Plant Archives Vol. 25, Supplement 2, 2025 pp. 736-745 e-ISSN:2581-6063 (online), ISSN:0972-5210

Plant Archives

Journal homepage: http://www.plantarchives.org

DOI Url : https://doi.org/10.51470/PLANTARCHIVES.2025.v25.supplement-2.093

DEFENCE PRIMING: A PROMISING APPROACH FOR SUSTAINABLE CROP PROTECTION

Srijan Samanta[1]*, Amitava Dutta[1] and Javed Akhtar[2]
[1] Department of Seed Science and Technology, Faculty of Agriculture,
Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, Nadia, West Bengal-741252, India,
[2] Department of Agronomy, Bidhan Chandra Krishi Viswavidyalaya, Nadia, West Bengal-741252, India.
Correspondence Email: srijansamanta0@gmail.com
ORCID ID: https://orcid.org/0009-0007-4650-2363

(Date of Receiving : 19-03-2025; Date of Acceptance : 27-05-2025)

ABSTRACT

The rapidly growing global population necessitates increased crop productivity, prompting a necessary shift towards sustainable agricultural practices to ensure the long-term efficiency of production. This comprehensive review advocates for the adoption of eco-friendly strategies, focusing on the promising approach of plant defence priming to address the challenges posed by biotic and abiotic stresses. While conventional methods such as transgenic crops and the use of chemical pesticides raise concerns, defence priming emerges as an affordable, efficient, and sustainable resistance strategy for enhancing crop protection in fragile ecosystems. The strategy involves subjecting plants preemptively to a modest dose of stress, leading to stronger and earlier responses to similar future challenges. The imprint of stress cues can persist across generations, contributing to stress memory retention.

***Keywords* :** Crop protection, defence priming, induced resistance, inheritable priming, stress memory.

Introduction

The global population is undergoing a rapid growth, with an annual increase rate of approximately 0.91% as of 2024 (worldometers.info). This burgeoning population necessitates a corresponding enhancement in the productivity of crops to sustainably meet the rising demand (Tiwari and Singh, 2021). However, crops are constantly subjected to a variety of biotic and abiotic stresses (Malook *et al.*, 2021) such as fungi, bacteria, insects, and drought, salinity, chilling etc. respectively. Besides the use of pesticides, various crop protection techniques have evolved, such as development of transgenic crops. Nonetheless, none of these methods proves to be a truly sustainable solution, each presenting moral, environmental, economic, social, or health concerns (Tiwari and Singh, 2021). Currently, crop production heavily depends on the use of pesticides to deter different stresses due to a lack of genetic resistance. Despite being effective, chemical-based plant defence not only poses environmental threats but also contributes to the depletion of consumers' health (Conrath *et al.*, 2015). Studies have shown that prolonged use of chemical-based pesticides can lead to soil degradation, water contamination, and adverse effects on non-target organisms such as pollinators and beneficial insects (Goulson, 2013). Additionally, the development of pesticide resistance in pests poses a significant threat to crop yields. The utilization of genetically modified (GM) crops also raises concerns like potential impacts on biodiversity and gene flow between GM and non-GM crops through pollen transfer, prompting ongoing debate regarding their sustainability. To overcome these challenges, the adoption of eco-friendly and economical practices such as priming and conservation agriculture is imperative (Rakshit and Singh, 2018). Priming serves as an effective tactic to shield plants from biotic and abiotic challenges, developed to mitigate the consequences of modern agriculture (Sarkar *et al.*, 2018). This technique emerges as an efficient form of resistance by preventing unnecessary metabolic processes in plants, contributing to the maintenance of plant health (Mauch-Mani *et al.*, 2017).

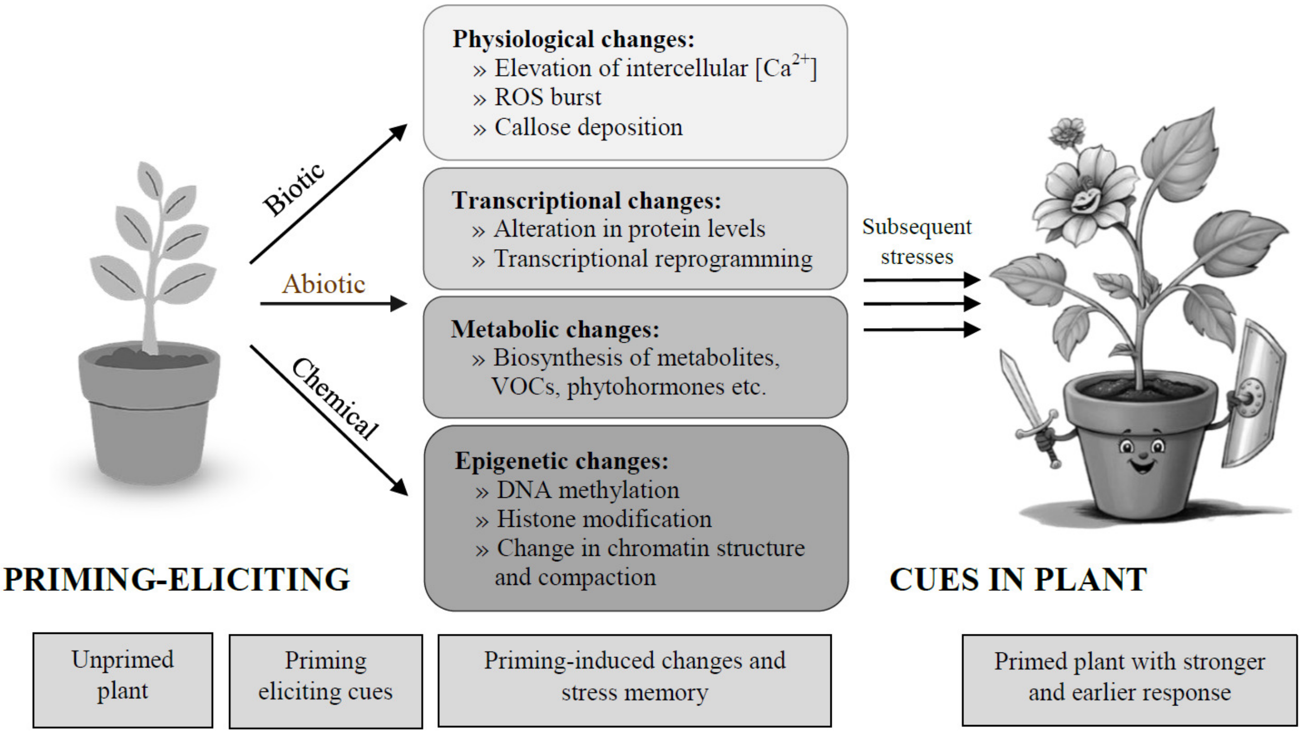
In the pursuit of a sustainable crop production strategy, researchers should focus on understanding the natural defence mechanisms of plants. Plants have evolved a diverse array of defence mechanisms (Zhou and Zhang, 2020), including leaf surface wax, thorns or trichomes, prickle, idioblast, cuticles, cell wall thickness, lignification, and various secondary metabolites with toxin-like properties to protect themselves from several biotic and abiotic stresses. Plants possess an innate immune system that regulates pre-programmed defence responses, but they can enhance their immune sensitivity in response to certain environmental cues (Hilker and Schmülling, 2019). Leveraging these built-in defence mechanisms can offer a promising approach for enhancing crop resilience to various stresses, thereby contributing to the development of more sustainable and efficient crop protection strategies.

