



Review

Beneficial Microorganisms as a Sustainable Alternative for Mitigating Biotic Stresses in Crops

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Abstract: Nowadays, population growth, the global temperature increase, and the appearance of emerging diseases in important crops generate uncertainty regarding world food security. The use of agrochemicals has been the “go-to” solution for the control of phytopathogenic microorganisms, such as *Magnaporthe oryzae*, causing blast disease in rice and other cereals; *Botrytis cinerea*, causing gray mold in over 500 plant species; and *Puccinia* spp., causing rust in cereals. However, their excessive use has harmed human health, as well as ecosystems (contaminating water, and contributing to soil degradation); besides, phytopathogens can develop resistance to them. The inoculation of plant growth-promoting microorganisms (PGPMs) to crops is a sustainable strategy for increasing the yield and quality of crops and mitigating biotic stresses. Likewise, PGPMs, such as *Pseudomonas*, *Bacillus*, and *Trichoderma*, can trigger a series of signals and reactions in the plant that lead to the induction of systemic resistance, a mechanism by which plants react to microorganism stimulation by activating their defense system, resulting in protection against future pathogen attack. These plant defense mechanisms help to mitigate biotic stresses that threaten global food security. Thus, the study of these mechanisms at molecular, transcriptomic, and metabolomic levels is indispensable to elucidate how stresses affect globally important crops.

Keywords: induced systemic resistance; systemic acquired resistance food security; biological control



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1. Introduction

As the world population is estimated to grow to more than 9 billion people by 2050, agriculture and the world’s crop production face significant challenges to increase production and yields. In addition, a shortage of arable land and the impact of climate change are also threats to food safety [1]. Plants experience natural stresses such as temperature change, water deficit, mineral deficiency, pests, and anthropogenic activities (an intensive application of herbicides, pesticides, fungicides, and fertilizers), which cause a loss in crop yield [2].

In plants, stress can be defined as any unfavorable condition or substance that affects or blocks a plant’s metabolism, growth, or development [3] and generally refers to environmental changes [4]. Thus, stress can be divided into two categories: abiotic and biotic. Abiotic stress refers to environmental factors such as physical or chemical, while biotic stress exposes plants to biological units such as diseases and predators [4].

Biotic stress in plants can be caused by one or multiple pathogens. Moreover, a type of phytopathogen can cause disease in different crops; due to this, plants have developed mechanisms of identification, control, and resistance to these diseases [5,6]. The reactions to biotic and abiotic stress negatively affect the crops since it limits their growth, development,

yield, and quality [7]. These can hamper the quality and proportion of agricultural products, threatening food security [8].

There are predictions of the significant effects on agricultural production caused by the global temperature increase by the end of the century [9,10]. Climate change can cause the appearance of new diseases and modify the severity of existing ones [11]. Pests and diseases are among the major causes of lost crop production, estimated as between 20% and 40% of losses to yield, with significant consequences for livelihoods, public health, and the environment [12]. The annual yield losses caused by crop pests and diseases are estimated at USD 220 billion [12]. Globally, three of the most important plant diseases caused by phytopathogenic fungi are rice blast disease (caused by *Magnaporthe oryzae*), gray mold (*Botrytis cinerea*), and rust (*Puccinia* spp.) [13,14]. The first one is the most destructive disease of rice worldwide; infections caused by *M. oryzae* lead to the annual destruction of approximately 10–30% of the rice harvested globally. Some analysts estimate that it destroys harvests that could feed 60 million people each year [15]. Gray mold is a disease caused by *B. cinerea*, having a host range of more than 500 plant species; it is especially damaging to fresh fruits and vegetables, making it the most important post-harvest disease, with annual economic losses easily exceeding USD 10 billion worldwide [16]. *Puccinia* spp. cause major crop losses, threatening food security and the sustainability of crop production in 31 countries across the world [17]. In wheat, three major rust pathogens (stripe rust (*P. graminis* f. sp. *striiformis*), stem rust (*P. graminis* f. sp. *tritici*), and leaf rust (*P. triticina*)) impact wheat production, causing losses of USD 4.3 to 5 billion annually, with resulting yield losses of 6–7 million metric tons per year [18]. However, the use of agrochemicals to maximize crop yields and control pests and diseases has had adverse repercussions on the environment and human health. Thus, sustainable agriculture through beneficial microorganisms is an effective way to satisfy the food demand and maintain functioning and healthy ecosystems [19]. The main objectives of this review are to summarize current knowledge on how different biotic stresses affect globally important crops and threaten world food security, and to focus on how plants combat these stresses through their defense systems.

2. Plants Biotic Stress: Interactions between Plants and Pathogens

Plants have a diversity of microorganisms inhabiting them, both below and above-ground, including endophytes (*Pseudomonas*, *Bacillus*, *Burkholderia*) [20], epiphytes (*Pseudomonas*, *Erwinia*, *Pantoea*) [21], phyllosphere (*Methylobacterium*, *Microbacterium*) [22], and/or rhizosphere (*Rhizobium*, *Agrobacterium*, *Pseudomonas*, *Stenotrophomonas*, *Bacillus*) [23,24]. These microorganisms can establish close and complex beneficial or pathogenic relationships with plants. The functions of microorganisms in plants are diverse and range from interactions that can be synergistic, antagonistic, and mutualistic, and they are modulated by multiple and complex biotic and abiotic factors [25]. In this sense, some microorganisms cause plant diseases (phytopathogens), generating production and quality losses, making them a considerable threat and some of the biggest obstacles to global food security, such as species of the genera *Botrytis*, *Colletotrichum*, *Fusarium*, *Magnaporthe*, *Mycosphaerella*, *Phytophthora*, *Puccinia*, *Sclerotinia*, and *Xanthomonas*, among many others [13,26,27]. However, several microorganisms have shown a beneficial effect on vegetal growth, development, and overall agricultural production (known as plant growth promoter microorganisms, PGPMs), increasing the interest in integrating them as alternatives to chemical products in sustainable agriculture [25]. Thus, knowing these plant–microorganism interactions, and the factors involved in them, can lead to a better understanding of how plants deal with biotic stresses and how to improve their management [28]. For example, in 2021, Nifakos et al. [29] used a genome mining approach and chemical analysis to elucidate the main mechanism of biocontrol of *Botrytis cinerea* by *Bacillus velezensis* Bvel1 in grape berries. They found that preventive treatment with Bvel1 cell culture before *B. cinerea* inoculation strongly suppressed fungal growth and significantly reduced the incidence of gray mold on red globe grapes. Their analysis showed that Bvel1 is capable of producing and secreting

