African Journal of Biological Sciences

Effectors: A Key Modulator of Plant Biotic Interactions

Theertha Thanikkal Surendran[1], Sidhardh H. Menon[2], Smitha Mony Sreedharan[1,3*]

[1]Amity Institute of Microbial Technology, Amity University, Noida, Uttar Pradesh, [2] Amrita School of Biotechnology, Amrita Vishwa Vidyapeetham, Amritapuri, Kollam

[3]Corresponding author: smsreedharan@amity.edu, Phone No: +91 9871556257

Amity institute of microbial technology, Amity University, Noida, Uttar Pradesh, India.

Article History
Volume 6, Issue 5, 2024
Received: 05 apr 2024
Accepted: 10 May 2024
doi: ***10.33472/AFJBS.6.5.2024. 4575-4601***

Abstract

Effector-mediated interactions play a crucial role in shaping plant health, disease dynamics, and ecosystem stability. This research delves into understanding the mechanisms and ecological impacts of effectors in plant biotic interactions. The research problem underscores the necessity of unraveling effector mechanisms for effective disease management and sustainable agriculture. Research aims include reviewing diverse effector roles, investigating molecular mechanisms of pathogen colonization, analyzing effector targets, and assessing ecological consequences. Methodologically, this study integrates literature review, molecular biology, and environmental analyses. Molecular techniques and field experiments are employed to identify effector targets and assess ecological impacts. Findings reveal insights into plant-pathogen dynamics, including identifying novel effectors and mechanistic understanding of effector-host interactions. Recommendations emphasize the development of integrated disease management strategies, the promotion of sustainable agricultural practices, and the need for further research on effector targets and non-pathogenic organism effectors. Ultimately, this study advances our understanding of effector-mediated interactions and offers avenues for sustainable disease management in agriculture.

Keywords: Effectors, Plant defense, Herbivory, ETI, PTI, ETS

Introduction

Plants despite their silent stature, engage in diverse biotic interactions ranging from microscopic fungi to large mammals throughout their lifetime to shape their surrounding niche and ecosystem thereby influencing evolutionary dynamics for their sustenance in nature. One of the most prominent is plant herbivore interaction which in today's world has more importance due to their imminent role in linking primary production with food chain. The selective pressure imparted on both plant and their interacting partners has driven the evolution of various defense strategies by plants and anti-defense strategies by herbivores including the production of various secretory as well as volatile secondary metabolites. One such strategy employed by the interacting partners is production of effector molecules which are secreted into plant system to hijack their machinery for favoring their spread and survival. Whether promoting symbiosis or manipulating plants to attract pathogens, the role of effectors reflects their importance in plant interactions.

At the center of symbiotic relationships, such as mycorrhizal and pollinator relationships, effectors serve as molecular messengers, exchanging nutrients and communicating between partners. On the other hand, in interactions such as herbivory and pathogenic attack, effectors act as weapons, allowing pathogens to disrupt plant defenses and exploit host resources (Kamoun, 2006). Although progress has been made in understanding the interactions between agents, many questions remain unanswered. Elucidating the molecular mechanisms underlying effector functions and their environmental impacts requires an interdisciplinary approach combining genomics, biotechnology and environmental science [Win, 2012]. Moreover, the translation of scientific results into agriculture and ecosystem management requires collaboration between researchers, policy makers and stakeholders (Pieterse, 2014)

Plant Biotic Interaction

From cooperative symbiosis to conflict, Plant biotic interactions have a profound impact on the structure, dynamic and functioning of ecosystems. A mutually beneficial partnership is essentially a symbiotic relationship in which both types of collaboration benefit. The relationship between flowers and pollinators is a prime example of this phenomenon. Flowers gift nectar and pollen to pollinators, and pollinators can increase seed production by facilitating the exchange of pollen grains (Bronstein, 2015). This beneficial combination is essential for the proliferation of many plant species and the maintenance of ecosystem biodiversity. Another beneficial partnership occurs between plants and mycorrhizal fungi. Mycorrhizal symbiosis involves the relationship between bacteria and roots, where fungi provide valuable nutrients to plants in exchange for photosynthetically produced carbohydrates (Smith and Read, 2008). This symbiotic relationship plays an important role in cycling, soil structure and plant communities, especially in nutrient-poor environments. In contrast to mutualistic relationship, hostile relationships include competition, herbivory, predation, and parasitism, in which one organism takes advantage of another. Herbivory is an important antagonistic interaction involving the consumption of tissues by herbivores. Herbivory can have significant effects on plant growth, reproduction, and population dynamics. Plants have evolved many defense mechanisms against herbivores, including physical structures such as spines and chemical compounds such as secondary metabolites.