Plant defence priming is a strategy that involves pre-stressing the plant with a modest dose of stress, which helps the plant to mount stronger and earlier responses to subsequent biotic or abiotic stress (Hilker and Schmülling, 2019; Kerchev *et al.*, 2020; De Kesel *et al.*, 2021). This priming strategy, associated with Induced Resistance (IR) such as Systemic Acquired Resistance (SAR), Induced Systemic Resistance (ISR), and Mycorrhiza-Induced Resistance (MIR; Reimer-Michalski and Conrath, 2016; Mauch-Mani *et al.*, 2017), relies on the concept of immune memory. This memory retains the modifications or information obtained from the initial stress perception facilitating a swift and effective response to future challenges (Ramirez-Prado *et al.*, 2018; Yang *et al.,* 2022). Defence priming has the potential to be a highly effective pre-sowing enhancement technique that is environment-friendly and can effectively induce plant immune memory (Jogaiah *et al.*, 2020; Joshi *et al.*, 2021; Martínez-Aguilar *et al.*, 2021; Yadav *et al.*, 2021; Kappel *et al.*, 2022). While this strategy alone may not offer comprehensive protection against all stressors, its broad-spectrum effectiveness, enduring durability, and potential inheritance to future plant generations make it a vital, appealing component of integrated disease management (Tiwari and Singh, 2021). In this review, we aim to shed light on the establishment and maintenance of this priming phenomenon, encompassing the initial stimuli and subsequent changes in plants, to advocate for a more robust and efficient crop protection strategy. We also discuss transgenerational immune-memory aspects associated with defence priming.

Plant Defence Priming

The induction of a primed state in the plant immune system can be initiated by various biological, physical, and chemical cues (Yang *et al.*, 2022). These priming responses serve as preparatory measures to anticipate forthcoming biotic or abiotic challenges. Defence priming represents a chemical-free approach to fortify plant protection, which could be alternatively referred to as green vaccination (Tiwari and Singh, 2021). Typically, pathogenic agents and their derived molecules could act as primary signalling elements to activate plant defence priming (Abdul Malik *et al.*, 2020). Advantageous interactions with root-colonizing microbes may act as potential contributors to the establishment of a primed state (Yu *et al.*, 2022). Intriguingly, certain abiotic stresses, such as extreme temperatures and mechanical injury could prime the plant immune system, a phenomenon referred to as ‘cross-priming’ or ‘cross-tolerance’ (Liu *et al.*, 2022). It refers to a process whereby exposure to one form of stress enhances the plant's ability to tolerate a range of stresses (Katam *et al.*, 2020; Liu *et al.,* 2022). It is well established that abiotic stresses generally exhibit many similarities in their impacts and associated responses by plants, especially signaling pathways (Perincherry *et al.,* 2021). The overlapping of these stress responses, and the activation of common defense mechanisms enable plants to develop efficient acclimation mechanisms for cross-tolerance. Moreover, herbivore-associated signals such as physical contacts, oral secretions, and oviposition fluids could also be capable of inducing priming responses (Mauch-Mani *et al.*, 2017).

Initially, it was believed that plants exposed to a priming stimulus did not undergo metabolic changes, and no alterations in gene expression occurred until the plant encountered a challenging infection. However, recent advancements in -omics techniques have revealed that priming stimuli elicit direct changes in plants that are essential for enhanced defence (Balmer *et al.*, 2015).



Priming-eliciting cues in plant

Plants exhibit an extraordinary ability to sense a wide array of environmental signals, enabling them to adapt effectively and respond to their surroundings. These signals, originating from several biotic, as well as chemicals and abiotic stimuli, serve as triggers for the initiation of priming, functioning as cautionary indicators.

❖ Biotic-stimulating agents

Biotic factors encompass living organisms within an ecosystem, including animals, plants, microorganisms, and others. Various living organisms or their derivatives have the potential to enhance the plant defence system, thereby rendering the plant more resilient and responsive to subsequent challenges.

i) ***Pathogenic stimuli*:** Stimuli originating from the pathogens themselves or their molecular derivatives can serve as priming agents. Pathogen-induced molecules are commonly referred to as PAMPs (Pathogen-Associated Molecular Patterns) and effectors, while those released by host plant in response to an attack are denoted as DAMPs (Damage-Associated Molecular Patterns; Dodds and Rathjen, 2010). These molecular patterns are not confined solely to pathogenic microorganisms; rather, they are also evident in beneficial microbes, for which the terminology Microbe-Associated Molecular Pattern (MAMP) is employed (Pieterse *et al.*, 2014). Plants recognize pathogen-derived molecules through specific protein receptors, such as pattern recognition receptors or resistance proteins. After this recognition, plants activate their induced defence, which is called Pathogen-triggered immunity (Couto and Zipfel, 2016). Prominent examples of PAMPs include several structural molecules such as lipopolysaccharides and flagellin derived from bacteria, chitin from fungi, and β-glucans found in fungi and oomycetes (Thomma *et al.*, 2011). Lipopolysaccharides and flg22 (flagellin peptide with 22 amino acids) stand out as well-established priming PAMPs (Flury *et al.*, 2013).

ii) ***Microbial stimuli:*** Beneficial microbes, specifically plant growth-promoting rhizobacteria (PGPR) and plant growth-promoting fungi (PGPF), exert favourable effects by inducing systemic resistance through dynamic interactions with their hosts, thus capable of initiating defence priming. However, it is essential to establish a symbiotic interaction between microorganisms and plants to ensure successful priming. This necessitates the suppression of local immune responses in the host by microbes. Several studies have provided evidence that PGPRs such as *Pseudomonas* spp., *Serratia* spp., *Bacillus* spp., as well as PGPFs like *Trichoderma* spp., nonpathogenic strains of *Fusarium* spp., *Serendipita indica* (root-colonizing mycorrhiza-like endophytic fungi) and arbuscular mycorrhizal fungi (AMFs) such as *Glomeromycota* spp., are widely recognized for their ability to induce priming in plants (Pieterse *et al.*, 2014; Kloepper *et al.*, 2004).

