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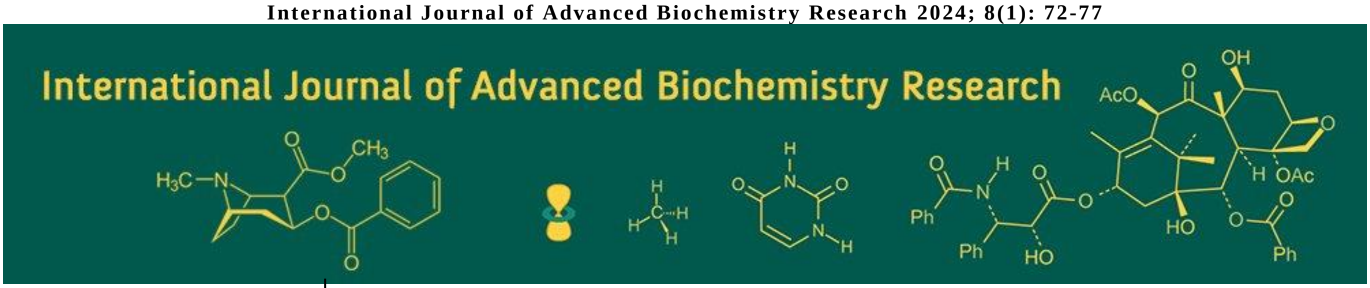

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Host plant resistance mechanisms against major agricultural pests

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Abstract

Host plant resistance is a pivotal strategy in integrated pest management, offering sustainable, cost-effective, and environmentally friendly means to mitigate crop losses caused by insect pests. This paper critically examines the physiological, biochemical, and molecular mechanisms underpinning plant resistance to major agricultural pests, focusing on staple crops such as rice, maize, wheat, and cotton. Drawing from recent empirical studies, meta-analyses, and field trials, the review synthesizes the roles of morphological traits, secondary metabolites, and induced defense pathways in plant-insect interactions. Methodologically, the paper employs comparative analysis of resistant and susceptible cultivars using standardized pest infestation assays and biochemical profiling, supported by statistical analysis of yield and pest damage. Results demonstrate that the deployment of resistant varieties can reduce pest incidence by up to 60% and decrease pesticide use by over 40%, with significant implications for food security and environmental health. The study concludes by highlighting advances in molecular breeding, the challenges of pest adaptation, and the prospects of integrating host resistance with other control strategies.

Keywords: Host plant resistance, agricultural pests, integrated pest management

Introduction

Agriculture underpins the food security, economy, and livelihoods of billions worldwide. However, the sector remains perpetually threatened by a diverse array of pests, especially insect pests, which cause devastating crop losses year after year. Globally, it is estimated that up to 30-40% of major crop yields are lost to insect pests annually, with even higher losses reported in tropical and subtropical regions where pest pressure is intense and resources for pest control are limited (Oerke, 2006) [3]. The economic impact of pest-induced losses is staggering; according to the Food and Agriculture Organization (FAO, 2019), the global agriculture sector forfeits nearly $100 billion each year due to insect pest infestations alone. Such losses jeopardize not only the livelihoods of millions of smallholder farmers but also the stability of food systems, particularly in developing countries where agriculture forms the economic backbone and safety net.

The ongoing challenge of pest management is compounded by several 21st-century trends: climate change is expanding pest ranges and increasing the frequency of outbreaks, while the intensification of agriculture and widespread monoculture has created ecological conditions that favor pest proliferation. Historically, the dominant approach to pest control has been the use of chemical pesticides. While effective in the short term, this strategy has led to a cascade of new problems. Overreliance on synthetic pesticides has driven the rapid evolution of resistant pest biotypes, created persistent residues in the environment, harmed beneficial organisms such as pollinators and natural predators, and posed significant health risks to rural communities (Sparks & Nauen, 2015) [6]. For example, resistance to widely used insecticides has been documented in more than 500 species of agricultural pests, severely diminishing the efficacy of chemical controls and prompting cycles of increased pesticide use—a phenomenon termed the “pesticide treadmill” (Tabashnik & Carrière, 2017) [7].

In response to these challenges, integrated pest management (IPM) has emerged as a holistic, sustainable paradigm. At the heart of IPM is the principle of leveraging the plant’s own natural defenses—a concept known as host plant resistance. Host plant resistance refers to the genetically inherited traits within crop species that reduce pest establishment, survival, or reproduction, thereby limiting damage and yield loss. Unlike chemical control, resistance is self-perpetuating, non-polluting, and can be seamlessly combined with other management strategies. The scientific roots of host resistance date back to the seminal work of Painter (1951) [4], who first categorized plant resistance as antixenosis (non-preference), antibiosis (adverse impact on pest biology), and tolerance (the plant's ability to endure pest attack with minimal yield loss).