Competition for resources such as light, water, food and space is an important aspect of plant interactions and social dynamics, whether intraspecific or interspecific. Competition creates the structure and diversity of plants by influencing species distribution, community composition, and ecosystem function. Plants use a variety of strategies to compete with neighboring plants, including acquisition, allelopathy, and shading. Allelopathy is when plants release biochemical chemicals that inhibit the growth or development of other nearby plants. Many plants produce allelochemicals to defend against competition, herbivory, and pathogen attacks. For example, the black walnut tree (Juglans nigra) secretes juglone, which is toxic to many plant species and inhibits the growth of nearby plants. Positive interactions too occur in plant communities, where nurses or symbionts often use support. One plant species facilitates the growth or survival of another species (Bruno et al., 2003). For example, nitrogen-fixing bacteria and mycorrhizal fungi form symbiotic relationships with plants, contributing nutrients and promoting plant growth in nutrient-deprived environments (Van der Heijden et al.,2008).

The plant-biotic relationship plays an important role in the ecosystem's structure, functioning and quality. Interactions between plants and the biota help maintain the ecosystem's stability and the conservation of biodiversity by enhancing food quality and pollination, as well as the growth of plants. These interactions also influence the abundance and diversity of plant and animal species by influencing population dynamics, species distribution, and the ecosystem's productivity (AgriOS, 2005).

Additionally, plants interact with ecosystem processes such as carbon sequestration, soil formation, and nutrient cycling, creating significant impacts on global biogeochemical cycles and climate control. Understanding the mechanisms and consequences of plant-biotic interactions is important for predicting ecosystem responses to environmental change and developing conservation and management strategies to preserve biodiversity and ecosystem services.

Molecular Signaling in Plant Herbivore interaction

Plant-herbivore communication drives an evolutionary arms race, with both adapting to each other's tactics. This interaction entails complex molecular pathways. When plants sense herbivore attacks, they activate defense mechanisms through intricate signaling involving hormones like jasmonic acid and salicylic acid. Perception of damage triggers signaling cascades via pattern recognition receptors, leading to defense gene activation and the production of compounds like phytoalexins and volatile organic compounds (VOCs). These substances deter herbivores or attract their predators. Environmental factors like light and temperature influence these interactions. Understanding these molecular networks is vital for developing eco-friendly pest management strategies.

Pattern-Triggered Immunity (PTI)

Pattern-triggered immunity (PTI) is an important part of plant defense. PTI is initiated when genes recognize conserved molecular patterns associated with potential pathogens, called pathogen-associated molecular patterns (PAMPs). PAMPs are molecules that are generally essential for bacterial survival and is conserved across a wide range of organisms, making them ideal targets for plant immunity (Zipfel, 2014). Recognition of PAMPs by plant cells is mediated by pattern recognition receptors (PRRs) on the surface of the plant. PRRs are specific receptor proteins that bind to specific PAMP molecules. Following binding, PRR initiates a signaling pathway that ultimately activates the immune response, including the production of antibodies, cell walls, and activation of immune system genes (Bigeard et al., 2015). The signaling cascade caused by PAMP perception involves phosphorylation events and activation of protein kinases and phosphatases. Importantly, the mitogen-activated protein kinase (MAPK) signaling pathway plays an important role in PTI signaling. MAPK cascades relay signals from PRRs to downstream components, ultimately leading to activation of the immune response (Meng and Zhang, 2013).

When PTI is activated, the plant sends out defense mechanisms designed to limit the growth and spread of pathogens. These defense responses include the production of phytoalexins and pathogenesis-related (PR) proteins, strengthening of cell walls through the release of callose and lignin, and the generation of reactive oxygen species (ROS) as part of the oxidative burst (Pieterse et al . 2013). , 2012). Phytoalexins are secondary metabolites synthesized by plants in response to pathogens and play an important role in inhibiting pathogen growth. PR proteins contain many proteins involved in many aspects of plant defense, including protease inhibitors, chitinases, glucanases, and lipid modification proteins. These proteins promote plant defense by targeting different parts of the bacterial cell wall or interacting with bacterial virulence factors (Van Loon et al., 2006).

PTI-PAMP-induced immunity is an important part of plant defense and the first line of defense. By knowing how to maintain molecular structures associated with different types of pathogens, plants can initiate a rapid and effective immune response without needing to be specific about a particular pathogen. Additionally, PTI provides the plant with an effective level of immunity against many diseases, including bacteria, fungi and some viruses. This general defense is good for plants living in many places where they may encounter many diseases (Dodds and

Rathjen, 2010). Additionally, PTIs play an important role in maintaining the plant's immune system so that it can better protect against the next pathogen. Activation of PTI leads to changes in gene expression and accumulation of immune-related defenses, leading to better readiness to respond to future infections. This priming effect, known as systemic acquired resistance (SAR), enables plants to develop faster and stronger defenses against pathogens (Durrant and Dong, 2004). Understanding the mechanisms by which PTI-PAMPs trigger disease resistance is important for plant health and agriculture. By elucidating the molecular basis of plant resistance, scientists can develop strategies to increase plant resistance and increase crop yields.

One approach involves plant engineering to improve PTI responses by controlling PRRs or downstream candidates. By adapting PTI guidance methods, researchers aim to develop crops resistant to various diseases, reduce the need for pesticides, and promote permaculture practices (Nicaise et al. et al., 2009).