iii) ***Herbivore-derived stimuli:*** The arthropod-associated stimuli inducing plant defence responses encompass a spectrum of both biological and physical origins. Biological stimuli comprise oral secretions, insect-associated microbes, insect-associated molecular patterns (IAMPs), and oviposition signals (Hilker and Fatouros, 2015; Howe and Jander, 2008). Concurrently, physical signals can be manifested as repeated spatiotemporal patterns and trichome sensing of insects traversing leaf surfaces (Hilker and Meiners, 2010; Peiffer *et al.*, 2009; Howe and Jander, 2008). Furthermore, herbivore-induced plant volatiles (VOCs), such as esters, jasmonates, aldehydes, phenols, etc. have been identified as potent priming elicitors, as they act as stimuli, activating the innate defence system in affected plants and neighbouring plants alike (Frost *et al.*, 2008). A recent in-depth study of herbivore-induced plant volatiles has elucidated the presence of indole in the volatile blend released by infested leaves which triggers priming by enhancing the terpene levels in systemic leaves and neighbouring plants, a phenomenon referred to as airborne priming (Erb *et al.*, 2015).

❖ Abiotic-stimulating agents

Abiotic factors refer to non-living components within an ecosystem that contribute to its environmental conditions, such as temperature, light, water, and salinity. Various forms of abiotic stimuli including mechanical stimulation through repetitive leaf rubbing or bending (Benikhlef *et al.*, 2013), wounding (Chassot *et al.*, 2008), submergence (Hsu *et al.*, 2013), exposure to ultraviolet light or ozone (Yalpani *et al.*, 1994) and heavy metal stress (Winter *et al.*, 2012) can induce resistance in plants. However, the precise role of defence priming induced by abiotic factors remains unclear (Mauch-Mani *et al.*, 2017). When using temperature, salinity or other abiotic agents as stimulating cues, it is crucial to apply the dose in a calculated manner. Failure to do so may result in adverse effects on plants, and priming may not occur at all (Singh *et al.*, 2014).

❖ Chemical-stimulating agents

Exogenous applications of various chemical compounds, frequently derived from natural sources, have been shown to have the capability to act as priming stimuli. This review provides an overview of some widely recognized chemical agents with well-understood modes of action.

i) ***Defence-related Phytohormones:*** Jasmonic acid (JA), Salicylic acid (SA), and their derivatives could induce plant defence priming when applied exogenously (Mauch-Mani *et al.*, 2017).

ii) ***Synthetic inducers:*** Potent priming inducers include functional SA analogues such as N-cyanomethyl-2-chloro Isonicotinic acid (NCI), 2,6-dichloroisonicotinic acid (INA- first synthetic compound to induce defence priming in the lab), Benzothiadiazole (BTH), Acibenzolar-S-methyl (ASM), and Isotianil.

iii) ***Plant metabolites and related synthetic chemicals:*** Recently identified defence priming agents include Sulforaphane (SFN), β-amino acids like (R)-beta-homoserine (RBH), Glycerol, and the enzyme Ascorbate oxidase (AO) (Buswell *et al.*, 2018; Zhou and Wang, 2018; Li *et al.*, 2020; Singh *et al.*, 2021).

iv) ***Nanomaterials:*** The distinctive physicochemical features of nanoparticles and nano-emulsions make them increasingly utilized in plant defence priming (do Espirito Santo Pereira *et al.*, 2021).

Among these priming agents, functional SA-analogs like BTH/ASM; β-aminobutyric acid (BABA)- a non-protein amino acid, and chitin polymeric derivative- Chitosan are commonly used for commercial application (Yassin *et al.*, 2021).

Priming-induced Changes and Adaptive Responses

Following the perception of stimulus, a biological process of acquiring priming unfolds until exposure to a challenging stressor. This process encompasses various changes, preparing the plant for enhanced responsiveness when confronted with challenges. These changes manifest at physiological, molecular, and epigenetic levels. They can transpire within seconds or hours after stimulation; can be transient or maintained throughout the lifespan of a plant and may even be inherited by reproductive tissues, to subsequent generations. Diverse priming stimuli may induce similar changes as well as distinct ones. Here are some changes associated with defence priming.

❖ **Physiological Changes:** Upon detecting invading pathogens, plants trigger different defence responses, such as elevating cytoplasmic calcium concentration ($[Ca^{2+}]_{cyt}$), reactive oxygen species (ROS) burst, and callose deposition (Balmer *et al.*, 2015; Cao *et al.*, 2017; Hake and Romeis, 2019). For instance, pretreatment with polypeptide extract from dry mycelium of *Penicillium chrysogenum* (PDMP) enhances disease resistance against tobacco mosaic virus (TMV) in tobacco plants by increasing callose deposition around plasmodesmata (Li *et al.*, 2021b). Interestingly, membrane depolarization resulting from an elevation in cytosolic calcium concentration (Jeworutzki *et al.*, 2010), can initiate electrical signalling which transmits the local perceptions to undamaged leaves and activates Jasmonic Acid signalling in those leaves (Mousavi *et al.*, 2013). Elevated levels of intracellular calcium, often preceding the onset of reactive oxygen species (ROS) generation (Beneloujaephajri *et al.*, 2013), are commonly referred to as the ROS burst. Nonetheless, maintaining precise regulation of ROS homeostasis (fine balance between production and scavenging) appears to play a critical role in the process of priming (Pastor *et al.*, 2013).

