Induced Resistance Mechanism in Plant and Its Importance in Agriculture

ABSTRACT

The search for a successful and efficient natural phenomenon of induced resistance in plants was prompted by the harmful effects that chemical pesticides and their degradation products had on the environment and human health. Ray was the first to identify plant resistance to diseases in 1901. When arabidopsis plants were injected with the pathogenic bacteria Pseudomonas fluorescens, which colonises roots, induced resistance was initially observed in these plants. There are two different kinds of induced resistance: induced biochemical defense and induced structural defense. Biochemical defense includes phytoalexins, PR-proteins, and secondary metabolites; structural defense includes cytoplasmic reactions, cell wall defense structure, and histological defense structure (development of cork layers, abscission layer, and tylose). Induced systemic resistance (ISR) and systemic acquired resistance (SAR) are the foundation of the induced resistance process. While the defense mechanism in ISR is mediated by jasmonic acid and ethylene and additionally triggered by non-pathognic rhizobacteria (Pseudomonas fluorescens), the defense mechanism in SAR is salicyclic mediated, namely alterations in gene expression. Plants can develop resistance to specific diseases by applying exogenous doses of 2, 6-dichloroisonicotonic acid and benzo-thiadiazole-7-carbothioic acid S-methyl ester (BTH). Induced resistance in plants, while still poorly understood, offers up new possibilities for plant protection and presents a viable strategy for sustainable agriculture and environmentally friendly disease control. It continues to be a problem for both basic and practical research.

Keywords: Induced resistance mechanism; acquired resistance; plant resistance; agriculture; pathogenesis related proteins (PRs); benzothiadiazole; Induced systemic resistance (ISR).

1. INTRODUCTION

A vast array of harmful pathogens and pests, including as fungus, oomycetes, bacteria, viruses, nematodes, and insect herbivores, constantly attack plants in the natural world. Plant pathogens are often classified as either biotrophs or necrotrophs based on their lifestyles. While biotrophs get their nourishment from living host tissues primarily by means of specialized feeding structures called haustoria that invade the host cell without disturbing it, necrotrophs first kill their hosts, frequently by producing phytotoxins. Hemi-biotrophs, on the other hand, are plant pathogens that exhibit both lifestyles based on their life cycle.

Currently, the majority of plant disease control strategies rely on the application of fungicides, bactericides, and insecticides—chemical substances poisonous to plant invaders, causal agents, or vectors of plant illnesses. However, new safe disease control techniques are desperately needed due to the harmful effects of these drugs or the consequences of their breakdown on the environment and human health. A growing amount of data on the natural phenomena of induced resistance has been gathered since the late 1950s, and in the past ten years, this evidence has been successfully applied in practice [1]. The resistance in plants induced by pathogens was first recognized in 1901 [2,3]. These phenomena might be crucial for the survival of plants in their natural habitat by compiling field observations [4]. Convincing proof was gathered only in the 1960s, when reproducible models employing the tobacco plant were established [5]. Greenhouse and field trials in the laboratory of Kuc and coworkers open the way to the current understanding of induced resistance as a plant protection technique [1], this is supported by various authors from throughout the world [6,7,8,9,10]. Utilising the

special ability of plants to fight pathogens, the induced resistance may reduce the need for toxic chemicals in the management of disease and, as a result, be suggested as a different, unconventional, non-biocidal, and environmentally friendly method of protecting plants and, consequently, of promoting sustainable agriculture.

2. INDUCED RESISTANCE

Increased expression of a plant's innate defense mechanisms against various diseases that are triggered by different external causes is known as induced resistance. It's common to use the words “induced resistance” (IR) and “acquired resistance” (AR interchangeably. Induced resistance can manifest itself as either local (LAR) or systemic (SAR) depending on how it does so. The term “induced systemic resistance” (ISR) was coined recently to describe the resistance that non-pathogenic rhizobacteria inoculate into plant roots, hence inducing resistance in the leaves of the plants. When the pathogenic bacteria *Pseudomonas fluorescens* was injected into Arabidopsis plants, a unique form of induced resistance was initially observed in the leaves. These plants demonstrated resistance against the bacterial leaf disease *Pseudomonas syringae* pv. Tomato [11]. Rhizo-bacteria-mediated ISR has also been demonstrated against fungi, bacteria and viruses in Arabidopsis, carnation, vegetable crops (bean, cucumber, radish, tobacco and tomato) [6].

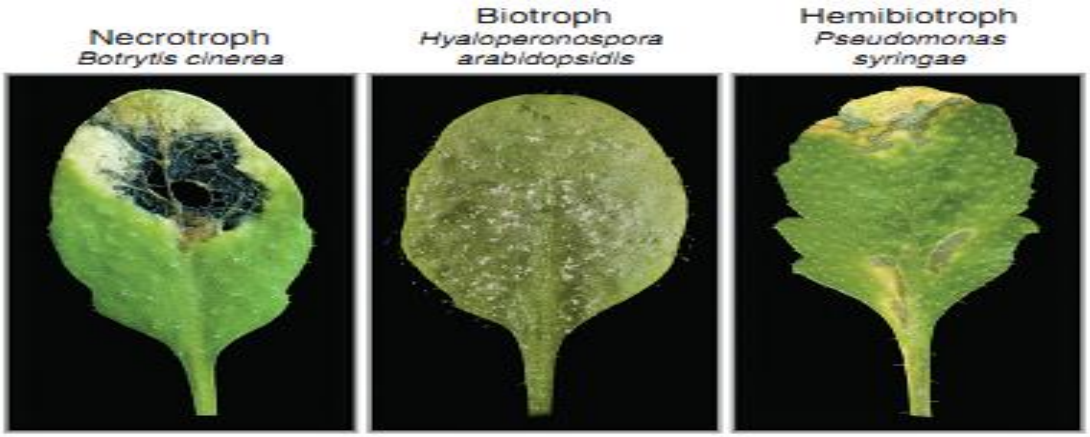


Fig. 1. Disease symptoms on Arabidopsis leaves caused by the necrotrophic fungus biotrophic oomycet and hemibiotrophic bacterium

3. CLASSIFICATION OF INDUCE RESISTANCE

Mainly two types of induce resistance found in plants *viz*., Induced Structural Defenses and Induce Biochemical Defenses.

I. Induced Structural Defenses

It is commonly understood that for a pathogen to produce infection, it must first penetrate. If the pathogen enters the host, parenchymatous cells prevent it from moving around and spreading. Expression of resistance depends on the presence of defense structures such as cuticles, waxes, the structure of the epidermal cell wall, natural openings, etc., either prior to penetration or during its development in response to the pathogen infecting the host. The majority of pathogens first infiltrate their hosts through wounds and other natural openings, after which they cause varying degrees of infection. Plants typically respond by producing one or more types of defense structures, which are more or less successful in protecting the plant from additional pathogen invasion, even after the disease has pierced the produced defense structures. Cell wall defense structures are created in the walls of invading cells; histological defense structures are formed in deeper tissues ahead of the pathogen. Cytoplasmic defense reactions are formed in the cytoplasm of the attacked cells. Lastly, the plant may be protected from additional invasion by the necrotic or hypersensitive defense reaction that results from the death of the invaded cell.