Additionally, a deeper understanding of the PTI signaling pathway may inform the development of new disease control strategies, such as the use of PAMP mimetics or elicitors to stimulate immune responses.These bio based methods show promise in controlling plant diseases while reducing environmental impacts associated with fungicides and fungicides(Newman et al., 2013).

Effector-triggered susceptibility (ETS)

Effector-triggered susceptibility (ETS) is a phenomenon observed in plant-pathogen interactions in which the pathogen produces chemical molecules that regulate cellular processes, resulting in multiplex infection. Unlike the immune response to infection (PTI), which involves recognition of microbial protection patterns, ETS uses host interactions to promote infection. Effector-triggered susceptibility involves the interaction between the affected organism and the affected host. Pathogens deliver effector molecules into the host cell to regulate cellular processes and limit host defense responses. This effect can target many aspects of plant resistance, including signaling pathways, defense-related proteins and regulatory mechanisms (Jones & Dangl, 2006).

Effector proteins frequently utilize or interact with host proteins to facilitate bacterial colonization and transmission. For example, some interventions cause the host's proteins to hijack cellular processes, while others inhibit immune signaling or downregulate immune proteins (Chisholm et al., 2006). By targeting key components of the plant's immune system, the virus can bypass the host's defenses and spread successfully. Besides the immune response, host interactions also play an important role in ETS. Susceptibility factors are whether the organism uses proteins or cellular processes to promote infection. These factors may include receptor proteins, signaling components, transcription factors, and regulatory proteins involved in the immune response (Cui et al., 2015).

Viruses often target factors that affect the host's immune system and suppress the immune response. For example, some affect target receptor proteins or signaling components to interfere with the immune system, while others affect the regulation of transcription or regulatory processes to alter gene expression and promote infection (Cui et al., 2015).

Effector-triggered susceptibility plays an important role in plant defense evasion and pathogen virulence. The virus can suppress the immune system and promote infection by targeting the host's response to the virus, resulting in increased disease and crop loss. ETS allows pathogens to pass through immune plants and spread effectively, ultimately leading to growth and spread of disease. Additionally, ETS helps bacteria control the host's body and cell processes to create a favorable environment for growth and development. By altering the host's immune response, pathogens can obtain necessary nutrients, suppress immune responses, and overcome the immune system (Chisholm et al., 2006). The ability to manipulate the host's biology provides a better selection for the pathogen and improves its ability to infect.

Table 1: Types of Effector-triggered susceptibility (ETS) and the Effector proteins and Host plant identified with it.

Types	**Plant species and effectors**
Directly targeting components of plant immune signaling pathways, thereby suppressing host defenses and promoting pathogen colonization.	Pseudomonas syringae effector AvrPtoB
Manipulating host cellular machinery to create a more conducive environment for pathogen growth.	Phytophthora sojae effector Avr3a
Mimicking host proteins or interfering with host cellular processes to subvert immune responses.	Xanthomonas campestris effector XopQ
Target host transcription factors to manipulate gene expression and promote pathogen virulence.	Magnaporthe oryzae effector AvrPiz-t

Manipulate host hormone signaling pathways to promote susceptibility.	Gibberella zeae effector FgVelB
Interfere with host metabolic processes to facilitate pathogen growth and reproduction.	Ustilago maydis effector Pep1

Effector-Triggered Immunity (ETI)

In the complex process of plant-pathogen interactions, effector-triggered immunity (ETI) is an important defense mechanism for plants against invading pathogens. Unlike patterned immunity (PTI), which relies on recognition of conserved microbial patterns, ETI is activated when plant defense proteins recognize specific pathogens. Effector-triggered immunity (ETI) is initiated when plant resistance (R) proteins directly or indirectly recognize specific pathogens. R proteins are plant-encoded intracellular receptors that monitor the intracellular environment for the presence of pathogen effectors. Following effector recognition, the R protein becomes a transcription factor leading to activation of downstream events (Jones and Dangl, 2006). Activation of R proteins leads to signaling that ultimately leads to a protective response, including the production of antibodies, cell walls, and activation of the immune system. In particular, the acute response (HR), characterized by local cell death at the site of invasive disease, is the hallmark of ETI and can limit the growth and spread of disease (Dodds and Rathjen, 2010). R proteins are highly specific for certain pathogens, allowing the plant to develop an immune system against certain pathogens. This specificity is achieved by direct or indirect recognition of the pathogen by the R protein, usually associated with protein-protein interactions or detection of changes affecting the target (Jones and Dangl, 2006). Specific recognition of antibodies by the R protein enables plants to use the target immune system to avoid defense strategies used by invading pathogens. This property is important for ETI to effectively protect plants against various pathogens and reduce the mutation rate associated with weakened immune systems (Dodds and Rathjen, 2010).

The elucidation of ETI mechanisms has significant implications for plant breeding and crop protection. By identifying and characterizing R proteins and their corresponding pathogen effectors, researchers can develop molecular markers for use in breeding programs aimed at introgressing resistance traits into crop varieties. Insights into ETI signaling pathways and defense mechanisms can inform the design of novel strategies for disease management and crop protection. By harnessing the power of ETI, researchers can develop innovative approaches for engineering plant immunity, such as the manipulation of R protein signaling networks or the deployment of synthetic immune receptors with broad-spectrum activity against multiple pathogens (Dodds & Rathjen, 2010).