- **Transcriptional Changes:** Pathogen infections and priming stimuli lead to significant transcriptional reprogramming (Gauthier *et al.*, 2014; Schenk *et al.,* 2014), resulting in distinct transcriptome changes. This reprogramming subsequently induces significant alteration in protein levels in primed plants (Balmer *et al.,* 2015), including increased expression of proteins associated with pattern recognition receptors and coreceptors (Tateda *et al.,* 2014). In some cases, BABA may directly induce pathogenesis-related (PR) proteins (Baccelli and Mauch-Mani, 2016), while lipopolysaccharides can transiently increase the enzymatic activity of a tyrosine decarboxylase (Newman et al., 2002). These changes in the protein level enhance the plants' responsiveness to subsequent pathogen infections (Yang *et al.,* 2022).
- **Metabolic Changes:** Priming initiates metabolic changes in the biosynthesis of both primary and secondary metabolites, tricarboxylic acid, VOCs, and phytohormones in plants, preparing them for imminent pathogen attacks (War *et al.*, 2011; Brosset and Blande, 2022). For instance, treatment with BABA induces resistance to *Botrytis cinerea* by altering sucrose content and phenylpropanoid metabolism in Grape berries (Li *et al.*, 2021a). Studies on common mycelial networks of AMPs found that plants connected by common mycelial networks can share signals and respond collectively to stress. These signals may include priming-initiated substances like amino acids and lipids (Bago *et al.*, 2002) or electrical signals mediated by changes in calcium levels (Mousavi *et al.*, 2013).
- **Epigenetic Changes:** Epigenetics encompasses changes that modulate the activation of specific genes without affecting the underlying DNA genetic code sequence. These changes can be stable and heritable through cell division and influence the regulation of gene expression. Specific epigenetic processes comprise paramutation, bookmarking, imprinting, gene silencing, X-chromosome inactivation, position effect, transvection, and regulation of histone modifications. Following priming, plants undergo significant epigenetic transformations such as changes in DNA methylation and histone modification (methylation and acetylation). It impacts the chromatin structure and compaction at promoter regions and potentially destabilizing adjacent chromatin regions. This process facilitates the accessibility of transcription components (Conrath *et al.*, 2015). Histone posttranslational modifications that alter compaction include well-characterized examples such as acetylation of histone H_3 at lysine 9 (H_3K_9ac) and trimethylation of histone H_3 at lysine 27 ($H_3K_{27}me_3$; Zhou *et al.*, 2010). Although epigenetic changes can be stable and heritable across generations, it's essential to note that not all epigenetic changes are necessarily passed on to offspring. The inheritance of epigenetic modifications depends on various factors, including the type of modification, its location within the genome, and environmental influences. A recent study carried out on common bean (*Phaseolus vulgaris*) showed that priming with BABA and INA induces resistance against *Pseudomonas syringae* pv. *phaseolicola* through distinct transcriptomic reprogramming involving alterations in the expression of defence genes and modifications in histone marks (mainly $H_3K_4me_3$ and $H_3K_{36}me_3$) at the promoter-exon regions of defence-associated genes (Martinez-Aguilar *et al.*, 2016).

Stress memory and its inheritance

The stress memory phase immediately follows the priming event (Stief *et al.*, 2014), involving the retention of information related to the stress cue even after the stress has ceased. While most of these changes are transient and return quickly to baseline levels after normal conditions are restored, in certain cases, stress memory may extend to offspring, referred to as inter or trans-generational stress memory (Lämke and Bäurle, 2017). The establishment of long-term memory typically necessitates mitotic stability and chromatin-based mechanisms (Hepworth *et al.*, 2018; Le Gac *et al.*, 2018; Song *et al.*, 2012).

Plants have the ability to 'forget' previously acquired information about stress through a process called protein degradation (Araujo *et al.*, 2011). The most prevalent protein degradation process in plants involves ubiquitination linked with the 26S proteasome (ubiquitin-proteasome pathway) and autophagy. Importantly the process autophagy acts in a target-oriented manner (Sedaghatmehr *et al.*, 2018). The recognition of targets by phagosomes in autophagy raises questions about how phagosomes recognize their targets. Avin‑Wittenberg (2018) summarizes the state of the art regarding (selective) autophagy caused by abiotic stress. Autophagy receptor proteins, which bind to ATG8, a ubiquitin-like protein, facilitate the recognition of the substrates. Phytohormones, metabolites, and ROS all interact closely with the autophagic process. Phytohormones such as abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), and auxins have been shown to regulate autophagy in plants (Han *et al.*, 2011; Liao and Bassham, 2020). Metabolites like sugars, amino acids, and organic acids serve as energy sources and signaling molecules linked to autophagy regulation (Liu and Bassaham, 2012). Therefore, the establishment and deletion of stress memory are intricately regulated by precise mechanisms involving a diverse array of mediators.

Plant intergenerational immune memory is generally unstable during meiosis, impacting only one stress-free generation. Plant transgenerational immune memory, on the other hand, is meiotically stable and can persist through two or more stress-free generations (Ramírez-Carrasco *et al.*, 2017). For every case of transgenerational stress memory, the possibility of an epigenetic basis must be confirmed. Plants have been found to have epialleles, which can express themselves differently in genetically identical individuals due to epigenetic modifications (Lamke and Baurle, 2017). This modification is independent of changes in DNA sequence, which is significant. Therefore, it is imperative to distinguish between intergenerational stress memory (detectable in the first stress-free generation) and transgenerational memory (which is detectable until at least the second stress-free generation). The avoidance of autophagy or ubiquitination in transgenerational immune inheritance by plants is not fully understood. Still, it may involve epigenetic modification in promoter regions of chromatin, which destabilizes chromatin structure.

The inheritance of stress memory raises questions about how it occurs. Heritable epialleles with distinct DNA methylation patterns may be a part of chromatin-based mechanisms of this inheritance (Cortijo *et al.*, 2014). DNA methylation occurs in various genomic regions, including gene promoters and transposable elements (Law and Jacobsen, 2010). Evidence suggests that DNA cytosine methylation is involved in the generational transmission of plant immune memory, as demonstrated by Luna *et al.* (2012) in a study on Pst DC3000 (*Pseudomonas syringae* pathovar tomato (Pst) strain, DC3000)-triggered systemic acquired resistance (SAR).

Another possibility is the inheritance of modified histones through either nucleosome recycling or the copying of modifications onto newly incorporated histones. The extent to which both processes occur is still under study (Alabert *et* al., 2015). The contribution of histone modification to the generational transmission of plant immune memory has been supported by current evidence. For instance, BABA treatment in potato could enhance the resistance against the oomycete pathogen *Phytophthora infestans*, and this pronounced disease resistance could be transmitted to at least one stress-free generation (Meller *et al.*, 2018). This is associated with enhanced deposition of permissive epigenetic mark $H_3K_4me_2$ at SA-responsive genes in both BABA-primed (F0) parent plant and its progeny (F1) in the absence of *P. infestans* challenge. This research showed that the epigenetic mark $H_3K_4me_2$ may help pass immune memory down through generations.

