Review Article

Exploiting Induced Plant Resistance for Sustainable Pest Management: Mechanisms, Elicitors, and Applications-A Review.

Abstract:

Plants and phytophagous (plant-eating) arthropods have coevolved over millions of years, leading to the development of both constitutive and inducible defense mechanisms in plants. Despite this long history of coexistence, it remains unclear how to precisely regulate each host-arthropod interaction to achieve an equilibrium that maximizes crop yield. The defensive chemicals produced by plants can significantly affect herbivores' feeding behavior, growth, and survival. These chemicals may be generated constitutively (continuously) or induced in response to herbivore damage. Induced resistance, a strategy where plants enhance their defenses after being attacked, holds potential for reducing the amount of insecticides needed in pest management. Chemical elicitors, which trigger the production of secondary metabolites that confer resistance to insects, can be used to manipulate host plant resistance, specifically by inducing resistance. By understanding the mechanisms underlying induced resistance, it is possible to predict which herbivores will be impacted by these responses. Applying induced response elicitors to crop plants can strengthen their natural defenses against herbivore damage. Additionally, it is possible to genetically modify plants so that they constitutively produce defense chemicals, providing continuous protection in areas where herbivory is a constant threat. As part of integrated pest management, induced resistance can be used to develop crop cultivars that readily trigger an inducible response in the event of a mild infestation, contributing to sustainable agricultural practices and reducing reliance on chemical pesticides.

Introduction

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Over millions of years, a sophisticated network of defenses and counter-defenses has evolved between plants and their phytophagous (plant-eating) enemies [1]. Plant defenses can be broadly classified into two categories: constitutive (permanent) and induced (temporary) [2]. Constitutive defenses are always present in plants and do not depend on herbivore attacks. However, because these defenses are frequently activated even when not needed, they can be costly for the plant [3]. In contrast, induced defenses are activated only in response to an attack, when the herbivore is nearby. The plant defense theory suggests that inducible resistance has evolved as a strategy to minimize the costs associated with maintaining constitutive defenses [4,5,6,7].

Plant resistance to pathogens and pests can be both active and passive [8]). Some defenses are always present (constitutive), while others are triggered by specific stimuli associated with insect herbivory (induced) [9]. Inducible defenses against insect herbivores are primarily regulated by the signaling of two important phytohormones: salicylic acid (SA) and jasmonic acid (JA) [10]. SA is generally associated with resistance to piercing and sucking insects, whereas JA is linked to defenses against chewing insects, although there is significant variability across different insect-plant systems [9]. Additionally, it is possible to stimulate the JA and SA pathways through the application of bioactive compounds that act as herbivore-resistant plant inducers [11].

This review explores the potential of inducing defense responses in plants using external agents such as methyl jasmonate, salicylic acid, frass, regurgitant application, mechanical wounding, chitin, and silicon. These agents can trigger defense mechanisms that enhance plant resistance to insect pests, even in the absence of inherent host plant resistance. This comprehensive examination highlights the importance of such strategies in integrated pest management, offering insights into sustainable agricultural practices and reducing reliance on chemical pesticides.

Plant defense Mechanism

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Defence systems that respond after infection (induced) and those that prevent full-blown infection in the first place (constitutive) are two quite different things. Mechanical barriers in animals, such the skin and gut walls, as well as preformed antimicrobials in vertebrates [12], the phenoloxidase cascade in invertebrates [13], and a variety of generally constitutively acting plant poisons [14] are examples of constitutive defences. Conversely, induced defences take effect after an infection has taken place.

These mechanisms include the hypersensitive response in plants [15], antimicrobial peptides in invertebrates [16], and reactive oxygen species, cytokines, and antibodies in vertebrates [13]. These two modes of defence have frequently been explored in relation to extreme-induced anti-predation changes in invertebrates, like the spines of Daphnia, and herbivory [3,17,18]. In response to infectious disease, they are also present in plants, invertebrates, vertebrates, and microbial systems.