a mixture of bioactive diffusible secondary metabolites (iturin A2, surfactin A-C13 and -C15 isoforms, oxydifficidin, L-dihydroantcapsin, bacillibactin) and specialized metabolites (azelaic acid) that are known to exert a strong antifungal activity and/or trigger host plant defenses against pathogens [29].

Plants are healthy when they carry out their physiological functions to the best of their genetic potential [5]. Microbial pathogens (such as fungi, bacteria, viruses, and/or nematodes) cause plant diseases and biotic stress that limit this potential and cause considerable losses in agriculture, horticulture, and forestry, which is known as a disease [5,30].

Plant disease results from the interaction between the plant, the pathogen, and the environment. This concept is known as the disease triangle and states that for a disease to occur, a susceptible plant host, a virulent pathogen, and the proper environmental conditions are required, as a lack of any of these three factors results in the disease failing to develop (Figure 1) [27].

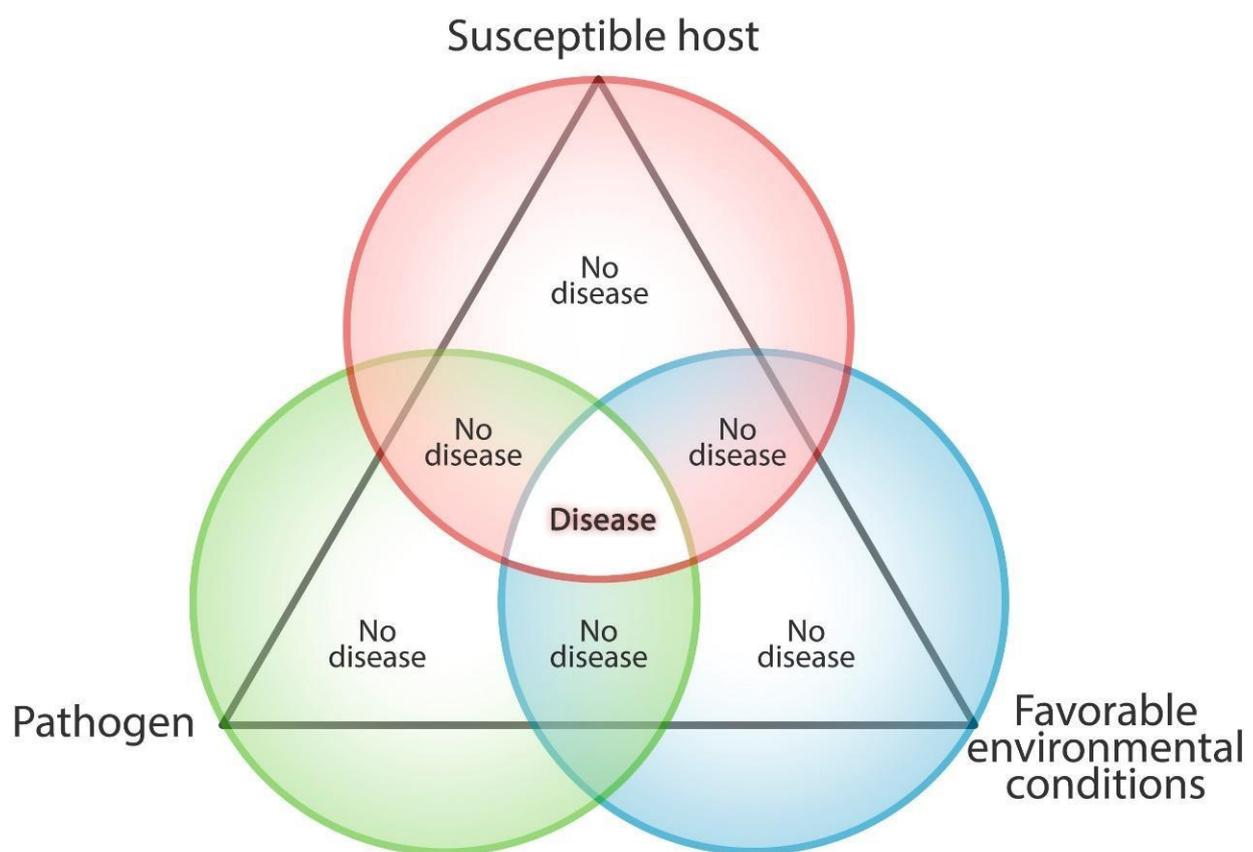


Figure 1. Disease triangle showing the interactions needed for the development of biotic stress in plants.

Phytopathogens generate the natural resistance of plants, which combines the effects of barriers and inducible mechanisms, based on physical (waxy cuticle, active closure of stomatal pores) and biochemical (ROS accumulation, hypersensitive response, PAMP-triggered immunity) defenses [31]. For a pathogenic microorganism to infect a plant, there must be (i) a union to the surface to begin with the degradation of physical and chemical barriers of the host, (ii) a production of toxins, and (iii) an inactivation of the plant defenses [32]. After the pathogen achieves infection successfully, a disease is developed (Table 1) and biotic stress is present.

Table 1. Interactions between pathogens and host plants.