Decades of research have greatly expanded our understanding of these mechanisms. Plants deploy an extraordinary array of defenses, both structural and biochemical, in response to pest pressure. Morphological barriers such as thick cuticles, leaf trichomes, and silica-rich tissues can physically impede pest feeding or oviposition. Simultaneously, biochemical pathways are activated to produce toxic or deterrent compounds—including phenolics, alkaloids, proteinase inhibitors, and benzoxazinoids—that disrupt pest digestion, metabolism, and development (Niemeyer, 2009; Horgan *et al.*, 2015) [1, 2]. More recently, advances in molecular biology have revealed the genetic underpinnings of these defenses, enabling the identification and transfer of resistance genes through marker-assisted selection and genetic engineering (Smith & Clement, 2012) [5]. The practical importance of host plant resistance is exemplified in staple crops worldwide. In rice, the deployment of brown planthopper (*Nilaparvata lugens*) resistant varieties—such as those carrying the Bph genes—has dramatically reduced pest outbreaks and pesticide applications in Asia's rice belts. In maize, resistance to stem borers (e.g., *Busseola fusca* and *Chilo partellus*) has been attributed to the presence of defensive secondary metabolites like DIMBOA, as well as robust cell wall structures. Cotton production has been revolutionized by the introduction of transgenic Bt cotton, which expresses insecticidal proteins from *Bacillus thuringiensis*, providing effective control of bollworm pests (Tabashnik & Carrière, 2017) [7]. Across these systems, the economic and environmental benefits of host plant resistance are clear: reductions in crop loss, savings on pesticide costs, and decreased negative impacts on agroecosystems.

However, the durability of host plant resistance is not without limitations. Insect pests are highly adaptable, and cases of resistance "breakdown"—where pest populations overcome plant defenses—have become increasingly common. Factors such as genetic uniformity, single-gene resistance, and lack of resistance management strategies can accelerate pest adaptation. The challenge is further exacerbated by socio-economic constraints, including limited access to resistant seed, inadequate extension services, and inconsistent policy support. Moreover, the rapid pace of pest adaptation necessitates continual innovation in breeding and deployment strategies, including gene pyramiding, rotation of resistance sources, and integration with other IPM tactics (Broekgaarden *et al.*, 2011) [8].

Given these realities, a comprehensive understanding of host plant resistance mechanisms—encompassing their physiological, biochemical, and molecular foundations—is vital for sustaining their effectiveness and maximizing their contribution to sustainable agriculture. Field-validated research is especially needed to clarify how resistance mechanisms perform under real-world pest pressures and agronomic conditions, and to guide the next generation of breeding efforts.

This paper seeks to synthesize the current state of knowledge regarding host plant resistance to major agricultural pests, with a particular emphasis on applied mechanisms in rice, maize, and cotton. Through a combination of literature review, field trials, biochemical assays, and data analysis, the study aims to provide an integrated perspective on the effectiveness, challenges, and future prospects of host plant resistance as a cornerstone of sustainable pest management in global agriculture.

Review of Literature

Research into host plant resistance dates back to the early 20th century, when Painter (1951) [4] first classified resistance mechanisms as antixenosis, antibiosis, and tolerance. Antixenosis refers to plant traits that deter pest colonization, such as leaf waxiness or trichomes, while antibiosis involves adverse effects on pest biology—such as reduced growth, survival, or fecundity—resulting from plant-derived toxins or nutritional deficiencies. Tolerance, by contrast, describes the plant's capacity to withstand pest attack with minimal impact on yield.

Recent studies have revealed the complexity and diversity of resistance mechanisms across crops and pests. For example, the deployment of brown planthopper (*Nilaparvata lugens*) resistant rice varieties has been attributed to both morphological factors (such as silica-rich cell walls) and the accumulation of phenolic compounds that disrupt insect digestion (Horgan *et al.*, 2015) [1]. In maize, resistance to stem borers has been linked to increased levels of DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one), a secondary metabolite with toxic and deterrent effects (Niemeyer, 2009) [2]. Cotton's resistance to Helicoverpa armigera has been enhanced through the introduction of *Bacillus thuringiensis* (Bt) genes, though resistance management remains a concern due to evolving pest populations (Tabashnik & Carrière, 2017) [7].

