

Chapter 6

Role of Microbial Bioagents as Elicitors in Plant Defense Regulation



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Abstract Plants are constantly challenged by an array of potential pathogens like fungi, bacteria, viruses, insects, nematodes, etc., which lead to a significant loss to plant yield. Plants commonly overcome these phytopathogens by showing resistance through plant defense mechanisms. Several general microbe elicitors allow plants to mitigate the harmful effects of pathogenic microbes by enhancing the capability of plants to identify anonymous pathogenic agents and act as surveillance systems for plants. Elicitors are small drug-like compounds released by pathogens that are composed of molecules like oligosaccharides, lipids, peptides, and proteins, and they activate various kinds of defense responses in plants. They deliver information to plants through perception and identification of signaling molecules by cell surface-localized receptors, which is followed by the triggering of signal transmission pathways that commonly induces the synthesis of active oxygen species (AOS), phytoalexin production, production of defense enzymes, and the aggregation of pathogenesis-related (PR) proteins. This article chiefly highlights the role of microbial elicitors in improving plant defense mechanisms as well as their modes of action that have been used to boost up the plant immune system.

Keywords Microbial bioagents · Elicitors · Plant defense regulation · Systemic acquired resistance · Phytopathogens

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6.1 Introduction

In the course of development, plants are systematically challenged by a broad range of biotic stresses in their natural habitat, such as fungi, bacteria, viruses, insects, nematodes, etc. There are numerous choices available for the plants to protect themselves from the disease (Abdul Malik et al. 2020). Plants usually overcome these biotic stresses by activating their separate defense pathways according to perceived signals from potential pathogens (Sarma et al. 2015; Barupal et al. 2020). There is an intricate type of defense mechanism employed by plants to detect microorganisms based on elicitor molecules produced during plant–pathogen interaction. Numerous elicitors of microbial origin belonging to distinct chemical groups have been identified, i.e., glycopeptides, carbohydrate polymers, glycoproteins, and lipids. This elicitor perception is followed by the stimulation of signal transmission pathways that commonly induces the synthesis of active oxygen species, production of phytoalexin, accumulation of pathogenesis-related proteins, deposition of callose, strengthening of the cell wall of plant cell related to phenyl propanoic compounds, and production of defense enzymes (Van Loon and Van Strien 1999; Patel et al. 2019). Active oxygen species (AOS) induce localized or fast death of limited cells at the site of infection, which induces a hypersensitive response in host plants to restrict the growth of invading pathogens. Activation of hypersensitive response (HR) results in the development of resistance in uninfected distal parts of the host plant to upcoming infection, which is called systemic acquired resistance (SAR) (Thakur and Sohal 2013). Systemic acquired resistance is mainly relying up on salicylic acid, where the first set of reactions brings on a complex modification in gene expression, enzymatic action, and metabolic changes (Garcia-Brugger et al. 2006; Barupal et al. 2019). Salicylic acid-dependent reaction is stimulated by biotrophic pathogens and distinct types of elicitors. Several microbial elicitors allow plants to mitigate the harmful effects of pathogenic microbes by enhancing the capability of plants to identify anonymous pathogenic agents and act as surveillance systems for plants (Newman et al. 2013). Elicitors are small drug-like compounds composed of molecules like oligosaccharides, lipids, peptides, and proteins, which activate various kinds of defense responses in plants. They are either secreted by pathogens or plants or pathogen cell walls by hydrolytic enzymes. Elicitor-activated signal transduction pathways bring on a hypersensitive response and systemic acquired resistance type of defense responses against a broad range of pathogens (Garcia-Brugger et al. 2006). Microbial biocontrol agents suppress the growth of phytopathogens through a wide array of distinct modes of actions. The most important advantage of using microbial biocontrol agents is that they display specificity for a particular pathogen and are expected to be harmless to nontarget species (Hussain et al. 2020a, b). In the last few decades, many studies have been done on the broad range of applications of microbial biocontrol agents in the plant disease management data given in Table 6.1 (Kokalis-burelle et al. 2002; Mavrodi et al. 2012; Singh et al. 2020). Environmentally friendly and sustainable attributes of biocontrol agents have driven profound investigation into the promising microbial