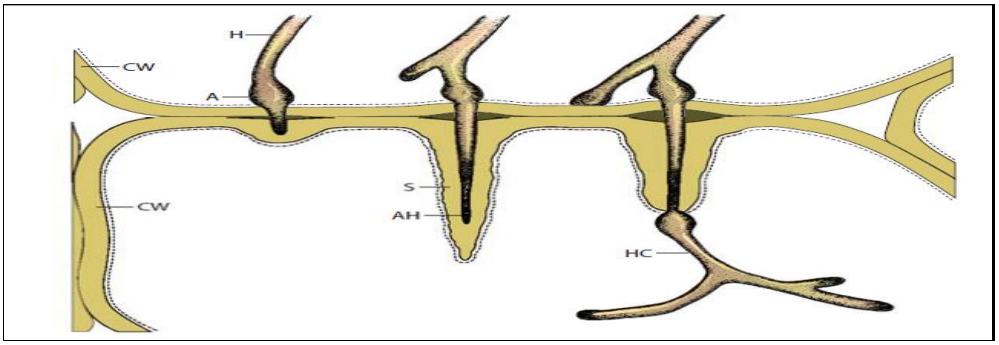


Fig. 2.Formation of a sheath around a hypha (H) penetrating a cell wall (CW). (A: Appressorium; AH: Advancing hypha still enclosed in sheath; HC: hypha in cytoplasm; S: Sheath)

A) Cytoplasmic defense reaction

The plant cell cytoplasm surrounds the hyphae clump in a few instances of slowly growing, weakly pathogenic fungi, such as the mycorrhizal fungi and weakly pathogenic *Armillaria* strains that cause chronic diseases or conditions that are almost symbiotic. In these cases, the plant cell nucleus is stretched to the breaking point. In certain cells, the protoplast vanishes and fungal growth accelerates due to an overriding cytoplasmic response. But in some of the infected cells, the nucleus and cytoplasm become larger. The cytoplasm thickens and becomes granular, containing a variety of particles and structures. At last, the pathogen's mycelium breaks down and the invasion comes to an end.

B) Cell wall defense structures

Cell wall defense structures include modifications to the cell wall's morphology or modifications generated from the pathogen's invading cell. These structures appear to have little function as defense systems. On the other hand, three primary varieties of these structures have been noted in plant diseases.

- When incompatible microorganisms come into contact with parenchyma cells, their outer layer of the cell wall swells and creates amorphous, febrillar components that trap and enclose the bacteria, preventing them from multiplying.

- In response to many infections, cell walls thicken, generating a substance that resembles cellulosic matter. However, this material is frequently mixed with cross-linked phenolic compounds to strengthen its resistance to penetration.

- Upon fungal pathogen invasion, cellulose papillae are deposited on the inner side of cell walls. Cells appear to start producing papallae a few minutes after being wounded and two to three hours after being exposed to microbes. While repairing cellular damage appears to be the primary role of papillae, they also appear to keep pathogens from entering cells later on, particularly if papillae are present prior to inoculation. Occasionally, cellulosic (callose) materials that have penetrated a cell wall and grown into the cell lumen of fungi encase the tips of their hypha. These materials then absorb phenolic compounds and form a sheath or lignin tuber around the hypha.

C) Histological Defense Structures (Defense structures formed after infection)

i. Formation of cork layers

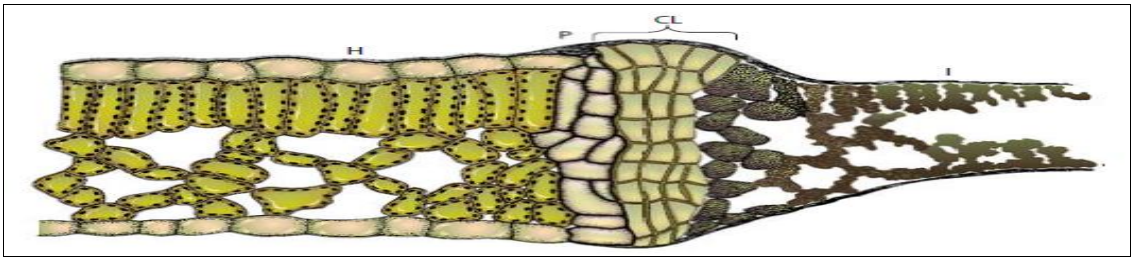


Fig. 3.Formation of a cork layer (CL) between infected (I) and healthy (H) areas of leaf. P, phellogen. [12]

Plants that are infected with fungi, bacteria, viruses, or nematodes develop many layers of cork cells beyond the site of infection due to the pathogen's released chemicals stimulating the host cells. The cork layers stop the transmission of any harmful substances and prevent the disease from invading areas beyond the original lesion. Moreover, cork layers starve the pathogen of nutrition by blocking the transfer of water and nutrients from the healthy to the infected area. Thus, the cork layers define the boundaries of the dead tissues, including the pathogen. These tissues may stay in situ and form necrotic lesions, or patches, that are surprisingly consistent in size and shape for a given host-pathogen combination. Resistant plant clones limit the growth of the fungus in tree cankers, as those on cypress trees produced by the fungus *Seiridium cardinale*, by creating ligno-suberized boundary zones, which consist of four to six layers of cells with suberized cell walls. Contrarily, the two to four discontinuous layers of suberized cells found in sensitive clones allow the fungus to repeatedly pass through the imperfect barrier.

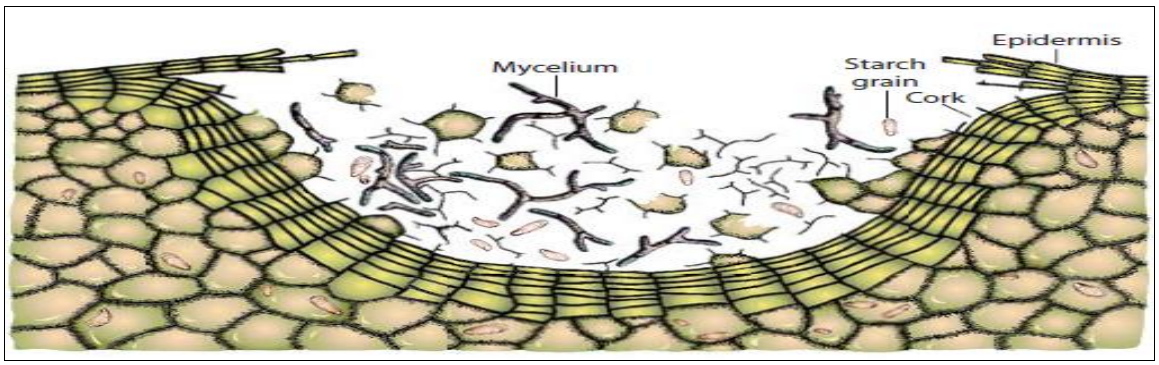


Fig. 4.Formation of a cork layer on a potato tuber following infection with Rhizoctonia. [13]

ii. Formation of Abscission Layers

On young, active leaves of stone fruit trees, abscission layers occur following infection by various fungus, bacteria, or viruses. A space created between two circular layers of leaf cells encircling the infection site are known as an abscission layer. The core region of the infection is totally isolated from the rest of the leaf when it infects, dissolving the middle lamella between these two layers of cells throughout the thickness of the leaf. This area eventually shrivels, dies, and sloughs off, bringing the infection with it. Gradually, this area shrivels, dies, and sloughs off, carrying with it the pathogen.