Pathogen	Host	Disease	Type	Reference
<i>Ustilago maydis</i>	Corn	Smut	Biotrophic	[33]
<i>Phytophthora capsici</i>	Tomato, pepper, other solanaceous, and cucurbit plants	Root rot, stem necrosis, foliar blight, and fruit rot	Hemibiotrophic	[34]
<i>Botrytis cinerea</i>	Strawberry, grape, raspberry, blackberry	Gray mold, post-harvest rots	Necrotrophic	[35]
<i>Bipolaris sorokiniana</i>	Wheat	Blotch spot	Necrotrophic	[36]
<i>Fusarium oxysporum</i>	Cucumber	<i>Fusarium</i> wilt	Hemibiotrophic	[37]
<i>Septoria nodorum</i> Berk	Wheat	Glume blotch	Hemibiotrophic	[38]
Tobacco mosaic virus	Tobacco	Mosaic virus disease	Biotrophic	[39]
<i>Agrobacterium tumefaciens</i>	Wild grape species (<i>Vitis riparia</i>)	Formation of tumors, rod-shaped, crown gall disease	Biotrophic	[40]
<i>Erysiphe orontii</i>	Tobacco	Powdery mildew diseases	Hemibiotrophic	[41]
<i>Fusarium solani</i>	Orange trees (<i>Citrus sinensis</i> L. Osbeck)	Darkening of the vascular system	Hemibiotrophic	[42]
<i>Erwinia amylovora</i>	Apple trees	Fire blight disease	Semi-necrotrophic or necrotrophic	[43]

3. Plants' Response to Biotic Stress: Systemic Acquired Resistance (SAR)

The first line of defense of plants against pathogens and biotic stress is their physical barriers, such as the waxy cuticle and active closure of stomatal pores, but depending on whether the pathogen is a virus, bacteria, or filamentous microorganism, the pathogen possesses mechanisms to overcome those barriers [44]. Pathogens that can overcome these barriers access the plant's apoplast, where the pathogen is perceived and recognized through transmembrane proteins called pattern recognition receptors (PRRs), which recognize specific, conserved microbial features named pathogen-associated molecular patterns (PAMPs) [44,45]. Successful pathogens deploy a diversity of effectors that suppress PAMP-triggered immunity (PTI) through susceptibility (S) proteins (effector targets), allowing plant cell infection and resulting in effector-triggered susceptibility (ETS). For pathogen detection, plants have evolved mechanisms that specifically recognize and respond to pathogens' effectors. This interaction was observed between pathogens carrying single dominant genes (avirulence genes) that caused them to be recognized by plant hosts carrying single dominant resistance (R) genes, leading to the gene-for-gene interaction [46,47]. Thus, when pathogens are recognized and fail to cause disease, they are called avirulent pathogens, the host is called resistant, and the interaction is called incompatible [48]. On the other side, in the absence of gene-for-gene recognition, the pathogen is virulent, the host is susceptible, and the interaction is compatible, resulting in pathogen proliferation within the plant cells and the onset of disease and biotic stress in the plant host [47,48].

PTI is the first active plant response to pathogen recognition. PTI consists of diverse cellular responses, including reactive oxygen and calcium bursts, mitogen-activated protein kinase (MAPK) signaling, plant hormone responses, transcriptional reprogramming, and cell wall fortification [47,49]. One of the earliest physiological responses in PTI is an influx of extracellular Ca^{2+} in the cytosol (a calcium burst). It induces the opening of other membrane transporters (influx of H^+ , efflux of K^+ , Cl^- , and NO_3^-), which results in an extracellular alkalization and depolarization of the plasma membrane [37]. These changes are detected by Ca^{2+} sensors, such as calmodulin (CaM), calmodulin-like protein (CML), or calcium-dependent protein kinase (CDPK), and it signals the hypersensitive response (HR), a programmed cell death at the site of infection, as well as rapid production of reactive oxygen species (ROS) [50].

The generation and accumulation of ROS include hydrogen peroxide (H_2O_2), superoxide anion, and hydroxyl radicals [51]. H_2O_2 is an active signaling molecule and its accumulation results in a variety of cellular responses as hypersensitive cell death [52], and blocks the cell cycle progression [53]. It also functions as a developmental signal for the onset of secondary wall differentiation and is an activator of mitogen-activated protein kinases (MAPKs) [51].

A local HR is often associated with the onset of systemic acquired resistance (SAR) in distal plant tissues, as signals derived from cells undergoing the HR contribute significantly to the induction of defense gene transcription in adjacent cells [54,55]. These include mechanisms such as salicylic acid (SA) accumulation, pathogenesis-related (*PR*) gene expression, and long-lasting resistance to pathogen infection [56] (Figure 2).