Table 2: Various Defense Responses in ETI and their corresponding Effectors/ Elicitors identifies with their herbivores & host plants

Insect Species	**Plant Species**	**Elicitor/ Effector**	**Mechanism of Defense Response in ETI**	**Reference**
Thrips	Soybean	Thrips-derived effector proteins, e.g., HopX1, HopAB2	Induction of systemic acquired resistance (SAR) pathway, inducing defense-related gene expression and reinforcement of cell walls to resist thrips infestation	Wang et al.,2020
Beetles	Maize	Beetle-produced elicitors, e.g., CAZyme, PPO	Activation of defense-related enzymes, such as polyphenol oxidase (PPO), and accumulation of defensive compounds, including phenolic compounds and defense proteins, to deter beetle feeding	Wang, H., & Gurr, G.M,2019
Leafhoppers	Rice	Leafhopper-secreted effector proteins, e.g., Hsap1, OsEPIC4	Activation of defense-related signaling pathways, such as jasmonic acid (JA) and ethylene (ET) pathways, leading to increased resistance against leafhopper feeding and oviposition	Xu et al.,2018

Aphids	Tomato	Aphid-derived effector proteins Eg. Avirulence (Avr) proteins	Recognition of Avr proteins by R proteins triggers hypersensitive response (HR), leading to localized cell death and resistance against aphids	Jones et al.,2006
Whiteflies	Arabidopsis	Whitefly secreted effectors, e.g., MpC002, Me10 protein	Activation of defense-related genes and production of antimicrobial compounds to inhibit whitefly feeding and reproduction	Kaloshian et al.,2005

Effectors

Effectors refer to small, secreted molecules that modify the structure and function of host cells, either facilitating infection or triggering a defense response. Effectoromics research has primarily examined these molecules in interactions between plants and pathogens, where their impact on virulence in the plant host is assessed, determining whether they promote resistance or susceptibility to plant diseases. Effectors produced by plant-pathogenic microorganisms like fungi, oomycetes, and bacteria play crucial roles in disease development. Interestingly, effectors from non-pathogenic plant organisms such as endophytes perform similar functions but lead to different outcomes for plant health. Endophyte effectors typically assist in establishing mutualistic relationships with plants and enhance plant health by inducing systemic resistance against pathogens. In contrast, pathogenic effectors primarily suppress the plants immune response, leading to disease establishment.

Effectors are pathogen proteins that modify host cell structure and physiology which plays a crucial role in either facilitating infection or triggering a defense response. These molecules have been identified not only in pathogens but also in non-pathogenic organisms like mycorrhizae and rhizobacteria, underscoring their significance in various ecological interactions with plant hosts. Effectors are defined as secreted or translocated molecules that influence interactions between organisms, typically benefiting the producer organism. They induce changes in the physical and physiological characteristics of other organisms, and sometimes even in the producer organism itself, affecting their interactions with others. While effectors can take various forms such as proteins, secondary metabolites, or small RNAs, the majority of characterized effectors are proteins. They play roles in microbial penetration and proliferation within the host, suppression of host immune responses, and nutrient acquisition. Despite being encoded in the genome of an organism, the secreted or translocated gene products primarily function within the plant host.

Effectors facilitate the colonization of the plant host by pathogens or endophytes through various means, including evading detection by the host, controlling host gene expression, disrupting phytohormone defense pathways, and affecting host protein trafficking. Key targets of bacterial, oomycete, and fungal effectors often encompass host proteases, the ubiquitin-proteasome system, autophagy components, reactive oxygen species (ROS) regulation, immune receptors, and phytohormones. Upon leaving the producer organism, effectors may localize to the host apoplast or the cytoplasm, with many targeting intracellular organelles. Techniques such as fluorescence protein-tagging combined with confocal microscopy and protein-protein interaction assays like co-immunoprecipitation and yeast-2-hybrid assays are commonly employed to identify effector targets in model plants that are genetically transformable (Todd& Jewel Nicole Anna,2022)

