

JOURNAL PRE-PROOF

This is an early version of the article, published prior to copyediting, typesetting, and editorial correction. The manuscript has been accepted for publication and is now available online to ensure early dissemination, author visibility, and citation tracking prior to the formal issue publication.

It has not undergone final formatting or technical editing by the journal's editorial team. Content is subject to change in the final Version of Record.



To differentiate this version, it is marked as **“PRE-PROOF PUBLICATION”** and should be cited with the provided DOI. A visible watermark on each page indicates its preliminary status.

The final version will appear in a regular issue of JPPR, with final metadata, layout, and pagination.

Please cite this article as:

Adewinle A.A., Togola A. Plant defense mechanisms against insect herbivores: ecological insights for sustainable pest management. Journal of Plant Protection Research. DOI: 10.24425/jppr.2026.7313

Review

Plant defense mechanisms against insect herbivores: ecological insights for sustainable pest management

Adeshina Ayodeji Adewinle^{1*}, Abou Togola² 

¹ Department of Entomology, University of Kentucky Research and Education Center, Princeton, USA

² Global Maize Program, International Maize and Wheat Improvement Center (CIMMYT), ICRAF Campus, United Nations Avenue, Gigiri, Kenya

*Corresponding address: adeshinaadewinle@gmail.com

Received: May 18, 2026

Accepted: August 31, 2026

Pre-proof Publication: October 8, 2026

Responsible Editor: Jacek Twardowski

DOI: 10.24425/jppr.2026.7313

Abstract

Insect herbivory remains a major constraint on agricultural productivity and ecosystem stability worldwide. Plants have evolved diverse structural, chemical, and inducible defense mechanisms that reduce herbivore damage while shaping ecological and evolutionary interactions across trophic levels. Beyond direct deterrence, plant defenses influence herbivore specialization, multitrophic interactions, and community structure, generating dynamic feedback between plants and insects. Although plant defense biology has been extensively examined from molecular and evolutionary perspective, there is potential need to explicitly connect these mechanisms to applied pest management frameworks. Here, we integrated structural barriers, secondary metabolite production, inducible signaling pathways, and herbivore-induced plant volatiles within a unified ecological context and examined how these traits influence herbivore performance, specialization, and adaptation. We further evaluated how plant defense traits can be incorporated into durable integrated pest management (IPM) strategies through selective breeding, a resistance trait pyramid, ecological intensification, and adaptive monitoring. By bridging mechanistic defense biology with ecological theory and agricultural implementation, this review summarized pathways for harnessing plant-based resistance to reduce insecticide reliance and promote resilient agroecosystems.

Keywords: induced plant defenses, integrated pest management (IPM), plant defense mechanisms, plant-insect interactions, secondary metabolites, sustainable agriculture

1. Introduction

Plants are persistently challenged by insect herbivores, which represent one of the most widespread and economically important biotic stresses in agricultural ecosystems worldwide. Insect herbivory can reduce plant growth, reproduction, and yield, and is a major cause of global crop losses (Savary *et al.* 2019). Globally, insect pests are responsible for reducing major crop yields by approximately 10–16% annually, even under current management practices, highlighting the substantial impact of herbivory on food security (Oerke 2006; Savary *et al.* 2019). Herbivore attack can also impair plant physiological processes by reducing photosynthetic activity and altering primary metabolism (Zhou *et al.* 2009). Consequently, sustained insect feeding may lead to reductions in plant size, growth, and seed production (Züst and Agrawal 2017; Endara *et al.* 2023). As immobile organisms, plants rely on a diverse array of defense mechanisms to mitigate herbivore damage rather than escaping attack, making plant defense a central component of plant–insect interactions (War *et al.* 2012; Mahanta *et al.* 2025)

Insect herbivores exert strong selective pressure on plants, shaping the evolution of physical, chemical, and inducible defense strategies (Howe and Jander 2008; Mithöfer and Boland 2012; Vasantha-Srinivasan *et al.* 2025). Structural defenses such as thorns, spines, and trichomes can impede insect feeding or oviposition, whereas chemical defenses mediated by secondary metabolites, including alkaloids, terpenoids, and phenolics, may deter feeding or negatively affect insect development and survival (Erb and Reymond 2019). These constitutive defenses provide continuous protection but may also incur metabolic costs that influence plant fitness under varying environmental conditions.

In addition to constitutive defenses, many plants deploy inducible defense responses that are activated following herbivore attacks. These herbivore-induced defenses are often regulated through phytohormonal signaling pathways, particularly those involving jasmonic acid, salicylic acid, and ethylene (Wasternack and Song 2017). Induced responses may include the production of toxic secondary metabolites, proteinase inhibitors, or volatile organic compounds (VOCs) that function as indirect defenses by attracting natural enemies such as predators and parasitoids of herbivores (Turlings and Erb 2018). Such inducible strategies enable plants to balance defense investment with growth and reproduction, particularly in environments where herbivore pressure is variable.

The expression of plant defense traits is influenced by ecological and evolutionary trade-offs, including allocation constraints between growth, reproduction, and resistance (Huot *et al.* 2014; He *et al.* 2022). These trade-offs contribute to co-evolutionary dynamics between plants and insect herbivores, often resulting in herbivore specialization and the evolution of counteradaptations that circumvent plant defenses (Agrawal 2020). Understanding these interactions is critical for predicting pest outbreaks and for developing effective strategies to mitigate insect pest impacts in agroecosystems.

In agricultural systems, plant defense mechanisms form the foundation of host plant resistance and represent a key component of integrated pest management (IPM). Enhancing or exploiting plant defense traits can reduce reliance on synthetic insecticides, slow the evolution of pest resistance, and support more sustainable crop protection strategies (Schuman and Baldwin 2016; Stenberg 2017). Although plant defense against insect herbivores has been extensively investigated from molecular, biochemical, and ecological perspectives, recent advances have highlighted the need for a more integrated framework that connects mechanistic understanding with practical crop protection. Contemporary research emphasizes that plant defense should not be viewed simply as a collection of structural or chemical traits, but as a multidimensional system encompassing resistance and tolerance, constitutive and induced responses, and direct and indirect defense mechanisms operating across multiple biological scales. Such an integrated perspective is increasingly important because the effectiveness of plant defenses depends not only on their molecular basis but also on environmental conditions, herbivore feeding guilds, natural-enemy interactions, and agricultural management practices (Souza 2025). Recent reviews further argue that translating mechanistic knowledge into operational host-plant resistance and integrated pest management (IPM) remains one of the major challenges for sustainable crop protection, particularly under increasing climatic variability and evolving pest populations. Consequently, greater emphasis is now being placed on linking ecological theory, defense mechanisms, and practical implementation to improve the durability and field performance of plant defense traits (Zhou *et al.* 2024; Souza 2025).

In this review, we aimed to (1) synthesize structural, chemical, and inducible plant defenses within a unified ecological framework, (2) examine how these defense traits shape herbivore performance and multitrophic interactions, and (3) evaluate how plant defense mechanisms can be strategically

incorporated into sustainable IPM programs. By explicitly linking mechanistic defense biology with applied agronomic practices, this review attempted to clarify how plant-based resistance can contribute to resilient agroecosystems.

1.2 Search Strategy and Literature Selection

This manuscript was prepared as a narrative review to synthesize current knowledge on plant defense mechanisms against insect herbivores and their relevance to sustainable pest management. Literature was identified through searches of Web of Science, Scopus, Google Scholar, and PubMed using combinations of keywords including *plant defense*, *host-plant resistance*, *antixenosis*, *antibiosis*, *tolerance*, *plant–insect interactions*, *herbivore-induced plant volatiles*, *integrated pest management*, and *plant immunity*. Priority was given to peer-reviewed literature published between 2020 and 2026, with the literature search updated through July 2026. Earlier publications were retained when they represented seminal contributions or foundational concepts essential for understanding plant defense mechanisms. Preference was given to peer-reviewed original research articles, mechanistic studies, field-based investigations, and recent review papers, particularly those involving major agricultural crop systems. Conference abstracts, non-peer-reviewed publications, and studies lacking sufficient methodological detail were generally excluded unless they provided important historical context. As a narrative review, this manuscript did not aim to provide an exhaustive systematic assessment of all available studies but rather a critical synthesis of representative and influential literature relevant to the objectives of this review.

2. Characterization of Plant Defense Mechanisms Against Insect Herbivores

Plants have evolved a wide range of defense strategies to reduce damage caused by insect herbivores. These defenses operate at multiple levels and may act before, during, or after herbivore attacks.