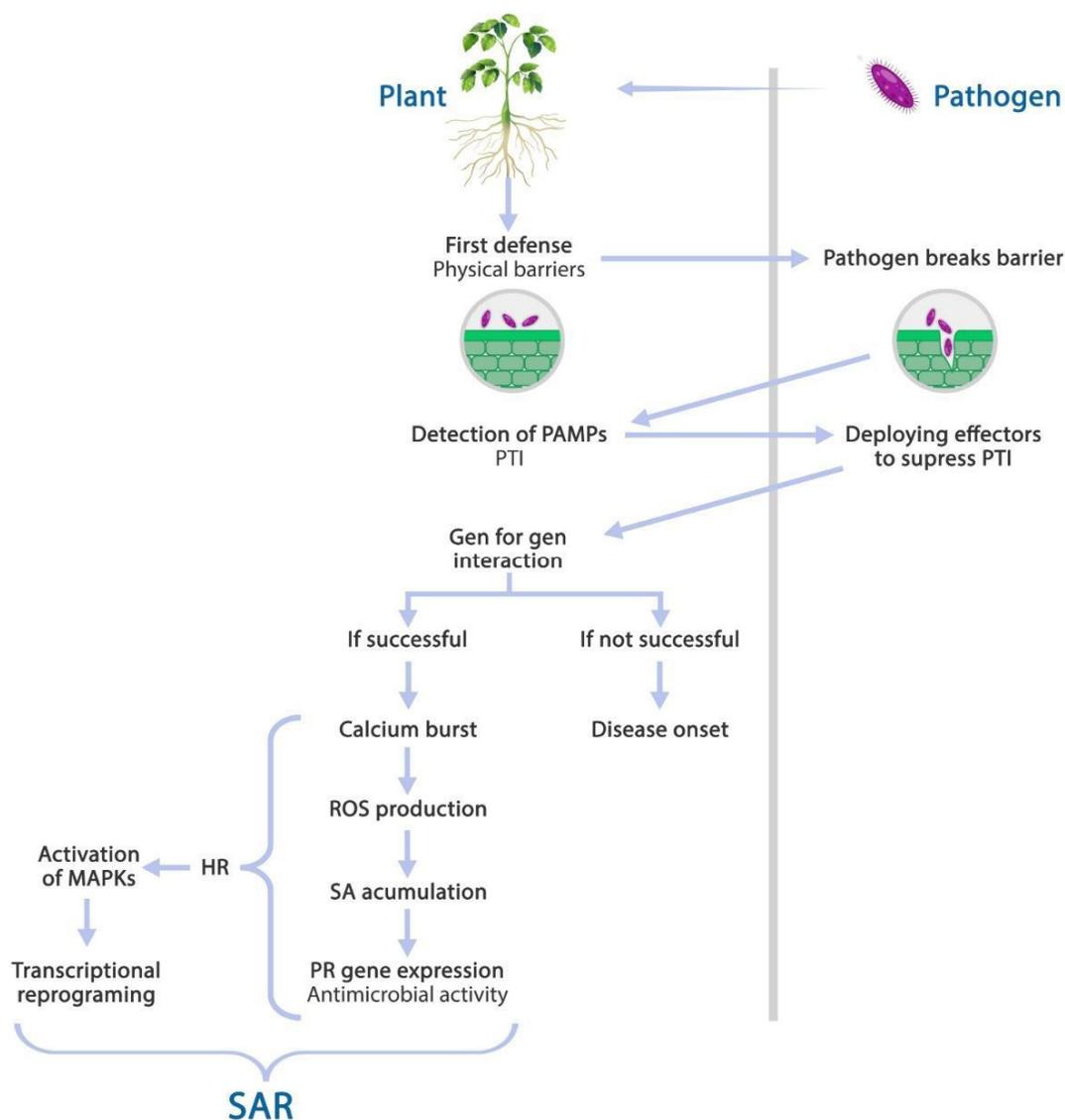


Figure 2. Activation of the systemic acquired resistance, through the interaction of plants and pathogens.

HR cell death leads to the activation of SA signaling throughout the whole plant. After the accumulation of SA, a part is converted to methyl salicylate (MeSA), which works as a phloem-mobile SAR signal [56]. MeSa can quickly spread through systemic tissue but does not induce defense gene expression alone. Once in systemic tissue, MeSa is modified to SA by the methyl esterase SABP2 [57,58]. SA levels rise, activating various presumed defense effector genes, including *PR* genes [35]. SAR signaling downstream of SA is controlled by

the protein nonexpressor of *PR* gene 1 (NPR1), which, upon SA-induced redox changes in the cell, converts from its oligomeric form to monomers; then, it is transported from the cytosol into the nucleus, where it acts as a transcriptional coactivator for the TGA transcription factors to induce the expression of a large set of *PR* genes [59,60]. *PR* proteins accumulate intercellularly in vacuoles and have antimicrobial activity; for example, *PR2* protein is a glucanase, *PR3* and *PR8* are chitinases, *PR9* is a peroxidase, and *PR1* has been shown to inhibit germination of oomycetes and have antifungal activity [50,59,61]. Disease resistance is given by diverse *PR* proteins that act together so that the overexpression or silencing of a single one does not significantly affect the resistance or susceptibility of the plant to a range of pathogens [58].

As mentioned before, H_2O_2 , produced during the HR, is an activator of MAPKs, which are conserved protein kinases that establish signaling modules where MAPK kinase kinases (MAPKKKs) activate MAPK kinases (MAPKKs) which in turn activate MAPKs. In plants, upon detecting biotic or abiotic stress, MAPKs participate in the signal transduction to the nucleus, allowing adequate transcriptional reprogramming to occur during defense [49,62]. In plant immunity and defense, transcriptional reprogramming is a highly dynamic and controlled process, considered the main link between signal transduction and the implementation of induced defense mechanisms [49,63].

The other two types of plant defense compounds are phytoalexins and phytoanticipins. The first ones are produced by the plant host as a direct response to pathogen detection, whereas phytoanticipins are produced before an attack and are only converted to their toxic forms post-pathogen perception, as a constitutive chemical barrier against the microbial attack [45,49,64]. All of these mechanisms, signaling, and metabolic pathways act together to stop pathogen infection and mitigate biotic stresses in the host plant; thus, systemic acquired resistance is a mechanism of defense that confers long-lasting protection against a broad spectrum of microorganisms [58].

There are research studies that focused on elucidating the mechanisms of SAR activation in different pathogen–plant host systems. One of them was carried out by Iakimova et al. [65], where they analyzed the morphological features of the HR and the contribution of signaling events resulting from ethylene production, ROS generation, and gene expression of a caspase-1-like protease (VPE) to *Erwinia amylovora*-induced cell death in spot-inoculated apple leaves. They observed that HR phenotypically resembled both the resistant and susceptible genotypes, expressing a similar pattern of distinguishable micro HR lesions that progressed into confined macro HR lesions, and the morphology of dead cells (protoplast shrinkage and retraction from cell wall) in apple leaves resembled necrotic programmed cell death (PCD). ROS accumulation and elevation of ethylene levels were similar in both cultivars, but in the resistant apple cultivar, an early and late increase in VPE gene expression was detected, suggesting that VPE might be an underlying component of the response to *E. amylovora* in resistant apple cultivars and that *E. amylovora* triggers leaf resistance response that is manifested through cell death [65].