A very recent study on hyperosmotic stress priming confirmed intergenerational stress memory in the progeny of plants stressed during their vegetative development for at least two successive generations (Wibowo *et al.*, 2016). However, this memory was reset after one stress-free generation, indicating an environmental adaptation that is rapidly lost in the absence of stress. According to other studies, the mother (maternal component) seems to be the primary source of inheritance for this intergenerational stress memory. The mechanistic understanding of the inheritance of stress memory remains fragmented. The involvement of DNA methylation, histone modification, and siRNA pathways has been observed in several genetic analyses. Still, the involvement of other mechanisms, such as the transfer of memory in the form of metabolites or proteins through seeds or embryos, remains a possibility. The possible role of phytohormone levels in seeds has been explored in some cases but not yet substantiated (Wibowo *et al.*, 2016; Slaughter *et al.*, 2012; Rasmann *et al.*, 2012).

Benefits and Challenges

Efficient induction of Transgenerational Immune Priming holds promises for empowering impoverished farmers to collect their seed stocks of more resistant crop varieties, thereby making their food production less vulnerable to pests and disease outbreaks. Defence priming, once initiated, endures throughout a plant's lifespan, and can be inherited epigenetically by subsequent generations. Several studies indicate that defence priming can enhance resistance to certain pathogens, but it may concurrently heighten susceptibility to others due to hormonal cross-link between salicylic acid (SA) and jasmonic acid (JA)

(Vos *et al*., 2013). The necessity for priming arises only in the presence of disease pressure. Primed plants exhibit superior growth and seed germination under such conditions. However, in disease-free environments, primed plants may display reduced plant growth than non-primed plants (Tiwari and Singh, 2021). This indicates that priming is advantageous only when there is disease pressure; otherwise, it may hinder crop yield by allocating metabolites unnecessarily for defence activation. Therefore, the utility of defence priming in areas with less severe disease and pest infestations is debatable, as it may impose unnecessary metabolic costs on plants.

Future Directions

Advancements in nanotechnology have yielded numerous nanomaterials for crop protection (Do Espirito Santo Pereira *et al*., 2021). Exogenous applications of nanomaterials in defence priming have shown efficacy in conferring disease resistance and stimulating crop immune memory (Quiterio-Gutiérrez *et al*., 2019; Shelar *et al*., 2021). A successful strategy for crop protection may eventually involve the use of those exogenous priming triggers.

Despite significant strides in seed priming for crop protection, much remains to be understood about plant immune memory and its efficient application in sustainable agriculture. Anticipated progress in unravelling the molecular basis of stress memory could pave the way for climate-resilient crops. Discovering any universal stress memory regulators and decoding different stress memory mechanisms will be intriguing areas of investigation. Additionally, further research into priming memory may offer valuable insights for developing stress-tolerant cultivars and expediting crop improvement initiatives.

Conclusion

Seed priming emerges as a viable strategy for improving crop production in fragile ecosystems. The extent of this study illustrated molecular bases of plant defence priming and immune memory, presenting recent advances and outlining future directions for leveraging seed priming in crop protection. As knowledge of plant immune memory advances and priming methodologies evolve, incorporating seed priming into future agriculture could offer novel avenues for improved crop protection. Successful adoption hinges on addressing awareness gaps, as many promising technologies have yet to reach farmers' fields. Strategic policy interventions to fortify extension services are crucial for elevating these technologies to widespread implementation. Further research on seed priming should consider the benefits of defence priming to restore ecosystems and promote sustainable agricultural production.

Author Contributions

Author A.D. contributed to the conceptualization of the manuscript and author S.S. and J.A. contributed to the drafting and revision of the manuscript.

Acknowledgement

The authors gratefully acknowledge Dr. Nasim Ali, Associate Professor, Department of Agricultural Biotechnology, Bidhan Chandra Krishi Viswavidyalaya, for his valuable guidance and insightful contributions that significantly improved the quality of this manuscript.

Conflict of interest

Authors declare no competing interests.

References

Abdul Malik, N.A., Kumar, I.S., and Nadarajah, K. (2020). Elicitor and receptor molecules, orchestrators of plant defence and immunity. *International Journal of Molecular Sciences.* **21**(3),963-970.

Alabert, C., Barth, T. K., Reverón-Gómez, N., Sidoli, S., Schmidt, A., Jensen, O. N., , A., and Groth A. (2015). Two distinct modes for propagation of histone PTMs across the cell cycle. *Genes and Development*. **29**(6),585-590.

Araujo, W.L., Tohge, T., Ishizaki, K., Leaver, C.J., and Fernie, A.R. (2011). Protein degradation-An alternative respiratory substrate for stressed plants. *Trends in Plant Science*, **16**(9),489-498.

Avin-Wittenberg, T. (2018). Autophagy and its role in plant abiotic stress management. *Plant, Cell & Environment*, **42**(3),1045–1053.

Baccelli, I., and Mauch-Mani, B. (2016). Beta-aminobutyric acid priming of plant defence, the role of ABA and other hormones. *Plant Molecular Biol*ogy, **91**(6),703–711.

Bago, B., Zipfel, W., Williams, R. M., Jun, J., Arreola, R., Lammers, P. J., Pfeffer, P. E., and Shachar-Hill, Y. (2002). Translocation and utilization of fungal storage lipid in the arbuscular mycorrhizal symbiosis. *Plant Physiology*, **128**(1),108-124.

Balmer, A., Pastor, V., Gamir, J., Flors, V., and Mauch-Mani, B. (2015). The ‘prime-ome’, towards a holistic approach to priming. *Trends Plant Science*, **20**(7), 443-452.

Beneloujaephajri, E., Costa, A., L’Haridon, F., Metraux, J. P., and Binda, M. (2013). Production of reactive oxygen species and wound-induced resistance in Arabidopsis thaliana against Botrytis cinerea are preceded and depend on a burst of calcium. *BMC Plant Biology*, **13**,160.

Benikhlef, L., L’Haridon, F., Abou-Mansour, E., Serrano, M., Binda, M., Costa, A., Lehmann, S. and Métraux, J.P. (2013). Perception of soft mechanical stress in Arabidopsis leaves activates disease resistance. *BMC Plant Biology*, **13**,133.

Brosset, A., and Blande, J. D. (2022). Volatile-mediated plant-plant interactions, volatile organic compounds as modulators of receiver plant defence, growth, and reproduction. *Journal of Experimental Botany,* **73(2)**,511–528.

Buswell, W., Schwarzenbacher, R. E., Luna, E., Sellwood, M., Chen, B., Flors, V., Pétriacq, P., and Ton, J. (2018). Chemical priming of immunity without costs to plant growth. *New Phytologist,* **218**(3), 1205–1216.

Cao, X. Q., Jiang, Z. H., Yi, Y. Y., Yang, Y., Ke, L. P., Pei, Z. M., and Zhu, S. (2017). Biotic and abiotic stresses activate different Ca^{2+} permeable channels in Arabidopsis. *Frontiers Plant Science,* **8,**83.