2.1 Conceptual framework of plant defense mechanisms

Plant defense against insect herbivores is best understood as a multidimensional system rather than a single classification scheme. Several complementary dimensions are used to describe plant defense, each representing a different biological aspect of protection. At the whole-plant level, defenses operate through resistance, which reduces herbivore colonization, feeding, survival, or reproduction, or through tolerance, which allows plants to maintain growth and productivity despite

herbivore injury (Cohenille *et al.* 2026). Based on the timing of expression, defenses may be constitutive, being continuously present before herbivore attack, or induced, being activated in response to herbivore feeding or oviposition. According to their mode of action, defenses may also be direct, acting on herbivores through physical barriers or defensive metabolites, or indirect, enhancing plant protection by recruiting predators and parasitoids through herbivore-induced signals. These defense strategies are mediated through structural, chemical, molecular, and ecological mechanisms that often interact rather than function independently. Organizing plant defense within this multidimensional framework provides a clearer understanding of the diversity of defense strategies and facilitates their application in host plant resistance and integrated pest management programs (Stout *et al.* 2024; Souza 2025).

2.2 Resistance mechanisms

Resistance mechanisms reduce herbivore colonization, feeding, survival, development, or reproduction through a combination of structural, chemical, constitutive, induced, direct, and indirect defenses. Although these mechanisms differ in their modes of action, they share the common function of reducing herbivore fitness or damage. The following subsections describe the principal resistance mechanisms that plants employ against insect herbivores.

Structural (physical) defenses in plants can be broadly grouped into three major categories: (1) surface-level barriers such as trichomes and waxy cuticles, (2) tissue-level mechanical reinforcement including leaf toughness and lignification, and (3) mineral-based fortification such as silicon deposition in grasses. Although these defenses differ in structure and modes of action, they share the common function of limiting herbivore access and reducing feeding efficiency. Physical defenses represent one of the most direct mechanisms by which plants reduce insect herbivory by creating mechanical barriers that limit tissue accessibility, increase handling time, and interfere with feeding or oviposition. These defenses are typically constitutively expressed and include traits such as thorns, spines, leaf toughness, thick cuticles, wax layers, and epidermal outgrowths such as trichomes (Hanley *et al.* 2007; Massey and Hartley 2009; Johnson *et al.* 2024). Physical barriers can reduce herbivore performance by slowing feeding rates, damaging mouthparts, or reducing the efficiency of nutrient extraction. In many cases, these traits alter herbivore behavior before feeding even begins, contributing to antixenosis (non-preference) resistance mechanisms.

Structural defenses are continuously expressed and relatively stable over time, making them the first line of resistance in both natural ecosystems and agricultural crops. Among structural defenses, epidermal outgrowths such as trichomes have received particular attention due to their functional diversity and importance in crop resistance. In tomato (*Solanum lycopersicum*), high densities of glandular trichomes reduce feeding and oviposition by lepidopteran pests such as *Helicoverpa armigera* and interfere with whitefly settlement (Hanley *et al.* 2007; Peiffer *et al.* 2009; Erb and Reymond 2019). Similarly, in cowpea (*Vigna unguiculata*), elongated and dense trichomes have been associated with resistance to the legume pod borer *Maruca vitrata*, limiting larval establishment and feeding damage (Togola *et al.* 2017).

Beyond surface-level defenses, plants also reinforce internal tissues to mechanically resist herbivore feeding. Leaf toughness and cuticle thickness also contribute significantly to plant resistance. In maize, increased leaf toughness and other physical traits have been associated with reduced feeding damage and slower development by generalist herbivores such as *Spodoptera frugiperda*, compared to more susceptible genotypes (Santos *et al.* 2020; Mason *et al.* 2022). Tougher tissues can limit chewing efficiency, extend larval development time, and increase exposure to natural enemies, thereby contributing to plant resistance. Structural components such as lignin and silica further decrease tissue digestibility and can accelerate wear on insect mouthparts, thereby reducing herbivore performance (Massey and Hartley 2009). Structural defenses are particularly important in perennial crops and long-living plant species due to their constitutive and long-lasting nature.

Silicon-based structural defenses are particularly important in grasses. In rice (*Oryza sativa*), increased silicon deposition in leaves has been shown to reduce damage from the rice stem borer *Chilo suppressalis* by increasing leaf abrasiveness and decreasing larval feeding efficiency (Reynolds and Keeping 2009; Acevedo *et al.* 2021; Bathoova *et al.* 2025). Silicon-mediated resistance represents a form of structural fortification that directly impairs herbivore performance while maintaining plant growth.

2.3 Chemical defenses

Chemical defenses represent one of the most extensively studied components of plant resistance to insect herbivores and involve secondary metabolites that influence insect behavior, physiology, and survival (War *et al.* 2012; Fürstenberg-Hägg *et al.* 2013). Unlike primary metabolites required for

growth and development, these compounds function primarily in ecological interactions and are often central to plant–herbivore coevolution (Howe and Jander 2008; Erb and Reymond 2019; Mostafa *et al.* 2022). Plant secondary metabolites may act as feeding deterrents, acute toxins, digestion inhibitors, or disruptors of insect endocrine and metabolic pathways (Mithöfer and Boland 2012; Schuman and Baldwin 2016). Major classes of defensive compounds include alkaloids, terpenoids, phenolics, glucosinolates, and cyanogenic glycosides, each differing in biosynthetic origin and mode of action (Wink 2010; Moles *et al.* 2013).

Chemical defenses can be constitutively expressed or induced in response to herbivore attack (Karban and Baldwin 1997; Heil and Ton 2008). Constitutive defenses provide continuous protection but may incur allocation costs, whereas inducible defenses allow plants to regulate defense investment in response to herbivore damage, often mediated by jasmonic acid signaling pathways (Howe and Jander 2008; Erb and Reymond 2019). The diversity and specificity of secondary metabolites also influence herbivore specialization, as generalist insects are typically more susceptible to plant toxins, while specialists often evolve detoxification mechanisms or sequestration strategies (Després *et al.* 2007; Ali and Agrawal 2012). Consequently, chemical defenses not only affect individual herbivore performance but also structure ecological communities and evolutionary trajectories in plant–insect systems.

A well-studied example is the glucosinolate - myrosinase system found in Brassicaceae crops. When plant tissues are damaged, glucosinolates are hydrolyzed into reactive compounds such as isothiocyanates, which reduce the performance of generalist herbivores including *Spodoptera* species and other chewing insects (Hopkins *et al.* 2009). However, specialist herbivores such as *Pieris rapae* have evolved biochemical adaptations, including the expression of nitrile-specifier proteins and other adaptive gene responses that mitigate the toxic effects of glucosinolate-myrosinase defenses in Brassicaceae hosts, illustrating the co-evolutionary dynamics between plant chemical defenses and insect adaptation (Okamura *et al.* 2019).

Phenolic compounds also play an important defensive role in legumes. Elevated concentrations of phenolics have been associated with reduced feeding efficiency and impaired development of aphids and other piercing–sucking insects, suggesting antibiosis mediated through oxidative stress or disruption of nutrient assimilation (Wójcicka 2010; Barbehenn and Constabel 2011; Togola *et al.* 2017).

In addition to alkaloids and glucosinolates, polyphenolic compounds such as tannins represent an important class of defensive metabolites that function primarily through interference with insect digestion rather than acute toxicity. Tannins can bind to dietary proteins and digestive enzymes in the insect gut, forming indigestible complexes that reduce nitrogen assimilation and nutrient availability (Barbehenn and Constabel 2011). This reduction in protein utilization lowers conversion efficiency and often results in prolonged larval development time, decreased growth rates, and reduced fecundity. Unlike fast-acting toxins, tannins typically exert chronic, sublethal effects that cumulatively reduce herbivore fitness. The defensive effectiveness of tannins depends on both their chemical structure and the feeding strategy of the herbivore.

Generalist herbivores are often more susceptible to tannin-rich tissues, whereas some specialists have evolved counteradaptations such as tannin-binding proteins or elevated gut pH to mitigate their effects (Barbehenn and Constabel 2011). Tannin-based defenses are widespread across woody plants and many crops, particularly legumes and tree species, where they contribute to reduced palatability and herbivore performance. These compounds therefore represent a form of quantitative defense, in which high concentrations reduce overall digestibility rather than directly poisoning herbivores.

By reducing herbivore growth rates and extending developmental periods, tannins may also indirectly enhance biological control by increasing exposure time to predators and parasitoids. This highlights how even sublethal chemical defenses can have cascading ecological effects within multitrophic systems.