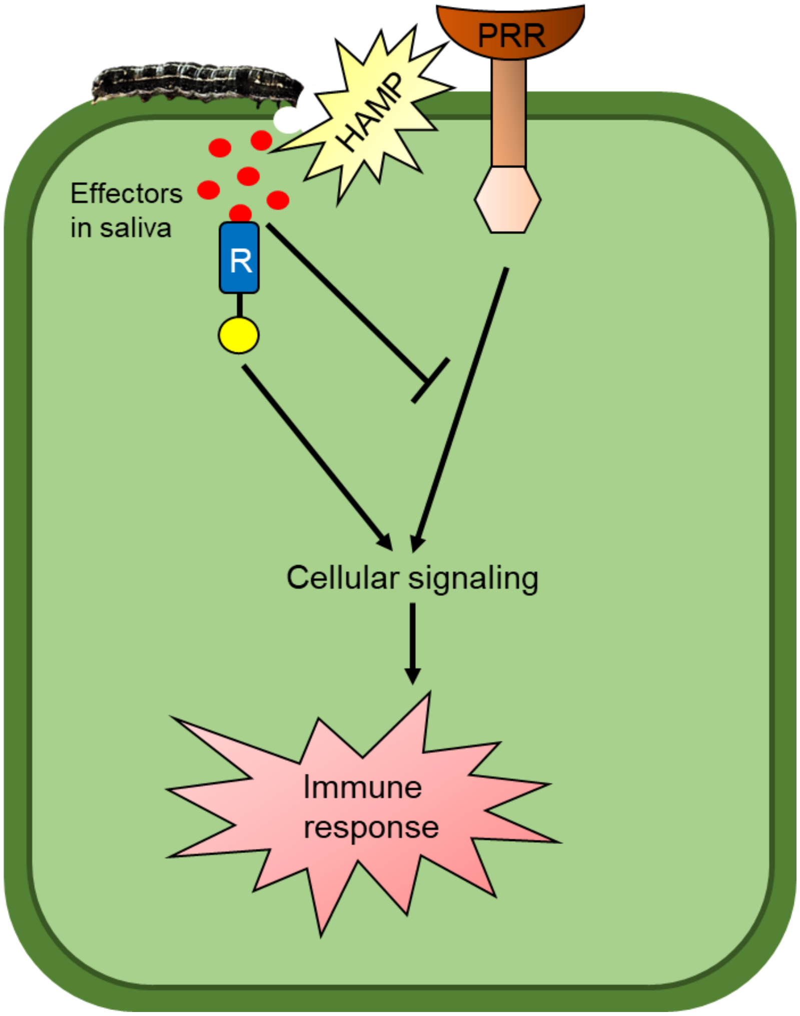

Fig 1: Effector Mechanism in plant Defense

Diversity Of Effectors in Plant Biotic Interactions

The diversity of effectors in plant-pathogen interactions shapes biotic stress responses, driving a co-evolutionary arms race. These specialized proteins manipulate host cellular processes and suppress plant defenses, facilitating infection and disease development. The Phytophthora species, a group of oomycete pathogens, deploy a broad range of effector proteins like RXLR and CRN to facilitate infections in various crop plants, leading to severe diseases (Haas et al., 2009). These RXLR effectors are particularly adept at entering host cells and suppressing immune responses, a common strategy among eukaryotic pathogens (Whisson et al., 2007). Fungal pathogens like Ustilago maydis employs effectors to suppress host immunity and alter metabolism, aiding pathogen nutrition and reproduction. The effector Pep1 crucially suppresses the host's oxidative burst, facilitating disease establishment (Doehlemann et al., 2009). Bacterial pathogens like **Pseudomonas syringae** use the type III secretion system (T3SS) to deliver effectors directly into the plant cytoplasm. Effectors like AvrPto and AvrPtoB exhibit dual roles in triggering and suppressing immune responses, highlighting the nuanced interplay in plant-pathogen interactions (Xiang et al., 2008).

Mode & Mechanism of Effectors

1. Breaking down Physical Barriers-Manipulation of Host Plant Stomatal Defenses, Degradation of Plant Cell Walls, Attacking Plasmodesmata–Callose Regulation, Destruction of the Host Plant Cytoskeleton.

2. Creating Conditions Favorable to Infestation by Construction of Hydrophobic Space, Induction of Extracellular Alkalinization.

3. Protecting or Masking Themselves by Inhibition of PTI, Antagonism with Anti-Microbial Compounds in Plants

4. Interfering with Host Plant Cell Physiological Activities by Regulation of Plant Gene Transcription, Degradation of Host Plant RNA, Interference with Plant Cell Degradation Pathways, Interference with Host Plant Protein Function, Interference with Host Vesicle Transport.

5. Manipulating Plant Downstream Immune Responses by Interference with Plant Hormone Signaling, Utilization of RNA Silencing Strategy, Regulation of Reactive Oxygen Species Generation, Manipulation of Plant Cell Death(Zhang et al.,2022)

Table 3. Major Effector proteins identifies with herbivores and their host plants.

S.No	**Insect species**	**Plant species**	**Elicitor/effectors**	**Mechanism of defense response**	**References**
1.	*Bemisia tabaci*	*N.tabacum*	*BtArmet*	Enhances whitefly performance & taget the tobacco NtCYS6	Du et al., 2022
2.	*Nilaparvata lungens; Laodelphax striatellus*	*O.sativa*	*CaM*	Enables BPH fecundity; supresses H2O2 aacumlation as well as callose depositiiton	Fu et al., 2022
3.	*Schizaphis graminum*	*N.tabacum*	*Sg2204*	Suppression of JA and SA pathways also causes BAX/INF1 induced cell death in tobacco	Zhang et al., 2022a
4.	*Nilaparvata lugens*	*O.sativa*	*Sm9723*	Enables BPH feeding as well as suppression of SA pathway	Zhang et al., 2022b
5.	*Nilaparvata lungens*	*O.sativa*	*NlugOBP11*	Supresses SA pathway & enables BPH feeding	Liu et al., 2021
6.	*Laodelphax striatellus*	*Oryza sativa*	Vitellogenin	H2O2 suppression and weakening of	Ji et al.2021