Table 6.1 Biocontrol agents and their target phytopathogens

Biocontrol agents	Crop	Pathogen	References
<i>Bacillus polymyxa</i>	Rice (<i>Oryza sativa</i>)	<i>Rhizoctonia solani</i> , <i>Pyricularia grisea</i>	Kavitha et al. (2005)
<i>Trichoderma viride</i> , <i>Trichoderma harzianum</i> , <i>Pseudomonas fluorescens</i>	Groundnut (<i>Arachis hypogaea</i>)	<i>Macrophomina</i> <i>phaseolina</i>	Karthikeyan et al. (2006)
<i>Acremonium strictum</i> , <i>Trichoderma harzianum</i>	Tomato (<i>Solanum lycopersicum</i>)	<i>Meloidogyne incognita</i>	Goswami et al. (2008)
<i>Trichoderma harzianum</i>	Tomato (<i>Solanum lycopersicum</i>)	<i>Meloidogyne javanica</i>	Sahebani and Hadavi (2008)
<i>Trichoderma viride</i>	Soybean (<i>Glycine max</i>)	<i>Fusarium oxysporum</i> f. sp. <i>adzuki</i> , <i>Pythium arrenomanes</i>	John et al. (2010)
<i>Trichoderma harzianum</i> , <i>Pseudomonas fluorescens</i> , <i>Bacillus subtilis</i>	Safflower (<i>Carthamus tinctorius</i>)	<i>Macrophomina phaseolina</i> (root rot disease)	Govindappa et al. (2010)
<i>Paecilomyces lilacinus</i>	Tomato (<i>Solanum lycopersicum</i>)	<i>Meloidogyne incognita</i>	Oclarit and Cumagun (2009)
<i>Trichoderma asperellum</i>	Cocoyam (<i>Xanthosoma sagittifolium</i>)	<i>Pythium myriotylum</i>	Mbarga et al. (2012)
<i>Verticillium chlamydosporium</i> , <i>Photorhabdus luminescens</i>	Cucumber (<i>Cucumis sativus</i>)	<i>Meloidogyne incognita</i>	Zakaria et al. (2013)
<i>Bacillus amyloliquefaciens</i>	Wheat (<i>Triticum aestivum</i>)	<i>Fusarium graminearum</i> (<i>Gibberella zeae</i>)	Dunlap et al. (2013)
<i>Bacillus</i> spp.	Ginseng (<i>Panax ginseng</i>)	<i>Fusarium</i> c.f. <i>incarnatum</i>	Song et al. (2014)
<i>Bacillus cereus</i>	Thale cress (<i>Arabidopsis thaliana</i>)	<i>Pseudomonas syringae</i>	Chowdhury et al. (2015)

candidates for the production of elicitors. In this chapter, we address the role of microbial elicitors in improving plant defense mechanisms as well as their modes of action that have been used to boost up the plant immune system.

6.2 Elicitors

Elicitors are small drug-like compounds composed of molecules like oligosaccharides, lipids, peptides, and proteins, which activate various kinds of defense responses in plants. Elicitors produced by pathogenic agents can be classified into two groups: general elicitors and specific elicitors (Montesano et al. 2003). General elicitors are engaged in the conventional resistance, which has the capacity to trigger defense reactions in both host and nonhost plants, whereas race-specific elicitors