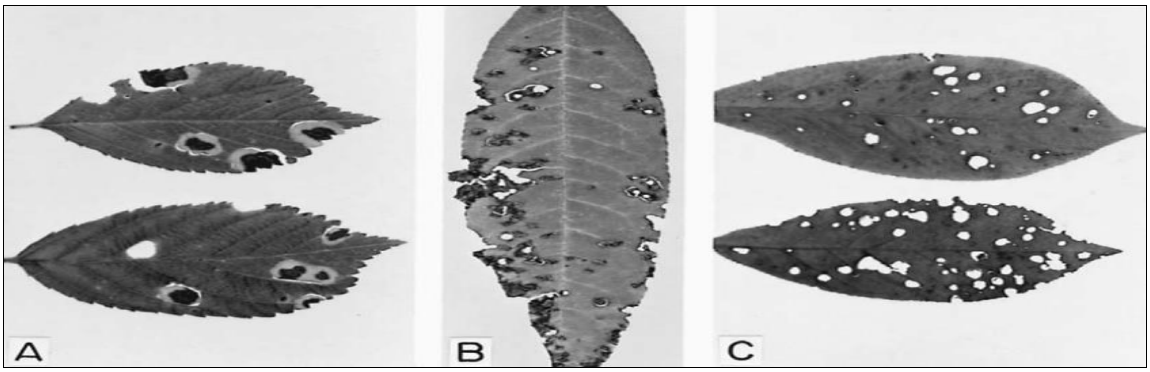


Fig. 5.Schematic formation of an abscission layer around a diseased spot of a Prunus leaf. (A–C) Leaf spots and shot holes caused by Xanthomonas arboricola pv. pruni bacteria on (A) ornamental cherry leaves; characteristic broad, light green halos form around the infected area before all affected tissue falls off, (B) on peach, and (C) on plum. The shot hole effect is particularly obvious on the plum leaves

iii. Formation of Tyloses

Tyloses are formed in the xylem vessels of the majority of plants in response to a variety of stressors and during the majority of diseases that invade the xylem. Tyloses are overgrowths of neighbouring parenchymatous cells' protoplasts that poke through pits into xylem vessels. Tyloses have cellulosic walls and have the potential to fully clog a vessel due to their size and quantity.

iv. Deposition of Gums

Gum secretion is most frequently found on stone fruit trees. Gums play a protective role because they are rapidly deposited in the intercellular spaces and within the cells around the infection locus, creating an impenetrable barrier that encloses the pathogen completely. After that, the infection isolates itself, starves, and eventually perishes.

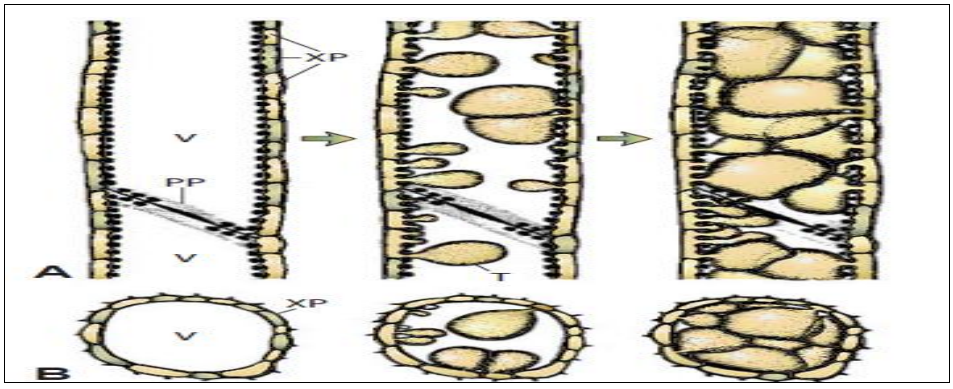


Fig. 6.Development of tyloses in xylem vessels. Longitudinal (A) and cross section (B) views of healthy vessels (left) and of vessels with tyloses. Vessels at right are completely clogged with tyloses. PP, perforation plate; V, xylem vessel; XP, xylem parenchyma cell; T, tylosis

II. Biochemical defense mechanism

Plants release inhibitors as a means of defending themselves against their surroundings. These substances include phytoalexins, PR proteins, and secondary metabolic products such as 2,6-dichloro-isonicotinic acid (INA), BTH, salicylic acid, Jasmonic acid etc.,

Phytoalexins: Phytoalexins are phenolic compounds, derived from the Greek words *Phyto*, which means plant, and *Alexin*, which means warding off component. They are not found in healthy plants;

instead, they are created when a plant is stimulated by a pathogen or by a mechanical or chemical harm. They are low molecular weight antibacterial chemicals that are only created when the parasite and host cells come into contact. The resistant state is limited to the tissue that the fungus has colonised and the immediate surrounding area, and it is not inherited.

PR Proteins: "Pathogenesis related proteins" (PRs) are a class of plant-coded proteins that are activated by various stressors. They are thought to play a significant role in both general stress adaption and plant defense against pathogenic restrictions. They are defined as proteins encoded by the host plant but induced only in pathological or related situations. Pathological conditions refer to all types of infected states, not just the resistant, hypersensitive responses in which PRs are most common; they also include parasitic attack by nematodes, insects, and herbivores. Among the PRs, a protein has to be newly expressed upon infection but not necessarily in all of them. Abiotic stress conditions alone are insufficient as a criterion for PR inclusion.

These factors suggest that the aspects of PR induction are more important than other distinguishing qualities like chemical composition or cellular location [14]. Originally, molecular and molecular-genetic methods in tobacco have identified five primary groups of PRs, (PR-1 to PR-5) which are arranged in decreasing order of electrophoretic mobility. Every group has a number of individuals with comparable characteristics. Each group consists of several members with similar properties [15] (Table 1). Group PR-1 is the most prevalent, accounting for 1-2 percent of all leaf proteins. The proteins of group 5 have been dubbed thaumatin-like (TL) proteins because they exhibit a notable degree of amino acid sequence homology with the protein that tastes sweet in the fruits of the tropical plant *Thaumatococcus daniellii* [16].

Table 1.PR proteins induced in Samsun tobacco (NN genotype) by TMV infection [15]

Group	Acidic PR proteins		Basic PR proteins		Function
	Name	Mol wt (KD)	Name	Mol wt (KD)	
1	1a	15.8	16 KD	16.0	Unknown
	1b	15.6			
	1c	15.5			
2a	2	39.7	Gluc .b	33.0	β- 1.3-gluconase
	N	40.0			
	O	40.6			
	Q^+	36.0			
2b	O^+	25.0			β- 1.3-gluconase
3	P	27.5	Ch 32	32.0	Chitinase
	Q	28.5	Ch 34	34.0	
4	s1	14.5			Unknown
	r1	14.5			
	s2	13.0			
	r2	13.0			
5a	R	24.0	Osmotin	24.0	Unknown thaumatic type proteins
	S	24.0			
5b			45 KD	45.0	Unknown

"The majority of PRs have nematicidal, insecticidal, antifungal, antibacterial, and, as recent research has demonstrated, antiviral properties. The main causes of PRs' toxicity are their hydrolytic, proteinase-inhibiting, and membrane-permeabilizing properties. Therefore, fungal cell walls, which include glucans, chitin, and proteins, can be weakened and broken down using hydrolytic enzymes (β-1,3-glucanases, chitinases, and proteinases), while gram-positive bacteria can be disrupted by PR-8 because of its lysozyme activity" [17,18,19]

4. RELEVANCE OF PRs TO DISEASE RESISTANCE

a) Stronger accumulation of PRs in inoculated resistant as compared to susceptible plants. Besides previous data, substantiating this statement, differential responses of resistant/susceptible plants were reported in tomato plants, inoculated with *Cladosporium fulvum* [20]; *Phytophthora infestans*-infected potato [21]; *Venturia inaequalis*-inoculated apple [22]; *Pseudomonas syringae*-infected grapevine [23]; *Xanthomonas campestris* pv. *vesicatoria* and TMVPo- infected hot pepper [24, 25].

b) Important constitutive expression of PRs in plants with high level of natural disease resistance. This correlation was observed in several pathosystems, such as apple – *Venturia inaequalis* [26], tomato – *Alternaria solani* [27] and potato – *Phytophthora infestans* [28].

c) Significant constitutive expression of PRs in transgenic plants over expressing PR genes accompanied by increased resistance to pathogens. Thus, increased tolerance to *Peronospora tabacina* and *Phytophthora parasitica* var. *nicotianae* was recorded in tobacco overexpressing PR1a gene [29]. Transgenic rice and orange plants overexpressing thaumatin-like PR-5 revealed increased tolerance to *Rhizoctonia solani* and *Phytophthora citrophthora*, respectively [30, 31], while transgenic potato over expressing PR-2 and PR-3 improved resistance to *Phytophthora infestans* [32]. *Puccinia graminis f. sp. hordei* in the leaves of barley [33].

d) Accumulation of PRs in plants in which resistance is locally or systemically induced. Generalizing this broad research area it can be stated that PRs are recognized as markers of the systemic acquired resistance (SAR), and PRs genes are involved in the list of the so-called SAR-genes [34]. Some SAR-inducing chemicals *viz*., benzothiadiazole (BTH), β-aminobutyric acid (BABA) or 2,6-dichloroisonicotinic acid (DCINA) are harmless commercially supplied compounds and have promising practical application as novel tools in plant protection (Edreva, 2004 and references therein).

