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REVIEW ARTICLE

Advancements in induced systemic resistance: Mechanisms, applications and integration for sustainable crop protection and climate adaptation

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Abstract

Induced Systemic Resistance (ISR) is an important biological defense mechanism in plants, which enhances their resistance to a wide range of pathogens and abiotic stresses. ISR is triggered by beneficial microorganisms, particularly Plant Growth Promoting Rhizobacteria (PGPR) and involves complex molecular interactions among key signaling pathways, including salicylic acid (SA), jasmonic acid (JA), ethylene (ET), abscisic acid (ABA) and Reactive Oxygen Species (ROS). This review explores the mechanistic basis of ISR, focusing on the molecular crosstalk and epigenetic memory that primes plants for enhanced stress tolerance. The integration of ISR with climate resilience strategies is highlighted, addressing the potential of ISR to mitigate the impacts of climate variability, including heatwaves, floods and elevated CO_2 levels. Additionally, practical challenges such as field-level validation, cost-effectiveness and formulation development are discussed, alongside the technological innovations that may enhance ISR applications in sustainable agriculture. This work aims to provide a comprehensive understanding of ISR's molecular foundations and its potential for climate-resilient agriculture, with a focus on scalable and economically viable solutions. Future directions, including the integration of ISR with precision agriculture and the use of biotechnological advancements such as CRISPR-Cas systems, offer promising avenues for enhancing ISR efficiency and expanding its applicability across diverse agricultural systems. This review aims to contribute to the development of ISR-based strategies that can promote long-term agricultural sustainability and global food security.

Keywords: CRISPR-Cas systems; jasmonic acid (JA); rhizobacteria; salicylic acid (SA); sustainable agriculture

Introduction

In pursuing sustainable and resilient agricultural practices, developing creative ways to improve plant health and productivity has become critical. Agriculture today faces several challenges, including the growing demand for food production, climate change and the overuse of chemical inputs, which have detrimental effects on the environment and human health (1). According to the Food and Agriculture Organization, by 2050, global food production needs to increase by 60 % to meet the demands of a growing population, with recent projections estimating the world population will reach 9.7 billion by 2050 (2). As of 2025, the global population stands at approximately 8.2 billion and food insecurity continues to rise, affecting nearly 295 million people worldwide-an increase for the sixth consecutive year (3). Food price inflation remains high, with over 60 % of countries experiencing food price increases above overall inflation rates, further straining access to nutritious food. While global wheat and rice production are projected to reach record highs in 2025, regional disparities persist due to climate-related yield losses and disease outbreaks. Fertilizer consumption in India is projected to rise steeply, with states like Punjab and Haryana already exceeding 250 kg/hectare, raising concerns about environmental sustainability and runoff pollution. Furthermore, climate change is expected to reduce maize yields by up to 24 % globally by 2030, while increasing the frequency of extreme weather events that threaten crop productivity and farmer livelihoods (3, 4). According to the Food and Agriculture Organization, by 2050, global food production needs to increase by 60 % to meet the demands of a growing population. Furthermore, excessive use of chemical fertilizers and pesticides has contributed to soil degradation, loss of biodiversity and pollution of water bodies, particularly in regions with intensive agriculture, such as the Indo-Gangetic Plains in India (5, 6). Alongside these challenges, urbanization, land degradation and water scarcity continue to exacerbate the pressure on traditional farming systems, requiring innovations that promote both food security and environmental sustainability.

Over the past decades, several strategies have been implemented to address these agricultural challenges. Conventional approaches include the use of improved crop varieties, chemical fertilizers and synthetic pesticides to enhance crop yields and manage pests. Integrated Pest Management (IPM) combines biological, cultural and chemical methods to minimize pest damage while reducing environmental impact (7). Precision agriculture, which leverages data and technology to optimize resource use, has also gained momentum in recent years (8). Additionally, organic farming and agroecological practices emphasize the use of natural inputs and biodiversity to maintain soil health and ecosystem balance. While these solutions have contributed to increased productivity and sustainability, each comes with limitations. For example, chemical-based methods can lead to resistance in pests and pathogens, while organic and agroecological approaches may face scalability and yield challenges (9, 10). Therefore, there is a growing demand for innovative and sustainable solutions such as ISR, that can complement existing practices and enhance the long-term resilience of agricultural systems.

Induced Systemic Resistance (ISR), a natural plant defense mechanism activated by beneficial microorganisms, particularly bacteria. ISR provides plants with the ability to fend off a wide range of pathogens by activating their innate immune systems, preparing them for future invasions (9, 10). This mechanism has been widely studied in several crops, particularly in Southeast Asia, where rice, wheat and chili are staple crops heavily affected by diseases. Studies have shown that bacterial agents can significantly reduce disease incidences in these crops, improving yields while reducing reliance on chemical inputs (11, 12). In the broader context of plant defense mechanisms, ISR is one component of the plant's innate and induced immune responses. While chemical inputs have been crucial in modern agriculture, they come with side effects, including the development of resistant pathogens, negative environmental impact and health risks for both farmers and consumers (13). ISR, through microbial interventions, offers a sustainable alternative. For instance, small RNAs play a critical role in plant-microbe interactions, helping regulate the plant's immune response (14). This mechanism is not only effective but also environmentally friendly, as demonstrated by field studies where ISR-induced plants show improved resilience to pests and diseases without the need for synthetic pesticides (12, 15).

Recent research on ISR against bacteria in India highlights the role of PGPR in enhancing plant defense mechanisms. PGPR-mediated ISR involves the production of various compounds like lipopolysaccharides, siderophores and volatile organic compounds that trigger plant immunity (16). The activation of ISR involves long-distance systemic signaling, primarily through JA and ethylene pathways, although SA may also play a role (14). Beneficial microbes stimulate hormone signaling, including salicylic acid, JA and ethylene pathways, leading to the expression of defense-related genes and the synthesis of secondary metabolites (5). The molecular basis of ISR involves recognition at the plant cell surface, early cellular immune events, systemic signaling and activation of defense mechanisms. While like systemic acquired resistance, ISR has specific molecular aspects that differentiate it (17). However, there are challenges in fully integrating ISR-based treatments into mainstream agriculture. One of the main hurdles is the variability of ISR responses across different plant species and environments. For example, the effectiveness of bacterial ISR can be influenced by factors such as soil type, climate and crop variety, which may limit its application in certain regions (18). Moreover, while significant strides have been made in understanding the molecular mechanisms of ISR, more research is required to develop strains of bacteria that are consistently effective across diverse agricultural ecosystems (19, 20). Microbiome research advances, including studies of the plant-associated microbiota and the microbial dynamics in soil and rhizosphere environments, offer new possibilities for enhancing ISR efficiency. Developing targeted microbial consortia, genetically modified microbes and advanced delivery mechanisms, such as encapsulation, will further optimize ISR applications. Furthermore, ISR can complement other sustainable practices, such as agroecology and IPM, enhancing the ecological sustainability of agricultural systems.

This review discusses the diverse field of ISR, concentrating on its underlying processes, the role of bacteria in inducing systemic resistance and the potential applications of these phenomena in modern agriculture. By bridging the gap between fundamental research and practical application, ISR holds the promise of reducing the global dependency on chemical inputs, enhancing crop resilience and ultimately contributing to global food security in a rapidly changing climate (1, 21). Additionally, the review highlights the importance of regional studies, such as those in rice-producing areas of Asia, where microbial ISR has shown promising results, particularly in combating diseases like rice blast and bacterial leaf blight (22).