Similarly, Moya-Elizondo and Jacobsen [65] demonstrated that *Bacillus mycoides* reduced the severity of *Fusarium* crown rot of wheat by 10% compared to water control, by inducing high concentrations of peroxidase and endochitinase, which makes it difficult for *Fusarium* to penetrate. Thus, *Bacillus mycoides* can induce SAR in wheat plants [66].

4. Interactions between Plants and Plant Growth-Promoting Microorganisms for Mitigating Biotic Stresses

As mentioned previously, PGPM has a beneficial effect on plant growth and development. Nevertheless, besides growth promotion through diverse mechanisms, PGPM can also protect plants from diseases and control phytopathogens [67], and therefore can alleviate biotic stresses in plants for sustainable agriculture.

PGPM has a diversity of mechanisms to defend and protect plants from pathogens, whether directly or indirectly. Some PGPMs, such as *Bacillus*, *Pseudomonas*, and *Trichoderma*, interact with plants by inducing resistance or priming without directly interacting with the

targeted pathogen [67–69]. Others act directly by interfering with the pathogen via nutrient and niche competition (as *Trichoderma* spp. and *Pseudomonas* spp.), parasitism (*Trichoderma* spp.), and antibiosis (*Bacillus* spp., *Pseudomonas* spp., and *Streptomyces* spp.) [67,70,71]. The result of these interactions is varied and hardly predictable, and the response depends, to a greater extent, on the interactions of biochemical and physiological compatibility [72]. Soil microorganisms have the particularity of proliferating and developing rapidly, taking advantage of the nutritional variety of the soil. This type of microorganism interacts with the rhizosphere, forming a niche highly dependent on the exudates of the plant roots, such as *Azospirillum*, *Bacillus*, *Trichoderma*, and *Rhizobium* [69,73–75]. As PGPMs and plants interact, they establish specialized relationships whereby gene expression results in the synthesis of metabolites (i.e., flavonoids, strigolactone, malic acid, pectin, citrate, and sugars), which play an essential role in effective communication [76,77].

Plant–microorganism communication can be studied through signalomics, which describes the metabolomics approaches employed to decipher the chemical communications occurring within the rhizosphere [71]. Rhizosphere microorganisms, such as *Azospirillum*, *Bacillus*, *Trichoderma*, and *Rhizobium* [69,74,75], establish symbiotic interactions with plants, secreting or emitting molecules beneficial to the plant (Table 2). These molecules can be phytohormones, volatile organic compounds (VOCs), and quorum-sensing signals such as N-acyl homoserine lactones (AHLs) [78–80].

Table 2. Beneficial microorganisms for plants.

Beneficial Microorganism	Host	Function	Reference
<i>Bacillus megaterium</i> , <i>Bacillus paralicheniformis</i> , and <i>Bacillus cabrialesii</i>	Wheat (<i>Triticum turgidum</i> L. subsp. <i>durum</i>)	Growth promotion	[81]
<i>Pseudomonas veronii</i> R4	Vid (Thompson Seedless)	Induced systemic resistance (ISR) defense for leaves and roots	[82]
<i>Bacillus velezensis</i> XT1	Tomato and strawberry plant	Growth promotion and biocontrol	[83]
<i>Bacillus cabrialesii</i>	Wheat (<i>Triticum turgidum</i> L. subsp. <i>durum</i>)	Biocontrol	[84]
<i>Bacillus subtilis</i> Cohn, <i>Bacillus thuringiensis</i> Berliner	Wheat	Plant resistance	[38]
<i>Pseudozyma churashimaensis</i>	Pepper	Elicits systemic defense against bacterial and viral pathogens	[85]
<i>Pseudomonas fluorescens</i> WCS417r	<i>Arabidopsis thaliana</i>	Local resistance of roots	[86]
<i>Bacillus pumilus</i> EN16, <i>Bacillus subtilis</i> SW1	Tobacco	Systemic resistance	[39]
<i>Trichoderma koningiopsis</i> Th00	Tomato	Induced systemic resistance (ISR) controlling <i>Fusarium</i> sp.	[87]
<i>Gliocladium roseum</i>	Tobacco	Induced systemic resistance (ISR) controlling <i>Erysiphe orontii</i>	[41]
<i>Bacillus</i> sp. FSQ1	Common bean (<i>Phaseolus vulgaris</i>)	Biological control	[88]
<i>Priestia</i> sp. TSO9	Wheat (<i>Triticum turgidum</i> L. subsp. <i>durum</i>)	Plant growth-promoting	[89]
<i>Bacillus paralicheniformis</i> TRQ65	Wheat (<i>Triticum turgidum</i> L. subsp. <i>durum</i>)	Biological control agent and plant growth-promoting	[90]
<i>Bacillus</i> sp. TSO2	Wheat (<i>Triticum turgidum</i> L. subsp. <i>durum</i>)	Biocontrol	[91]
<i>Trichoderma harzianum sensu lato</i> TSM39	Wheat (<i>Triticum turgidum</i> L. subsp. <i>durum</i>)	Biocontrol	[92]
<i>Rouxiella badensis</i> SER3	Strawberry	Biocontrol	[93]

5. Induced Systemic Resistance (ISR)

A practical method of biological control is the extensive use of non-pathogenic rhizosphere-associated microbial species, known as PGPMs [94,95]. This type of biological

control is used as an alternative to synthetic pesticides. These microorganisms have a fundamental role in the ecology of the agroecosystem, promoting plant growth [96] through different mechanisms, such as metabolite production, atmospheric nitrogen fixation, and/or making nutrients assimilable by the plant [97,98]. PGPMs (such as *Trichoderma* [99] and *Bacillus* [100]) are free-living and colonize the rhizosphere of plants, forming part of the plant microbiome [96], which consists of microorganisms present in leaves, rhizosphere, pollen, and other parts of the plant. The microbiome is reactive to biotic and abiotic plant interaction conditions, helping the plant to absorb nutrients and tolerate several types of stress [101,102].