				OSWRKY71 related defense	
7.	*Helicoverpa armigera*	*Arabidopsis thaliana*	HARP1	Inhibition of JAZ degradation resulting in reduced JA defense.	Chen et al.2019
7.	*Acyrthosiphon pisum*	*N.tabacum*	*Armet*	SA pathway elicitor, also enables aphid feeding	Wang et al., 2015a;Cui et al.,2019
8.	*Nilaparvata lugens*	*O.sativa*	*NISP7*	Mediate tricin metabolism and enables BPH feeding	Rao et al., 2019
9.	*Bemisia tabaci*	*S.lycopersicum*	*BtFer1*	Enables whitefly survival and suppress JA pathway	Su et al., 2019
10.	*Nilaparvata lungens*	*N.tabacum*	*Nl32*	Induced a dwarf phenotype, defensive gene expression and callose deposition in the plant	Rao et al., 2019
11.	*Marcosiphum euphorbiae*	*S.lycopersicum* & *N.benthamiana*	Me 10	Interact with TFT7 increasing the performance and survivability	Atamian et al.2013; Chaudhary et al.2019
12.	*Bemisia tabacai*	*Nicotiana tabacum*	BT56	Interacts with NTH202 and increases SA	Xu et al.2019b

				defense decreases JA gene expression	
13.	*Nilapervata lugens*	*O.sativa*	Endoβ 1-4emdoglucanase	Degrades plant cell and increases insect fecundity and survival	Ji et al.2017
14.	*Nilapervata lungens*	*Oryza sativa*	NISEF1	Decreases cytosolic Ca^{2+} levels upon infestation resulting in defensive suppression	Ye et al.2017
15.	*Tetranychus evansi*	*N.benthamiana*	Te84	Chlorophyll induction and reduction of SA maker gene expression	Villarroel et al.2016
16.1	*Acyrrthosiphon pisum*	*N.benthamiana*	MIF	Reduce cell death and callus deposition	Naessens et al.2015
17.	*Mayetiola destructor*	*Triticum spp.*	SSGP-17	Hijack plant proteosome and block basal immunity by mimicking E3 ligase.	Zhao et al.2015
18.	*Acyrthosiphon pisum*	*N.tabacum*	ACE-1 & ACE-2	Enable aphid feedoing and survival	Wang et al., 2015b
19.	*Myzus*	*Arabidopsis*	Mp1	VPS52	Pitino and

	persicae	*thaliana*		interaction resulting in vesicle like relocalization and aphid virulence upscaling in Arabidopsis	Hogenhout 2013
20.	*Helicoverpa zea*	*Solanum lycopersicum*	ATPases	Helps in the suppression of direct defense	Wu et al.2012
21.	*Myzus persicae*	*Nicotiana benthamiana*	Mp10	Direct defence suppressal	Bos et al.2010
22.	*Myzus persicae*	*N.benthamiana*	MpC002	Suppression of direct defense	Bos et al.2010
23.	*Helicoverpa zea*	*N.tabacum*	GOX	Nicotine production suppression	Musser et al.2002
24.	*Helicoverpa zea*	*Solanum lycopersicon*		Elicits direct defense	Musser et al.2005
25.	*Helicoverpa exigua*	*Nicotiana tabacum*		Increases H2O2 and SA accumulation, supresses JA and ET related defense	Diezel et al.2009

Effectors of Chewing Pests Insects

Chewing herbivores, like caterpillars and beetles, cause significant damage to host plants as they feed, releasing various signals that influence plant defenses. These signals can have both positive and negative effects on the herbivores. Herbivore-Associated Molecular Patterns (HAMPs) are substances produced by these insects that help trigger plant defenses, hindering insect growth. Conversely, certain compounds, called effectors, suppress plant defenses, making the plant more susceptible to further damage by chewing herbivores. Chewing insects possess a mouth structure designed for chewing, comprising the labrum, mandibles, first maxillae, second maxillae, hypopharynx, and epipharynx. Positioned centrally, the labrum resembles a rectangular flap. The mandibles, occurring in pairs, feature toothed edges on their inner surfaces and employ two sets of transverse muscles for food mastication. Paired as well, the first maxillae hold food, while the second maxillae aid in pushing masticated food into the mouth. The hypopharynx contains a single median tongue-like structure, with the opening of the salivary duct situated beneath it. The epipharynx, housing taste buds, is a small membranous piece located at the base of the labrum (Kahl, 1982; Felton et al., 1999; Stotz et al., 1999). The oral secretion (OS), comprising regurgitant and saliva, from chewing insects contains active molecules that significantly influence plant defense responses, distinct from typical mechanical damage (Hogenhout and Bos, 2011; Chen and Mao, 2020). Recent research indicates that besides secretions from glands and digestive systems, insect waste (frass) and symbiotic organisms associated with herbivores also play crucial roles in adjusting plant defenses.