are released by specialized pathogens involved in *R* gene-mediated signal transduction (Gowthami 2018). General elicitors have the capacity to trigger defense in both nonhost and host plants through the realized incidence of potential pathogens (Onaga and Wydra 2016). Commonly, general elicitors are found in the cell walls of pathogens as structural constituents, for example, glucan, flagellin, chitin, and lipopolysaccharides (LPS) (Abdul Malik et al. 2020). Elicitor molecules act as ligands and generally bind to the specific receptor proteins located on the surface of plant cell membranes. According to the molecular pattern of elicitors recognized by receptors, an intracellular defense signaling has been triggered, which is echoed by the synthesis of secondary metabolites (Gowthami 2018; Zehra et al. 2021). It has long been recognized that microbial elicitors can induce many cellular defense responses in plants. Currently, elicitors of microbial origin have also been stated as microbe- or pathogen-associated molecular patterns (MAMPs or PAMPs). Following MAMP recognition, production of reactive nitrogen species, ion fluxes across the membrane, medium alkalinization, reactive oxygen species, and ethylene synthesis lead to activate plant pattern-triggered immunity (PTI) against broad range of microbial attack (Wu et al. 2014). Newman et al. (2013) stated that N-acetyl-chito-oligosaccharides, i.e., chitin oligomers, a fungal cell wall-derived elicitor molecule, can activate several defense responses in monocot as well as dicot plants. In recent years, numerous MAMPs and their corresponding PRRs have been recognized, such as flagellin, peptidoglycan, elongation factor (Tu), lipopolysaccharides, β -glucans from oomycetes and Ax21, fungal chitin, etc. (Newman et al. 2013).

6.2.1 Microbial Agents as a Source of Elicitors

Induction of plant defense response is a crucial step during plant–pathogen interaction via several factors. The first step of inducible response is carried out by the plant by the perception of molecules derived by microbes known as elicitors. While the plant perceives these molecules, it results in a plant response that provides effective resistance toward pathogens; hence, they can be described as “defense elicitors” (Wiesel et al. 2014). These elicitors may be of proteinaceous, polysaccharide, laminarin, and other chemical nature. Apart from the pathogenic role of microbes, there are some beneficial microbes that live in plant tissue as endophytes, plant growth promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), and some algae, oomycetes, and viruses also play a significant role in inducing resistance in plants (Siah et al. 2018; Yadav and Meena 2021). The primary work of these elicitors is to induce production of reactive oxygen species (ROS) or oxidative burst, which ultimately evokes plant defense responses like cross-linking of plant cell wall proteins, upregulation of defense-related genes, stimulation of synthesis of phenolic compounds (phytoalexins), and induction of hypersensitive response (Low and Merida 1996). The biological agents evoke plant defense via several modes like production of siderophores, antibiotic secretion, lytic enzyme production,

hyperparasitism, and inducing systemic response (ISR); all mechanisms are induced by secretion of elicitor molecules (Pieterse et al. 2014; Navarro et al. 2019; Singh et al. 2020).

6.2.2 Some Potent Elicitor-Producing Microbial Agents

6.2.2.1 Fungi

Fungal groups possess some cell wall breakdown products like chitin, β -glucans, and mannoproteins that act as potent elicitors and can evoke defense response; for example, yeast extract can be used widely for the study of defense response in plants via closing of stomata and peroxidase-mediated ROS production (Khokon et al. 2010). *Sclerotinia* culture filtrate elicitor1 (SCFE1) is a proteinaceous elicitor secreted by *Sclerotinia sclerotiorum* that induces BAK1-dependent PTI responses in *A. thaliana* (Zhang et al. 2013). Among fungal-derived elicitors, chitin and chitosan (a deacetylated derivative of chitin) are potent elicitors that increase resistance in plants toward several fungal and bacterial pathogens (Hadrami et al. 2010). Fungal cell wall polysaccharides, especially chitin and carboxymethyl cellulose, are active elicitors that stimulate synthesis and accumulation of a secondary metabolite tolytoxin (phytoalexin) in a cyanobacterium *Scytonema ocellatum*, which provides chemical defense against fungal pathogens (Patterson and Bolis 1997; Meena and Samal 2019). Transcription of retrotransposons is also carried out by some fungal genera to increase host defense; for example, application of crude extracts of *Trichoderma viride* induces transcription of *Tnt1* gene, which accumulates capsidiol (a phytoalexin) in tobacco plants (Pouteau et al. 1994; Meena and Swapnil 2019). Some other examples also suggest transcription activation by fungal elicitors as it has been seen in *Phaseolus vulgaris* where plant cells show upregulation of genes related to phytoalexin metabolism such as phenylalanine ammonium lyase (PAL) and chalcone synthase (CHS) (Lawton and Lamb 1987). Some other species of *Trichoderma* like *T. virens* induce plant defense response by producing an elicitor named Sm1 (small protein 1), which triggers an increased production of reactive oxygen species in seedlings of monocot and dicot plants and proves as a potent elicitor in defense against foliar pathogen *Colletotrichum* sp. (Djonović et al. 2006). *Trichoderma harzianum* is also reported as an inducer of antioxidant defense system in tomatoes against Fusarium wilt disease (Zehra et al. 2017a, b). It is reported that oxidative burst during plant defense is dependent on external calcium (Ca^{+2}) and protein kinase activity (Schwacke and Hager 1992). Hypersensitive response is also stimulated by the same fungus in *Vitis vinifera* by increasing the level of endogenous H_2O_2 , which ultimately activates oxidative phenolic metabolism in respective plants (Calderón et al. 1993). A proteinaceous elicitor PeaT1 produced by *Alternaria tenuissima* enhances plant defense response against tomato aphid (*Myzus persicae*), which is evidenced by accumulation of defense-related substances such as jasmonic acid (JA), salicylic acid (SA), and ethylene (ET) (Meena et al. 2017a, b; Basit et al.