Mechanisms Involved in Induced Systemic Resistance (ISR)

ISR is a critical method used by plants to strengthen their immune systems (23). Unlike localized responses to pathogen invasion, ISR relies on systemic signaling pathways to prepare the entire plant for future encounters with potential hazards which include various biotic stresses, including pathogens and parasites, that affect plants (24). This section discusses the necessity of understanding the underlying mechanisms that drive ISR for sustainable agriculture.

Priming of defense responses

Priming in ISR of plants improves the plant's ability to resist pathogen attacks, wounding and osmotic stress by increasing the activation of cellular defensive mechanisms (25, 26). Priming is the process of pre-treating plants with systemic resistance inducers such as salicylic acid or benzothiadiazole, which results in the direct activation of defense-related genes and prepares the cells for enhanced elicitation of another set of defensive genes (24, 25). This priming mechanism has been demonstrated in a variety of plant models, including parsley cell cultures and *Arabidopsis* plants, where pre-treatment with systemic resistance inducers improves subsequent defense gene activation and callose production in response to pathogen infection, wounding and osmotic stress (27). Furthermore, priming has been linked to the activation of several defense-related genes and the accumulation of defense-related chemicals, demonstrating its importance in improving plant defense mechanisms (28, 29). Defense priming is a series of stages that begin with stimulation from pathogenic or beneficial fungi, bacteria, rhizobacteria, arthropods and abiotic stressors (30, 31). During the priming phase, the plant perceives these stimuli, which causes a moderate induction of numerous chemicals and activities known as the "priming fingerprint" (32). Some components in this fingerprint may be common to several stimuli. When confronted by an adversary, primed plants have a better perception of the threat, allowing them to build a stronger defense in the post-challenge primed state (33). Scientists have recently discovered more details about how this system works in different plants. A key part of this defense involves proteins inside the plant that help turn on protective genes. In a plant called Arabidopsis, one important protein, NPR1, teams up with another group of proteins called TGA transcription factors to activate defense genes (like PR-1) that respond to a chemical signal called SA. This binding helps the plant build a stronger, whole-plant (systemic) defense called systemic acquired resistance. Scientists have even studied how these proteins fit together, showing that a part of NPR1 called the ankyrin repeat is very important for this process (34). Along with SA, another plant hormone called JA is also very important for helping plants defend themselves. Helpful microbes like *Trichoderma harzianum* can trigger this defense by breaking down certain blocker proteins (called JAZ repressors). This allows other proteins (MYC2) to switch on genes that help the plant respond through the JA pathway (35).

In rice, the plant can detect a substance called chitin from friendly fungi using special sensors called LysM receptor kinases (like CERK1). This starts a chain reaction inside the plant (called a MAP kinase cascade) and turns on defense-related proteins like WRKY45, helping the plant prepare to fight off disease (36). Epigenetic regulation also contributes to the priming process. For example, in maize, colonization by *Bacillus velezensis* has been shown to reduce DNA methylation at the promoters of key defense genes, enhancing their expression upon pathogen challenge (37). Recent studies have shed light on the role of transcription factors in priming for ISR. The chromatin regulator MOM1 is a negative regulator of defense priming induced by certain compounds (38). Studies further explored the gene networks involved in ISR, identifying key transcription factors such as LHY, WRKY28, MYB31 and RRTF1 (38). Another highlighted the role of the transcriptional coactivator NPR1 in the chemical priming of plant defense responses (39). A proteomic perspective was provided, showing that *Trichoderma* root colonization can activate plant proteins to counteract pathogen infection, with a focus on the phenylpropanoid pathway (40). These studies collectively underscore the complex interplay of transcription factors and other molecular mechanisms in priming for ISR.

Molecular signaling in ISR

Salicylic acid : The role of SA in the initiation of ISR is crucial, as it activates plant defense against various pathogens (41, 42). SA is involved in both basal and resistance gene-mediated defense, as well as Systemic Acquired Resistance (SAR) (43). The simultaneous activation of SAR and ISR, both of which require the key regulatory protein NPR1, results in an additive effect on the level of induced protection against pathogens (44, 45). However, the primary signaling components activating SA biosynthesis and linking to pathogenesis-related (PR) protein accumulation are not well understood (46, 47). SA plays a crucial role in inducing SAR in plants. It does so by inhibiting catalase activity, leading to an increase in hydrogen peroxide (H_2O_2) levels, which in turn triggers the expression of defense-related genes associated with SAR (48). However, the role of H_2O_2 as a second messenger of SA in SAR signaling is still debated, with some studies suggesting that H_2O_2 may induce SAR gene expression through SA accumulation (49-51). The essential role of SA in SAR is further supported by the finding that transgenic plants with reduced SA levels are defective in inducing acquired resistance (52). Overall, SA's ability to inhibit antioxidant enzymes and promote the accumulation of active oxygen species is a key mechanism in inducing plant resistance (53). Various studies have been done that collectively underscore the diverse and important roles of SA in inducing systemic resistance in various hosts. Researchers highlighted the significance of SA in systemic acquired resistance (SAR), with others emphasizing its cooperation with other SAR-inducing chemicals and others identifying its role in activating BIN2 kinase, which in turn enhances the expression of pathogenesis-related (PR) genes (53-55). Further, the relationship between SA and strigolactones was also explored, showing that the latter can modulate SA-mediated disease resistance (56). Lastly, the potential of SA in enhancing heat stress resistance was also demonstrated in Pleurotus ostreatus through metabolic rearrangement (56).

Jasmonic acid : Recent research has highlighted the crucial role of JA in plant responses to various stresses, including biotic and abiotic stressors (57, 58). JA regulates a wide range of physiological and biochemical processes, such as root growth, reproductive development and defense mechanisms (59, 60). Its signaling pathways, particularly those related to environmental signal perception, biosynthesis and metabolism, have been extensively studied (60). JA is a key player in conferring tolerance to abiotic stresses through its antioxidant potential and crosstalk with other plant growth regulators, making it a valuable target for enhancing plant resilience (61, 62).

JA exhibits a dual role in plant stress responses by mediating both biotic and abiotic stress tolerance mechanisms. In response to biotic stressors like herbivores and pathogens, JA activates defense pathways that enhance the plant's ability to counter these threats by inducing specific defense-related genes. Conversely, under abiotic stress conditions such as drought, salinity and heat, JA orchestrates physiological adjustments to balance growth and stress tolerance. This dual function is mediated by the accumulation of JA-Ile, a bioactive form of JA, which promotes the degradation of JAZ proteins via the SCF^COI1 complex. The removal of JAZ repressors leads to the activation of key transcription factors, such as MYC2, that drive the expression of stress-responsive genes and promote resilience (63).

Notably, JA also contributes to ISR by beneficial microbes. For instance, indigenous endophytic bacteria and N-decanoyl-homoserine lactone have been shown to activate the JA pathway in tomato plants, leading to ISR (14, 64). Additionally, JA-induced β-cyclocitral confers resistance to bacterial blight in rice (65). However, its dual role is further underscored by findings that jasmonic acid oxidase 2 can suppress basal defense responses against *Botrytis cinerea*, suggesting that JA may act as both a positive and negative regulator depending on the context and type of stress (66).