PRs members induced in resistant or SAR- expressing plants, as well as PRs from transgenic resistant plants exhibit high antimicrobial activity [36,21,37], this suggesting their direct role in disease resistance. 2,6-dichloro-isonicotinic acid (INA): The first activator described was 2,6-dichloro-isonicotinic acid (INA). INA induced systemic resistance against a broad range of pathogens in several plant species and made available widely for research as well as effective in decreasing foliar diseases in green beans *Phaseolus vulgaris* [38, 39] in growth chamber and the field (Table 1). It decreased powdery mildew in cucumber [40] and barley [41], and infections by *Cercospora beticola* in sugar beet [42] and also powdery mildew in roses [43].

The provided evidence outlines the significance of pathogenesis-related proteins (PRs) in plant defense mechanisms. Here's a breakdown of the supporting evidence:

a) Differential accumulation of PRs in resistant vs. susceptible plants: Previous data and subsequent studies indicate stronger accumulation of PRs in inoculated resistant plants compared to susceptible ones [44]. Examples include studies on tomato plants infected with *Cladosporium fulvum* [20], *Phytophthora infestans*-infected potato [21], *Venturia inaequalis*-inoculated apple [22], *Pseudomonas syringae*-infected grapevine [23] and *Xanthomonas campestris* pv. *vesicatoria* and TMVPo-infected hot pepper [24,25].

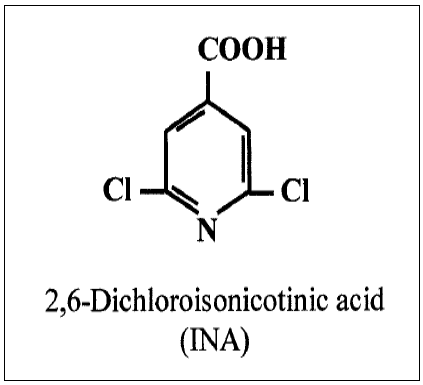
b) Constitutive expression of PRs in plants with high natural disease resistance: Correlation observed in various pathosystems such as apple with *Venturia inaequalis* [26], tomato with *Alternaria solani* [27], and potato with *Phytophthora infestans* [28]. PR mRNAs proposed as molecular markers in potato breeding programs.

c) Increased resistance to pathogens in transgenic plants over expressing PR genes: Examples include tobacco over expressing PR1a gene showing increased tolerance to *Peronospora tabacina* and *Phytophthora parasitica* var. *nicotianae* [29], transgenic rice and orange plants over expressing thaumatin-like PR-5 exhibiting increased tolerance to *Rhizoctonia solani* and *Phytophthora citrophthora*, respectively [30, 31], and transgenic potato over expressing PR-2 and PR-3 showing improved resistance to *Phytophthora infestans* [32].

d) Accumulation of PRs in plants with induced resistance: PRs are recognized as markers of systemic acquired resistance (SAR). Examples include studies using SAR-inducing chemicals like benzothiadiazole (BTH), β-aminobutyric acid (BABA), or 2,6-dichloroisonicotinic acid (DCINA), which have promising practical applications in plant protection. Induced PRs exhibit high antimicrobial activity, suggesting their direct role in disease resistance. Overall, these lines of evidence highlight the multifaceted roles of PRs in plant defense against pathogens, including their differential accumulation in resistant vs. susceptible plants, constitutive expression in naturally resistant plants, enhanced resistance in transgenic plants over expressing PR genes, and induction in plants with induced resistance mechanisms.

Table 2. Recognized and proposed families of pathogenesis-related proteins

Family	Type member	Properties
PR-1	Tobacco PR-1a	unknown
PR-2	Tobacco PR-2	β-1,3-glucanase
PR-3	Tobacco P, Q	chitinase type I, II, IV, V, VI, VII
PR-4	Tobacco "R"	chitinase type I, II
PR-5	Tobacco S	thaumatin-like
PR-6	Tomato Inhibitor I	proteinase-inhibitor
PR-7	Tomato P_{6g}	endoproteinase
PR-8	Cucumber chitinase	chitinase type III
PR-9	Tobacco "lignin-forming peroxidase"	peroxidase
PR-10	Parsley "PR1"	"ribonuclease-like"
PR-11	Tobacco class V chitinase	chitinase type I
PR-12	Radish Rs-AFP3	defensin
PR-13	*Arabidopsis* THI2.1	thionin
PR-14	Barley LTP4	lipid-transfer protein



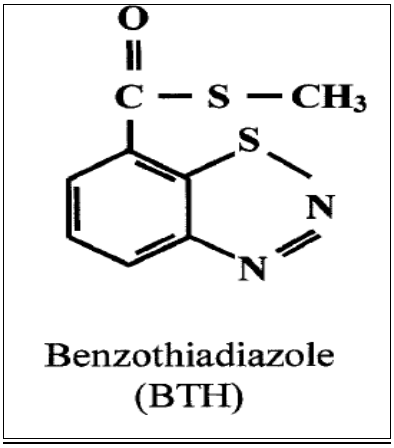
2,6-Dichloroisonicotinic acid (INA)

2,6- Dichloro-isonicotinic acid (INA) is described as the first activator of systemic resistance in plants. It has been shown to induce systemic resistance against a broad range of pathogens across various plant species. Some notable findings regarding its effectiveness were proven in green beans (*Phaseolus vulgaris*). Results revealed that INA decreased foliar diseases, both in growth chamber experiments and field trials [38, 39], INA decreased powdery mildew infections in cucumber [40] and barley [41] and infections caused by *Cercospora beticola* in sugar beet plants [42]. INA was effective in reducing powdery mildew infections in roses [43]. These findings suggest that INA is a potent inducer of systemic resistance and has practical applications in managing various foliar diseases in diverse plant species.

Table 3. Control of plant diseases by INA

Crops	Disease/ Pathogen	Reference
Barley	Powdery Mildew/ *Erysiphe graminis*	[41]
Rose	Powdery Mildew/*Spheerotheca fuliginea*	[43]
Cucumber	Anthracnose/ *Colletotrichum lagenarium*	[45]
Green Bean	Anthracnose/ *Uromyces appendiculatus*	[38, 39]

5. BENZOTHIADIAZOLE (BTH)



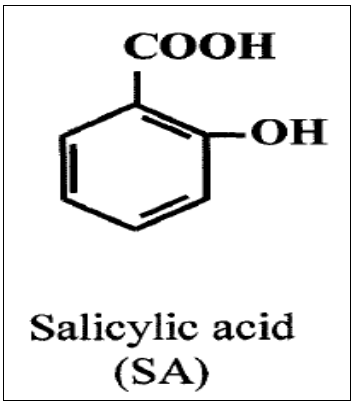
Benzothiadiazole
(BTH)

Benzothiadiazole (BTH) is another activator of systemic resistance in plants, with particularly notable efficacy observed in various pathosystems involving wheat, rice, tobacco, and some vegetable crops. Early application of BTH during wheat growth effectively protected against powdery mildew for the entire season and provided some protection against leaf rust and Septoria leaf spot [46]. BTH was registered for commercial use in Europe in 1996 specifically for controlling powdery mildew in wheat. Its application decreased infections by fungi, bacteria, and viruses in tobacco [47] and Arabidopsis [48]. It significantly reduced rust severity when sprayed onto faba bean leaves four days before challenge inoculation with *Uromyces viciae-fabae* spores. These findings underscore the effectiveness of BTH in providing systemic resistance against a range of pathogens across various plant species, making it a valuable tool for disease management in agricultural settings.