2021). PeaT1 is also responsible for systemic acquired resistance (SAR) in tobacco plants (Mao et al. 2010). Other than the above described fungal genera, there are several fungi that are sources of potent elicitors and regulate plant defense responses as given in Table 6.2.

6.2.2.2 Bacteria

In addition to fungal-derived elicitors, bacteria-derived elicitors have also been shown to regulate plant defense mechanisms and reduce pathogen infections in plants. There are several pieces of evidence that justify this statement, for example, *Ralstonia solanacearum* produce extracellular polysaccharides (EPS), which trigger a defense response in tomato plants in the case of bacterial wilt (Milling et al. 2011). Gram-negative bacteria-derived lipopolysaccharides (LPS)-mediated induction resistance is also shown in many crop plants (Erbs and Newman 2012). At concentrations of 1 g/ml, lipopolysaccharides from *Xanthomonas campestris* induce transcription of genes of β -1,3-glucanase, which ultimately shows defense responses in turnip (Newman et al. 1995). Cold shock protein (Csp)-related elicitor activity has been detected in bacterial extracts; there are many aromatic and basic side chains of csp domains that are necessary for elicitor activity; hence, RNA-binding motif RNP-1 of bacterial cold shock proteins that are highly conserved is recognized as an elicitor signal in *Nicotiana sylvestris* plant (Felix and Boller 2003). The two bacterial microbe-associated molecular patterns (MAMPs) are flagellin and the elongation factor Tu (EF-Tu), which are recognized by a variety of plant species (Deslandes and Rivas 2012). *Botrytis cinerea* and *Erwinia carotovora* produce a wide array of elicitors that enhance the expression of conserved plant defense-associated genes such as *HrpN* gene and show responses like shrinkage of cytoplasm, programmed cell death (PCD), etc. in *Physcomitrella patens* (de León et al. 2007). *Hrp* genes are crucial for HR response in plants; Wei et al. (1992) reported that *hrp* genes (*hrpN*) of *Erwinia amylovora* encode harpin, a proteinaceous elicitor, which shows HR necrosis in respective plants. Surfactin lipopeptide is secreted by *Bacillus* sp., which triggers induced systemic response in host plants and defense responses like oxidative burst, etc. (Cawoy et al. 2014). In elicitation, not only free-living or plant-associated bacteria but also animal-associated bacteria are also involved; for example, it is observed that insects named *Helicoverpa zea*, gut-associated bacteria, induce defenses in tomatoes indirectly by secreting a salivary elicitor that induces expression of genes of defense-related enzymes like polyphenol oxidase and jasmonic acid (JA) and suppression of pathogenesis-related genes of salicylic acid (SA) response (Wang et al. 2017). Twenty-three bacteria isolated from gut segments of *Spodoptera exigua*, *Agrotis segetum*, and *Mamestra brassicae* produce surfactants such as *N*-acylglutamine, which is recognized as a potent elicitor for plant defense response (Spiteller et al. 2000). There are several other bacterial groups identified as sources of elicitors, which are mentioned in Table 6.2.