Alkaloids and other nitrogen-containing secondary metabolites also contribute to plant resistance in several crop systems. In Solanaceous plants, glycoalkaloids such as α -tomatine impair the growth and survival of lepidopteran larvae, including *Helicoverpa* species, by disrupting membrane integrity and digestion (Friedman 2002; You and Van 2021). In cotton (*Gossypium hirsutum*), gossypol and related terpenoid aldehydes reduce feeding and development of bollworms and other chewing herbivores (Stipanovic *et al.* 2006; Cope 2025). These examples illustrate the diversity of plant secondary metabolites involved in chemical defense against herbivorous insects.

The production of defensive metabolites is rarely uniform across plant tissues. Instead, plants frequently allocate chemical defenses selectively to organs that contribute most strongly to fitness, such as young leaves, meristems, and reproductive tissues. This pattern of targeted allocation is

consistent with predictions from the Optimal Defense Theory (ODT), which proposes that plants should invest disproportionately in defending tissues that are either highly valuable or particularly vulnerable to herbivory (Stamp 2003; Boege and Marquis 2005). Because young tissues often have higher photosynthetic potential and future reproductive value, damage to these organs may carry greater fitness consequences than damage to older leaves. Empirical studies support these predictions. For example, higher concentrations of defensive metabolites have been observed in expanding leaves than in mature foliage of several plant species, including crops and woody plants (Boege and Marquis 2005).

Similarly, reproductive tissues such as flowers and developing seeds often contain elevated levels of toxic or deterrent compounds, reflecting their direct contribution to plant fitness. Such spatial variation in defense expression can influence herbivore feeding patterns, promoting selective herbivory on less-defended tissues and shaping plant–insect interaction dynamics. Uneven distribution of chemical defenses also interacts with herbivore specialization (Jan *et al.* 2026; Feng *et al.* 2026). Generalist herbivores may preferentially attack older, less-defended tissues, whereas specialists may evolve adaptations that allow them to exploit highly defended organs. Consequently, ODT not only explains patterns of within-plant defense allocation but also provides a mechanistic framework linking plant chemistry to herbivore behavior, performance, and evolutionary trajectories (Mobarak *et al.* 2025).

The diversity of plant secondary metabolites involved in herbivore defense across crop systems is summarized in Table 1.

Table 1. Examples of plant chemical defenses in major crop systems, their target insect herbivores, mechanisms of action, and ecological significance for integrated pest management.

Crop/Plant Species	Defensive Compound/Class	Target Insect Pest	Mode of Action	Ecological/IPM Significance	Reference
Brassicaceae(e.g., cabbage, mustard)	Glucosinolates Isothiocyanates	<i>Spodoptera</i> spp. and other generalist chewing insects	Toxic hydrolysis products disrupt metabolism and reduce herbivore performance	Provides broad-spectrum resistance against generalist herbivores and serves as	Hopkins <i>et al.</i> (2009)

				an important source of resistance traits in Brassica breeding programs.	
Brassicaceae	Glucosinolates	<i>Pieris rapae</i>	Specialist detoxification enables tolerance to glucosinolate breakdown products	Demonstrates plant–herbivore coevolution and highlights the importance of considering herbivore adaptation when developing durable host-plant resistance.	Hopkins <i>et al.</i> (2009)
Cowpea (<i>Vigna unguiculata</i>)	Phenolics and related secondary metabolites	Cowpea aphid (<i>Aphis craccivora</i>)	Antibiosis through reduced feeding efficiency and impaired development	Supports breeding for enhanced chemical resistance against sap-feeding pests while reducing dependence on insecticides.	Togola <i>et al.</i> (2017)
Solanaceous plants (tomato)	Glycoalkaloids (α -tomatine)	<i>Helicoverpa</i> spp.	Disrupt membrane integrity and digestive processes	Contributes to natural resistance against chewing insects and provides valuable traits for host-plant resistance breeding.	Friedman (2002); You and Van (2021)
Cotton (<i>Gossypium hirsutum</i>)	Gossypol and terpenoid aldehydes	Bollworms and other chewing insects	Feeding deterrence and impaired larval development	Illustrates how naturally occurring defensive metabolites can suppress economically important pests while complementing other IPM tactics.	Stipanovic <i>et al.</i> (2006); Cope (2025)

Multiple plant species	Tannins	Generalist herbivores	Bind digestive enzymes and dietary proteins, reducing nutrient availability	Slow herbivore growth, prolong larval development, and may indirectly improve biological control by increasing exposure to predators and parasitoids.	Barbehenn and Constabel (2011)
------------------------	---------	-----------------------	---	---	--------------------------------

2.4 Induced and Indirect Defenses

In addition to constitutive structural and chemical defenses, many plants rely on inducible defenses that are activated in response to insect attack. Induced responses allow plants to allocate defensive resources dynamically, increasing protection when herbivore pressure is high while minimizing metabolic costs when risk is low.

Herbivore attack activates complex phytohormone signaling networks that regulate induced plant defenses. Jasmonic acid (JA) is the principal signaling pathway involved in defense against chewing herbivores, whereas salicylic acid (SA) plays a more prominent role in responses to many phloem-feeding insects and pathogens (Roychowdhury *et al.* 2025; Tonga and Ali 2026). Ethylene (ET) acts as an important regulatory signal that modulates both JA- and SA-mediated responses depending on the herbivore feeding guild and environmental context. Rather than functioning independently, these signaling pathways interact through synergistic and antagonistic crosstalk to regulate the production of proteinase inhibitors, defensive secondary metabolites, and herbivore-induced plant volatiles while balancing defense with plant growth. Recent studies further demonstrate that some insect herbivores manipulate JA-SA signaling interactions to suppress host defenses, highlighting the dynamic nature of plant-insect interactions and the importance of hormone crosstalk in developing durable host plant resistance and sustainable pest management strategies (Vasanth-Srinivasan *et al.* 2025; Li *et al.* 2025). Plants also employ indirect defenses through the release of herbivore-induced plant volatiles (HIPVs), which mediate multitrophic interactions by influencing the behavior of predators, parasitoids, neighboring plants, and even other herbivores. HIPVs consist of diverse blends of green leaf volatiles, terpenoids, benzenoids, and other volatile organic compounds whose composition depends on plant genotype, herbivore species, feeding intensity, and environmental conditions (Qian *et al.* 2024).

Recent studies further demonstrate that insect behavioral responses are often determined by specific blends of volatile organic compounds rather than by individual compounds acting alone. For example, synthetic blends of plant-derived volatile organic compounds have been shown to influence host-location behavior in leaf beetles, highlighting the importance of volatile composition and concentration in mediating insect orientation (Piesik *et al.* 2020b). Likewise, wheat plants damaged by the striped shieldbug emit characteristic volatile blends that alter insect behavior, demonstrating the ecological significance of herbivore-induced volatile emissions in cereal cropping systems (Sendel *et al.* 2022). In addition, volatile signaling is not restricted to insect herbivory; pathogen-induced volatile emissions can also contribute to defense priming and plant-to-plant communication, illustrating the broader ecological functions of volatile organic compounds in plant defense (Piesik *et al.* 2015a).

Although numerous laboratory and olfactometer studies have demonstrated that HIPVs attract natural enemies, attraction alone does not necessarily result in increased parasitism, reduced pest populations, or improved crop yield under field conditions. Their effectiveness can be influenced by volatile concentrations, emission timing, weather conditions, surrounding vegetation, and the complexity of the local food web (Carmo *et al.* 2025). Consequently, current research emphasizes that HIPVs should be viewed as promising components of integrated pest management rather than universally reliable biological control tools. Further field validation is needed before their widespread deployment in agricultural systems (Qian *et al.* 2024; Carmo *et al.* 2025).

Inducible defenses are also well documented in rice–planthopper interactions. Feeding by the brown planthopper (*Nilaparvata lugens*) activates jasmonate-mediated defense pathways that reduce subsequent infestation and increase plant resistance (Zhou *et al.* 2015). Together, constitutive and inducible defenses represent complementary strategies rather than mutually exclusive alternatives. The balance between constitutive and inducible defenses reflects broader physiological trade-offs between growth and defense investment. According to the Growth–Differentiation Balance Hypothesis (GDBH), originally proposed by Herms and Mattson (1992) and Fiorucci (2020), plants face resource allocation constraints that limit their ability to simultaneously maximize growth and defensive compound production. When resources such as nitrogen and carbon are abundant, plants may prioritize rapid growth, potentially reducing allocation to costly constitutive defenses. Conversely, under moderate resource limitation or

elevated herbivore pressure, plants may divert resources toward defensive metabolite synthesis or structural reinforcement.