Table 4. Control of plant diseases by BTH

Crops	Disease/ Pathogen	Reference
Tobaco	Blue mould/ *Peronaspora tobacina*	[47]
Tomato	Bacterial spot/ *Xanthomonas spp*	
Wheat	Powdery Mildew/ *Erysiphe graminis*	[46]

6. SALICYLIC ACID



Salicylic acid
(SA)

Salicylic Acid (SA) is a compound derived from the Latin word *salix* - metabolism of salicin, found in the bark of willow trees. It belongs to the group of phenolic acids and is also classified as a beta hydroxy acid. This colorless crystalline organic acid serves various functions in organic synthesis and acts as a plant hormone. In addition to its role as a compound similar to aspirin (acetylsalicylic acid), SA is well-known for its use in anti-acne treatments. Salts and esters derived from salicylic acid are termed salicylates. Salicylic acid exhibits several physiological effects in plants. It reverses the closure of stomata caused by abscisic acid [49]. Exogenous application of salicylic acid improves the yield in crops [50]. SA retards ethylene synthesis; stimulates photosynthetic machinery and increase the

chlorophyll content [51]. Recent research has identified salicylic acid as a crucial component in signaling pathways that induce systemic acquired resistance against pathogenic infections [52, 53, 54].

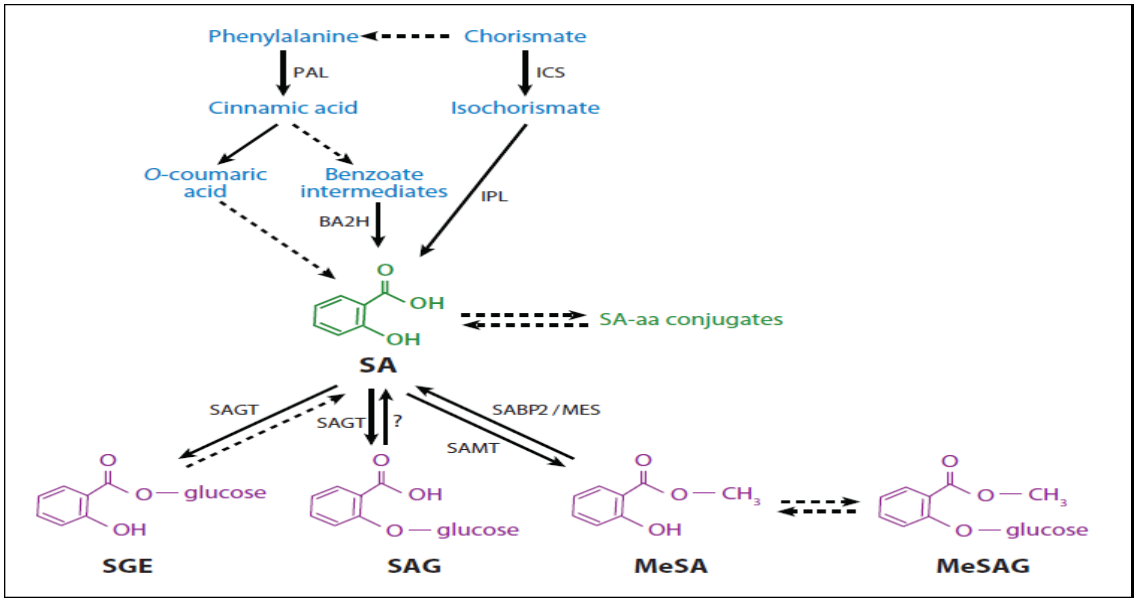


Fig. 7. Simplified schematic of pathways for SA biosynthesis and metabolism as adapted from Garcion & M´etraux [55]. Abbreviations: PAL, phenylalanine ammonia lyase; ICS, isochorismate synthase; IPL, isochorismate pyruvate lyase; BA2H, benzoic acid-2-hydroxylase; SA, salicylic acid; SAGT, SA glucosyl transferase; aa, amino acid; SAMT, SA methyl transferase; SABP2, SA-binding protein 2; MES, methyl esterase; SGE, salicyloyl glucose ester; SAG, SA O-β-glucoside; MeSA, methyl salicylate; Me SAG, methyl salicylate O-β-glucoside

7. SALICYLIC ACID BIOSYNTHESIS

Salicylic acid (SA) in plants can be synthesized through two distinct enzymatic pathways, both of which require the primary metabolite chorismite [56, 57]. Chorismate-derived l-phenylalanine can be converted into SA via either benzoate intermediates or coumaric acid via a series of enzymatic reactions initially catalyzed by Phenylalanine Ammonia Lyase (PAL). Alternatively, chorismate can be converted into SA via isochorismate in a two-step process involving Isochorismate Synthase (ICS) and Isochorismate Pyruvate Lyase (IPL) (Fig. 7) [58, 59, 60]. This pathway is responsible for the bulk of pathogen-induced SA synthesis in plants such as Arabidopsis, *Nicotiana benthamiana* and tomato [60, 61, 62]. Arabidopsis, for example, encodes two ICS enzymes, with ICS1 being responsible for approximately 90% of SA production induced by pathogens or UV light. Mutants lacking functional ICS1 show compromised SA production and pathogen resistance [56]. Interestingly, even in mutants lacking functional ICS1, residual SA in an *ics1/ics2* indouble mutant indicates that the *ICS* pathway is not the only source of SA in *Arabidopsis*. Most of the SA produced in plant is subsequently converted into SA *O-β*-glucoside (SAG) by a pathogen-inducible SA glucosyl transferase (SAGT) (Fig. 7) [63, 64, 65, 66, 67].

In Arabidopsis, there are two enzymes responsible for the conversion of salicylic acid (SA) into its glucoside form, SA O-β-glucoside (SAG), known as SA glucosyltransferases (SAGTs). One of these enzymes exhibits a preference for converting SA into SAG, while the other forms a less abundant SA derivative called salicyloyl glucose ester (SGE) [68]. SA is believed to be synthesized primarily in chloroplasts, as indicated by various studies [56, 58, 60]. However, in tobacco, it has been observed that SAGT localizes to the cytosol [69]. Once SAG is formed in the cytosol, it undergoes active transport into the vacuole. Inside the vacuole, SAG may function as an inactive storage form of SA,

which can be converted back into SA when needed [68, 69, 70]. This process likely contributes to the regulation of SA levels and its availability for signaling pathways involved in plant defense responses.

8. JASMONIC ACID

Jasmonic Acid (JA) is a plant hormone derived from the fatty acid linolenic acid and belongs to the jasmonate class of plant hormones. It is synthesized via the octadecanoid pathway from linolenic acid. The primary function of JA and its metabolites is to regulate various plant responses to both abiotic and biotic stresses, as well as influencing plant growth and development processes. It regulates stress responsesas it plays a crucial role in mediating plant responses to various stresses, including defense against herbivores, pathogens, and environmental stresses. It also regulates several aspects of plant growth and development, including growth inhibition, senescence, tendril coiling, flower development, and leaf abscission. JA is responsible for tuber formation in certain plants such as potatoes, yams, and onions. In addition to this, it can be converted into various derivatives, including esters such as methyl jasmonate, and can also be conjugated to amino acids. There is evidence suggesting that JA may play a role in pest control. Some researchers have explored its use as a spray applied to seeds prior to planting, which stimulates the natural anti-pest defenses of the plants. Hence, Jasmonic Acid is a versatile plant hormone involved in regulating a wide range of physiological processes, including stress responses, growth, and development. Its potential applications in pest control and plant defense make it an area of interest for researchers and agricultural practitioners alike.