Chassot, C., Buchala, A., Schoonbeek, H. J., Metraux, J. P., and Lamotte, O. (2008). Wounding of Arabidopsis leaves causes a powerful but transient protection against Botrytis infection. *Plant Journal*, **55**(4),555-567.

Conrath, U., Beckers, G. J., Langenbach, C. J., and Jaskiewicz, M.R. (2015). Priming for enhanced defence. *Annual Review of Phytopathol*ogy, **53**(1), 97–119.

Cortijo, S., Wardenaar, R., Colomé-Tatché, M., Gilly, A., Etcheverry, M., Labadie, K., Caillieux, E., Hospital, F., Aury, J-M., Wincker, P., Roudier, F., Jansen, R. C., Colot, V., and Johannes, F. (2014). Mapping the epigenetic basis of complex traits. *Science*, **343**(6175),1145-1148.

Couto, D., and Zipfel, C. (2016). Regulation of pattern recognition receptor signalling in plants. *Nature Reviews Immunology*. **16**(9), 537-552.

De Kesel, J., Conrath, U., Flors, V., Luna, E., Mageroy, M. H., Mauch-Mani, B., Pastor, V., Pozo, M. J., Pieterse, C. M. J., Ton, J., and Kyndt, T. (2021). The induced resistance lexicon, Do's and don'ts. *Trends Plant Science*, **26** (**7**),685–691.

Do Espirito Santo Pereira, A., Oliveira, H. C., Fraceto, L. F., and Santaella, C. (2021). Nanotechnology potential in seed priming for sustainable agriculture. *Nanomaterials (Basel)* **11(2)**, 267.

Dodds, P. N., and Rathjen, J. P. (2010). Plant immunity, towards an integrated view of plant-pathogen interactions. *Nature Reviews Genetics*, **11**,539-548.

Erb, M., Veyrat, N., Robert, C.A., Xu, H., Frey, M., Ton, J., and Turlings, T. C. J. (2015). Indole is an essential herbivore-induced volatile priming signal in maize. *Nature Communications* **6**,6273.

Flury, P., Klauser, D., Schulze, B., Boller, T., and Bartels, S. (2013). The anticipation of danger, microbe-associated molecular pattern perception enhances AtPep-triggered oxidative burst. *Plant Physiology*, **161**(4),2023-2035.

Frost, C. J., Mescher, M. C., Carlson, J. E., and De Moraes, C. M. (2008). Plant defence priming against herbivores, getting ready for a different battle. *Plant Physiology*. **146**(3),818-824.

Gauthier A, Trouvelot S, Kelloniemi J, Frettinger P, Wendehenne D, Daire, X., Joubert, J-M., Ferrarini, A., Delledonne, M., Flors, V., and Poinssot, B. (2014). The sulfated laminarin triggers a stress transcriptome before priming the SA- and ROS-dependent defences during grapevine's induced resistance against *Plasmopara viticola*. *Plos One*, 13(3), e0194327.

Goulson, D. (2013). An overview of the environmental risks posed by neonicotinoid insecticides. *Journal of Applied Ecology*, **50**(4), 977–987.

Hake, K., and Romeis, T. (2019). Protein kinase-mediated signalling in priming, immune signal initiation, propagation, and establishment of long-term pathogen resistance in plants. *Plant Cell and Environment,* **42**(3), 904–917.

Han, S., Yu, B., Wang, Y., Liu, Y. (2011). Role of plant autophagy in stress response. *Protein Cell* **2**(10),784-791.

Hepworth, J., Antoniou-Kourounioti, R. L., Bloomer, R. H., Selga, C., Berggren, K., Cox, D., and Dean, C. (2018). Absence of warmth permits epigenetic memory of winter in *Arabidopsis*. *Nature Communications,***9**, 639.

Hilker, M., and Fatouros, N. E. (2015). Plant responses to insect egg deposition. *Annual Review of Entomology*, **60**,493–515.

Hilker, M., and Meiners, T. (2010). How do plants "notice" attack by herbivorous arthropods? *Biological reviews of the Cambridge Philosophical Society*, **85**(2),267-280.

Hilker, M., and Schmülling, T. 2019. Stress priming, memory, and signalling in plants. *Plant, Cell and Environment* **42**(3), 753–761.

Howe, G. A., Jander, G. (2008). Plant immunity to insect herbivores. *Annual Review of Plant Biology*, **59**,41–66.

Hsu, F. C., Chou, M. Y., Chou, S. J., Li, Y. R., Peng, H. P., and Shih, M. C. 2013. Submergence confers immunity mediated by theWRKY22 transcription factor in Arabidopsis. *Plant Cell,* **25**(7),2699–2713.

Jeworutzki, E., Roelfsema, M. R., Anschutz, U., Krol, E., Elzenga, J. T., Felix, G., Boller, T., Hedrich, R., and Becker, D. (2010). Early signaling through the Arabidopsis pattern recognition receptors FLS2 and EFR involves Ca-associated opening of plasma membrane anion channels. *Plant Journal*, **62**(3),367-378.

Jogaiah, S., Satapute, P., De Britto, S., Konappa, N., and Udayashankar, A. C. (2020). Exogenous priming of chitosan induces upregulation of phytohormones and resistance against cucumber powdery mildew disease is correlated with localized biosynthesis of defence enzymes. *International Journal of Biological Macromolecules,* **162**,1825–1838.

Joshi, S. M., De Britto, S., and Jogaiah, S. (2021). Myco-engineered selenium nanoparticles elicit resistance against tomato late blight disease by regulating differential expression of cellular, biochemical and defence responsive genes. *Journal of Biotechnology,* **325**,196–206.

Kappel, L., Kosa, N., and Gruber, S. (2022). The multilateral efficacy of chitosan and Trichoderma on sugar beet. *Journal of Fungi (Basel*), **8(2)**, 137-160.

Katam, R., Shokri, S., Murthy, N., Singh, S. K., Suravajhala, P., Khan, M. N., Bahmani, M., Sakata, K., and Reddy, K. R. (2020). Proteomics, physiological, and biochemical analysis of cross tolerance mechanisms in response to heat and water stresses in soybean. *PloS one*, **15**(6),e0233905.

Kerchev, P., Meer, T.V.D., Sujeeth, N., Verlee, A., Stevens, C. V., Breusegem, F. V., and Gechev, T. (2020). Molecular priming as an approach to induce tolerance against abiotic and oxidative stresses in crop plants. *Biotechnology Advances*. **40**,107503.

Kloepper, J. W., Ryu, C. M., and Zhang, S. (2004). Induced systemic resistance and promotion of plant growth by Bacillus spp. *Phytopathology,* **94**(11),1259–1266.