Empirical studies support this trade-off framework. For example, nitrogen fertilization can increase plant growth rates while simultaneously reducing concentrations of certain defensive secondary metabolites in crops and wild plants (Huot *et al.* 2014; Züst and Agrawal 2017). Similarly, fast-growing annual species often rely more heavily on inducible defenses that are activated following herbivory, whereas long-lived perennials may invest more in constitutive defenses due to prolonged exposure to herbivores over their lifespan. These patterns illustrate how plants dynamically adjust defense expression in response to environmental conditions, herbivore pressure, and life-history strategy.

Understanding this growth–defense trade-off is essential for interpreting variation in plant resistance across environments and for predicting how agricultural practices such as fertilization, irrigation, or high-density planting may inadvertently influence plant susceptibility to insect herbivores.

2.5 Tolerance Mechanisms

Although resistance mechanisms such as antixenosis and antibiosis reduce herbivore preference, survival, or reproduction, tolerance represents a distinct defense strategy in which plants minimize the fitness costs of herbivore injury while maintaining growth and reproductive performance (Kalske and Kessler 2023; Zhao 2024). Tolerance is achieved through mechanisms such as compensatory growth, resource reallocation, enhanced photosynthetic activity, and developmental plasticity, allowing plants to recover from damage without directly reducing herbivore performance (Zhao 2024). Because tolerant plants exert less direct selection pressure on herbivore populations than resistance traits, tolerance has been proposed as a complementary and potentially more durable component of sustainable pest management. However, the expression of tolerance depends on plant genotype, resource availability, herbivore pressure, and environmental conditions, highlighting the importance of integrating tolerance with other defense mechanisms rather than relying on it alone (Salgado-Luarte *et al.* 2023; Kalske and Kessler 2023).

3. Ecological and Evolutionary Consequences of Plant Defense Mechanisms

Plant defense mechanisms against insect herbivores have far-reaching ecological and evolutionary consequences beyond the immediate reduction in herbivore damage. By influencing herbivore host choice, feeding behavior, performance, and population dynamics, plant defenses shape patterns of species interactions, specialization, and community structure across ecosystems (Gong and Zhang 2014; Endara 2023).

One of the most important ecological consequences of plant defense is its role in driving insect herbivore specialization. Rather than simply reducing herbivore abundance, plant defenses act as selective filters that favor herbivores capable of overcoming specific structural or chemical barriers. Over evolutionary time, these reciprocal selective pressures promote physiological, biochemical, and behavioral counteradaptations that enable specialist herbivores to exploit defended host plants while restricting the success of generalists (Ali and Agrawal 2012; Agrawal 2020). The mechanistic examples presented in Section 2, including glucosinolate detoxification in Brassicaceae specialists and cardenolide sequestration in milkweed herbivores, illustrate these adaptive processes and demonstrate how plant defenses contribute to ecological specialization and coevolution rather than functioning solely as barriers to herbivory.

Many herbivores evolve narrow host ranges in response to plant chemical and structural defenses, developing physiological or behavioral adaptations that allow them to tolerate or exploit defended plants. This specialization can reduce interspecific competition among herbivores but may also increase vulnerability to changes in host availability or defense expression (Ali and Agrawal 2012; Jones *et al.* 2022). As a result, plant defenses contribute to the diversity and stability of plant–insect communities.

Plant defense traits also influence ecological interactions beyond the plant–herbivore interface by affecting predators, parasitoids, and other organisms within multitrophic food webs (Nishu *et al.* 2026). As discussed in Section 2, herbivore-induced plant volatiles (HIPVs) provide one of the best-studied examples of indirect defense by recruiting natural enemies. Ecologically, these interactions extend the effects of plant defense beyond individual plants and can strengthen biological control by altering predator–prey and parasitoid–host relationships (Wyckhuys *et al.* 2025). However, the magnitude of these effects varies considerably between cropping systems because volatile emission, natural-enemy responses, and environmental conditions jointly

determine whether attraction ultimately translates into meaningful pest suppression under field conditions (Dicke and Baldwin 2010; Turlings and Erb 2018; Carmo *et al.* 2025).

Defensive compounds can alter herbivore quality as prey, affecting predator and parasitoid performance and shaping food-web dynamics. In some cases, plant defenses indirectly benefit higher trophic levels by slowing herbivore growth or increasing exposure time to natural enemies, while in other cases they may reduce prey suitability and weaken top-down control (Mooney *et al.* 2012). These cascading effects highlight the need to consider plant defense within a multitrophic ecological context.

Although numerous studies demonstrate that plant defenses influence herbivore specialization and multitrophic interactions, much of the available evidence originates from laboratory, greenhouse, or short-term experiments. Field studies frequently report greater variability because defense expression depends on plant genotype, environmental conditions, herbivore community composition, and interactions with natural enemies (Russavage *et al.* 2025; Al-Amri 2026). Consequently, reductions in herbivore performance observed under controlled conditions do not always translate into consistent reductions in pest populations or economically significant yield protection in commercial cropping systems. This context dependency highlights the importance of integrating mechanistic studies with long-term field validation when developing defense-based pest management strategies (Stout *et al.* 2024; Souza 2025).

From an evolutionary perspective, plant defense strategies are central to coevolutionary interactions between plants and insect herbivores. Reciprocal selection pressures can lead to evolutionary “arms races,” in which plants evolve increasingly effective defensive traits while herbivores evolve counteradaptations that restore their ability to feed and reproduce.

The evolutionary consequences of plant defense are evident in the repeated emergence of herbivore counteradaptations, including behavioral avoidance, target-site modification, sequestration of defensive compounds, and enhanced detoxification capacity (Farhan *et al.* 2026). Together, these adaptations illustrate the reciprocal selection that underpins plant-herbivore coevolution and explain why resistance traits that are highly effective against one herbivore species may be less effective against specialists that have evolved mechanisms to circumvent plant defenses (Després *et al.* 2007; Agrawal 2020).

However, not all plant–herbivore interactions follow this escalating pattern. In some systems, selection favors defense diversification or inducibility rather than increased toxicity, leading to more dynamic and context-dependent evolutionary outcomes (Ehrlich and Raven 1964; Agrawal and Fishbein 2006).

Variation in plant defense expression across environments contributes to ecological and evolutionary complexity in plant–herbivore interactions. Environmental factors such as nutrient availability, water stress, and herbivore pressure can influence both the type and intensity of defense expressed (Pearse *et al.* 2018; Sobral *et al.* 2021; Wang *et al.* 2023; Li *et al.* 2024). Environmental modulation of plant defense traits can generate spatial and temporal heterogeneity in herbivore pressure, thereby influencing population dynamics and local adaptation in both plants and insects. Such variability is particularly relevant under changing environmental conditions, where mismatches between plant defenses and herbivore life histories may alter established interaction patterns (Agrawal 2020; Pearse *et al.* 2020)

Overall, plant defense mechanisms extend far beyond reducing herbivore damage at the individual plant level. By influencing herbivore specialization, multitrophic interactions, community assembly, and evolutionary trajectories, plant defenses shape ecosystem functioning across spatial and temporal scales. Recognizing these broader ecological consequences provides the conceptual foundation for translating mechanistic knowledge into durable host plant resistance and ecologically informed integrated pest management strategies, which are discussed in the following section.

4. Implications for Agriculture and Integrated Pest Management

Plant defense mechanisms provide a foundational biological tool for reducing insect herbivory in agricultural systems and form the basis of host plant resistance within IPM programs. By incorporating resistant cultivars into cropping systems, pest populations can be suppressed before they reach economic thresholds, reducing the need for chemical interventions.

Physical defense traits have been successfully exploited in crop improvement programs. Structural defenses have been incorporated into crop improvement programs through both conventional breeding and selection of resistant cultivars. In rice, variation in silicon uptake and deposition capacity among genotypes has been associated with reduced feeding damage by planthoppers such

as *Nilaparvata lugens*, and breeding programs have selected cultivars with enhanced silica accumulation and leaf toughness to improve resistance (Ma and Yamaji 2006; Reynolds *et al.* 2009; Mitani-Ueno and Ma 2021). These traits increase tissue abrasiveness and reduce feeding efficiency, thereby lowering pest survival and fecundity.

