067

Viana P., Guimarães P., and Mendes S., 2022, Maize cultivars with native insect resistance-potential advances and challenges, Revista Brasileira de Milho e Sorgo, 21(2022): Special Issue https://doi.org/10.18512/rbms2022vol21e1250

Wang T., Wang K., Wang C., Zhao Y., Tao Z., Li J., Wang L., Shi J., Huang S., Xie C., and Li P., 2023, Combining QTL mapping with multiomics profiling reveals genetic control of corn leaf aphid (*Rhopalosiphum maidis*) resistance in maize, Journal of Experimental Botany, 3: 21. https://doi.org/10.1093/jxb/erad113

Warburton M., Woolfolk S., Smith J., Hawkins L., Castano-Duque L., Lebar M., and Williams W., 2023, Genes and genetic mechanisms contributing to fall armyworm resistance in maize, The Plant Genome, 16(2): e20311 https://doi.org/10.1002/tpg2.20311

Yang Q., Balint-Kurti P., and Xu M., 2017, Quantitative Disease Resistance: Dissection and Adoption in Maize, Molecular Plant, 10 (3): 402-413. https://doi.org/10.1016/j.molp.2017.02.004