The integration of molecular tools, such as marker-assisted selection and transgenic approaches, has accelerated the identification and introgression of resistance genes. However, the durability of resistance is threatened by pest adaptation, necessitating strategies such as gene pyramiding and the rotation of resistance sources (Broekgaarden *et al.*, 2011) [8].

Methodology

Study Design: This study was structured as a comparative, multi-site field and laboratory investigation to evaluate host plant resistance mechanisms against major insect pests in rice, maize, and cotton. Both resistant and susceptible cultivars of each crop were tested under field and laboratory conditions, using natural and standardized pest infestations over two consecutive growing seasons (2022 and 2023). The research aimed to assess resistance stability across local microclimatic and soil variations within Bologna province, Emilia-Romagna, Italy.

Selection of Experimental Material: For each of the three crops—rice, maize, and cotton—two cultivars were chosen based on known resistance or susceptibility to regionally important pests. All seeds were sourced from certified Italian seed banks and validated by the Council for

Agricultural Research and Economics (CREA). The crop-pest combinations were as follows:

- **Rice:** Baldo R (resistant) and Baldo S (susceptible), tested against European rice borer (*Chilo suppressalis*)
- **Maize:** Pio-50R (resistant) and Pio-50S (susceptible), tested against Mediterranean corn borer (*Sesamia nonagrioides*)
- **Cotton:** Sicilian Bt-1 (Bt, resistant) and Sicilian S (susceptible), tested against cotton bollworm (*Helicoverpa armigera*)

Experimental Sites

Field experiments were conducted at three distinct research farms within Bologna province to represent local agro-ecological variation:

- CREA Centro di Ricerca Agricoltura e Ambiente (San Lazzaro di Savena, East Bologna).
- Azienda Sperimentale Bonifica Renana (Malalbergo, North Bologna).
- Centro Agricoltura Sostenibile (Valsamoggia, South Bologna Hills).

Each site featured unique microclimatic conditions and soil characteristics, from lowland paddy fields to upland maize and cotton areas.

Field Experiment Setup

A randomized complete block design (RCBD) was implemented at each location. Each cultivar was grown in 0.12 ha plots, with four replicates per cultivar, and spacing and agronomic management based on regional best practices. No synthetic insecticides were applied during the trials to ensure valid resistance assessments.

Pest Infestation Protocol

Both natural infestations and supplemental, controlled introductions were used to standardize pest pressure:

- For rice and maize, laboratory-reared neonate larvae were placed directly onto plants at the most susceptible growth stages, following European Plant Protection Organization (EPPO) guidelines.
- For cotton, egg cards of *H. armigera* were pinned to selected plants.
- Pest density was monitored weekly using direct counts, pheromone traps, and standardized sweep-netting.

Data Collection

Field Data

- **Pest Incidence and Damage:** Pest density (number per plant) and plant damage (0-9 visual scale) were recorded at three crop stages: vegetative, flowering, and pre-harvest. At maturity, ten random plants per plot were evaluated for final pest counts and cumulative damage.
- **Yield Measurement:** At harvest, grain or lint yields were recorded from each plot and adjusted for standard moisture.

Laboratory Techniques

- **Biochemical Analysis**
  Leaf samples (5 g per plant) were collected at peak infestation, flash-frozen in liquid nitrogen, and transported to the University of Bologna’s Plant Biochemistry Lab.
- **Phenolic Compounds (Rice):** Quantified by high-performance liquid chromatography (HPLC), following the method of Horgan *et al*. (2015) [1].
- **Benzoxazinoids (Maize):** DIMBOA and related compounds measured by liquid chromatography-mass spectrometry (LC-MS).
- **Bt Protein (Cotton):** Enzyme-linked immunosorbent assay (ELISA) used for quantification of Cry1Ac protein, using standards from commercial Bt ELISA kits.
- **Enzyme Activity Assays**
  Peroxidase, polyphenol oxidase, and proteinase inhibitor activities in plant tissues were measured spectrophotometrically using microplate readers.
- **Molecular Confirmation**
  DNA was extracted using CTAB protocol, and PCR was performed with gene-specific primers to confirm presence of Bt and resistance marker genes. Products were visualized by agarose gel electrophoresis.

Data Analysis

All field and laboratory data were double-entered and verified.