A representative example of host plant resistance is found in soybeans, where Resistance to Aphis glycines (Rag) genes has been successfully incorporated into breeding programs for soybean aphid management. Among these, Rag1 and Rag2 are the best-characterized resistance loci and confer protection primarily through antibiosis and antixenosis, thereby reducing aphid colonization, survival, and reproduction (Natukunda *et al.* 2020a; Natukunda *et al.* 2021b). More recently, pyramiding multiple Rag genes has been shown to improve the durability of resistance compared with single-gene cultivars by delaying the evolution of virulent aphid biotypes. Nevertheless, the continued emergence of virulent biotypes capable of overcoming Rag-mediated resistance demonstrates that host plant resistance should be integrated with complementary IPM tactics rather than deployed as a stand-alone management strategy (Natukunda and MacIntosh 2020; Lewis *et al.* 2025). Chemical defenses also contribute directly to pest suppression in agroecosystems. In maize, benzoxazinoids such as 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) have been shown to reduce the performance of generalist herbivores including *Spodoptera frugiperda* and other lepidopteran pests (Glauser *et al.* 2011; Bui *et al.* 2018). In Brassica crops, glucosinolate diversity influences susceptibility to both chewing and sap-feeding insects, shaping pest community composition and feeding preference (Halkier and Gershenzon 2006). These compounds may act through toxicity, feeding deterrence, or disruption of insect digestion and nutrient utilization.

Induced defenses further strengthen IPM by enhancing compatibility with biological control. Herbivore-induced plant volatiles released by cotton and maize have been shown to recruit parasitoids and predators, increasing natural enemy efficiency and contributing to population suppression of caterpillars and other herbivores (Kessler and Baldwin 2002; Turlings and Erb 2018). Such multitrophic interactions demonstrate that plant defense can extend beyond direct herbivore deterrence to influence entire ecological networks.

However, the deployment of single resistance traits may impose strong selection pressure on herbivore populations, leading to the increase of virulent genotypes capable of overcoming host

plant resistance (Xu *et al.* 2024). The durability of resistance therefore, depends not only on the resistance gene itself but also on deployment strategies, including gene combinations, refuge availability, spatial and temporal diversification, and integration with complementary IPM tactics (Ali and Zhuo 2025; Kumaraswamy *et al.* 2026). Recent studies emphasize that pyramid resistance genes can improve resistance durability in some systems, but its success depends on the independence of resistance mechanisms, the frequency of virulence alleles within pest populations, and associated fitness costs. Consequently, host plant resistance should be integrated with biological control, cultural practices, pest monitoring, and resistance management rather than being considered as a stand-alone solution for sustainable pest suppression (Stout *et al.* 2024; Souza 2025).

Despite considerable advances in identifying plant defense traits that suppress insect herbivores under controlled conditions, successful translation into commercial crop production remains challenging (Stout *et al.* 2024; Sansinenea *et al.* 2026). The effectiveness of many resistance traits is influenced by genotype-by-environment interactions, variation in pest pressure, and differences in herbivore communities across locations and growing seasons. In some cases, enhanced resistance may also be associated with trade-offs affecting plant growth, yield, grain quality, or compatibility with other desirable agronomic traits, making these characteristics more difficult to incorporate into elite cultivars. In addition, widespread adoption by growers depends on the availability of resistant seed, economic benefits relative to existing management practices, and integration with locally adapted IPM programs. Consequently, durable implementation of host plant resistance requires not only effective defense mechanisms but also rigorous multi-environment field validation and close collaboration between plant breeders, entomologists, agronomists, and producers to ensure that resistance traits remain both agronomically and economically sustainable (Stout *et al.* 2024; Souza 2025).

Similarly, adaptation to plant chemical defenses through enhanced detoxification has been documented in multiple herbivore species. Elevated expression of cytochrome P450 monooxygenases and other detoxification enzymes enables some lepidopteran pests to metabolize plant allelochemicals more efficiently, thereby reducing the effectiveness of toxin-based resistance traits (Després *et al.* 2007). In other systems, insects may exhibit behavioral avoidance, preferentially feeding on less-defended tissues or shifting host plants altogether.

Collectively, these examples demonstrated that the successful deployment of plant defense traits depends on integrating resistance mechanisms with ecological knowledge, crop improvement, and adaptive pest management practices. Rather than relying on individual defense traits, sustainable IPM should combine host-plant resistance with biological control, cultural practices, pest monitoring, and informed decision-making to improve resistance durability and reduce insecticide dependence. Such an integrated approach strengthens ecosystem services while promoting resilient and environmentally sustainable crop protection systems (Alves *et al.* 2026).

5. Conclusion and Future Directions

Plants have evolved a diverse and dynamic array of defense mechanisms to mitigate insect herbivory, ranging from physical barriers and chemical deterrents to inducible and indirect defenses that operate across multiple trophic levels. Collectively, these defense strategies influence herbivore feeding behavior, population dynamics, and the structure of plant-insect interactions. Rather than functioning independently, plant defenses are coordinated through complex ecological and evolutionary processes and are shaped by environmental conditions, herbivore pressure, plant developmental stage, and trade-offs between growth, reproduction, and resistance.

This review synthesized current knowledge on structural, chemical, constitutive, inducible, and indirect plant defense mechanisms within an ecological and agronomic framework. Together, the evidence demonstrated that these defense strategies function as interconnected components of an integrated defense system that influence herbivore performance, multitrophic interactions, and ecosystem functioning. Their coordinated action provides a strong ecological foundation for sustainable integrated pest management (IPM) by reducing pest populations while promoting environmentally responsible crop protection.

Future research should increasingly focus on understanding how plant defense traits function under variable environmental conditions, multiple abiotic stresses, and complex multitrophic interactions, particularly within managed agricultural systems. Integrating ecological, evolutionary, genetic, and agronomic perspectives will be essential for improving the deployment of host plant resistance in modern crop production. In practice, this integration includes identifying the genetic loci underlying structural, chemical, and inducible defenses through quantitative trait mapping, genomics, transcriptomics, metabolomics, and other advanced molecular approaches, followed by incorporating these traits into elite cultivars through conventional breeding, marker-

assisted selection, or emerging gene-editing technologies. Equally important are field-based evaluations that assess defense performance under realistic pest pressure, environmental variability, and interactions with natural enemies.

Achieving durable pest resistance will require integrating host plant resistance with complementary IPM tactics, including biological control, habitat diversification, crop rotation, resistance gene pyramiding, pest monitoring, and threshold-based insecticide applications. Long-term surveillance of pest populations for changes in virulence, detoxification capacity, or resistance evolution will also be essential for maintaining the effectiveness of resistant cultivars. Advances in high-throughput phenotyping, artificial intelligence-assisted breeding, and predictive ecological modeling offer unprecedented opportunities to accelerate the identification and deployment of durable resistance traits while improving decision-making in pest management.

Overall, plant defense mechanisms represent a cornerstone of sustainable agriculture and provide considerable potential for reducing reliance on synthetic insecticides while enhancing agroecosystem resilience. Continued integration of molecular biology, ecology, plant breeding, and adaptive IPM will be critical for developing resilient cropping systems capable of maintaining productivity under increasing pest pressure and a changing climate. By combining mechanistic understanding with ecological and evolutionary principles, future plant defense research can support the development of innovative, durable, and climate-resilient pest management strategies for sustainable global food production.

Acknowledgments

The authors wish to thank Dr. Nicholas M. Teets for providing thoughtful comments and constructive feedback that helped improve the clarity and focus of the manuscript.