There is evidence that root microorganisms can migrate to other parts of the plant, through the xylem apoplast, colonizing stems, and finally through leaves, establishing large populations [103]. These microorganisms play an essential role in antibiotic production, competition for nutrients, parasitism, and the production of suppressive metabolites (hydrogen cyanide, siderophores), as well as in the induction of systemic resistance or defense mechanisms in the plant against pathogen attack (Figure 3) [73].

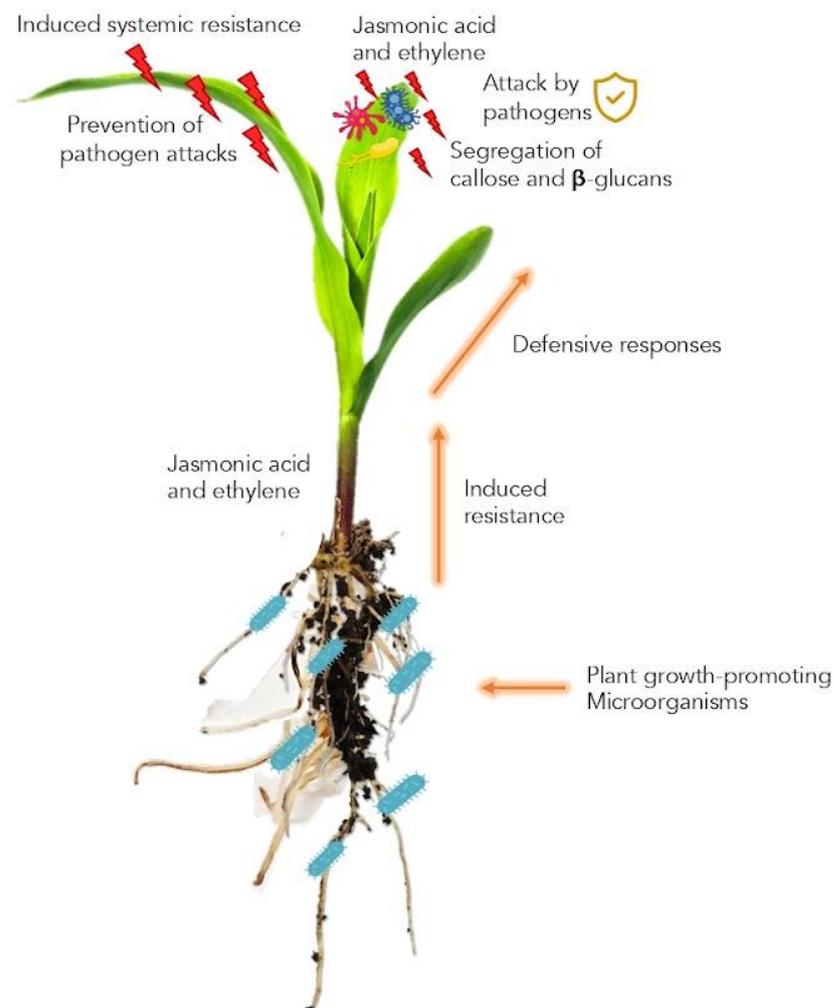


Figure 3. Priming generated by beneficial microorganisms in the rhizosphere, causing activation of resistance which may initially be local, but eventually becomes systemic by jasmonic acid and ethylene.

The plant-developed defense system related to the interaction with microorganisms is complex and is mainly activated by molecular patterns (MAMPs) based on surface recognition on the cell membrane [104,105]. MAMPs are protein fragments essential for microorganisms [104], such as flagellins in bacteria or β -glucans in fungi, that are absent in plants. MAMPs control the plant's colonization by beneficial microorganisms

and the signaling pathways for salicylic acid (SA), jasmonic acid (JA), and ethylene (ET), which play a crucial role in controlling the functions of these microorganisms inside the plant [102,106,107].

MAMPs in plants are recognized by pattern recognition receptors (PRR), which are located on the plant surface [108,109], and when in direct contact, start the signaling cascade that leads to the activation of resistance mechanisms. Another type of MAMP recognition pattern is leucine-rich repeats (LRRs), which are part of the PRRs found intracellularly, rich in leucine as their name indicates; however, when the immune response is activated by LRR, it is named MAMP-triggered immunity (MTI). Many of these receptors LRRs contain nucleotide binding sites (NBS-LRRs); these receptors function by detecting pathogen virulence proteins (effectors), and in turn, this immunity is called effector-triggered immunity (ETI) [108,110]. This type of resistance can recognize cellular modifications in plants and proteins produced by pathogens and terminate pathogen infection [111]. Likewise, ETI is gene-for-gene-resistant and prevents infection by biotrophic pathogens by generating programmed cell death [60,86,112].

MAMP recognition in leaves triggers oxidative response, leading to ethylene and nitric oxide synthesis and the activation of mitogen-activated protein kinase (MAPK) signaling cascades, leading to defense-related gene transcription, as well as segregation of callose and β -glucans at the site of plant infection as a physical barrier, preventing plant infection (Figure 3) [113,114].

Generally, the rhizosphere is constantly exposed to microbial interaction, which generates induced systemic resistance [113,115]. This mechanism refers to the action of generalized or systemic resistance or defense capacity, as well as non-generalized local resistance to pathogens or diseases [116]. When we refer to ISR in plants, we refer to a generalized or systemic resistance action, whereas when we use the term induced resistance (IR), we refer to local resistance that does not generalize to pathogens or diseases [116]. Both types of resistance develop by contact with non-pathogenic microorganisms, unlike systemic acquired resistance, in which a series of protective mechanisms are generated in the plant due to direct contact with one or several pathogens. This type of resistance is activated in plants by rhizosphere contact with plant growth-promoting fungi or bacteria and is mediated by ET and JA (Figure 3) [117,118].