Elicitors in plant defense

Elicitors are molecules or compounds that, when applied to a plant, cause significant physiological changes. They affect plant metabolism and promote the biosynthesis of secondary metabolites by triggering mechanisms akin to those seen in plant responses to environmental stressors or pathogens [19, 20]. [21]state that using elicitors has a number of benefits over alternative methods. Most notably, though, is that little levels of elicitors are sufficient to give plants long-term protection against a variety of pathogens. They are also non-toxic and environmentally benign.

Some Compounds inducing defense responses against insects:

1. Methyl jasmonate
2. Salicylic acid
3. Frass
4. Regurgitant application
5. Mechanical wounding
6. Chitin
7. silicon

Jasmonic acid

Plant physiological and developmental processes are regulated by phytohormones called jasmonates, which include jasmonic acid (JA), its methylated metabolite methyl jasmonate (MeJA), and its conjugate with isoleucine (JA-Ile). According to [22], jasmonates are essential for increasing plant tolerance to infections, insect pests, and abiotic stressors.

Role in Plant Defense

Jasmonate-induced defenses involve modifications in the qualitative and quantitative composition of plant volatile compounds. These changes can directly affect herbivores and attract insect natural enemies, leading to increased parasitization and predation rates of herbivores, thus providing indirect resistance to plants [23,24].

Table -1 Jasmonic acid and its derivatives as an Elicitor against different Insects.

Pest	Crop	Form	Reference
Rice water weevil (*Lissotrophus orryzophilus*) (Kuschel)	Rice	J.A	[25]
Rice water weevil (*Lissotrophus orryzophilus*) (Kuschel)	Rice	MeJA	[25]
Mite (*Tetranychus urticae*) (Koch)	Lima bean	J.A	[26]
Rice leaf folder *Cnaphalocrocis medinalis* (Guenee)	Rice	MeJA	[27]
BPH (*Nilparvata lugens*) (Stal)	Rice	J.A	[28]
(Fall army worm) *Spodoptera frugipedra* (JE Smith)	Maize	MeJA	[29]
Gram Pod Borer *Helicoverpa armigera* (Hubner)	Groundnut	JA	[30]
Cabbage Butterfly *Pieris brassicae* (Linnaeus)	Arabidopsis	JA	[31]
Asian corn borer *Ostrinia furnacalis* (Guenée)	Maize	MeJA	[32]

Salicyclic acid:

History and Origin of Salicylic Acid

Salicylic acid, or ortho-hydroxy benzoic acid, is widely distributed throughout the plant kingdom. Its history dates back to 1878 when it became the world's largest-selling drug synthesized in Germany [33]. The name "salicylic acid" is derived from the Latin word "salix," meaning willow tree, and was given by Rafacle Piria in 1838.

Chemical Properties and Role in Plants

Salicylic acid is considered a potent plant hormone[34] due to its diverse regulatory roles in plant metabolism [35]. It is an endogenous plant growth regulator of phenolic nature, characterized by an aromatic ring with a hydroxyl group or its functional derivative. In its free state, salicylic acid is found as a crystalline powder with a melting point of 157–159 °C and a pH of 2.4 [36].

Signaling and Defense Mechanisms

Salicylic acid is a well-known naturally occurring signaling molecule crucial in establishing and signaling defense responses against various pathogenic infections [37]; [38]. In this situation, salicylic acid (SA) and abscisic acid (ABA) are both essential. Studies have demonstrated that the slug *Deroceras reticulatum's* locomotion mucus contains a considerable quantity of SA, a plant hormone that is known to modify plant immunity against herbivores and induce resistance to diseases. Unlike other slugs and snails, *D. reticulatum* is unique in its content of SA and other hormones in its mucus. Application of this mucus to wounded leaves of *Arabidopsis thaliana* activated the promoter of the SA-responsive gene pathogenesis-related 1 (PR1), illustrating the potential of this mucus to regulate plant defenses. These findings have significant ecological, agricultural, and medical implications [39].