References

- Acevedo F.E., Peiffer M., Ray S., Tan C.W., Felton G.W. 2021. Silicon-mediated enhancement of herbivore resistance in agricultural crops. *Frontiers in Plant Science* 12: 631824. DOI: <https://doi.org/10.3389/fpls.2021.631824>
- Agrawal A.A. 2020. A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology* 101 (2): e02924. DOI: <https://doi.org/10.1002/ecy.2924>
- Agrawal A.A., Fishbein M. 2006. Plant defense syndromes. *Ecology* 87 (Suppl. 7): S132–S149. DOI: [https://doi.org/10.1890/0012-9658\(2006\)87\[132:PDS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[132:PDS]2.0.CO;2)
- Al-Amri S.M. 2026. Functional plasticity of crop volatiles: Integrating genetic regulation and ecological application for sustainable crop-pests management. *Journal of Agricultural and Food Chemistry* 74 (18): 14106–14126. DOI: <https://doi.org/10.1021/acs.jafc.5c13670>
- Alam A., Abbas S., Hussain H., Mehar I., Ahmad B., Khan K.A., Chen R. 2025. Molecular strategies for crop resistance: Advancing plant defense mechanisms against insect herbivores. *International Journal of Tropical Insect Science* 45: 2465–2488. DOI: <https://doi.org/10.1007/s42690-025-01668-4>
- Alves J.J.A., Silva I.F.P., Andrade A.B.A., Acácio R.D.S., Goulart H.F., Santana A.E.G. 2026. Sweet potato pests: Perspectives on the use of pheromones for control and monitoring. *Journal of Plant Protection Research* 66 (2): 135–147. DOI: <https://doi.org/10.24425/jppr.2026.1064>
- Ali H., Zhuo Z. (eds.). 2025. *Integrated Pest Management: Emerging Technologies and Sustainable Approaches*. 1st ed. CRC Press, Boca Raton, FL, USA, 252 pp. DOI: <https://doi.org/10.1201/9781003516538>
- Ali J.G., Agrawal A.A. 2012. Specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science* 17 (5): 293–302. DOI: <https://doi.org/10.1016/j.tplants.2012.02.006>
- Barbehenn R.V., Constabel C.P. 2011. Tannins in plant–herbivore interactions. *Phytochemistry* 72 (13): 1551–1565. DOI: <https://doi.org/10.1016/j.phytochem.2011.01.040>
- Bathoova M., Svubova R., Gimes L., Kostolani D., Slovakova L., Martinka M. 2025. The potential of silicon in crop protection against phloem-feeding and chewing insect pests: A review. *Journal of Experimental Botany* 76 (14): 3912–3926. DOI: <https://doi.org/10.1093/jxb/eraf102>

- Boege K., Marquis R.J. 2005. Facing herbivory as you grow up: The ontogeny of resistance in plants. *Trends in Ecology and Evolution* 20 (8): 441–448. DOI: <https://doi.org/10.1016/j.tree.2005.05.001>
- Bui H., Greenhalgh R., Ruckert A., Gill G.S., Lee S., Ramirez R.A., Clark R.M. 2018. Generalist and specialist mite herbivores induce similar defense responses in maize and barley but differ in susceptibility to benzoxazinoids. *Frontiers in Plant Science* 9: 1222. DOI: <https://doi.org/10.3389/fpls.2018.01222>
- Carmo E.B., Macedo-Rego R.C., Peñafior M.F.G. 2025. Herbivory by multiple arthropods does not hinder the attraction of natural enemies to plant volatiles: Insights from a meta-analysis. *Current Opinion in Insect Science* 69: 101347. DOI: <https://doi.org/10.1016/j.cois.2025.101347>
- Cochenille T., Baracchini C., Doury G., Six A., Tougeron K., Ameline A. 2026. Testing optimal defense theory: Root resistance selection in chicory (*Cichorium intybus*) reduces foliar defense and alters aphid performance and feeding behavior. *Pest Management Science*. DOI: <https://doi.org/10.1002/ps.70855>
- Cope R.B. 2025. Cottonseed toxicity. p. 973–986. In: "Veterinary Toxicology" (R.C. Gupta, ed.). Academic Press, London, UK. DOI: <https://doi.org/10.1016/B978-0-443-29007-7.00068-6>
- Després L., David J.P., Gallet C. 2007. The evolutionary ecology of insect resistance to plant chemicals. *Trends in Ecology and Evolution* 22 (6): 298–307. DOI: <https://doi.org/10.1016/j.tree.2007.02.010>
- Dicke M., Baldwin I.T. 2010. The evolutionary context for herbivore-induced plant volatiles: Beyond the "cry for help". *Trends in Plant Science* 15 (3): 167–175. DOI: <https://doi.org/10.1016/j.tplants.2009.12.002>
- Ehrlich P.R., Raven P.H. 1964. Butterflies and plants: A study in coevolution. *Evolution* 18 (4): 586–608. DOI: <https://doi.org/10.1111/j.1558-5646.1964.tb01674.x>
- Endara M.J., Forrister D.L., Coley P.D. 2023. The evolutionary ecology of plant chemical defenses: From molecules to communities. *Annual Review of Ecology, Evolution, and Systematics* 54: 107–127. DOI: <https://doi.org/10.1146/annurev-ecolsys-102221-045254>
- Erb M., Reymond P. 2019. Molecular interactions between plants and insect herbivores. *Annual Review of Plant Biology* 70: 527–557. DOI: <https://doi.org/10.1146/annurev-arplant-050718-095910>

- Farhan M., Pan J., Zhao J., Yang H., Zhang S. 2026. Aphid adaptation to plant secondary metabolites: Adaptive mechanism of resistance evolution and future prospects. *Horticulture Research* 13 (1): uhaf269. DOI: <https://doi.org/10.1093/hr/uhaf269>
- Feng R., Jia S., Hao Z., Moreira X. 2026. Species-specific responses of leaf herbivory and defenses along a latitudinal gradient. *Ecology* 107 (5): e70403.
- Fiorucci A.S. 2020. To grow or defend? More on the plant Cornelian dilemma. *Plant Physiology* 183 (2): 437–438. DOI: <https://doi.org/10.1104/pp.20.00497>
- Friedman M. 2002. Tomato glycoalkaloids: Role in the plant and in the diet. *Journal of Agricultural and Food Chemistry* 50 (21): 5751–5780. DOI: <https://doi.org/10.1021/jf020560c>
- Fürstenberg-Hägg J., Zagrobelny M., Bak S. 2013. Plant defense against insect herbivores. *International Journal of Molecular Sciences* 14 (5): 10242–10297. DOI: <https://doi.org/10.3390/ijms140510242>
- Glauser G., Marti G., Villard N., Doyen G.A., Wolfender J.L., Turlings T.C.J., Erb M. 2011. Induction and detoxification of maize 1,4-benzoxazin-3-ones by insect herbivores. *The Plant Journal* 68 (5): 901–911. DOI: <https://doi.org/10.1111/j.1365-3113X.2011.04740.x>
- Gong B., Zhang G. 2014. Interactions between plants and herbivores: A review of plant defense. *Acta Ecologica Sinica* 34 (6): 325–336. DOI: <https://doi.org/10.1016/j.chnaes.2013.07.010>
- Halkier B.A., Gershenzon J. 2006. Biology and biochemistry of glucosinolates. *Annual Review of Plant Biology* 57: 303–333. DOI: <https://doi.org/10.1146/annurev.arplant.57.032905.105228>
- Hanley M.E., Lamont B.B., Fairbanks M., Rafferty C.M. 2007. Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics* 8 (4): 157–178. DOI: <https://doi.org/10.1016/j.ppees.2007.01.001>
- He Z., Webster S., He S.Y. 2022. Growth–defense trade-offs in plants. *Current Biology* 32 (12): R634–R639. DOI: <https://doi.org/10.1016/j.cub.2022.04.070>
- Herms D.A., Mattson W.J. 1992. The dilemma of plants: To grow or defend. *The Quarterly Review of Biology* 67 (3): 283–335.
- Heil M., Ton J. 2008. Long-distance signalling in plant defence. *Trends in Plant Science* 13 (6): 264–272. DOI: <https://doi.org/10.1016/j.tplants.2008.03.005>

- Hopkins R.J., van Dam N.M., van Loon J.J.A. 2009. Role of glucosinolates in insect–plant relationships. *Annual Review of Entomology* 54: 57–83. DOI: <https://doi.org/10.1146/annurev.ento.54.110807.090623>
- Howe G.A., Jander G. 2008. Plant immunity to insect herbivores. *Annual Review of Plant Biology* 59: 41–66. DOI: <https://doi.org/10.1146/annurev.arplant.59.032607.092825>
- Huot B., Yao J., Montgomery B.L., He S.Y. 2014. Growth–defense trade-offs in plants: A balancing act to optimize fitness. *Molecular Plant* 7 (8): 1267–1287. DOI: <https://doi.org/10.1093/mp/ssu049>
- Jan U., Gul A., Ashraf N. 2026. Unveiling the arms race between plants and insects. p. 253–278. In: *Insect-Plant Interactions: Mechanisms and Strategies*. Volume 2 (Editor(s), eds.). Apple Academic Press, Palm Bay, FL, USA.
- Johnson S.N., Waterman J.M., Hartley S.E., Cooke J., Ryalls J.M., Lagisz M., Nakagawa S. 2024. Plant silicon defences suppress herbivore performance, but mode of feeding is key. *Ecology Letters* 27 (10): e14519. DOI: <https://doi.org/10.1111/ele.14519>
- Jones A.C., Felton G.W., Tumlinson J.H. 2022. The dual function of elicitors and effectors from insects: Reviewing the "arms race" against plant defenses. *Plant Molecular Biology* 109 (4): 427–445. DOI: <https://doi.org/10.1007/s11103-021-01203-2>
- Kalske A., Kessler A. 2023. Herbivory selects for tolerance and constitutive defence across stages of community succession. *Proceedings of the Royal Society B: Biological Sciences* 290 (1993): 20222458. DOI: <https://doi.org/10.1098/rspb.2022.2458>
- Karban R., Baldwin I.T. 1997. *Induced Responses to Herbivory*. University of Chicago Press, Chicago, IL, USA, 330 pp.
- Kessler A., Baldwin I.T. 2002. Plant responses to insect herbivory: The emerging molecular analysis. *Annual Review of Plant Biology* 53: 299–328. DOI: <https://doi.org/10.1146/annurev.arplant.53.100301.135207>
- Kumaraswamy S., Huang Y. 2026. Plant resistance: Scientific basis and latest research progress. *Frontiers in Plant Science* 17: 1789793. DOI: <https://doi.org/10.3389/fpls.2026.1789793>
- Lewis M.T., Poelstra J.W., Michel A.P. 2025. Host plant flooding stress in soybeans differentially impacts avirulent and virulent soybean aphid (*Aphis glycines*) biotypes. *Scientific Reports* 15 (1): 4897. DOI: <https://doi.org/10.1038/s41598-025-87561-z>