Mechanism of chewing pest on plants

Chewing insect pests are equipped with strong mandibles that enable them to ingest plant material, resulting in clear damage like defoliation and leaf skeletonization. Caterpillars, specifically, secrete digestive enzymes in their saliva that decompose plant cell walls, enhancing their ability to extract nutrients. (Felton and Tumlinson, 2008). Moreover, certain chewing insects, such as beetles, emit toxins or trigger the production of plant defense chemicals to bypass plant resistance and inhibit defenses triggered by herbivores (Agrawal, 2011).

Frass

Until Ray et al. (2015) presented their findings, the significance of effectors found in insect waste was overlooked. They demonstrated that maize plants could detect signals emitted by caterpillar waste. In maize, the deposition of caterpillar waste at feeding sites triggered the activation of pathogen defenses while simultaneously dampening herbivore defenses. This led to the accumulation of salicylic acid (SA), potentially suppressing levels of jasmonic acid (JA) (Ray et al., 2015). Subsequent research revealed that caterpillar waste utilized plant-derived chitinases PR4 and endochitinase A to either suppress plant defense mechanisms, stimulate susceptibility, or both, thereby enhancing the performance of herbivores on host plants (Ray et al., 2016a). Additionally, it was observed that waste from different caterpillars modulated plant defenses in various tissues and species (Ray et al., 2016b).

Effectors of Sucking Pests Insects

Piercing-sucking herbivorous insects, including aphids, whiteflies, and planthoppers, feed on plants using specialized mouthparts called stylets, which they utilize to puncture the plant surface and access the phloem sap. Piercing-sucking insects in the order Hemiptera display typical feeding behavior that suggests active suppression of plant defense. The mouthparts of these insects consist of the labrum, labium, and stylet, with the stylet being specifically adapted for piercing and sucking phloem sap from plants (Sogawa, 1982; Backus, 1988). The feeding process of piercing-sucking insects can be broadly categorized into three main phases: labial exploration, stylet penetration, and phloem-sap ingestion (Spiller, 1990; Hao et al., 2008; Cheng et al., 2013b; Will et al., 2013). Upon first encountering their host plants, insects move rapidly and repeatedly probe the plant surface to locate a suitable feeding site, crucial for their survival (Wang et al.,2023)

Sucking pest insects employ a diverse array of effectors to overcome plant defenses and manipulate host physiology. Vacuum-sucking insects secrete complex saliva mixtures into tissues during feeding. Salivary effectors include a variety of proteins, enzymes, and other molecules that support insects by inhibiting plant defenses, modulating plant signaling pathways, and altering plant metabolism (Elzinga et al., 2014). Some pesticides act pesticides or interfere with plant hormones to regulate the host's body and promote disease. This effect may involve plant hormones such as auxin or jasmonic acid causing changes in plant growth and development that are beneficial to insects, or voluntary interactions with hormones represent a way to protect against plant resistance (Kaloshian and Walling, 2016). Vacuum-sucking pests create an effect that disrupts the plant's immune system, allowing insects to escape and find and feed on the plant. This effect may interfere with the production of proteins involved in the immune system, interfere with the immune system, or prevent disease by interfering with the immune response (HR) induced by the immune system (Elzinga et al., 2014).

Mechanism of Sucking pest on plants

Sucking pests employ various tactics to aid in feeding and counteract plant defenses. For example, aphids release saliva containing specialized proteins into plant tissues, altering plant functions to create a more favorable environment for feeding. These proteins can manipulate plant defense pathways, impede wound healing, and modify the composition of phloem sap to improve nutrient absorption by the insect. (Elzinga et al., 2014) Conversely, whiteflies produce honeydew, a sweet substance abundant in nutrients, which can encourage the proliferation of sooty mold and attract additional pests, intensifying plant harm. (Ghanim et al., 2006). sucking pest effectors can also evade detection by plant defenses through a variety of mechanisms, such as masking recognition of the plant's sting, changing their patterns to avoid recognition, or evolving to attack the host (Kaloshian and Walling, 2016).

ROLE OF AI IN EFFECTORS

Effector proteins play a pivotal role in the complex interplay between pathogens and their host plants. Understanding the functions and mechanisms of action of these effectors is crucial for unraveling the molecular basis of plant-pathogen interactions and developing effective strategies for crop protection. Artificial Intelligence (AI) techniques have emerged as powerful tools for analyzing, predicting, and manipulating effector proteins, offering new insights and opportunities for research in this field.

Effector Prediction and Identification

One of the primary applications of AI in effector research is in the prediction and identification of novel effectors. Machine learning algorithms, such as Support Vector Machines (SVMs), Random Forests, and deep learning models, can analyze large-scale genomic and transcriptomic datasets to identify patterns and features associated with known effectors. By training these models on labeled datasets of known effectors and non-effectors, researchers can develop predictive models capable of distinguishing between potential effector proteins and other non-effector proteins within pathogen genomes (Sperschneider et al., 2018).