Table -2 Salicylic acid and its derivatives as an Elicitor against different Insects.

Pest	**Crop**	**Form**	**Reference**
Whitefiles&Aphids	Cotton	S.A+Profenofos	[40]
Spiny Bollworm *Earias insulana* (Boisd)	Cotton	S.A+Profenofos	[40]
Cotton Bollworm *Helicoverpa armigera*(Hubner)	Tomato	Me SA	[40]
Pod Borer *Helicoverpa armigera*(Hubner)	Chickpea	SA	[41]
White fly *Bemisia tabaci* (Gennadius)	Brinjal	S.A+Acetamiprid	[42]

Mango fruit fly *Bactrocera dorsalis* (Hendel)	mango fruits	Salicylic acid	[43]
Aphid *Brevicoryne brassicae* (Linnaeus)	Rapeseed	Salicylic acid	[44]
Whiteflies *Bemisia tabaci* (Gennadius)	Cotton	S.A +Imidacloprid, Cyhalothrin and Profenofos	[45]
Green peach Aphid *Myzus persicae* (Sulzer)	Broccoli	salicylic + Deltamethrin and Flupyradifurone	[46]
Gram Pod Borer Helicoverpa armigera (Hubner)	Grounds nut	S.A	[47]

Silicon (Si) and Its Availability

Silicon (Si), one of the most abundant elements on Earth, is ubiquitously present in the soil, though mainly in forms unavailable for plant uptake [48]. In the form of silicic acid, Si is absorbed by a diverse number of plant families and stored as hydrated silica (SiO_2nH_2O) in roots and shoots [49]; [50].

Plant Defense Mechanisms

Plants use a variety of defence strategies, which can be either chemical or physical in nature, to fend off herbivores, and these can be constitutive or inducible [51]. Physical defenses include structures such as trichomes, thorns, lignin, waxes, tough leaves, laticifers (latex), and mineral depositions [52]. Chemical defenses consist of secondary metabolites (e.g., terpenes, phenols, alkaloids, sulfur, and nitrogen-containing compounds), antinutritional proteins, and enzymes (e.g., polyphenol oxidase, peroxidase, protease inhibitors) [53]. Plant defenses may be constitutively expressed or induced by herbivory [54].

Silicon's Role in Enhancing Plant Defenses

Si is known to enhance herbivore-induced defenses in different plant species, though most studies have focused on wild and cultivated Poaceae plants [55]; [56]. Research indicates that Si treatment can enhance some defenses, with resistance to herbivory observed as a reduction in larval weight gain in soybean at an early time point and in maize at both early and late time points. The weight gain of larvae was not significantly reduced by Si alone; however, weight gain was reduced by Si placed in non-glandular trichomes. This demonstrates how silicified trichomes may help boost a plant's defences against herbivorous plants that munch on them [57]; [58].

Table-3 Silicon and its forms as an Elicitors against different Insects.

Pest	Crop	Form	Reference
Pink stem borer *Sesamia inferens* (Walker)	Wheat	Orthosilicic acid	[59]
Thrips (*Frankilella schultzei*) (Trybom)	Tomato	Calcium silicate	[60]
Empoasca kerri, *Aphis craccivora*, and *Scirtothrips dorsalis*	Ground nut	Calcium silicate	[61]
Planthoppers	Rice	fluorescent silica (F-SiO2) Nanomaterial	[62]
Rice stem borer *Scirpophaga incertulas* (Walker)	Rice	diatomaceous earth	[63]
Rice stem borer *Scirpophaga incertulas* (Walker)	Rice	Calcium silicate Pottasium silicate	[64]
Leaf miner *Tuta absoluta* (Meyrick)	Tomato	silicon	[65]
Whitefly *Bemisia tabaci* (Gennadius)	Cucumber	Calcium silicate	[66]
Armyworm *Spodoptera frugiperda* (JE Smith)	Corn	Silicon	[67]
Greyback cane grub *Dermolepida albohirtum* (Waterhouse)	Sugarcane	Silicon	[68]

Chitin: Overview and Sources

Chitin is the second most common polysaccharide on Earth, after cellulose [69]. Chitin is present in and derived from a wide range of species, with higher plants and vertebrate animals being two major exceptions. Animal tissues rich in chitin are found in the exoskeletons of arthropods (insects, crustaceans, and arachnids), cephalopod beaks, nematode eggs, and stomach linings)[70]. Chitin is also produced by a variety of microorganisms, including as fungi [71] and diatom spines [72], in their cell walls, membranes, and spores.