As shown in Fig. 1, JA improves tolerance to abiotic stresses through modulation of physiological and biochemical processes. Fig. 2 illustrates the involvement of JA in activating the Jasmonate-ZIM domain (JAZ) and Jasmonate-associated VQ-Motif GENE1 (JAV1) families, which are central to JA signaling and plant defense. Degradation of JAZ proteins releases transcription factors like MYC2, resulting in transcriptional reprogramming, activation of defense responses and modulation of growth. Furthermore, JA-mediated antioxidant defense systems enhance tolerance by increasing enzymatic and non-enzymatic antioxidant activities, reducing ROS accumulation and upregulating antioxidant enzyme genes (67). Altogether, the context-dependent dual nature of JA underscores its complex but vital role in stress adaptation and plant survival.

Ethylene (ET): Recent research has highlighted the crucial role of key signaling molecules, particularly ET, in the initiation of ISR in plants (68, 69). EIN3/EIL1 transcription factors have been identified as key regulators of ethylene signaling, playing a role in tuning the transcriptional regulation of ethylene response (70). In the interaction between strawberry plants and the plant growth-promoting bacterium *Azospirillum brasilense*, ethylene production and the up-regulation of genes associated with ethylene signaling have been shown to support the priming activation characteristic of ISR (71). Similarly, ethylene signaling is involved in *Azospirillum* sp-B510-induced disease resistance in rice. Furthermore, the role of ethylene in regulating physiological Fe responses in dicot plants has been supported by recent results (72, 73). ET promotes root hair development by activating master regulators EIN3/EIL1, which directly interact with genes controlling hair length and form a transcription complex with RHD6, enhancing root hair initiation

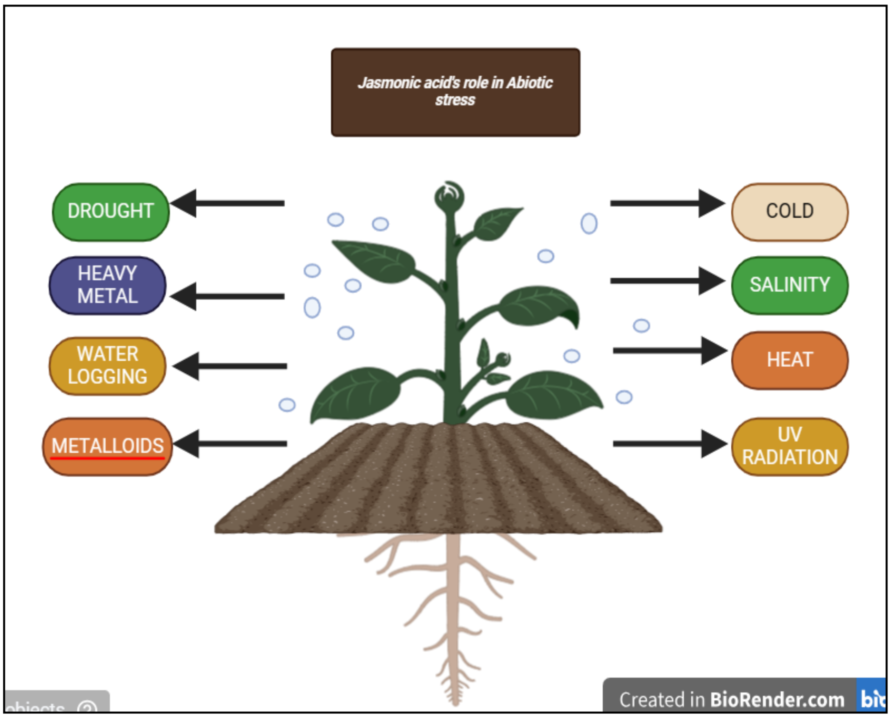

Fig. 1. Figure created using BioRender.com depicting the abiotic stresses in which JA is crucial in improving plant tolerance.

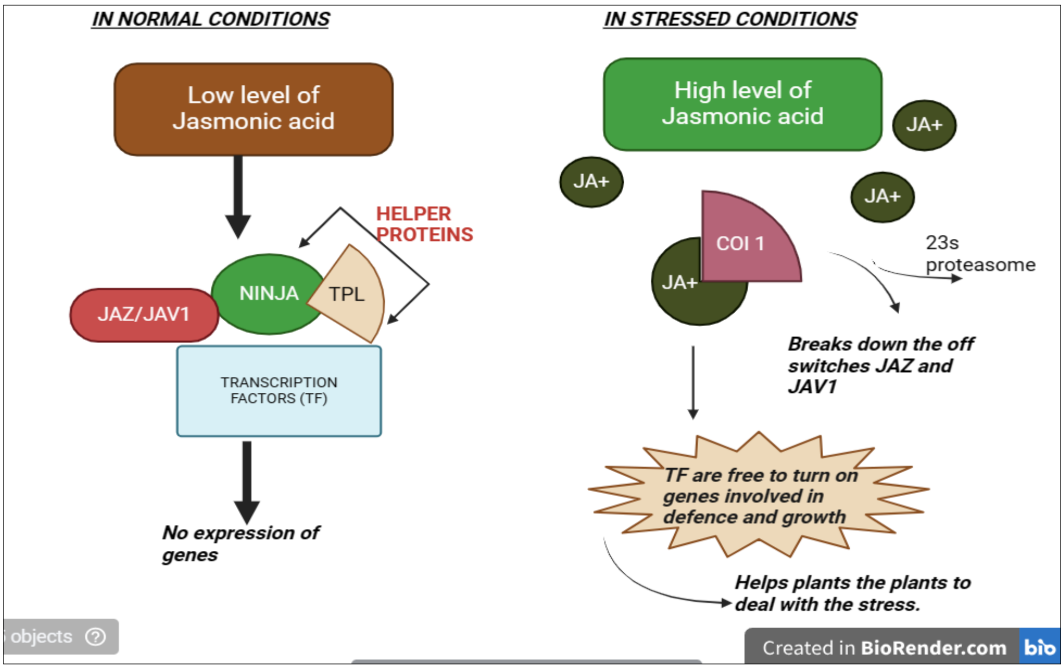

Fig. 2. Figure created using BioRender.com depicting the modulation of the JA signaling pathway under both (a) normal conditions and (b) stress conditions.

and elongation. This complex integrates ET signals with internal pathways, playing a central role in plant adaptability (74). These studies collectively underscore the significance of ethylene and its signaling in the initiation of ISR. Fig. 3 depicts the mechanism of ethylene, illustrating its activity both in the presence and absence thereof.