Table 6.2 Table showing elicitor producing microbial agents, host, and their mode of plant defense regulation

Microbial agent	Host	Mechanism of host defense regulation	References
Fungi			
<i>Trichoderma harzianum</i>	Sunflower	Induce resistance by increasing phenolics as well as stress enzymes	Singh et al. (2014), Swapnil et al. (2021)
<i>Trichoderma harzianum</i> T3	Grapevine	Enhance expression of defense-related genes	Banani et al. 2015
<i>Trichoderma viride</i>	Potato	Increase total phenol content	Rosyidah et al. (2014), Meena et al. (2020)
<i>Trichoderma viride</i>	Black gram	Induction of defense enzymes and total phenolic content	Surekha et al. (2014)
<i>Trichoderma asperellum</i>	Onion	Increase of glucanase, chitinase, and peroxidase activity	Guzmán-Valle et al. (2014)
<i>Trichoderma asperelloides</i>	<i>Arabidopsis</i>	Suppress nitric oxide generation, elicited by pathogen	Gupta et al. 2014
<i>Fusarium oxysporum</i> Fo47	Pepper	Production of caffeic, ferulic, and chlorogenic acids	Veloso et al. (2016)
<i>Penicillium oxalicum</i>	Pearl millet	Increase peroxidase and chitinase activity	Murali and Amruthesh (2015)
<i>Clonostachys rosea</i>	Canola	Upregulation of host genes involved in biosynthesis of jasmonic acid, ethylene, and auxin	Lahlali et al. (2014)
Arbuscular mycorrhizal fungi (AMF)			
<i>Glomus fasciculatum</i>	Tomato	Higher expression of genes involved in jasmonic acid biosynthesis	Nair et al. (2015)
<i>Funneliformis mosseae</i> , <i>Rhizophagus irregularis</i>	Wheat	Accumulation of polyphenolic compounds and reduction of pathogen conidia	Mustafa et al. (2016)

(continued)

Table 6.2 (continued)

Microbial agent	Host	Mechanism of host defense regulation	References
Bacteria			
<i>Bacillus subtilis</i> QST 713	Tomato	Increase expression of <i>Pin2</i> gene in host	Fousia et al. (2016)
<i>Bacillus cereus</i> AR156	<i>Arabidopsis</i>	Activation of PAMP-triggered immunity and ISR through NPR1- and SA-dependent signaling pathway in host	Niu et al. (2016), Meena et al. (2019)
<i>Bacillus amyloliquefaciens</i> S13-3	Tomato	Induction of ISR through antibiotic production	Yamamoto et al. (2015)
<i>Bacillus oryzae</i>	Rice	Induced systemic response in host	Chung et al. (2015)
<i>Paenibacillus polymyxa</i> CF05	Tomato	Induction of defense-related enzymes (PAL, SOD, and PPO) and accumulation of H ₂ O ₂ and phenolics in host plant	Mei et al. (2014)
<i>Pseudomonas</i> sp. LBUM223	Potato	Induction of defense-related genes like <i>LOX</i> , <i>PIN2</i> , <i>PAL-2</i> , <i>ERF3</i> , <i>ChtA</i> , <i>PR-1b</i> , <i>PR-2</i> , and <i>PR-5</i>	Arseneault et al. (2014)
<i>Streptomyces rochei</i> A-1	Apple	Increased activities of POD, CAT, SOD, PAL, β -1,3-glucanase, and chitinase , promoted H ₂ O ₂ generation, decreased lipid peroxidation , and upregulation of related genes	Zhang et al. (2016)
<i>Brevibacterium iodinum</i> KUDC1716	Pepper	Elicit systemic acquired resistance (SAR)	Son et al. (2014)
<i>Carnobacterium</i> sp. SJ-5	Soybean	Higher expression of defense-related proteins	Jain and Choudhary (2014)