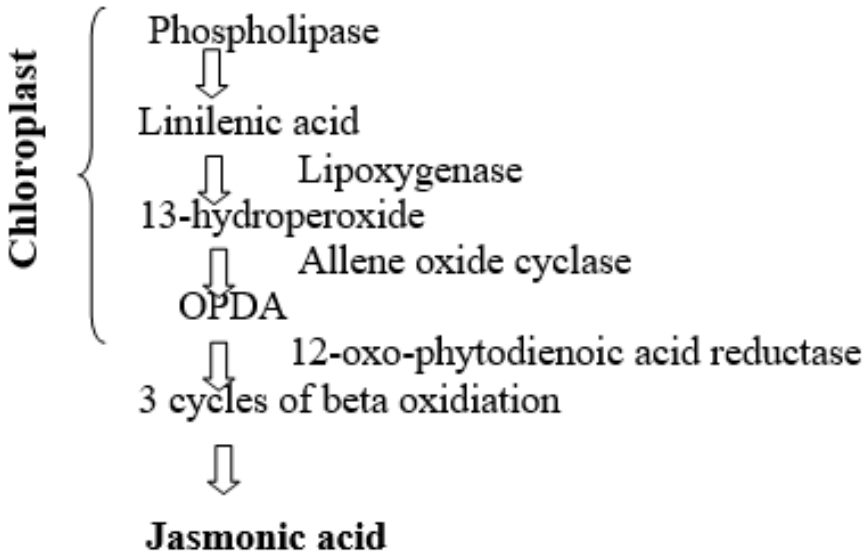


Fig. 8. Jasmonic Acid Biosynthesis- Octadecanoid pathway [71]

9. ISR RELATION TO SEED

Application of certain Plant Growth-Promoting Rhizobacteria (PGPR) strains to seeds or seedlings has been found to induce systemic resistance (ISR) in treated plants. ISR is a phenomenon where the plant's defense mechanisms are activated and primed to resist infection by pathogens [6, 72]. These findings highlight the potential of using PGPR as a sustainable strategy for enhancing plant health and reducing reliance on chemical pesticides and had played a crucial role in advancing our understanding of the interactions between plants and beneficial rhizobacteria and have paved the way for the development of sustainable agricultural practices aimed at enhancing plant health and reducing reliance on chemical pesticides. Certain PGPR strains when applied to seeds or seedlings, can trigger or stimulate ISR in plants. This means that the plant's immune system is activated, making it more resistant to pathogen attacks. ISR leads to the enhancement of the plant's natural defense mechanisms. This includes the activation of defense-related genes, production of antimicrobial

compounds, and strengthening of physical barriers against pathogens. ISR involves priming the plant's immune system, which means that it is prepared to respond more rapidly and effectively to pathogen attacks upon subsequent exposure. The induction of ISR by PGPR offers a promising approach for sustainable agriculture by reducing the need for chemical inputs and enhancing plant resilience to diseases. Overall, the application of certain PGPR strains to seeds or seedlings can lead to the induction of ISR in plants, providing a natural and eco-friendly means of enhancing plant immunity and health.

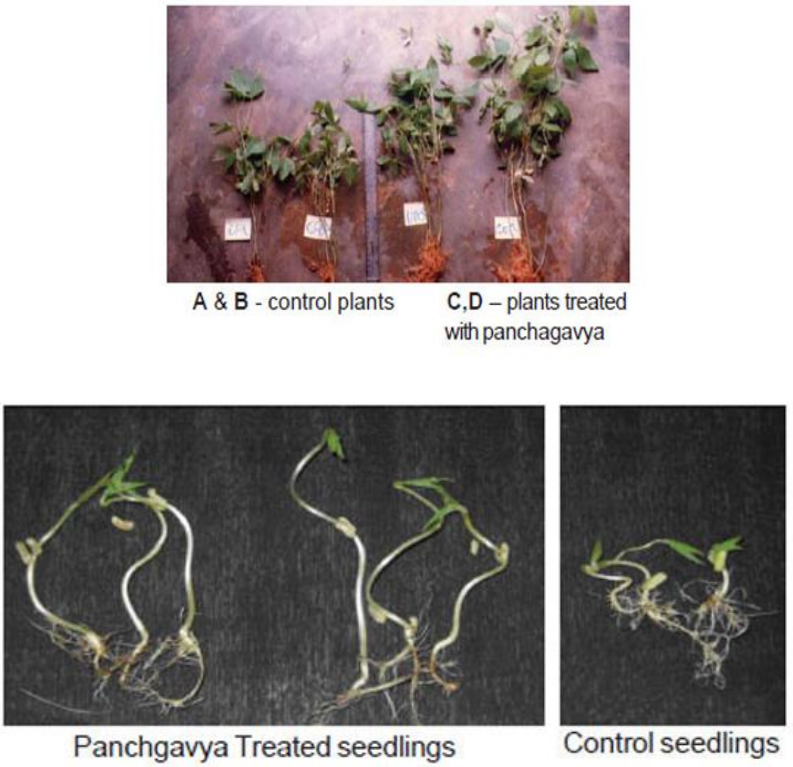


Fig. 9. Induced resistance through Panchagavya

Panchagavya is an organic formulation derived from five products of the cow: cow dung, urine, milk, curd and ghee. It has been reported to induce systemic resistance in plants and exhibit bio-pesticidal properties. Research conducted at the Department of Biotechnology, GITAM Institute of Technology, demonstrated that it up-regulates certain genes associated with the plant's pathogenesis pathway, thereby conferring disease resistance to the plants. The use of Panchagavya presents a sustainable alternative to chemical pesticides. By harnessing natural ingredients derived from cows, this organic formulation offers a holistic approach to plant health management. Furthermore, its ability to enhance systemic resistance in plants and regulate pathogenesis pathways suggests its potential as an eco-friendly and effective strategy for pest and disease control in agriculture.

10. SYSTEMIC RESISTANCE IN CHICKPEA AGAINST FUSARIUM WILT

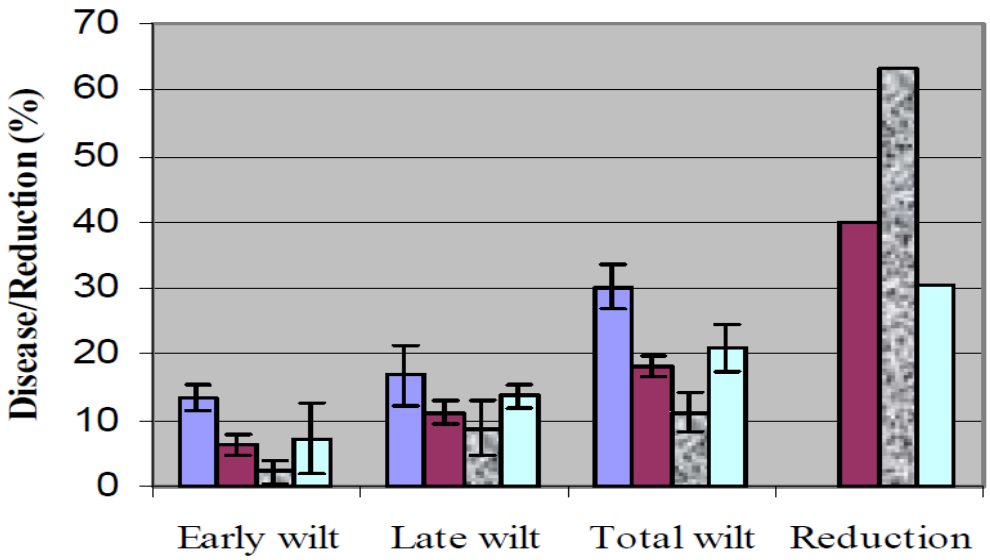


Fig.10. Effect of seed dressing with different chemicals on wilt disease incidence in chickpea grown in wilt sick field. Chickpea seeds were dressed with Salicylic acid (SA), Bezo (1,2,3)-thiadizole-7-carbothioic acid-S-methyl ester (Bion), K_2HPO_4 (Kp) and water (Con) for two hours before sowing