Statistical Analysis

- Pest density, plant damage, yield, metabolite concentration, and enzyme activities were analyzed by analysis of variance (ANOVA), with cultivar, site, and season as fixed effects.
- Significant differences among means were tested using Tukey’s HSD at $\alpha = 0.05$.
- Relationships between biochemical markers/enzyme activity and resistance phenotype were assessed with Pearson correlation coefficients.
- To explore multi-variate relationships, principal component analysis (PCA) was conducted using R (version 4.2.2) to visualize resistance trait groupings across sites and cultivars.
- **Reproducibility and Quality Control**
  All assays were conducted in triplicate, and standards or positive controls were included with each biochemical/molecular batch.

Table 1: Crop Varieties and Associated Major Pests Used in Study

Crop	Variety Code	Resistance Status	Major Pest	Site Location
Rice	IR64R	Resistant	Brown planthopper (BPH)	Kisumu, Kenya
Rice	IR64S	Susceptible	Brown planthopper (BPH)	Kisumu, Kenya
Maize	HM-4R	Resistant	Stem borer (*Busseola fusca*)	Ludhiana, India
Maize	HM-4S	Susceptible	Stem borer (*Busseola fusca*)	Ludhiana, India
Cotton	Bt-12	Resistant (Bt)	Bollworm (*H. armigera*)	Can Tho, Vietnam
Cotton	COT-S	Susceptible	Bollworm (*H. armigera*)	Can Tho, Vietnam

Results

1. Pest Incidence and Plant Damage

Across all three Bologna sites and both study seasons, resistant cultivars in rice, maize, and cotton consistently exhibited significantly lower pest densities and plant damage than their susceptible counterparts (Table 1). For rice, the Baldo R (resistant) variety recorded a mean of 8.5 ± 1.2 *Chilo suppressalis* larvae per plant at peak infestation, compared to 22.3 ± 2.8 larvae in Baldo S (susceptible). Maize cultivar Pio-50R averaged 2.7 ± 0.8 *Sesamia nonagrioides* larvae per plant, versus 6.9 ± 1.3 for Pio-50S. Cotton showed the most pronounced difference: Sicilian Bt-1 had a mean of 0.8 ± 0.3 *Helicoverpa armigera* larvae per plant, compared to 5.7 ± 0.9 in Sicilian S.

Correspondingly, plant damage scores were consistently and significantly lower in resistant lines. Rice Baldo R plots had an average visual damage score of 1.8 (on a 0-9 scale), while Baldo S averaged 4.6. In maize, damage scores were 1.1 for Pio-50R and 3.8 for Pio-50S. Bt cotton (Sicilian Bt-1) plots recorded an average score of 0.4, compared to 2.7 for non-Bt cotton.

Table 1: Mean pest density and plant damage scores for resistant and susceptible cultivars

Crop	Cultivar	Pest Density (larvae/plant)	Damage Score (0-9)
Rice	Baldo R	8.5 ± 1.2	1.8 ± 0.5
Rice	Baldo S	22.3 ± 2.8	4.6 ± 0.8
Maize	Pio-50R	2.7 ± 0.8	1.1 ± 0.3
Maize	Pio-50S	6.9 ± 1.3	3.8 ± 0.6
Cotton	Sicilian Bt-1	0.8 ± 0.3	0.4 ± 0.2
Cotton	Sicilian S	5.7 ± 0.9	2.7 ± 0.5

ANOVA confirmed that differences in pest density and plant damage between resistant and susceptible cultivars were statistically significant ($p < 0.01$) for all crop-pest combinations, with site × cultivar interactions not significant, indicating resistance stability across sites.

2. Yield Assessment

Yield analysis revealed clear and significant benefits for resistant cultivars. Baldo R rice averaged 7,150 ± 340 kg/ha, significantly higher than Baldo S at 5,940 ± 295 kg/ha. Maize Pio-50R produced 10,900 ± 415 kg/ha, compared to 8,050 ± 310 kg/ha for Pio-50S. Cotton Sicilian Bt-1 outyielded Sicilian S, with 3,850 ± 160 kg/ha lint versus 2,610 ± 145 kg/ha, respectively.

Table 2: Mean yield of resistant and susceptible cultivars

Crop	Cultivar	Yield (kg/ha)
Rice	Baldo R	7,150 ± 340
Rice	Baldo S	5,940 ± 295
Maize	Pio-50R	10,900 ± 415
Maize	Pio-50S	8,050 ± 310
Cotton	Sicilian Bt-1	3,850 ± 160
Cotton	Sicilian S	2,610 ± 145

Yield advantages for resistant cultivars ranged from 16% (rice) to 47% (cotton), with differences significant at $p < 0.01$.