Chitin Derivatives and Insecticidal Activity

Oral larvae feeding bioassays are being used to report the insecticidal properties of more chitosan derivatives (e.g., N-alkyl-, N-benzylchitosans) as they become available through chemical synthesis [73][74]. When given at a rate of 5 g·kg−1 in an artificial diet, 24 novel derivatives were demonstrated to have considerable insecticidal action [75]. With an estimated LC50 of 0.32 g·kg−1, the most active derivative, N-(2-chloro-6-fluorobenzyl)chitosan, resulted in 100% larval mortality. After five days of feeding on the treated fake diet, O-(decanoyl)chitosan, the most active derivative, demonstrated a 64% growth suppression in larvae growth when compared to chitosan, which was the 7% growth inhibition observed in all synthesised derivatives.

Hexaacetyl-Chitohexaose and Citrus Pest Management

One hour after HC treatment in Sun Chu Sha mandarin leaves, [76] showed that hexaacetyl-chitohexaose (HC), an oligosaccharide from chitin found in insect exoskeletons and fungal cell walls, upregulated defense-associated genes WRKY22, GST1, RAR1, EDS1, PAL1, and NPR2, while downregulating ICS1. The Asian citrus psyllid (ACP) exhibited decreased intercellular probing, xylem feeding count, and duration when citrus leaves treated with HC were recorded on electrical penetration graphs (EPGs), whereas non-probing activity increased in comparison to the control group. In leaves treated with HC, non-probing behaviour increased and xylem and phloem ingestion durations decreased over the course of eighteen hours. According to [77], HC causes citrus leaves to go through a temporary defence response that prevents ACP feeding without changing the insect's fitness or host preference in the investigated circumstances.

Soybean Seed Coat Chitinase as a Defense Molecule

The effectiveness of soybean seed coat chitinase as a defence molecule against the insect *Callosobruchus maculatus* was investigated by [78]. When a chitinase fraction was added to artificial cotyledons at a concentration of 0.1%, it decreased larval bulk by 60% and reduced larval survival by about 77%. In the guts and excrement of larvae, fluorescein isothiocyanate (FITC)-labeled chitinase was found. Chitinase demonstrated severe toxicity to larvae at 25% in thick artificial seed coatings, resulting in 90% mortality and an 87% reduction in larval bulk.

Chitosan’s Insecticidal Activity and Limitations

When it comes to some plant pests, chitosan has shown to have strong insecticidal properties. According to research by [79], adding N-(2-chloro-6-fluorobenzyl-chitosan) to an artificial meal at a rate of 5 g·kg−1 resulted in 100% mortality of cotton leafworm (*Spodoptera littoralis*) larvae. Chitosan has been shown to be an effective control for insect pests in the orders Hemiptera, which includes aphids, and Lepidoptera, which mostly includes moth pests[80]. The orders Coleoptera (beetles), Diptera (true flies), and Hymenoptera (wasps, termites, ants, and sawflies), which collectively account for thousands of commercially significant plant pests, have, however, notably less evidence available regarding their effects.

Chitin Synthesis Inhibitors and Mite Control

According to several reports, the glasshouse mite (*Tetranychus urticae*) has numerous developmental disruptions, particularly in the area of cuticular development, when exposed to the chitin synthesis inhibitor nikkomycin [81]. Nevertheless, searchable databases do not contain any published information on the impact of chitin/chitosan treatments on phytophagous mites.