Priming memory: Recent research has shed light on the phenomenon of plant immune memory, which enhances their

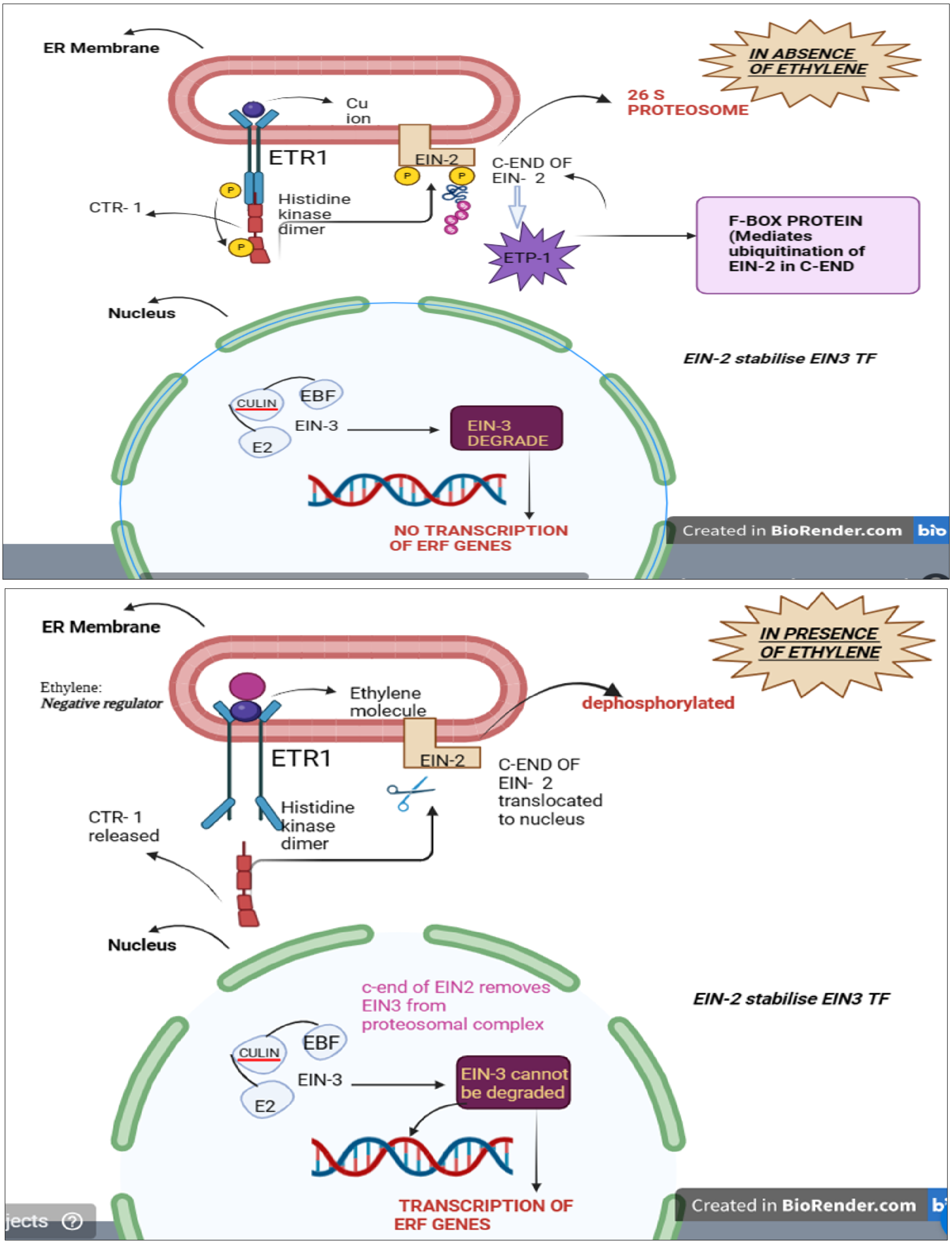

Fig. 3. Figure created using BioRender.com. It depicts the mechanism of ethylene and illustrates what occurs in its presence and absence. (a) shows how EIN2, after being phosphorylated, is degraded, consequently failing to stabilize the EIN-3 transcription factor, which prevents transcription of the Ethylene Response Factor (ERF) genes. On the other hand, (b) demonstrates how, in the presence of ethylene, CTR-1 (Constitutive Triple Response) is released and cleaves the C-terminal of EIN-2. This allows EIN-2 to enter the nucleus and stabilize the EIN-3 transcription factors, resulting in their release from the proteasomal complex and subsequent transcription of ERF genes, which regulate the expression of various defense-related activities.

ability to respond more rapidly to subsequent pathogen exposure (75, 76). This memory is established through physiological, transcriptional, metabolic and epigenetic changes and can be induced through seed priming (75). The immune memory is also influenced by interactions with beneficial microbes, which can boost the plant immune system (77). Furthermore, plants can develop acquired tolerance to multiple abiotic stresses through priming, with the molecular basis of this process being a key area of study (78). Studies explore the evolution of immune memory in insects, showing that it can be shaped by pathogen selection and can lead to the development of different immune strategies (77). In the context of recurrent *Staphylococcus aureus* infection, demonstrating the role of macrophages in conferring protective memory is seen (79). These studies collectively underscore the significance of priming memory in enhancing resistance to pathogens. The development of immune memory is a complex process influenced by various factors, including microbiota. Moreover, the role of microbiota in shaping the immune system and inducing memory responses (80, 81). This is particularly evident in innate immune cells, which can exhibit memory responses through the interaction between pattern recognition receptors and microbe-associated molecular patterns. The role of the environment and lifestyle in the development of immune memory was further emphasized, particularly in invertebrates (81, 82). Further a broader perspective, discusses the mechanisms of adaptation and memory in immunity, which are essential for immune cells to respond effectively to changing environments (83).

Priming memory and implications for crop breeding

Recent research has shed light on the phenomenon of plant immune memory, which enables plants to respond more rapidly and robustly to repeated pathogen attacks through physiological, transcriptional, metabolic and epigenetic changes. This immune memory can be established via seed priming or through beneficial microbe interactions and has been shown to confer acquired tolerance to multiple abiotic and biotic stresses (84). Importantly, the heritability of primed states where offspring inherit enhanced resistance traits offers promising avenues for crop breeding. For example, primed Arabidopsis plants exposed to β-aminobutyric acid (BABA) not only display heightened resistance to *Pseudomonas syringae* but also transmit this trait to subsequent generations, suggesting that priming memory can be stably inherited. Such findings highlight the potential for integrating priming strategies into breeding programs to develop crop varieties with durable, broad-spectrum resistance, reducing reliance on chemical pesticides and enhancing sustainable agriculture (85, 86).

Cross-talk between pathways

Plants exhibit ISR, a well-explored phenomenon triggered by local infections, where a salicylic-dependent signaling cascade activates broad and durable disease resistance against fungi, bacteria and viruses (87). This response entails alterations in cell wall composition, the production of pathogenesis-related proteins like chitinases and glucanases and the synthesis of phytoalexins (88). Notably, ISR interactions with herbivore-induced resistance mediated by JA may lead to cross-resistance or trade-offs, suggesting independent action of elicitation, signaling and defensive compound synthesis (88, 89). Phytohormone crosstalk, particularly involving SA, JA and ET, plays a crucial role in plant defenses against pathogens and insects, finely tuning resistance through a complex signaling network (90). These interactions are mediated by different molecular players, allowing plants to adapt their defense mechanisms against specific threats (88). Although essential for orchestrating responses to various stresses and inducing resistance, the specificity and compatibility of the signaling systems leading to induced resistance remain crucial for a functional understanding of plant responses (91). The cross-talk between signaling pathways is central to how plants tailor their defense responses against diverse pathogens and pests. For instance, in tomato, infection by *Pseudomonas syringae* activates the SA pathway, which can suppress JA-mediated defenses, making the plant more susceptible to necrotrophic pathogens like *Botrytis cinerea*. Conversely, herbivory by *Spodoptera exigua* induces JA signaling, which can antagonize SA-dependent resistance, illustrating the trade-offs that result from pathway cross-talk (92, 93). Another example is rice, where the interaction between SA and JA/ ET pathways determines resistance to *Magnaporthe oryzae* (rice blast) and *Xanthomonas oryzae* (bacterial blight), with the balance of these signals shaping disease outcomes. Understanding such interactions allows for more precise manipulation of plant immunity in breeding and crop management, enabling the development of varieties optimized for resistance to specific pathogens or stress combinations (94). The intricate crosstalk between signaling pathways in induced systemic resistance enables plants to adapt and defend against various biotic stresses, such as pathogens and herbivores, emphasizing the importance of understanding these interactions for effective plant disease management and crop protection (95).