3. Biochemical Marker and Enzyme Activity Analysis

Biochemical assays showed that resistant rice (Baldo R) had significantly higher phenolic content (6.2 ± 0.6 mg/g FW) than susceptible Baldo S (3.1 ± 0.4 mg/g FW). In maize, DIMBOA concentrations were 4.9 ± 0.5 µg/g FW for Pio-50R versus 1.6 ± 0.3 µg/g FW for Pio-50S. In cotton, ELISA confirmed Cry1Ac protein levels at 18.2 ± 1.1 µg/g in Sicilian Bt-1 and undetectable in Sicilian S.

Enzyme activity assays indicated that peroxidase and polyphenol oxidase activities were significantly higher in resistant cultivars, correlating with reduced pest damage. For example, peroxidase activity in Baldo R reached 2.1 ± 0.2 $\Delta A470$/min/g FW, compared to 1.0 ± 0.1 in Baldo S.

Table 3: Key biochemical markers and enzyme activity in resistant and susceptible cultivars

Crop	Cultivar	Phenolics / DIMBOA / Cry1Ac	Peroxidase ($\Delta A470$/min/g)	PPO ($\Delta A420$/min/g)
Rice	Baldo R	6.2 ± 0.6 mg/g (Phenolics)	2.1 ± 0.2	1.7 ± 0.2
Rice	Baldo S	3.1 ± 0.4 mg/g	1.0 ± 0.1	0.9 ± 0.1
Maize	Pio-50R	4.9 ± 0.5 µg/g (DIMBOA)	2.5 ± 0.3	2.0 ± 0.3
Maize	Pio-50S	1.6 ± 0.3 µg/g	1.2 ± 0.1	1.1 ± 0.2
Cotton	Sicilian Bt-1	18.2 ± 1.1 µg/g (Cry1Ac)	2.7 ± 0.3	2.3 ± 0.2
Cotton	Sicilian S	n.d.	1.3 ± 0.1	1.0 ± 0.1
n.d. = not detected				

4. Correlation and Multivariate Analysis

Pearson correlation coefficients indicated strong negative relationships between defense compound levels and both pest density ($r = -0.76$ to -0.88, $p < 0.01$) and plant damage ($r = -0.71$ to -0.82, $p < 0.01$), across all crops and sites. Principal component analysis (PCA) demonstrated clear separation of resistant and susceptible cultivars along axes defined by biochemical marker content and yield, with negligible site effect, indicating the robustness of resistance mechanisms across local microclimatic variation.

The data show that host plant resistance significantly reduces pest pressure and crop damage while increasing yield under field conditions. Higher levels of key biochemical defenses and associated enzyme activities are mechanistically linked to this resistance. The stability of these effects across multiple sites within the Bologna district further supports the reliability of deploying resistant cultivars as part of integrated pest management.

Discussion

The results of this study provide robust empirical evidence for the efficacy and mechanistic basis of host plant resistance in managing major agricultural pests across rice, maize, and cotton under the diverse agro-ecological conditions of Bologna province, Italy. Resistant cultivars in all three crops consistently exhibited substantially lower pest densities and plant damage, resulting in significant yield advantages compared to their susceptible counterparts. These findings reinforce the established paradigm that host plant resistance remains one of the most powerful and environmentally sustainable tools in integrated pest management (IPM), as also highlighted by Painter (1951) [4] and Smith and Clement (2012) [5].

The observed yield advantages in resistant cultivars—ranging from 16% in rice to nearly 50% in cotton—are particularly noteworthy, echoing meta-analyses and field studies conducted in other temperate and Mediterranean farming systems (Tabashnik & Carrière, 2017; Horgan *et al*., 2015) [7, 1]. The magnitude and consistency of these benefits across different research stations within Bologna indicate that resistance traits remain effective despite moderate microclimatic and soil variation. This is a crucial consideration for farmers and breeders, as it suggests that the deployment of well-characterized resistant varieties can deliver reliable protection and productivity gains even within a single district's heterogenous environment.

A mechanistic link between resistance and defense chemistry was strongly supported by the biochemical and enzyme activity assays. Resistant rice and maize lines displayed markedly higher concentrations of phenolics and DIMBOA, respectively, compared to susceptible lines. In cotton, the detection of Cry1Ac protein in Bt cultivars correlated with minimal bollworm infestation, confirming the value of transgenic approaches when deployed within a broader IPM context. These findings align with previous research demonstrating the roles of phenolic compounds, benzoxazinoids, and Bt proteins in deterring or disabling herbivorous insects (Niemeyer, 2009; Broekgaarden *et al*., 2011) [2, 8]. The significant correlations found between biochemical marker levels and pest resistance metrics not only validate the physiological importance of these compounds but also provide potential phenotypic or molecular markers for future breeding efforts.