Lämke, J., and Baurle, I. (2017). Epigenetic and chromatin‑based mechanisms in environmental stress adaptation and stress memory in plants. *Genome Biology,* **18**(1),124.

Law, J. A., and Jacobsen, S. E. (2010). Establishing, maintaining and modifying DNA methylation patterns in plants and animals. *Nature Reviews Genetics*, **11**, 204–220.

Le Gac, A., Lafon‐Placette, C., Chauveau, D., Segura, V., Delaunay, A., Fichot, R., Marron, N., Le Jan, I., Berthelot, A., Bodineau, G., Bastien, J. C., Brignolas, F., & Maury, S. (2018). Winter-dormant shoot apical meristem in poplar trees shows environmental epigenetic memory. *Journal of Experimental Botany*, **69**(20), 4821-4837.

Li, C., Wang, K., Lei, C., Cao, S., Huang, Y., Ji, N., Xu, F., and Zheng, Y. (2021a). Alterations in sucrose and phenylpropanoid metabolism affected by BABA-primed defence in postharvest grapes and the associated transcriptional mechanism. *Molecular Plant-Microbe Interactions*, **34**(11), 1250–1266.

Li, Y., Jiao, M., Li, Y., Zhong, Y., Li, X., Chen, Z., Chen, S, and Wang, J. (2021b). *Penicillium chrysogenum* polypeptide extract protects tobacco plants from tobacco mosaic virus infection through modulation of ABA biosynthesis and callose priming. *Journal of Experimental Botany,* **72**(10), 3526–3539.

Li, Y., Qiu, L., Liu, X., Zhang, Q., Zhuansun, X., Fahima, T., Krugman, T., Sun, Q., and Xie, C. (2020). Glycerol-induced powdery mildew resistance in wheat by regulating plant fatty acid metabolism, plant hormones cross-talk, and Pathogenesis-related genes. *International Journal of Molecular Science*, **21**(2),673.

Liao, C. Y. and Bassham, D. C. (2020). Combating stress, the interplay between hormone signaling and autophagy in plants. *Journal of Experimental Botany,* **71**(5),1723–1733.

Liu, Y. and Bassham, D. C. (2012). Autophagy, Pathways for self-eating in plant cells. *Annual Review of Plant Bio*logy, **63**,215–237.

Liu, H., Able, A. J., and Able, J. A. (2022). Priming crops for the future, rewiring stress memory. *Trends in Plant Science,* **27**(7), 699–716.

Luna, E., Bruce, T. J., Roberts, M. R., Flors, V., and Ton, J. (2012). Next-generation systemic acquired resistance. *Plant Physiology,* **158**(2), 844-853.

Malook, S. U., Xu, Y., Qi, J., Li, J., Wang, L., and Wu, J. (2021). Mythimna separata herbivory primes maize resistance in systemic leaves. *Journal of Experimental Botany,* **72**(10),3792–3805.

Martinez-Aguilar, K, Ramirez-Carrasco, G., Hernandez-Chavez, J. L., Barraza, A., Alvarez-Venegas, R. (2016). Use of BABA and INA as activators of a primed state in the common bean (*Phaseolus vulgaris* L.). *Frontiers in Plant Science sec. Biotechnology*, **7**,653.

Martínez-Aguilar, K., Hernández-Chávez, J. L., and Alvarez-Venegas, R. (2021). Priming of seeds with INA and its transgenerational effect in common bean (*Phaseolus vulgaris* L.) plants. *Plant Science,* **305**,110834.

Mauch-Mani, B., Baccelli, I., Luna, E., and Flors, V. (2017). Defence priming, an adaptive part of induced resistance. *Annual Review of Plant Biology,* **68**,485-512.

Meller, B., Kuźnicki, D., Arasimowicz-Jelonek, M., Deckert, J., and Floryszak-Wieczorek, J. (2018). BABA-primed histone modifications in potato for intergenerational resistance to *Phytophthora infestans. Frontiers in Plant Science,* **9**,1228.

Mousavi, S. A., Chauvin, A., Pascaud, F., Kellenberger, S., and Farmer, E. E. (2013). Glutamate receptor like genes mediate leaf-to-leaf wound signalling. *Nature*, **500**(7463),422-426.

Newman, M. A., von Roepenack-Lahaye, E., Parr, A., Daniels, M. J., and Dow, J. M. (2002). Prior exposure to lipopolysaccharide potentiates expression of plant defences in response to bacteria. *Plant Journal*, **29**(4),487-495.

Pastor, V., Luna, E., Ton, J., Cerezo, M., García-Agustín, P., and Flors, V. (2013). Fine tuning of reactive oxygen species homeostasis regulates primed immune responses in Arabidopsis. *Molecular plant-microbe interactions*, **26**(11),1334-1344.

Peiffer, M., Tooker, J. F., Luthe, D. S., and Felton, G. W. (2009). Plants on early alert, glandular trichomes as sensors for insect herbivores. *The New phytologist*, **184**(3),644-656.

Perincherry, L., Stępień, Ł., and Vasudevan, S. E. (2021). Cross-Tolerance and Autoimmunity as Missing Links in Abiotic and Biotic Stress Responses in Plants, A Perspective toward Secondary Metabolic Engineering. *International Journal of Molecular Sciences*, **22**(21),11945.

Pieterse, C. M., Zamioudis, C., Berendsen, R. L., Weller, D. M., Van Wees, S. C., and Bakker, P. A. (2014). Induced systemic resistance by beneficial microbes. *Annual review of phytopathology,* **52**,347–375.

Quiterio-Gutiérrez, T., Ortega-Ortiz, H., Cadenas-Pliego, G., Hernández-Fuentes, A. D., Sandoval-Rangel, A., Benavides-Mendoza, A., Cabrera-de la Fuente, M., and Juárez-Maldonado, A. (2019). The Application of Selenium and Copper Nanoparticles Modifies the Biochemical Responses of Tomato Plants under Stress by *Alternaria solani*. *International journal of molecular sciences*, **20**(8),1950.

Rakshit, A., and Singh, H. B. (Eds.). (2018). *Advances in seed priming* (pp. 147-183). Singapore, Springer.

Ramírez-Carrasco, G., Martínez-Aguilar, K., and Alvarez-Venegas, R. (2017). Transgenerational defence priming for crop protection against plant pathogens, a hypothesis. *Frontiers in Plant Science,* **8**,696.

Ramirez-Prado, J. S., Abulfaraj, A. A., Rayapuram, N., Benhamed, M., and Hirt, H. (2018). Plant immunity, from signaling to epigenetic control of defence. *Trends in plant science,* **23**(9),833–844.