Effector Function Prediction

Once potential effector proteins are identified, AI techniques can aid in predicting their functions and targets within host plants. Computational methods, such as protein structure prediction algorithms, homology modeling, and functional annotation tools, can leverage AI to infer the biological roles and mechanisms of action of effector proteins. By comparing effector sequences and structures to known proteins with annotated functions, researchers can predict the biochemical activities, protein-protein interactions, and subcellular localization of effector proteins, providing insights into their roles in pathogenesis (Savojardo et al., 2021).

Effector-Host Interaction Prediction

Understanding the intricate network of interactions between effectors and host proteins is essential for deciphering their roles in pathogenesis. AI techniques, such as network analysis, protein-protein interaction prediction algorithms, and deep learning models, can integrate diverse data sources, including genomic, transcriptomic, and proteomic data, to infer effector-host interaction networks. By analyzing these networks, researchers can identify candidate effector-target interactions, prioritize them for experimental validation, and elucidate the molecular mechanisms underlying effector-mediated manipulation of host physiology (Villani et al., 2021).

Effector Design and Engineering

AI-driven approaches can facilitate the rational design and engineering of novel effector proteins with desired properties. Computational protein design algorithms, such as Rosetta and FoldX, use AI techniques to simulate and optimize the sequences and structures of effector proteins in silico. By predicting the effects of mutations and modifications on effector function, stability, and specificity, researchers can design synthetic effector variants tailored for specific applications, such as enhancing pathogen virulence, eliciting host immune responses, or delivering cargo molecules for targeted gene editing or drug delivery (Lippow et al., 2007).

Effector-Based Crop Protection

Effector research guided by AI techniques can inform strategies for crop protection and disease management. By identifying key effectors involved in pathogenesis and host manipulation, researchers can develop targeted interventions, such as genetic engineering of resistant crop varieties or the design of effector-based vaccines or therapeutics for disease control. AI-powered platforms for effector analysis and prediction can accelerate the discovery and deployment of novel effector-based strategies for sustainable agriculture (Drechsler et al., 2019).

FUTURE PERSPECTIVE

Effector research, empowered by Artificial Intelligence (AI) techniques, is poised to revolutionize our understanding of plant-pathogen interactions and pave the way for innovative solutions in agriculture and crop protection. As we look towards the future, several exciting developments and emerging trends are shaping the landscape of effector research and its applications.

1. Integration of Multi-Omics Data: The advent of high-throughput sequencing technologies has generated vast amounts of genomic, transcriptomic, proteomic, and metabolomic data. AI-driven approaches for data integration and analysis will enable researchers to unravel the complex networks of effector-host interactions, identify novel effectors, and elucidate their functions in pathogenesis. By combining multi-omics data with AI algorithms, researchers can gain deeper insights into the molecular mechanisms underlying plant-pathogen interactions and develop targeted strategies for disease management.

2. Advancements in Structural Biology: Recent breakthroughs in structural biology, such as the development of deep learning-based protein structure prediction algorithms like AlphaFold2, are revolutionizing our ability to model and predict the three-dimensional structures of proteins, including effectors. AI-driven methods for protein structure prediction will facilitate the rational design and engineering of novel effector variants with desired

properties, enabling researchers to tailor effector proteins for specific applications in crop protection and biotechnology.

3. Implementation of Precision Agriculture: AI-driven platforms for effector analysis and prediction will play a crucial role in implementing precision agriculture practices. By leveraging AI techniques for real-time monitoring of pathogen populations, disease outbreaks, and environmental conditions, farmers can optimize the timing and deployment of control measures, minimize pesticide use, and maximize crop yields. Effector-based diagnostics and therapeutics developed through AI-driven research will enable targeted interventions for managing plant diseases with high precision and efficiency.

4. Harnessing the Power of Synthetic Biology: The convergence of AI and synthetic biology holds immense potential for engineering novel effector-based solutions for crop protection and biotechnology. AI-driven design algorithms can simulate and optimize effector sequences and structures in silico, enabling the development of synthetic effector variants with enhanced functionalities and tailored properties. Effector-based biotechnologies, such as effector-assisted gene editing, delivery of cargo molecules, and modulation of plant immunity, will revolutionize crop breeding, pest control, and sustainable agriculture practices.

Conclusion

Effector research, fueled by Artificial Intelligence, is at the forefront of innovation in plant pathology, crop protection, and agricultural biotechnology. By leveraging AI techniques for effector prediction, identification, function prediction, and engineering, researchers are advancing our understanding of plant-pathogen interactions and developing novel strategies for disease management and crop improvement. As we continue to harness the power of AI-driven approaches, we can expect significant breakthroughs in effector research, leading to the development of sustainable solutions for global food security challenges. Through collaboration across disciplines and integration of cutting-edge technologies, we can unlock the full potential of effector-based approaches and pave the way for a future where agriculture is resilient, efficient, and sustainable.

Author Contributions

T.T.S prepared the first the first draft of the manuscript. S.H.M edited and contributed significantly to the development of specific topics covered in the manuscript. S.M.S helped in planning the layout of the work. The present version of the manuscript has been examined by all three authors and approved, with their individual contributions added to improve the quality and breadth of the writing.

Acknowledgment

We thank Dr. Jyothilakshmi Vadassery and her lab members at NIPGR, New Delhi, India for the immense support.

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