Diversity of bacteria inducing ISR

Several PGPR strains have been identified for their ability to induce systemic resistance in plants (96). This section reviews the key genera and species of PGPR involved in ISR, such as *Pseudomonas, Bacillus* and *Rhizobium*. Non-pathogenic Fusarium certain non-pathogenic strains of *Fusarium* have been found to induce systemic resistance without causing disease. The paper discusses the potential of these strains as biocontrol agents and their mechanisms of action (Table 1).

Challenges and future directions

Integrative approaches and knowledge gaps in ISR research

The exploration of Induced Systemic Resistance (ISR) offers a promising pathway for sustainable crop protection. However, certain gaps in our understanding limit its broader application. Addressing these gaps through integrative approaches can enhance ISR's effectiveness and applicability in diverse agricultural settings. This section highlights three critical areas of improvement: unexplored microbial strains, regional or crop-specific insights and stress combination studies.

Unexplored microbial strains

Beneficial microbes play a pivotal role in inducing ISR, yet research has primarily focused on a few well-characterized strains, such as *Pseudomonas fluorescens* and *Bacillus subtilis*. While these strains have demonstrated significant efficacy, the potential of other microbial species or novel combinations of

Table 1. Overview of research on the potential of various bacterial strains as biocontrol agents and their mechanisms of action

Sl No	Strains	Pathogens	Diseases	Main resistance mechanisms	References
1	*Pseudomonas fluorescens* strains PF1 and FP7	*Rhizoctonia solani* Kuhn (Sexual stage: *Thanetophorus cucumeris* (Frank) Donk)	Sheath blight incidence in rice	*Pseudomonas fluorescens* strains PF1 and FP7 induced systemic resistance (ISR) in plants by activating defense genes, resulting in enhanced expression of peroxidase and chitinase enzymes. These enzymes played a crucial role in reducing disease severity, with chitinase potentially inhibiting fungal growth by degrading chitin in the fungal cell wall. Additionally, *Pseudomonas* strains exhibited plant growth-promoting activities, contributing to increased crop yield.	(131)
2	*Bacillus subtilis* MBI600	*Rhizoctonia solani*, *Pythium ultimum* and *Fusarium oxysporum* f.sp. radicis-lycopersici-Forl.	Fusarium crown and root rot	Showed efficacy as a plant growth-promoting rhizobacterium (PGPR) in tomato crops, promoting growth by inducing auxin production and enhancing nutrient uptake. It efficiently colonized tomato roots across various substrates, exhibiting antibiosis against soilborne pathogens. The BCA induced weak defense responses in early root colonization stages, but increased expression of defense-associated genes was observed at later stages.	(132)
3	*Rhizobium leguminosarum* bv. *viciae* Strain 33504-Mat209	Alfalfa Mosaic Virus	Alfalfa Mosaic Virus in Faba Bean Plants	The strain positively influenced physiological parameters, reduced disease occurrence and severity and decreased AMV accumulation. The protective mechanism involves the induction of SAR, activation of defense-related genes (PR-1 and PR-2), reduction in oxidative stress markers (H_2O_2 and MDA) and stimulation of the biosynthesis of polyphenolic compounds (such as chlorogenic acid and flavonoids), contributing to enhanced resistance against viral infections.	(133)
4	*Azospirillum lipoferum* strain AL-3	*Alternaria solani*	Early blight disease of potato	It acts through direct antagonism against the pathogen, induction of systemic resistance and modulation of defense-related responses, including the upregulation of pathogenesis-related genes, increased SA and hydrogen peroxide levels and enhancement of bound phenolic acids. These mechanisms collectively contribute to the plant's resistance against the fungal pathogen *Alternaria solani*, making *Azospirillum lipoferum* AL-3 a potential biocontrol agent for sustainable disease management in agriculture.	(82)
5	*Bacillus amyloliquefaciens* Strain TBorg1	Tobacco mosaic virus	Tobacco mosaic	The foliar application of TBorg1 culture filtrate (TBorg1-CF) reduced TMV infection, improved plant growth and induced systemic resistance. The mechanism involves the production of secondary metabolites, including phenolic compounds, by TBorg1-CF, resulting in enhanced antioxidant enzyme activities, reduced oxidative stress and increased expression of defense-related genes (C4H, HCT, CHI, PR-1, PR-2, PR-5), contributing to the control of TMV in tomatoes.	(134)
6	*Pseudomonas fluorescens* VSMKU3054	*Ralstonia solanacearum*	Bacterial wilts of tomato	The *Bacillus amyloliquefaciens* strain TBorg1 exhibited antiviral activity against Tobacco Mosaic Virus (TMV) in tomatoes. The foliar application of TBorg1 culture filtrate (TBorg1-CF) reduced TMV infection, improved plant growth and induced systemic resistance. The mechanism involves the production of secondary metabolites, including phenolic compounds, by TBorg1-CF, resulting in enhanced antioxidant enzyme activities, reduced oxidative stress and increased expression of defense-related genes (C4H, HCT, CHI, PR-1, PR-2, PR-5), contributing to the control of TMV in tomatoes.	(135)
7	*Paenibacillus polymyxa* J2-4	*Meloidogyne incognita*	*Meloidogyne incognita* infection in cucumber	Isolated from *M. incognita*-affected ginger plants, *Paenibacillus polymyxa* J2-4 demonstrates effective biocontrol against the nematode in cucumber. It reduces nematode mortality, inhibits infection on potted plants and induces plant resistance through SA and JA signaling. Genomic analysis reveals the presence of gene clusters for antimicrobial compounds, underscoring its potential as a safe biological control agent in agriculture.	(59)