On the other hand, this resistance can also be activated by priming caused by chemicals, environmental or abiotic factors, as well as other biological agents. Thus, once plants are in contact with the resistance elicitor or activator, a series of biochemical and molecular changes are triggered, but the plant's defense mechanisms are not directly activated until the plant is exposed to the biotic stress [119]. The importance of this priming for plant defense lies in their adjustment to unpredictable environments, which has been studied in a wide variety of crops, ranging from herbaceous to woody plants [119,120]. This mechanism can be local and occur only in one part of the plant, or systematically in the whole plant [116,121].

In this sense, in plants, the *NPR1* gene has been linked to both SAR and ISR, since its transcriptional role is necessary for ET synthesis and the cytosolic transcription of this gene in JA/ET signaling. *NPR1*, *NPR3*, and *NPR4* genes are related to PGPM establishment in roots, leading to ISR activation [60,94,122]. On the other hand, the role of plant lipoxygenases (LOX) is associated with resistance in plants, playing crucial roles in biotic and abiotic stress [123] and defending plants from pathogen attack by synthesizing oxylipins, compounds that oxidize pathogen fatty acids [105]. The pathogen defense mechanism of these is based on the enzyme LOX, which is involved in the synthesis of JA and ET, along with lipid deoxygenation [121]. Oxylipin synthesis is also associated with green leafy vegetables in the form of volatile compounds, which release these compounds to activate the defense system against pathogens due to volatile compounds, which can induce crop tolerance to biotic stress [124,125].

The enhancement of the expression of genes that regulate the JA and ET pathways (Table 3) leads to increased defense sensitivity at the cellular level, better known as priming

in ISR, and this in turn leads to gene overexpression of *AP2/ERF*, which is involved in regulating the jasmonate and ethylene pathways. One gene involved in this priming is *MYB72*, which is overexpressed when *Arabidopsis thaliana* are inoculated with PGPM, as well as regulation of iron homeostasis and the onset of ISR [126,127]. It has been found that after the onset of ISR, the accumulation of phytoalexins at the infection site is common, and phytoalexins are present in different types of stress. Long-distance signaling by jasmonate and ethylene causes stress in the plant, which leads to long-term adaptations to stresses at the whole-plant level [102,128].

Table 3. Genes involved in plant defense.

Gene	Function	Source	Reference
<i>CsChi23</i>	Antifungal activity	Cucumber	[81]
<i>Npr1</i>	AS-dependent regulatory factor to RSA	Vid (Thompson Seedless)	[82]
<i>Eir1</i>	Auxin efflux transport, being root-specific, RSI activation	Vid (Thompson Seedless)	[82]
<i>Lox2</i>	Lipoxygenase leading to JA biosynthesis, induced systemic resistance (ISR)	Vid (Thompson Seedless)	[82]
<i>Tlp1</i>	Antifungal activity	Vid (Thompson Seedless)	[82]
<i>AtTLP1</i>	Encodes a thaumatin-like protein with antimicrobial properties	<i>Arabidopsis thaliana</i>	[86]
<i>EIN2</i>	Ethylene signaling, chromoplast development	<i>Solanum lycopersicum</i> (tomato)	[129]
<i>JAR1</i>	JA signaling in root	<i>Arabidopsis thaliana</i>	[130]
<i>BAK1</i>	Co-receptor enabling detection of microbe-associated molecular patterns and induction of PTI	<i>Arabidopsis thaliana</i>	[131]
<i>ERF1</i>	Ethylene and jasmonate pathways in plant defense	<i>Arabidopsis thaliana</i>	[132]
<i>LOX</i>	Resistance to biotic and abiotic stress	<i>Arachis duranensis</i> , <i>Arachis ipaënsis</i> , <i>Cajanus cajan</i> , <i>Cicer arietinum</i> , <i>Glycine max</i> , <i>Lotus japonicus</i> , <i>Medicago truncatula</i>	[123]
<i>COI1</i>	JA signaling	Tomato plants	[133]
<i>JAR1</i>	Encodes a JA-amido synthetase that catalyzes the formation of jasmonoyl-l-isoleucine (JA-Ile)	<i>Arabidopsis thaliana</i>	[134]
<i>AP2/ERF</i>	Biotic and abiotic stresses responses	Tartary buckwheat (<i>Fagopyrum Tataricum</i>)	[135]
<i>PAL1</i>	SA-dependent signaling of the defense response to microbial pathogens	Pepper	[136]
<i>R2R3-MYB</i>	Initiate the ISR priming process	<i>Arabidopsis thaliana</i>	[137]

6. Induced Systemic Resistance as a Biocontrol Mechanism

Worldwide use of pesticides has intensified from a consumption of ~1.3 kg/ha in 1992 to 2.57 kg/ha in 2016, an increase of 97.69% [138]. A wide range of bacterial pathogens have developed resistance against commonly used chemicals including antibiotics, such as streptomycin [139]. In addition, the exhaustive use of chemically formulated pest controllers has triggered biodiversity problems such as the loss of pollinators over the years, a phenomenon that threatens biodiversity conservation and sustainable food production worldwide [140]. The use of insecticides can have lethal effects on non-target organisms and reach higher trophic levels through food [141], as well as generating problems for human health related to the use of synthetic agricultural inputs to maintain crop yields.