(continued)

Table 6.2 (continued)

Microbial agent		Host	Mechanism of host defense regulation	References
Oomycetes	<i>Pythium oligandrum</i>	Grapevine	Induction of genes related to phenylpropanoid pathways, PR proteins, oxylipins, and oxydo-reduction systems	Yacou et al. (2016)
	<i>Phytophthora parasitica</i>	Tobacco	Formation of physical barriers like phloem proteins, impregnation of pectin, etc. in the host plant	Lherminier et al. (2003)

6.2.2.3 Oomycetes

Oomycetes are taxonomically and structurally different from plants and fungi. There are several plant pathogenic oomycetes known, but genera *Phytophthora* and *Pythium* show superiority in causing disease of crop plants. The cell walls of these groups consist of several elicitor factors such as cellulose, glycan, and hydroxyproline-rich proteins. Some potent elicitors reported from oomycetes are CBEL, cryptogein, eicosapentaenoic acid, Pep-13, and INF1 (Wiesel et al. 2014). Necrosis and ethylene-inducing peptide 1 (Nep1)-like proteins (NLP) has been identified in dicot plants, which are associated with defense response in *Arabidopsis thaliana* (Qutob et al. 2006). In *Nicotiana benthamiana*, HR response is induced by INF1 elicitor of *Phytophthora infestans* (Kamoun et al. 1998). These responses are dependent on the receptor-like kinase SERK3/BAK1, required for multiple resistance responses in plants (Heese et al. 2007). Pathogenic species of *Phytophthora* release some extracellular and intracellular effectors into plants encoding protease or glucanase inhibitors to suppress pattern-triggered immunity in plants (Hein et al. 2009; Schornack et al. 2009). RXLR effector Avrblb2 of *P. infestans* prevents secretion of an immune-associated protease (Bozkurt et al. 2011). An intracellular RXLR effector named Avr3a of *P. infestans* interacts with potato E3 ubiquitin ligase CMPG1 and stabilizes it, which results in perturbation in cell death response induced by INF1 (Bos et al. 2010). The other examples of oomycete elicitors and plant defense regulations are mentioned in Table 6.2.

6.2.2.4 Virus

Among well-known elicitor-producing microbes like fungi, bacteria, and oomycetes, some viruses are also known that immunize plants and regulate their defense response. Plant virus coat proteins (CPs) can act as elicitors that triggers R-gene-mediated HR response (Moffett 2009). Several viral silencing suppressors

misregulate AUXIN RESPONSE FACTOR 8, which finally causes chlorotic symptoms in plants (García and Pallás 2015). Strain-specific P3 of *Soybean Mosaic Virus* G7 is identified as an elicitor for *Rsv1* (a single dominant resistance gene)-mediated HR response (Hajimorad et al. 2005). It is also observed that TMV replicase sequence of 126/183 kDa activates N-gene mediated hypersensitive response in tobacco plants (Padgett et al. 1997). BV1 protein of bean dwarf mosaic virus is also recognized as a determinant factor for the hypersensitive response and avirulence in French bean (*Phaseolus vulgaris*) (Garrido-Ramirez et al. 2000).

6.2.3 Mode of Action by Which Microbial Bioagents Bring About Plant Defense

The microbial bioagents show antagonism, competition, and parasitism against different pathogenic microbes. These activities of microbial bioagents provide defense to plants directly or indirectly, such as plant defense response stimulation. These mechanisms include antimicrobial compound production, competition for niches and nutrients, elicitation of plant defenses, etc. (Jamalizadeh et al. 2011; Compant et al. 2013; Hussain et al. 2020a). Different mechanisms of biocontrol agents, which have been shown in Fig. 6.1, are described in the following sections.