8	*Bacillus cereus* AR156	*Pseudomonas syringae* pv. tomato (Pst) DC3000.	Bacterial speck disease	The plant growth-promoting bacterium *Bacillus cereus* AR156 triggers ISR by activating both SA and JA/ET signaling pathways. This involves miR472-mediated posttranscriptional regulation, targeting a group of nucleotide-binding domain and leucine-rich repeat-containing proteins (CNLs), resulting in increased resistance against the pathogen *Pseudomonas syringae* pv. tomato (Pst) DC3000.	(136)
9	*Streptomyces* sp. SP5	*Fusarium oxysporum*	Fusarium wilt	*Streptomyces* sp. SP5 bioformulations act as biocontrol agents against *Fusarium oxysporum* by inducing systemic resistance in tomato and capsicum plants. The mechanism involves the production of secondary metabolites, such as lyophilized cells in the talc-kaolin bioformulation, leading to enhanced viability, resistance to environmental challenges and effective inhibition of *F. oxysporum*.	(137)
10	*B. megaterium* N8	*F. proliferatum*	Rice sheath rot	*Bacillus megaterium*, used as a biocontrol agent against plant diseases, acts as a PGPR. It colonizes the plant roots, enhancing host defenses against various pathogens. The strain N8 of *B. megaterium*, isolated from paddy soil, exhibits facultative endophyte behavior, reducing rice sheath rot disease incidence and mycotoxin accumulation. It promotes defense enzyme activities, alters the rhizosphere microbiome and induces systemic resistance, ultimately contributing to enhanced plant health and productivity.	(138)
11	*Enterobacter cloacae* PS14	*Ralstonia solanacearum*	Potato wilt	The antagonistic efficacy of *E. cloacae* PS14 is attributed to its ability to produce inhibitory substances, such as antibacterial agents. It induces a systemic resistance response in potato plants, involving increased production of SA, peroxidase, polyphenol oxidase and lipoxygenase. This dual mechanism enhances plant defense, suppresses pathogen growth and significantly reduces disease severity. Additionally, *E. cloacae* PS14 produces siderophores and hydrogen cyanide, contributing to its biocontrol potential against *R. solanacearum*. The findings support the promising application of *E. cloacae* PS14 in biological control strategies for plant diseases.	(139)
12	*Burkholderia contaminans* AY001	*Pseudomonas syringae*	Tomato Fusarium Wilt and Bacterial Speck Diseases	*Burkholderia contaminans* AY001, a novel strain belonging to the *Burkholderia cepacia* complex (Bcc), exerts biocontrol on Fusarium wilt disease in tomato plants through multiple PGPR traits, such as nitrogen fixation, phosphate and zinc solubilization, siderophore and indole-3-acetic acid (IAA) production. Despite lacking direct antibacterial activity against *Pseudomonas syringae* pv. tomato DC3000, AY001 induces systemic resistance (ISR) in tomato plants by upregulating defense -related genes in the JA/ET pathway, thereby enhancing resistance against bacterial pathogens. Additionally, the secondary metabolites identified in AY001's culture filtrate, including di(2-ethylhexyl) phthalate, octadec-9-enoic acid and 2-ethyl-1-hexanol, contribute to its biocontrol efficacy against various plant pathogens.	(140)
13	*Serratia plymuthica* IC1270	*Magnaporthe oryzae*	rice blast disease	The study indicates that IC1270-induced ISR acts as a double-edged sword, enhancing resistance to certain pathogens while increasing susceptibility to others. The mechanism involves ROS-mediated defense responses.	(141)
14	*Bacillus licheniformis* strain POT1	Genus: *Alfamovirus* , Family: *Bromoviridae*	Alfalfa mosaic virus in potato	The mechanism of *Bacillus licheniformis* strain POT1's antiviral activity involves the induction of plant defense responses, specifically the upregulation of genes in phenylpropanoid, chlorogenic acid and flavonoid biosynthetic pathways. The bacterial culture filtrate, containing secondary metabolites, activates ISR in potato plants against Alfalfa mosaic virus (AMV), leading to increased resistance by limiting viral accumulation, symptom severity and promoting the biosynthesis of various antimicrobial compounds, including polyphenols and flavonoids. Additionally, the ethyl acetate extract of POT1 is rich in pyrrolo(1, 2-a) pyrazine-1,4-dione, a compound with reported antiviral and antioxidant activities, suggesting its potential role in preventing viral replication.	(14242)

15	*Arthrobacter* spp. strain AA	*Zymoseptoria tritici*	Septoria tritici blotch (STB)	The research explored the influence of Mix-2, comprising Arthrobacter strain AA (AA) and *Paenibacillus* sp. strain B2 (PB2) (1:1), on wheat genotypes concerning root colonization and defense mechanisms. In Alixan, Mix-2 triggered substantial upregulation of genes involved in basal defense, JA signaling, phytoalexin and phenylpropanoid pathways, ROS pathway and defense and cell rescue. Similarly, in Cellule, Mix-2 induced the upregulation of genes associated with basal defense, JA signaling, phytoalexin and phenylpropanoid pathways, ROS pathway and defense and cell rescue. Mix-2 exhibited varying protective effects against Z. tritici strains across wheat genotypes and growth stages, highlighting its potential as a bioinoculant to enhance wheat resistance and growth in diverse conditions.	(143)
16	*Stenotrophomonas maltophilia* Sg3	*Nicotiana tabacum*	Cucumber mosaic virus (CMV)	*Stenotrophomonas maltophilia* Sg3 induces antiviral activity against Cucumber mosaic virus (CMV) in tobacco by significantly reducing virus accumulation, suppressing symptoms and promoting plant growth, possibly mediated by the production of the compound 2-naphthalene-sulfonic acid.	(144)
17	*Sphingomonas Strains*	*Pseudomonas syringae*		*Sphingomonas* spp. exhibit antagonistic effects through preemptive colonization of leaf surfaces, competing for nutrients like photoassimilates and potentially producing antimicrobial compounds. Their ability to protect plants is linked to their abundance on leaves and the utilization of specific organic compounds, indicating a nutritional niche overlap with the pathogen *P. syringae* pv. tomato DC3000. The findings suggest that these bacteria serve as effective antagonists in the phyllosphere, potentially strengthening plant defenses against foliar pathogens. While other mechanisms like competition for macroelements and space, as well as the stimulation of systemic host responses, are proposed, additional experiments are needed for validation.	(145)
18	*Lysobacter gummosus* OH17	*Magnaporthe oryzae, Rhizoctonia solani and Xanthomonas oryzae pv. oryzae.*	Rice blast, rice sheath blight, bacterial leaf blight	*Lysobacter gummosus* OH17 enhances disease resistance in rice by inducing overexpression of key genes in the jasmonic acid and ethylene pathways (OsACC, OsACO, OsERF3, OsLOX), resulting in increased production of pathogenesis-related proteins. These metabolic effects contribute to heightened resistance against major rice pathogens, including *Magnaporthe oryzae*, *Rhizoctonia solani and Xanthomonas oryzae* pv. oryzae.	(146)
19	*Xenorhabdus bovienii*	*Meloidogyne incognita*	Root-knot nematodes	*Xenorhabdus* inhibits *Meloidogyne incognita* by producing ammonium, a nematicidal compound that adversely affects the nematode, resulting in mortality.	(147)
20	*Klebsiella oxytoca*	*Potato virus Y (PVY)*	potato tuber necrotic ringspot disease (PVYNTN)	The exact mechanism through which *Klebsiella oxytoca* works to suppress the development of Potato virus Y (PVY) involves the activation of the host plant's innate immune system and/or the induction of systemic resistance. This activation or induction subsequently inactivates and/or inhibits PVY replication. The study suggests that *Klebsiella oxytoca* may enhance the natural defenses and detoxification processes in the host plant, leading to more rapid and effective responses to viral inoculation. Additionally, the application of *Klebsiella oxytoca* and biochar prior to PVY inoculation improves growth parameters, elevates the antioxidant system, modulates gene expression and activates plant defense marker genes in both SA and JA signaling pathways. These combined effects contribute to the suppression of PVY and enhance the plant's resistance to viral infection.	(148)
21	*Pasteuria penetrans*	*Meloidogyne incognita*	root galling in tomato and banana plants	In this work, the positive impact of specific bacteria, including *Pasteuria penetrans*, on controlling the nematode *Meloidogyne incognita* in tomato and banana plants. Through greenhouse and microplot experiments, plants treated with these bacteria exhibited improved growth, reduced root galling and decreased nematode reproduction compared to untreated plants. Notably, bacteria *like B. subtilis, P. fluorescens, A. radiobacter and B. cepacia* showed significant benefits in promoting plant growth and suppressing nematode damage. Changes in root gall size and shape in tomatoes suggest the potential activation of systemic resistance or defense mechanisms.	(149)