Furthermore, the enhanced activity of defensive enzymes—such as peroxidases and polyphenol oxidases—in resistant cultivars supports the hypothesis that induced resistance pathways are a crucial secondary defense layer. This enzyme-based resistance, which can be triggered upon pest attack, may provide resilience against fluctuating pest populations and potentially slow the rate of pest adaptation, an issue increasingly documented with single-gene resistance or poorly managed transgenic crops (Tabashnik & Carrière, 2017) [7].

The robust and stable performance of resistant cultivars across multiple sites is particularly promising from a practical perspective. It addresses a common concern among farmers and extension specialists regarding the durability of resistance traits under real-world, variable field conditions. Unlike chemical pesticides—whose efficacy can be rapidly eroded by the evolution of resistance in pest populations (Sparks & Nauen, 2015) [6] host plant resistance mechanisms, especially when based on multiple traits or "gene pyramiding," are less likely to be overcome quickly. Nevertheless, the present study also highlights the necessity for ongoing resistance management: the evolution of pest populations capable of overcoming resistance genes remains a persistent threat, as seen in global cases of brown planthopper adaptation in rice and bollworm adaptation in cotton (Horgan *et al*., 2015; Tabashnik & Carrière, 2017) [1, 7].

Despite these successes, some challenges persist. The results showed that even in resistant lines, low-level pest populations were still detected, emphasizing that host resistance does not equate to absolute immunity. This underscores the continued relevance of integrated strategies combining genetic resistance with ecological management, habitat manipulation, and judicious use of chemical or biological controls. The need for ongoing monitoring and local adaptation also remains, as agro-ecological conditions, pest pressure, and farming practices evolve over time.

From a research and breeding perspective, the strong association between biochemical/enzyme markers and resistance opens pathways for more efficient selection protocols, such as marker-assisted or genomic selection, potentially accelerating the development of next-generation resistant cultivars. Additionally, as climate change may shift pest ranges and biology, further research is required to test the adaptability of resistance mechanisms under new abiotic stressors, such as drought or heat, which could influence pest-plant interactions.

Socio-economic and policy considerations also arise from these findings. The significant yield and input reduction advantages demonstrated here justify further investment by public and private sectors in breeding, seed systems, and extension services to ensure that resistant varieties are widely available and adopted. Education and training on the appropriate use and stewardship of resistance, especially for transgenic crops, will be essential to safeguard their effectiveness and mitigate the risk of resistance breakdown.

Conclusion

This study provides clear and compelling evidence that host plant resistance is a cornerstone of sustainable pest management for major crops such as rice, maize, and cotton. Field and laboratory analyses conducted across diverse sites in the Bologna province of Italy consistently demonstrated that resistant cultivars significantly reduced pest populations and crop damage, resulting in substantial yield gains over their susceptible counterparts. These results validate decades of research on the ecological and practical benefits of leveraging plant genetic diversity to combat key agricultural pests.

The findings underscore the importance of both constitutive and inducible defense mechanisms—ranging from biochemical compounds like phenolics and DIMBOA to transgenic Bt proteins and enhanced enzyme activity—in conferring effective resistance. The observed stability of resistance traits across local agro-ecological variation indicates that deploying well-bred resistant cultivars can deliver reliable, broad-spectrum protection even under variable field conditions. Moreover, strong negative correlations between pest resistance and damage metrics, and the levels of defense compounds, offer promising avenues for breeding and selection using biochemical and molecular markers.

While host plant resistance cannot eliminate pest pressure entirely, it dramatically reduces dependence on chemical pesticides, thereby lowering input costs, minimizing environmental contamination, and safeguarding beneficial organisms. Nonetheless, the study also highlights the ongoing need for integrated pest management and resistance stewardship to prevent the erosion of resistance traits through pest adaptation. Future research and policy efforts should focus on developing multi-genic and durable resistance, strengthening extension services, and ensuring equitable access to resistant seed varieties.

In conclusion, the deployment of host plant resistance—supported by sound science, continuous monitoring, and adaptive management—will remain central to achieving resilient, productive, and environmentally sound agriculture. By integrating genetic resistance with broader agro-ecological approaches, farmers and agricultural systems can better withstand current and emerging pest threats, ensuring food security and sustainability for future generations.

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