PGPMs with controlling effects have been widely studied, of which the genus *Pseudomonas* and *Bacillus* are the most commercialized [142]. The adequate protection of plants by using biocontrol agents (BCA) is due mainly to the successful colonization of the host and the subsequent production of antibacterial properties, and the production of metabolites that induce systemic resistance and/or the subsequent induction of antibacterial properties [143]. The use of microorganisms capable of inducing ISR may be the key to crop pathogen protection sustainability [144]. For example, Peñafiel-Jaramillo et al. [82] analyzed a selection of genes (*Lox2*, *Tlp1*, *Eir1*, *NPR1*) in grapevine plants, which were activated for systemic resistance induced by rhizosphere microorganisms. The results showed that the *Tlp1* gene was related to the ability of *Pseudomonas* to develop the ethylene (ET) pathway-induced symbiosis complex. The *NPR1* gene was found in leaves and roots, with no significant differences between plants treated with phosphate-buffered saline (PBS) or *Pseudomonas veronii* R4. This proves how rhizosphere inoculation activates the induced systemic resistance state [82].

In another study, Jaimes-Suárez et al. [87] reported how induction of systemic resistance in tomatoes by *Trichoderma koningiopsis* Th003 delayed the *Fusarium* infection. They found that the incidence of root and collar rot in tomatoes was significantly reduced by 35% when compared to the control. The strain Th003 was positive to the induction of systemic resistance in plants since both microorganisms were inoculated spatially and not in direct contact; this effect can be attributed to the fact that *Trichoderma* stimulates the activity of PR proteins, such as β -1,3-endoglucanases and endochitinases in plants [87]. On the other hand, compared to traditional chemical control, resistance induced by biological agents does not have immediate and potent disease-reducing effects but has a long-lasting effect.

Resistance reactions begin soon after the use of the inducer and the effects generally persist for three weeks to two months, but resistance periods of up to six months have been reported [144]. In addition, plants become resistant to subsequent infections caused by different pathogens [5]. The major disadvantage of this type of resistance is that it can leave the plant unprotected from pathogen attack until the resistance is fully activated [118]. Thus, although ISR through PGPM has been vastly studied and described, research on it should continue, in order to seize its full potential as a method for the biocontrol of phytopathogens.

Exemplifying the above-mentioned ISR mechanisms, Li et al. [145] found that *Bacillus amyloliquefaciens* strain LJ02 can decrease powdery mildew fungal disease in cucurbits. Cucumber plants inoculated with this strain had a significant production of superoxide dismutase, peroxidase, polyphenol oxidase, and phenylalanine ammonia-lyase as compared to the control. In addition, the accumulation of free AS in cucumber leaves was observed, which was markedly increased in the 5-day treatment compared to the control, as well as overexpression of the *PR-1* gene, which is commonly related to SA expression. These findings indicate that *B. amyloliquefaciens* strain LJ02 can induce systemic resistance in cucumber plants [145].

Mathys et al. [146] analyzed the transcriptomic profile of *Arabidopsis thaliana* after inoculation of *Trichoderma hamatum* T382 in roots, which conferred greater resistance to the attack of the necrotrophic pathogen *Botrytis cinerea*; the analysis of ISR gene expression was carried out by using microarrays. Gene expression analysis allowed the identification of genes related to MAMP-triggered defense and the subsequent production of reactive oxygen species, as well as the identification of genes related to the synthesis of JA and SA. This confirms the activation of induced systemic resistance in *A. thaliana* by *T. hamatum* T382 [146].

In addition to transcriptomic analysis of these types of interactions, the root metabolome can show us what metabolites are being produced when PGPM–root interactions are occurring; however, it is a broad niche to analyze as the soil ecosystem is very complex [147]. Bacterial metabolomic analysis of PGPM helps us to elucidate which metabolites are ISR elicitors [147]. Fatima and Anjum [68] analyzed the metabolomic profile of *Pseudomonas aeruginosa* PM12 in tomato plants, finding an increase in the synthesis of phytoalexins

and phenolic compounds, as well as other RSI-related metabolites, concluding that the activation of this type of defense against *Fusarium* wilt was generated by PGPR [68].

7. Conclusions

Stresses generated by biotic factors in plants modify their normal physiological state, leading to the expression of defense genes, as well as the modification of growth and development. Interaction with pathogens can activate systemic acquired resistance (SAR) after a pathogen attack as a defense mechanism generating molecular cascades that lead to the synthesis of structural barriers and stomatal closure as a first line of defense. Subsequently, activation of programmed cell death can halt the progress of pathogens, and reactive oxygen species lead to the accumulation of oxidants, which attack the pathogen, inhibiting its proliferation. The synthesis of SA and MeSA is indispensable in this type of pathogen-generated biotic stress as they carry this pathogen alertness to other sites in the plant. Understanding this type of defense, as well as the genes expressed in it, is necessary for the control of pathogen-generated stress in crops. On the other hand, stress generated by beneficial microorganisms triggers a series of molecular processes in plants that lead to the activation of induced systemic resistance (ISR); this resistance is generally activated in the rhizosphere when microorganisms (PGPM) interact with it, generating benefits for the plant such as plant growth promotion—thanks to the increased absorption of nutrients in the root—and protection against pathogen attack due to molecular processes, where defense-related gene transcription and the segregation of callose and β -glucans at the site of plant infection act as a physical barrier, preventing plant infection. This type of defense (ISR) generates “beneficial stress” mediated by ET and JA. We can say that it is the equivalent of immunizing the plant against stress generated by pathogens, which results in a sustainable mechanism for pest control and crop adjustment to different stresses, in order to ensure global food security.

Comprehending the induction of these stresses in crops leads us to understand that the application of PGPMs helps reduce biotic and abiotic stresses, as PGPMs, thanks to signaling and establishment in the plant, generate a state of pre-alertness to pathogen attack, which is an alternative to the use of pesticides, being beneficial for the agroecosystem and economically speaking. The plant growth promotion provided by PGPMs helps to reduce the use of fertilizers by promoting plant growth and increasing agricultural production. However, there is still a long way to go in exploring metabolomic and transcriptomic approaches to plant–microorganism interactions and how they mitigate biotic stress.

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