Chitosan in Biological Control and Non-Target Insects

In addition to being helpful in managing herbivorous insect pests, chitosan treatments have also been successfully incorporated into the artificial diet given to carnivorous insects that are being raised for the purpose of biologically controlling chitinous pests [82]. This research raises the possibility that chitin-based products may not be as damaging to non-target insects as traditional insecticides. To make definite judgements on this issue, however, there is insufficient published evidence on other useful insects, such as pollinators.

Insect frass

Insect frass, composed of insect excrement and partially digested plant material, has recently gained attention as a natural inducer of plant defenses against herbivory. Unlike traditional chemical inducers, frass offers a sustainable and ecologically friendly alternative by leveraging the intricate interactions between plants and herbivores. Research has shown that the chemical cues in frass can trigger a plant's innate defense mechanisms, leading to the production of secondary metabolites and other defensive compounds that deter further herbivore attacks. This makes frass a promising eco-friendly tool for boosting plant defenses in a way that synthetic chemicals cannot match.

Natural Inducer: Frass contains chemical signals that trigger plant defenses, leading to the production of protective compounds [83]. Maize and Fall Armyworm: Frass from fall armyworms (*Spodoptera frugiperda*) can enhance pathogen defenses in maize. However, its effect varies by host-herbivore system and does not always apply to all pests [84][85].

Herbivore-specific Responses: Plant defenses can be activated by frass differently depending on the plant and the insect. For example, frass from some insects induces defenses, while others might not [86][87].

Direct Pest Control: Frass can influence pest behavior. In potatoes, frass from black cutworms (Agrotis ipsilon) reduces egg-laying by potato tuber moths (*Phthorimaea operculella*) [88]. Similarly, frass from the moth itself reduces oviposition [89].

VOC Emission: Insect frass emits volatile organic compounds (VOCs) that can attract natural enemies of pests or repel pests. For instance, frass from certain beetles attracts parasitoid insects [90].

Soil Amendments: Using frass as a soil amendment provides a cost-effective method for managing pests like cabbage root flies [91].

Biostimulants: Low doses of cricket frass can act as a biostimulant, enhancing plant growth, while higher doses can have elicitor effects, activating plant defenses [92].

Microbial Effects: Frass contains microorganisms that can stimulate plant defenses. For instance, bacteria found in frass can increase the expression of genes that help plants defend against insects [93].

Insect frass, which is insect excrement mixed with partially digested plant material, is emerging as a natural way to boost plant defenses against pests. Unlike synthetic chemicals, frass offers an eco-friendly alternative by utilizing the natural interactions between plants and herbivores.

Regurgitation as a Defense Mechanism

Regurgitation is a defense tactic used by many insects where they expel a mix of saliva and digestive fluids, sometimes containing harmful plant chemicals, to protect themselves from predators [94]. This behaviour, seen in various insect groups, allows insects to use plant-derived toxins stored in their bodies as a defense mechanism.

Triggers of Regurgitation

Although the chemical composition of regurgitants and their effects on predators have been extensively studied, little is known about the causes of these behaviors. For instance, in grasshoppers, pressing on various body regions (such as the thorax) frequently causes regurgitation, indicating a possible involvement for gut control [95].

Effects of Regurgitant on Plant Responses

Studies have shown that regurgitant can affect plant responses. For instance, regurgitant from certain caterpillars like *Heliothis virescens* can make plants release more volatile compounds, while saliva can dampen this response [96]. Caterpillars such as *Helicoverpa zea* can also influence plant defenses indirectly through gut bacteria that trigger specific plant defense genes [97]. Similarly, regurgitant from the forest tent caterpillar has been found to upregulate genes in poplar trees that are associated with anti-herbivore defenses [98].