- Li X., Zhang P., Jackson E., Zhang Y. 2025. Salicylic acid and jasmonic acid in plant immunity. *Horticulture Research* 12 (7): uhaf082. DOI: <https://doi.org/10.1093/hr/uhaf082>
- Li Z.X., Tan J.F., Yao N., Xie R.H. 2024. From trade-off to synergy: How nutrient status modulates plant resistance to herbivorous insects. *Advanced Biotechnology* 2: 37. DOI: <https://doi.org/10.1007/s44307-024-00045-5>
- Ma J.F., Yamaji N. 2006. Silicon uptake and accumulation in higher plants. *Trends in Plant Science* 11 (8): 392–397. DOI: <https://doi.org/10.1016/j.tplants.2006.06.007>
- Mahanta D.K., Komal J., Samal I., Bhoi T.K., Kumar P.D., Mohapatra S., Mastinu A. 2025. Plant defense responses to insect herbivores through molecular signaling, secondary metabolites, and associated epigenetic regulation. *Plant-Environment Interactions* 6 (1): e70035. DOI: <https://doi.org/10.1002/pei3.70035>
- Mason C.J., Ray S., Davidson-Lowe E., Ali J., Luthe D.S., Felton G.W. 2022. Plant nutrition influences resistant maize defense responses to the fall armyworm (*Spodoptera frugiperda*). *Frontiers in Ecology and Evolution* 10: 844274. DOI: <https://doi.org/10.3389/fevo.2022.844274>
- Massey F.P., Hartley S.E. 2009. Physical defences wear you down: Progressive and irreversible impacts of silica on insect herbivores. *Journal of Animal Ecology* 78 (1): 281–291. DOI: <https://doi.org/10.1111/j.1365-2656.2008.01472.x>
- Mitani-Ueno N., Ma J.F. 2021. Linking transport system of silicon with its accumulation in different plant species. *Soil Science and Plant Nutrition* 67 (1): 10–17. DOI: <https://doi.org/10.1080/00380768.2020.1845972>
- Mithöfer A., Boland W. 2012. Plant defense against herbivores: Chemical aspects. *Annual Review of Plant Biology* 63: 431–450. DOI: <https://doi.org/10.1146/annurev-arplant-042110-103854>
- Mobarak S.H., Basit A., Gui S.H., Hu C.X., Yu X.L., Felton G.W., Liu T.X. 2025. Volatile organic compounds as mediators in plant–herbivore interactions: Mechanisms and evolutionary consequences. *Entomologia Generalis* 45 (4): 975–990. DOI: <https://doi.org/10.1127/entomologia/3516>
- Mooney K.A., Gruner D.S., Barber N.A., Van Bael S.A., Philpott S.M., Greenberg R. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proceedings of the National Academy of Sciences of the*

- United States of America 107 (16): 7335–7340. DOI: <https://doi.org/10.1073/pnas.1001934107>
- Moles A.T., Peco B., Wallis I., Foley W.J., Poore A.G., Seabloom E.W., Hui F.K.C. 2013. Correlations between physical and chemical defences in plants: Trade-offs, syndromes, or just many different ways to skin a herbivorous cat? *New Phytologist* 198 (1): 252–263. DOI: <https://doi.org/10.1111/nph.12116>
- Mostafa S., Wang Y., Zeng W., Jin B. 2022. Plant responses to herbivory, wounding, and infection. *International Journal of Molecular Sciences* 23 (13): 7031. DOI: <https://doi.org/10.3390/ijms23137031>
- Natukunda M.I., MacIntosh G.C. 2020a. The resistant soybean–*Aphis glycines* interaction: Current knowledge and prospects. *Frontiers in Plant Science* 11: 1223. DOI: <https://doi.org/10.3389/fpls.2020.01223>
- Natukunda M.I., Hohenstein J.D., McCabe C.E., Graham M.A., Qi Y., Singh A.K., MacIntosh G.C. 2020b. Interaction between *Rag* genes results in a unique synergistic transcriptional response that enhances soybean resistance to soybean aphids. *BMC Genomics* 22: 887. DOI: <https://doi.org/10.1186/s12864-021-08147-3>
- Nishu Verma K., Noor S.A., Mathur V. 2026. Aboveground insect herbivory shapes plant-soil feedback and ecosystem resilience. *Biologia Futura* 77: 257–276. DOI: <https://doi.org/10.1007/s42977-025-00305-y>
- Oerke E.C. 2006. Crop losses to pests. *Journal of Agricultural Science* 144 (1): 31–43. DOI: <https://doi.org/10.1017/S0021859605005708>
- Okamura Y., Sato A., Tsuzuki N., Sawada Y., Hirai M.Y., Heidel-Fischer H.M. 2019. Differential regulation of host plant adaptive genes in *Pieris* butterflies exposed to a range of glucosinolate profiles in their host plants. *Scientific Reports* 9: 7256. DOI: <https://doi.org/10.1038/s41598-019-43703-8>
- Pearse I.S., Paul R., Ode P.J. 2018. Variation in plant defense suppresses herbivore performance. *Current Biology* 28 (12): 1981–1986. DOI: <https://doi.org/10.1016/j.cub.2018.04.070>
- Pearse I.S., LoPresti E., Schaeffer R.N., Wetzel W.C., Mooney K.A., Ali J.G., Weber M.G. 2020. Generalising indirect defence and resistance of plants. *Ecology Letters* 23 (7): 1137–1152. DOI: <https://doi.org/10.1111/ele.13512>

- Peiffer M., Tooker J.F., Luthe D.S., Felton G.W. 2009. Plants on early alert: Glandular trichomes as sensors for insect herbivores. *New Phytologist* 184 (3): 644–656. DOI: <https://doi.org/10.1111/j.1469-8137.2009.03002.x>
- Piesik D., Miler N., Lemańczyk G., Bocianowski J., Buszewski B. 2015a. *Botrytis cinerea* infection in three cultivars of chrysanthemum in 'Alchemist' and its mutants: Volatile induction of pathogen-infected plants. *Scientia Horticulturae* 193: 127–135. DOI: <https://doi.org/10.1016/j.scienta.2015.06.040>
- Piesik D., Bocianowski J., Sendel S., Krawczyk K., Kotwica K. 2020b. Beetle orientation responses of *Gastrophysa viridula* and *Gastrophysa polygona* (Coleoptera: Chrysomelidae) to a blend of synthetic volatile organic compounds. *Environmental Entomology* 49 (5): 1071–1076. DOI: <https://doi.org/10.1093/ee/nvaa082>
- Qian J., Zhu C., Jian G., Zeng L., Yang Y. 2024. Release patterns and potential utility of herbivore-induced plant volatiles in crops: A review. *Environmental and Experimental Botany* 219: 105659. DOI: <https://doi.org/10.1016/j.envexpbot.2024.105659>
- Reynolds O.L., Keeping M.G., Meyer J.H. 2009. Silicon-augmented resistance of plants to herbivorous insects: A review. *Annals of Applied Biology* 155 (2): 171–186. DOI: <https://doi.org/10.1111/j.1744-7348.2009.00348.x>
- Roychowdhury R., Hada A., Biswas S., Mishra S., Prusty M.R., Das S.P., Sarker U. 2025. Jasmonic acid (JA) in plant immune response: Unravelling complex molecular mechanisms and networking of defence signalling against pathogens. *Journal of Plant Growth Regulation* 44 (1): 89–114. DOI: <https://doi.org/10.1007/s00344-024-11264-4>
- Russavage E.M., Helms A.M., Thompson M.N., Szczepaniec A., Rooney W.L., Kerns D.L., Eubanks M.D. 2025. Indirect plant defense may provide economically important pest suppression in sorghum. *Pest Management Science* 81 (11): 7478–7488. DOI: <https://doi.org/10.1002/ps.8813>
- Salgado-Luarte C., González-Teuber M., Madriaza K., Gianoli E. 2023. Trade-off between plant resistance and tolerance to herbivory: Mechanical defenses outweigh chemical defenses. *Ecology* 111 (3): 617–629. DOI: <https://doi.org/10.1002/ecy.3860>
- Sansinenea E., Argente-Martínez L., Peñuelas-Rubio O., Hwang H., Toprak U., Mitra D., El-Shabasy A., Upadhyay S.K., Shin J.-H., Azizoglu U. 2026. Next-generation insect pest