Rasmann, S., De Vos, M., Casteel, C. L., Tian, D., Halitschke, R., Sun, J. Y., Agrawal, A. A., Felton, G. W., and Jander, G. (2012). Herbivory in the previous generation primes plants for enhanced insect resistance. *Plant Physiology*, **158**(2),854-863.

Reimer-Michalski, E. M., and Conrath, U. (2016). Innate immune memory in plants. *Seminars in immunology,* **28**(4),319-327.

Sarkar, D., Pal, S., Mehjabeen, M., Singh, V., Singh, S., Pul, S., *et al*. 2018. Addressing stresses in agriculture through bio-priming intervention, in Advances in Seed Priming, eds Rakshit, A. and Singh, H. B. (Singapore, Springer).107–113.

Schenk, S. T., Hernandez-Reyes, C., Samans, B., Stein, E., Neumann, C., Schikora, M., Reichelt, M., Mithöfer, A., Becker, A., Kogel, K. H., and Schikora, A. (2014). N-Acyl-Homoserine Lactone Primes Plants for Cell Wall

Reinforcement and Induces Resistance to Bacterial Pathogens via the Salicylic Acid/Oxylipin Pathway. *The Plant cell*, **26**(6),2708–2723.

Sedaghatmehr, M., Thirumalaikumar, V. P., Kamranfar, I., Marmagne, A., Masclaux‐Daubresse, C., and Balazadeh, S. (2018). A regulatory role of autophagy for resetting the memory of heat stress in plants. *Plant, Cell & Environment*, **42**(3),1054–1064.

Shelar, A., Singh, A. V., Maharjan, R. S., Laux, P., Luch, A., Gemmati, D., Tisato, V., Singh, S. P., Santilli, M. F., Shelar, A., Chaskar, M., and Patil, R. (2021). Sustainable agriculture through multidisciplinary seed nanopriming, prospects of opportunities and challenges. *Cell,* **10**(9),2428.

Singh, P., Yekondi, S., Chen, P. W., Tsai, C. H., Yu, C. W., Wu, K., and Zimmerli, L. (2014). Environmental history modulates Arabidopsis pattern-triggered immunity in a histone acetyltransferase1-dependent manner. *Plant Cell*, **26**(6),2676-2688.

Singh, R. R., Pajar, J. A., Audenaert, K., and Kyndt, T. (2021). Induced resistance by ascorbate oxidation involves potentiating of the phenylpropanoid pathway and improved rice tolerance to parasitic nematodes. *Frontiers in Plant Science,* **12**,713870.

Slaughter, A., Daniel, X., Flors, V., Luna, E., Hohn, B., and Mauch-Mani, B. (2012). Descendants of primed Arabidopsis plants exhibit resistance to biotic stress. *Plant Physiology*, **158**(2),835-843.

Song, J., Angel, A., Howard, M., and Dean, C. (2012). Vernalization-A cold-induced epigenetic switch. *Journal of Cell Science*, **125**(16),3723–3731.

Stief, A., Altmann, S., Hoffmann, K., Pant, B. D., Scheible, W. R., and Bäurle, I. (2014). Arabidopsis miR156 regulates tolerance to recurring environmental stress through SPL transcription factors. *The Plant Cell*, **26**(4),1792-1807.

Tateda, C., Zhang, Z., Shrestha, J., Jelenska, J., Chinchilla, D., Greenberg, J. T. (2014). Salicylic acid regulates Arabidopsis microbial pattern receptor kinase levels and signaling. *The Plant Cell*, **26**(10),4171-4187.

Thomma, B. P. H. J., Nurnberger, T., and Joosten, M. H. (2011). Of PAMPs and effectors, the blurred PTI-ETI dichotomy. *The Plant Cell,* **23**(1),4-15.

Tiwari, M., and Singh, P. (2021). Plant defence priming, A new tool for sustainable global food security, in *Agricultural innovations and sustainability*, vol. p. Ed. G. S. Shekhawat, (An Imprint of Agrobios (India), Jodhpur, Agrobios Research),133–153.

Vos, I. A., Pieterse, C. M., and Van Wees, S. C. (2013). Costs and benefits of hormone‐regulated plant defences. *Plant Pathology*, **62**(1),43-55.

War, A. R., Sharma, H. C., Paulraj, M. G., War, M. Y., and Ignacimuthu, S. (2011). Herbivore induced plant volatiles, their role in plant defence for pest management. *Plant signaling & behavior,* **6**(12),1973–1978.

Winter, T. R., Borkowski, L., Zeier, J., Rostás, M. (2012). Heavy metal stress can prime for herbivore-induced plant volatile emission. *Plant, cell & environment*, **35**(7),1287–1298.

Yadav, M., Dubey, M.K., Upadhyay, R.S. (2021). Systemic Resistance in Chilli Pepper against Anthracnose (Caused by *Colletotrichum truncatum*) Induced by *Trichoderma harzianum, Trichoderma asperellum and Paenibacillus dendritiformis*. *Journal of fungi (Basel, Switzerland),* **7**(4),307.

Yalpani, N., Enyedi, A. J., León, J., and Raskin, I. (1994). Ultraviolet light and ozone stimulate accumulation of salicylic acid, pathogenesis-related proteins and virus resistance in tobacco. *Planta*, **193**(3),372-376.

Yang, Z., Zhi, P., and Chang, C. (2022). Priming seeds for future, Plant immune memory and application in crop protection. *Frontiers in Plant Science*, **13**,961840.

Yassin, M., Ton, J., Rolfe, S. A., Valentine, T. A., Cromey, M., Holden, N., and Newton, A.C. (2021). The rise, fall and resurrection of chemical-induced resistance agents. *Pest Management Science,* **77**(9),3900–3909.

Yu, Y., Gui, Y., Li, Z., Jiang, C., Guo, J., and Niu, D. (2022). Induced Systemic Resistance for Improving Plant Immunity by Beneficial Microbes. *Plants,* **11**(3),386.

Zhou, J., Wang, X., He, K., Charron, J. B., Elling, A. A., and Deng, X. W. (2010). Genome-wide profiling of histone H_3 lysine 9 acetylation and dimethylation in Arabidopsis reveals correlation between multiple histone marks and gene expression. *Plant Molecular Biology*, **72**(6),585-595.

Zhou, J. M., and Zhang, Y. (2020). Plant Immunity, Danger Perception and Signaling. *Cell*.**181**(5),978-989.

Zhou, M., and Wang, W. (2018). Recent advances in synthetic chemical inducers of plant immunity. *Frontiers Plant Science,* **9**,1613.