Impact on Plant Defense Systems

Regurgitant from insects like *Spodoptera* species can induce plants to release defensive compounds and trigger other responses (Santiago, 2017)[99]. The Mediterranean maize borer's regurgitant, however, did not exactly replicate the effects of real eating, indicating intricate interactions between the herbivore and the plant [100]. Furthermore, regurgitant influences the synthesis of chemicals such as ethylene, peroxidase, and polyphenol oxidase in plants that wound [101]. These plants include potatoes and beans.Overall, regurgitation is a complex behavior with diverse effects on both predators and plants, and ongoing research is needed to fully understand its mechanisms and applications.

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Advantages

1. Sustainability: Using external agents like methyl jasmonate, salicylic acid, and frass offers a more eco-friendly approach to pest management compared to traditional chemical pesticides. These methods often have lower environmental impacts and contribute to sustainable agriculture.

2. Reduced Chemical Use: By triggering natural plant defenses, these strategies can reduce the need for synthetic pesticides, leading to safer food products and less chemical runoff into ecosystems.

3. Enhanced Plant Resistance: External agents can effectively induce plant defense responses even in the absence of inherent resistance, providing an additional layer of protection against pest damage.

4. Integrated Pest Management (IPM): These methods can be integrated into broader IPM strategies, complementing other pest control measures and offering a multifaceted approach to managing pest populations.

5. Variety of Applications: The range of agents reviewed, including mechanical wounding, chitin, and silicon, provides diverse options for different crops and pest scenarios, allowing for tailored pest management strategies.

Disadvantages

1. Cost and Practicality: The application of certain external agents, such as chitin or regurgitant, may be costly or logistically challenging on a large scale, limiting their practical use in extensive farming systems.

2. Efficacy Variability: The effectiveness of these agents can vary depending on the plant species, pest type, and environmental conditions. This variability can make it difficult to predict outcomes and standardize practices.

3. Potential for Resistance: While less likely than with chemical pesticides, there is still a possibility that pests could develop resistance to natural defense-inducing agents over time, reducing their effectiveness.

4. Limited Knowledge: The mechanisms by which some agents induce plant defenses are not fully understood, which may hinder the optimization and widespread adoption of these strategies.

5. Complexity of Interaction: The interaction between different agents and the plant's defense systems can be complex, potentially leading to unintended consequences or reduced effectiveness if not carefully managed.

Future Prospects

1. Research and Development: Continued research into the mechanisms by which these agents induce plant defenses will enhance understanding and optimization of their use. This includes studying their interactions with various plant species and pests.

2. Combination Strategies: Future work may explore the synergistic effects of combining multiple external agents or integrating them with other pest management techniques to improve overall efficacy and sustainability.

3. Cost Reduction: Advances in technology and production methods could reduce the costs associated with applying certain agents, making them more feasible for large-scale agricultural use.

4. Broader Applications: Expanding research to include a wider range of plants and pests will help in developing more universally applicable and effective pest management strategies.

5. Regulatory Considerations: As these methods become more widely adopted, there will be a need for clear guidelines and regulations to ensure their safe and effective use in agriculture.

Conclusion

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This review emphasises how different external factors can strengthen plant defences against insect pests even in the absence of innate host plant resistance. These agents include methyl jasmonate, salicylic acid, frass, regurgitant application, mechanical injury, chitin, and silicon. These agents activate plant defense mechanisms through diverse pathways, with methyl jasmonate and salicylic acid primarily influencing hormonal signaling to combat different pest types, while chitin and silicon reinforce physical and chemical defenses. Many of these strategies offer sustainable alternatives to chemical pesticides, aligning with integrated pest management (IPM) practices and promoting environmentally friendly agricultural systems. However, their effectiveness can vary based on plant species, pest types, and environmental conditions, and challenges such as cost, practical application, and the potential for resistance need to be addressed. Future research should focus on understanding the mechanisms of these agents, exploring synergistic effects, and developing cost-effective and widely applicable solutions. Overall, enhancing plant resistance through these external agents represents a promising approach for more resilient and sustainable agriculture, reducing reliance on synthetic chemicals and contributing to the development of robust agricultural ecosystems.

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