- management: Genetic innovations and emerging biocontrol strategies. *Frontiers in Plant Science* 17: 1868879. DOI: <https://doi.org/10.3389/fpls.2026.1868879>
- Santos L.F.C., Ruiz-Sánchez E., Andueza-Noh R.H., Garruña-Hernández R., Latournerie-Moreno L., Mijangos-Cortés J.O. 2020. Leaf damage by *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) and its relation to leaf morphological traits in maize landraces and commercial cultivars. *Journal of Plant Diseases and Protection* 127 (1): 103–109. DOI: <https://doi.org/10.1007/s41348-019-00276-y>
- Savary S., Willocquet L., Pethybridge S.J., Esker P., McRoberts N., Nelson A. 2019. The global burden of pathogens and pests on major food crops. *Nature Ecology and Evolution* 3: 430–439. DOI: <https://doi.org/10.1038/s41559-018-0793-y>
- Sobral M., Sampedro L., Neylan I., Siemens D., Dirzo R. 2021. Phenotypic plasticity in plant defense across life stages: Inducibility, transgenerational induction, and transgenerational priming in wild radish. *Proceedings of the National Academy of Sciences of the United States of America* 118 (33): e2005865118. DOI: <https://doi.org/10.1073/pnas.2005865118>
- Sendel S., Bocianowski J., Buszewski B., Piesik M., Mayhew C.A., Piesik D. 2022. Volatile organic compounds released by wheat as a result of striped shieldbug feeding and insect behaviour. *Journal of Applied Entomology* 146 (6): 710–724. DOI: <https://doi.org/10.1111/jen.12997>
- Souza B.H. 2025. Host plant resistance: Is it time for a new model? *Neotropical Entomology* 54 (1): 82.
- Stamp N. 2003. Out of the quagmire of plant defense hypotheses. *The Quarterly Review of Biology* 78 (1): 23–55. DOI: <https://doi.org/10.1086/367580>
- Stenberg J.A. 2017. A conceptual framework for integrated pest management. *Trends in Plant Science* 22(9): 759–769. DOI: <https://doi.org/10.1016/j.tplants.2017.06.010>
- Stipanovic R.D., Lopez J.D. Jr., Dowd M.K., Puckhaber L.S., Duke S.E. 2006. Effect of racemic and (+)- and (–)-gossypol on the survival and development of *Helicoverpa zea* larvae. *Journal of Chemical Ecology* 32 (5): 959–968. DOI: <https://doi.org/10.1007/s10886-006-9052-9>
- Stout M.J., Bernaola L., Acevedo F. 2024. Recent history and future trends in host-plant resistance. *Annals of the Entomological Society of America* 117 (3): 139–149. DOI: <https://doi.org/10.1093/aesa/saae006>

- Togola A., Boukar O., Belko N., Chamarthi S.K., Fatokun C., Tamò M., Oigiangbe N. 2017. Host plant resistance to insect pests of cowpea (*Vigna unguiculata* L. Walp.): Achievements and future prospects. *Euphytica* 213: 239. DOI: <https://doi.org/10.1007/s10681-017-2030-1>
- Tonğa A., Ali J. 2026. Jasmonate-mediated plant responses to sap-sucking herbivores: A comprehensive review with emerging implications. p. 59–104. In: *Insect-Plant Interactions: Mechanisms and Strategies*. Volume 2. Apple Academic Press, Palm Bay, FL, USA. DOI: <https://doi.org/10.1201/9781779644305-3>
- Turlings T.C., Erb M. 2018. Tritrophic interactions mediated by herbivore-induced plant volatiles: Mechanisms, ecological relevance, and application potential. *Annual Review of Entomology* 63: 433–452. DOI: <https://doi.org/10.1146/annurev-ento-020117-043507>
- Vasanth-Srinivasan P., Noh M.Y., Park K.B., Kim T.Y., Jung W.J., Senthil-Nathan S., Han Y.S. 2025. Plant immunity to insect herbivores: Mechanisms, interactions, and innovations for sustainable pest management. *Frontiers in Plant Science* 16: 1599450. DOI: <https://doi.org/10.3389/fpls.2025.1599450>
- War A.R., Paulraj M.G., War M.Y., Ignacimuthu S. 2012. Mechanisms of plant defense against insect herbivores. *Plant Signaling and Behavior* 7 (10): 1306–1320. DOI: <https://doi.org/10.4161/psb.21663>
- Wasternack C., Song S. 2017. Jasmonates: Biosynthesis, metabolism, and signaling by proteins activating and repressing transcription. *Journal of Experimental Botany* 68 (6): 1303–1321. DOI: <https://doi.org/10.1093/jxb/erw443>
- Wang X., Kang J., Wang H., Wang S., Tang B., Lu J. 2023. Phenotypic plasticity plays an essential role in the confrontation between plants and herbivorous insects. *CABI Agriculture and Bioscience* 4 (1): 58. DOI: <https://doi.org/10.1186/s43170-023-00201-2>
- Wink M. (ed.). 2010. *Annual Plant Reviews*. Volume 40: *Biochemistry of Plant Secondary Metabolism*. Blackwell Publishing Ltd., Chichester, UK, 464 pp. DOI: <https://doi.org/10.1002/9781444320503>
- Wójcicka A. 2010. Cereal phenolic compounds as biopesticides of cereal aphids. *Polish Journal of Environmental Studies* 19 (6): 1337–1343.
- Wyckhuys K.A.G., Bushley K., Gratton C., Gurr G.M., Pozsgai G., Tschardt T., Wanger T.C., Lu Y., Elkahky M. 2025. Restoring functional farmland biodiversity for biological pest control.

Trends in Plant Science 30 (10): 1097–1110. DOI: <https://doi.org/10.1016/j.tplants.2025.03.012>

- Xu Y., Ghorri N., Hussain S., Xu X., Su Z., Zhang D., Bai G. 2024. Evaluating a worldwide wheat collection for resistance to Hessian fly biotype "Great Plains". *Frontiers in Plant Science* 15: 1402218. DOI: <https://doi.org/10.3389/fpls.2024.1402218>
- You Y., van Kan J.A. 2021. Bitter and sweet make tomato hard to (b)eat. *New Phytologist* 230 (1): 90–100. DOI: <https://doi.org/10.1111/nph.17104>
- Zhao G. 2024. Plant compensatory growth: Its mechanisms and implications to agricultural sustainability under global environmental changes. *International Journal of Sustainable Development and World Ecology* 31 (3): 348–360. DOI: <https://doi.org/10.1080/13504509.2023.2289475>
- Zhou W., Arcot Y., Medina R.F., Bernal J., Cisneros-Zevallos L., Akbulut M.E. 2024. Integrated pest management: An update on the sustainability approach to crop protection. *ACS Omega* 9 (40): 41130–41147. DOI: <https://doi.org/10.1021/acsomega.4c06628>
- Zhou G., Qi J., Ren N., Cheng J., Erb M., Mao B., Lou Y. 2009. Silencing *OsHI-LOX* makes rice more susceptible to chewing herbivores but enhances resistance to phloem feeders. *The Plant Journal* 60: 638–648. DOI: <https://doi.org/10.1111/j.1365-313X.2009.03988.x>
- Züst T., Agrawal A.A. 2017. Trade-offs between plant growth and defense against insect herbivory: An emerging mechanistic synthesis. *Annual Review of Plant Biology* 68:513–534. DOI: <https://doi.org/10.1146/annurev-arplant-042916-040856>