microbial consortia remains largely untapped. For instance, emerging evidence suggests that less-studied genera like *Paenibacillus*, *Serratia* and *Burkholderia* could harbor unique ISR-inducing traits. These microbes may produce distinct metabolites or signaling molecules capable of triggering enhanced plant immune responses (60, 97). For example, *Paenibacillus polymyxa* was shown to induce ISR in tomato plants against *Fusarium oxysporum*, improving both yield and pathogen resistance (98). Similarly, *Serratia plymuthica* enhanced ISR in cucumber by upregulating defense genes associated with the JA/ET pathway (99). *Burkholderia phytofirmans* PsJN has also demonstrated ISR potential across multiple crops, including grapevine and Arabidopsis (100, 101).

Moreover, the concept of microbial consortia-where multiple strains work synergistically is a promising area for research. Such consortia could target multiple plant defense pathways simultaneously, potentially increasing ISR efficacy against a broader range of pathogens (102). For example, combining a strain that activates the SA pathway with another that enhances JA or ET signaling could yield more robust and comprehensive resistance. A notable example is the synergistic use of *Bacillus amyloliquefaciens* in chili, which triggered both SA and JA/ET pathways, offering broad-spectrum resistance against bacterial and fungal pathogens (103). Systematic screening and functional validation of these underexplored microbes and their interactions will be essential to advancing ISR-based solutions.

Regional or crop-specific inputs

In real-field conditions, plants are rarely subjected to a single stressor. Instead, they often face biotic and abiotic stresses, such as pathogen attacks coinciding with drought or salinity. Understanding how ISR mechanisms function under such combined stress scenarios is crucial for developing resilient agricultural systems. Current research has largely focused on ISR against isolated biotic stresses, leaving a significant gap in knowledge regarding its efficacy in multi-stress environments (92, 96). For example, drought can cause changes in a plant's body that may disrupt the signals needed to start ISR, which depends on molecules like SA, JA and ET. On the other hand, ISR can help plants deal with drought and other stresses by boosting their antioxidant defenses and keeping cells stable (104). Studies that mimic these combined stresses can help us understand how they interact. Also, using modern tools like transcriptomics and metabolomics can reveal how ISR and stress responses work together at the molecular level (105). Doing focused research in this area can greatly improve both scientific knowledge and real-world farming practices. By studying less-known helpful microbes, creating specific solutions for different crops and regions and understanding how plants handle multiple stresses at once, we can make ISR a strong and flexible method for sustainable farming. These combined efforts are key to making crops stronger and more productive in today's changing climate.

Mechanistic approach: This review gave us the idea of the mechanistic depth of ISR involving complex molecular crosstalk between key signaling pathways, such as SA, JA and ET, with other stress response pathways like ABA and ROS. These interactions reveal that while ISR pathways promote systemic defense, ABA can antagonize SA- or JA-mediated responses, requiring a balanced regulatory mechanism, particularly under drought or salinity stress. ROS, acting as secondary messengers, amplify ISR signaling through MAPK cascades, a phenomenon validated through co-treatment experiments using ISR-inducing PGPR strains and ABA/ROS modulators, coupled with transcriptional and reporter-based assays. Another emerging area is ISR-induced epigenetic memory, where heritable changes, such as DNA methylation, histone modifications (e.g., H3K4me3) and non-coding RNAs, prime plants for enhanced stress tolerance across generations (97, 98). Techniques like CRISPR-based epigenome editing and RNA-seq analysis of ISR-primed progeny could unlock new breeding strategies for resilient crops (106, 107). Furthermore, advances in omics technologies, including transcriptomics and proteomics, have uncovered novel ISR markers and regulatory elements. RNA-seq highlights ISR-specific transcription factors like TGA and WRKY families, while proteomics identifies pathogenesis-related proteins and enzymes crucial for defense (108, 109). Additionally, non-coding RNAs, such as miRNAs and lncRNAs, play vital roles in modulating ISR, as seen in miR393's regulation of auxin signaling (110). These discoveries, validated through gene silencing, overexpression and comparative omics analyses, provide a comprehensive understanding of ISR's molecular foundations and its potential for sustainable agriculture.

Practical applications and challenges

The application of ISR in agriculture holds immense potential for sustainable pest and disease management. However, the transition from controlled laboratory studies to practical field-level applications presents significant challenges that must be addressed to realize ISR's full potential.

Field-level validation

One of the key challenges in implementing ISR strategies lies in translating promising laboratory results into consistent field success. While lab experiments are typically conducted under controlled, optimal conditions, real-world agricultural environments are far more variable and unpredictable. Factors such as soil type, temperature, moisture levels and crop management practices can significantly influence the survival, activity and effectiveness of ISR-inducing agents. Moreover, the presence of native microbial communities may alter or inhibit the performance of introduced beneficial microbes, raising concerns about the reliability of ISR under diverse field conditions (111).

Despite these challenges, several field studies have reported successful applications of ISR. For instance, PGPR applied as seed treatments or soil drenches in cucumber fields have led to disease suppression, improved early-season growth and yield increases of up to 75 % (112). In chickpea, seed treatments using chemical inducers such as Bion, salicylic acid and K_2HPO_4 have been shown to reduce Fusarium wilt incidence by as much as 63 %, with noticeable improvements in yield (113). Similarly, treatments targeting Ascochyta blight demonstrated significant disease reduction, with salicylic acid and Bion emerging as particularly effective agents (113). Additionally, various *Bacillus* species have proven capable of eliciting ISR in multiple crops, offering broad-spectrum protection by activating distinct signaling pathways compared to *Pseudomonas*-induced ISR (114). Collectively, these examples provide strong evidence for the potential of ISR as a viable and sustainable disease management strategy under field conditions.

Another critical aspect is cost-effectiveness. The scalability of ISR technologies requires a detailed cost-benefit analysis to ensure their economic viability for farmers. High production costs, storage requirements and the potential need for repeated applications can deter widespread adoption. Addressing these challenges requires interdisciplinary research and collaboration among microbiologists, agronomists and economists to optimize ISR technologies for field deployment.

Biocontrol formulation development

Effective ISR application requires innovative formulations to ensure microbial survival and targeted delivery. Techniques like microencapsulation (e.g., using alginate or chitosan) protect microbes from environmental stress and allow controlled release in the rhizosphere. Seed coating is another practical method, enabling early root colonization and reducing application frequency. Emerging nanocarriers and biodegradable films enhance stability and adherence to plant surfaces. Formulations must also maintain viability during storage; thus, cryoprotectants (like trehalose) and dry carriers are used. Combining ISR agents with biofertilizers or micronutrients is also being explored for added benefits in the field (14, 62, 115).

Integration with climate resilience

Using ISR in farming shows strong potential for dealing with climate-related challenges (116). However, extreme weather like heatwaves, floods, or high CO_2 levels can change how plants defend themselves and how helpful microbes perform (117). For example, high temperatures can affect the production of plant defense hormones such as SA, JA and ET, which are important for ISR. Studying these effects can help improve the use of ISR in regions facing tough climates.