Fusarium wilt, caused by *Fusarium oxysporum* f. sp. *ciceri*, is a significant disease affecting chickpea crops. The fungus invades the plant's vascular tissues, leading to severe wilting of foliage by obstructing xylem transport and impeding water movement [73, 74]. *Fusarium oxysporum* f. sp. *ciceri* can survive as a facultative saprophyte in both seeds and soil, remaining viable for up to six years in the absence of susceptible hosts [75]. In recent years, there has been increasing interest in the process of induced resistance as a method for managing plant diseases. Induced resistance involves priming plants' defense mechanisms to better withstand pathogen attacks [76]. Certain environmentally safe chemicals have been identified as effective inducers of systemic resistance [77]. Salicylic acid, acetyl salicylic acid, and benzo (1,2,3)-thiadizole-7-carbothioic acid - S-methyl ester (Bion) have been shown to induce systemic resistance in chickpea against Fusarium wilt disease under controlled environments [78, 79]. Induced systemic resistance in chickpea against wilt disease caused by *Fusarium oxysorum* f.sp. *ciceri* by treating the seeds with benzo (1,2,3)-thiadizole-7-carbothioic acid - s- methyl ester (Bion), salicylic acid (SA) and di- potassium hydrogen phosphate (K_2HPO_4) [80]. Results revealed a reduction in disease incidence in both types of applications, with seed dressing being more effective than soaking. Bion dressing exhibited the highest reduction in wilt disease (63%), followed by SA (40%) and K_2HPO_4 (30%). When seeds were soaked in these chemicals, Bion and SA showed reductions of 41% and 24%, respectively, while no reduction was observed with K_2HPO_4 soaking. Although there was a slight increase in yield with all treatments in both applications, the differences were statistically non-significant. Therefore, seed dressing with Bion, SA, or K_2HPO_4 can effectively reduce Fusarium wilt incidence in chickpea, with Bion exhibiting the highest efficacy. These findings highlight the potential of induced systemic resistance as a sustainable strategy for disease management in chickpea cultivation.

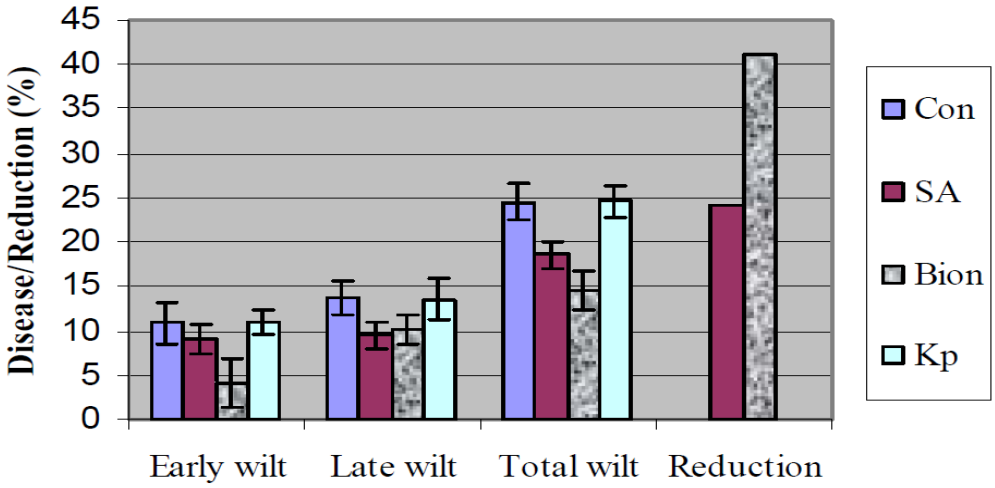


Fig.11. Effect of seed soaking with different chemicals on wilt disease incidence in chickpea grown in wilt sick field. Chickpea seeds were soaked in aqueous solutions of Salicylic acid (SA), Bezo (1,2,3)-thiadizole-7-carbothioic acid-S-methyl ester (Bion), K_2HPO_4 (Kp) and water (Con) for two hours before sowing

The effects of salicylic acid seed priming on the growth and biochemical attributes of wheat under saline conditions was reported [81]. The experiment involved soaking wheat seeds of cv. Inqlab and S-24 in water or a 100 mg L-1 salicylic acid solution for 24 hours before sowing them in sand salinized with 0, 50, or 100 mM NaCl. Pots were sprayed with ¼ strength Hoagland's nutrient solution during the experiment. Salt stress significantly reduced all growth parameters, such as shoot and root length, and shoot and root dry weights. However, the application of salicylic acid mitigated the adverse effects of salinity on growth, indicating a positive role of salicylic acid in promoting growth under saline conditions (Table 5). Salinity led to a decrease in chlorophyll a and b content and the chlorophyll a/b ratio in both wheat lines. However, the reduction in the chlorophyll a/b ratio was lower in the salt-tolerant wheat line S-24 (Table 6). This observation suggests that the chlorophyll a/b ratio could serve as a useful marker for selecting salt-tolerant wheat varieties. Salt stress resulted in a significant increase in the accumulation of reducing, non-reducing, and total soluble sugars in the leaves of 14-day-old wheat seedlings in both cultivars. The salt-tolerant line S-24 exhibited higher sugar content, indicating its potential as a marker for salt tolerance in wheat. (Table 7). Overall, the findings suggest that salicylic acid seed priming can alleviate the adverse effects of salt stress on wheat growth and biochemical attributes. Additionally, the study identifies potential markers, such as chlorophyll content and soluble sugars accumulation, for selecting salt-tolerant wheat varieties.

The experiment involved growing sunflower seedlings in dark conditions for 9 days, after which etiolated cotyledons were transferred into Petri dishes containing various concentrations of salicylic acid (SA) solutions. These cotyledons were then incubated in the dark for 14 hours and subsequently exposed to light for 3 hours. The study examined the effects of different SA concentrations on chlorophyll, carotenoid content, protein amount, and peroxidase (POD) activity in the cotyledons. The highest SA concentration (1000 µM) exhibited a toxic effect on growth, as evidenced by a decrease in total chlorophyll, carotenoid content, and protein amount. Lower concentrations of SA (0.1 µM and 10 µM) led to significant increases in chlorophyll and carotenoid content compared to the control group. Specifically, a 2-fold increase in chlorophyll content was observed with 10 µM SA, while a 3.5-fold increase in carotenoid content was observed with 0.1 µM SA through stimulation effect. Protein amount increased in all concentrations of SA except the highest concentration (1000 µM), indicating a potential regulatory effect of SA on protein synthesis. Peroxidase (POD) activity was stimulated in all concentrations of SA solutions, suggesting an activation of defense mechanisms in response to SA treatment. However, the difference in POD activity was not significant at the lowest SA concentration (0.001 µM) [82].