ISR also supports environmental health. Healthier plants grow more and store more carbon, helping to reduce CO_2 in the atmosphere. The good microbes involved in ISR can also improve soil health by increasing microbial diversity, which supports better nutrient cycling and carbon storage. This shows that ISR can be useful not only for protecting crops but also for fighting climate change. Future research should explore how ISR can be combined with climate-smart farming methods like crop rotation, agroforestry and conservation agriculture. New technologies such as microbe coating could help ISR work better under extreme weather.

Climate-adaptive ISR strategies are already being used in some crops. For example, in sugarcane farming, predictive modeling, pest monitoring and precision agriculture are used to manage climate-related pest problems (118). In India, farmers are using crop diversification, efficient water use and local ISR-based methods to cope with changing climates (119). In coastal areas, strategies like marsh elevation and shoreline protection help adapt to sea-level rise (120). These examples show how ISR can be part of larger, climate-resilient farming systems.

Also, recent tools have made it easier to measure and track carbon storage. Technologies like InSAR (Interferometric Synthetic Aperture Radar) have helped measure carbon capture in peatlands (121). Remote Sensing (RS) and GIS are low -cost and accurate ways to measure carbon over large areas (122, 123). These tools use sensors like optical, radar and LiDAR to estimate plant biomass and carbon, especially in dry regions (123). Still, measuring carbon precisely is a challenge and using fixed targets instead of changing baselines may improve accuracy (124). These advancements are essential for managing carbon and helping agriculture respond to climate change.

Quantitative analysis and predictive models

The integration of quantitative analysis and predictive modeling is vital for advancing the practical application of ISR in sustainable agriculture. Predictive modeling tools offer a strong framework to understand and forecast ISR activation dynamics across varying crops, climatic conditions and soil types. Such models can simulate interactions between plants and ISR-inducing microbial strains under diverse environmental conditions, providing insights into optimal scenarios for ISR activation. These models are capable of precisely evaluating the biological, chemical and physical properties of soil, offering potential applications in predicting crop yields (88). For instance, computational approaches like machine learning algorithms and systems biology models can predict the influence of specific soil microbiomes and environmental stressors on ISR efficacy. These tools not only enhance our understanding of ISR mechanisms but also assist in formulating precision agriculture strategies tailored to specific regional requirements. Systems biology approaches, integrating multi-omics datasets and network analyses, offer comprehensive insights into plant-pathogen interactions (125). Environmental stressors like acidity and metalloid poisoning significantly impact soil microbial diversity and enzymatic activity, which can be analyzed using machine learning tools (126).

Economic impact studies are equally crucial to evaluate the feasibility of large-scale adoption of ISR-based practices. By conducting comprehensive cost-benefit analyses, researchers can assess the economic viability of using ISR-inducing agents compared to traditional pest and disease management methods (127). This involves quantifying the reduction in chemical pesticide use, improvements in crop yield and the potential cost savings for farmers. Additionally, such studies can explore the long-term benefits of ISR adoption, including improved soil health, reduced environmental degradation and enhanced sustainability in agricultural systems (71). Socioeconomic analyses further broaden the perspective by addressing the implications of ISR on farming communities. Scaling up ISR practices may lead to shifts in labor dynamics, market structures and policy frameworks. For smallholder farmers, particularly in developing regions, ISR can serve as an accessible and cost-effective alternative to expensive chemical inputs, potentially improving livelihoods and food security. However, economic models must also account for initial investments in microbial inoculants, field-level validation processes and potential barriers to market entry.

By combining predictive modeling and economic analyses, future research can pave the way for informed decision-making, fostering the widespread adoption of ISR-based practices. This dual approach ensures that ISR not only meets ecological and scientific goals but also delivers tangible benefits to farmers and agricultural stakeholders worldwide.

Technological innovations

The integration of technological advancements in biotechnology and precision agriculture offers transformative opportunities for enhancing ISR mechanisms and applications. These innovations not only improve the efficacy of ISR but also make its implementation more feasible and scalable for modern agricultural practices.

Biotechnology and genetic engineering

Recent breakthroughs in gene-editing tools, particularly CRISPR -Cas systems, have opened new avenues for tailoring ISR traits in both plants and microbes (128). Genetic engineering can be employed to modify ISR-inducing microbial strains to enhance their survival, colonization efficiency and resistance-inducing capabilities under diverse environmental conditions. For example, targeted edits in genes regulating the biosynthesis of volatile organic compounds, lipopolysaccharides and siderophores can amplify their role in triggering plant immune responses. Similarly, CRISPR-Cas technology can be utilized to engineer plant genomes, enhancing their sensitivity to microbial elicitors and boosting the efficiency of ISR pathways. Such modifications include fine-tuning SA, JA and ET signaling networks, as well as introducing or activating stress-resilient traits through epigenetic mechanisms. These advancements hold promise for creating crop varieties that are inherently more resistant to a wide range of biotic and abiotic stresses.

Precision agriculture integration

Precision agriculture, driven by sensors, data analytics and Artificial Intelligence (AI), offers a powerful platform to optimize the application of ISR-inducing agents. Sensors can monitor soil health, microbial diversity and plant physiological responses in real-time, enabling site-specific application of beneficial microbes (129). AI algorithms can analyze these data streams to predict disease outbreaks and recommend tailored ISR-inducing interventions (130). For instance, microbial consortia can be applied at precise dosages and timings to ensure maximum efficacy under varying climatic and soil conditions. Additionally, advanced delivery mechanisms such as seed coatings and encapsulated formulations can be integrated into precision agriculture systems to ensure sustained microbial viability and gradual release in the field.

By leveraging these technological innovations, the full potential of ISR can be harnessed to enhance crop resilience, reduce chemical inputs and achieve sustainable agricultural intensification in a rapidly changing global environment.

Conclusion

ISR, particularly through PGPR, stands out as a promising strategy for achieving sustainable agriculture. This review has highlighted the diversity of beneficial microorganisms, their molecular mechanisms including the pivotal roles of SA, JA and ET and the importance of priming memory in shaping plant immunity. The intricate crosstalk between these signaling pathways enables plants to mount precise and robust defenses, while PGPR contribute to enhanced plant growth, stress tolerance and disease suppression. To fully harness the potential of ISR, future research should prioritize the elucidation of strain-specific mechanisms, the integration of omics approaches and the translation of laboratory findings to field conditions. There is a pressing need to explore the long-term impacts of ISR on crop productivity, soil health and ecosystem resilience, as well as to assess its compatibility with existing agricultural practices and crop varieties. Interdisciplinary collaboration among plant biologists, microbiologists, agronomists, breeders and data scientists will be essential for developing holistic management strategies that combine ISR with other sustainable practices. By fostering such collaborations, the agricultural community can accelerate the development of resilient crop varieties, reduce reliance on chemical inputs and address the challenges posed by climate change and global food security.

In summary, advancing ISR research and its practical application requires a concerted, interdisciplinary effort. By bridging fundamental discoveries with real-world implementation, ISR can become a cornerstone of sustainable agriculture and a key contributor to future global food security.

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Authors' contributions

DS drafted the manuscript. JS and AJD were responsible for formatting the manuscript. MB and RN conceptualized the study and reviewed the entire work. All authors read and approved the final version of the manuscript.

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