11. DIFFERENT INDUCED CHEMICALS RESPONSES ON WHEAT

Table 5. Germination and seedling indices of wheat cultivar as affected by the interaction of PEG

PEG%	SA mM	Germination (%)	Mean germination time (d)	Vigor index	Shoot length (mm)	Root length (mm)	Shoot dry weight mg/plant	Root dry weight mg/plant	Electrolyte leakage (%)
0	0.0	92.50ab	1.42d	378.22abc	129.25a	280.75a	74.50b	27.46d	37.12f
	0.1	100.00a	1.54cd	410.50a	129.75a	280.75a	84.50a	34.13b	35.14f
	0.5	100.00a	1.34d	408.75a	128.75a	280.00a	83.83a	37.46a	35.52f
10	0.0	87.50bc	2.02b	361.57bcd	87.50d	326.75b	14.50f	25.20de	71.62b
	0.1	90.00abc	1.99b	391.72abc	93.50c	341.75b	37.83e	31.20 c	50.21d
	0.5	92.50ab	1.72c	4.6.40ab	99.00b	339.25b	41.16d	34.46ab	40.78f
20	0.0	75.00d	2.71a	295.75e	66.50g	324.25b	8.16i	24.60e	90.54a
	0.1	80.00cd	2.25b	330.23de	74.50f	334.75b	11.16h	34.40b	70.85b
	0.5	91.00ab	2.10b	356.87cd	79.00e	337.50b	13.50g	36.80ab	60.54c

In each column, means with similar letter are not significantly different (DMART, p > 0.05)

Table 6. Effect of salicylic acid on germination of two wheat cultivars as affected by PEG

SA (mM)	Germination (%)	Mean germination time (d)	Vigor index	Shoot length (mm)	Root length (mm)	Shoot dry weight (mg/plant)	Root dry weight mg/plant	Electrolyte leakage (%)
0.0	85c	2.04a	345.18cc	94.41c	309.58c	32.38c	25.73b	66.41a
01	90b	1.94a	3.77.48b	99.25b	319.08b	42.83b	33.12a	52.11b
0.5	95a	1.72b	390.67a	102.25a	328.91a	46.5a	35.30a	45.61c

In each column, means with similar letter are not significantly different (DMART, p > 0.05)

Salicylic acid (SA), play important roles in regulating a number of physiological processes in plants and is a common plant-produced phenolic compound found to signal molecules for modulating plant responses to environmental stresses [83]. It is now clear that SA provides protection against a number of abiotic stresses such as heat stress in mustard seedlings [84], chilling damage in different plants [85, 86], heavy metal stress in barley seedlings [87] and drought stress in wheat plants [88].

Table 7. Effect of salisylic acid pre- treatment on root, shoot dry weights and root/shoot ratio of *T. aestivum* and *H. vulgare* after 8 days (g/ seedling)

	T. aestivum			***H. vulgare***		
Group	**Root(g)**	**shoot(g)**	**Root/Shoot**	**Root(g)**	**shoot(g)**	**Root/Shoot**
C	0.022	0.096	0.229	0.017	0.055	0.309
S	0.010	0.027	0.370	0.010	0.034	0.294
SAW	0.034	0.142	0.239	0.021	0.086	0.244
SAS	0.024	0.099	0.242	0.020	0.061	0.328

*C=Control S=Treated with 150mM NaCl after 6 h in water SAW =Treated with 0.05 mM SA and then in water SAS= Treated with 0.05 mM SA and then in 150 mM NaCl *=Significant at P<0.5 **=Significant at P<0.1 ***=Significant at P<0.05*

12. *Trichoderma spp.*AS INDUCER

It was reported by authors that, several BCF, as well as various plant growth–promoting rhizobacteria (PGPR) have been shown to efficiently help plants overcome abiotic stresses, such as salinity and drought, in both field crops and trees [89, 90, 91, 92, 93, 94]. The ability of maize plants grown from seeds treated with *T. harzianum* to resist water deficit has been demonstrated in the field, and the enhanced deep rooting clearly contributes [95]. Moreover, in *Trichoderma* inoculated cacao seedlings, drought-induced changes such as stomatal closure and reduction of net photosynthesis were delayed under drought compared with non-inoculated plants, allowing plants to continue growing [90]. In maize, it has been shown that in addition to induction of carbohydrate metabolism and photosynthesis-related proteins, the stress factors in the field are water deficit. *T. harzianum* added as seed treatment (tomato) or as a soil treatment (*Arabidopsis*) largely to improve the germination at osmotic potentials of up to 0.3 M Pa starch content of the leaves was higher in t*richoderma*-inoculated plants [96]. A number of other stresses are also alleviated. *T. harzianum* has recently been shown to improve resistance to heat and cold (seedlings of tomato were imbibed at 25^0C for 1 day, then exposed to either 10^0C or 35^0C, and then returned to 25^0C). Seedlings were much less damaged by the temperature extremes in the presence of *T. harzianum*. *Trichoderma* also increased potassium content of plants [94, 97]. Salt stress is well known to reduce potassium uptake, and in several systems increasing potassium uptake ameliorated salt-induced damage [98]. Lipopeptides such as fengycin and surfactin of Bacillus act as elicitors to induce plant resistance [99]. *Bacillus pumilus* strain S2–3–2 application led to the production of indole-3-acetic acid (IAA) that enhanced the tobacco plant growth [100]. Treatment by *Rhizobium leguminosarum* bv. *viciae* 33504-Alex1, a nitrogen-fixing strain, in soil or via foliar application enhanced plant growth and significantly reduced both the disease severity and incidence of bean yellow mosaic virus (BYMV) in faba beans [101].

Beneficial microbes play a crucial role in stimulating the host plant's immune response by being recognized as Microbe-Associated Molecular Patterns (MAMPs) by Plant Pattern Recognition Receptors (PRRs). To establish a symbiotic relationship with the host plant, these beneficial microbes have evolved mechanisms to minimize the activation of the host's immune system. However, the balance between efficient recognition and the strength of the host immune response needs further study. The interaction between beneficial microbes and plants involves a complex network of genes and transcription factors that participate in defense responses. Signaling crosstalk occurs among pathways involving salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and mitogen-activated protein kinase (MAPK) cascades. These pathways coordinate downstream defense responses and are activated by beneficial microorganisms in an NPR1-dependent pathway. Furthermore, non-coding RNAs induced by beneficial microorganisms play a significant role in regulating host development and resistance to pathogens. Genome-wide profiling of microRNAs (miRNAs) and subsequent functional verification are crucial aspects for future exploration. RNA interference technology holds promise as a method to control plant diseases and pests. [102].

Those are able to stimulate defense responses of host plants through different pathways, thereby endowing plants with resistance to multiple pathogens. *Bacillus amyloliquefaciens*, *B. atrophaeus, B. cereus, Pseudomonas fluorescens*, etc., were demonstrated to be effective against fungal, bacterial, and viral invasion through ISR. Recent studies suggested that beneficial microbes induce early plant ISR events, including, but not limited to, increased expression of pathogenesis-related PR genes, enhanced activities of defense-related substances, such as phenylalanine ammonia-lyase, polyphenol oxidase, peroxidase, β-1, 3 glucanase, and chitinase, and accumulating reactive oxygen species [103, 104]. Although the initial research disregarded the involvement of SA in beneficial microbe-induced systemic resistance, recent studies have shown that beneficial microorganisms can control plant disease through activating SA and JA/ET signaling pathways. Beneficial microbes, such as Bacillus and Trichoderma, showed the ability to increase the expression of SA and JA/ET marker genes PR1 and LOX2, respectively, and increased the content of SA and JA in plants [105, 106, 107]. Studies have shown that beneficial microbes such as *Bacillus and Trichoderma* induce early plant-induced systemic resistance (ISR) events, including increased expression of pathogenesis-related (PR) genes, enhanced activities of defense-related substances, and accumulation of reactive oxygen species. While initial research overlooked the involvement of SA in beneficial microbe-induced systemic resistance, recent studies have demonstrated that these microbes can activate both SA and JA/ET signaling pathways. This activation results in increased expression of SA and JA/ET marker genes and higher levels of SA and JA in plants. So, beneficial microbes induce systemic resistance in plants through various pathways, ultimately enhancing plant defense mechanisms against pathogens. Understanding these interactions can lead to the development of novel strategies for sustainable disease management in agriculture.

13. CONCLUSION

Although not fully understood, induced resistance in plants opens new horizons in plant protection, being a promising tool for eco-friendly disease control and sustainable agriculture. It remains a challenge for both fundamental and applied research.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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