6.2.3.1 Antagonisms

In antagonism, actions of one organism inhibit or obstruct the normal growth and development of other organisms appearing in its near vicinity. If these types of organisms inhibit phytopathogens, they can be used as biocontrol agents against pests and pathogens (Heydari and Pessarakli 2010). According to Shoda (2000), microorganisms that have capability to multiply in the rhizospheres are regarded as ideal biocontrol agents. Microorganisms colonize in the root of the host, produce some metabolites, and secrete into the root system, which are toxic to pathogens and directly suppress the pathogen growth. These metabolites directly offer protection to the host or sometimes trigger defense in the host plant (Nihorimbere et al. 2012; Chandran et al. 2020). The elicitation of the host plant defense system by microbial bioagents is known as direct antagonism (Ab Rahman et al. 2018).

6.2.3.2 Parasitism

In parasitism, one microorganism is ubiquitous for another. The microbial bioagents produce lytic enzymes like glucosaminidases and chitinases, which lead to the degradation of the cell wall of phytopathogens (Guigón-López et al. 2015). Urbina et al. (2016) investigated the role of enzymes synthesized by *Candida oleophila*

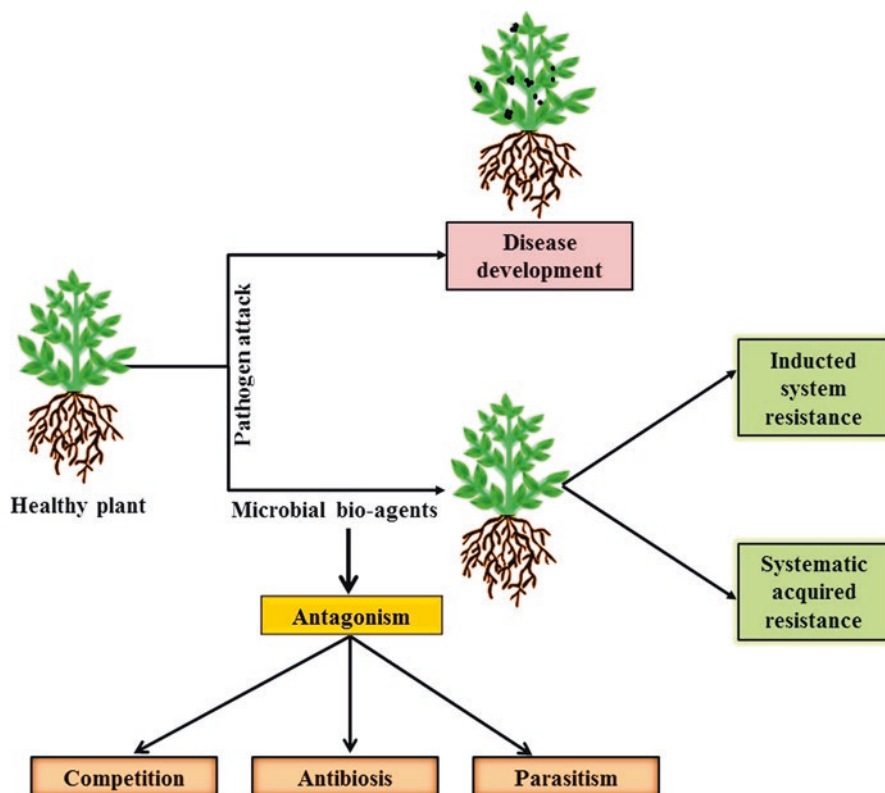


Fig. 6.1 Diagrammatic representation of different antagonistic action and plant defense induced by microbial bio-agents

(extracellular 3-glucanase $\text{exo-}\beta\text{-1}$) in biocontrol of *Penicillium expansum* causing apple spoilage. Moreover, many researchers reported different antagonistic microbial species (Meena et al. 2017c, d). Jeffries (1995) reported that *Rhizoctonia solani* could be controlled using 30 different hyperparasitic species belonging to 16 genera. Powdery mildew, which is caused by an obligate biotrophic pathogen, was controlled with eight hyperparasites by Hijmegen and Buchenauer (Hijmegen and Buchenauer 1984). In a study, it was observed that *Pseudomonas flocculosa* release some cell wall lytic enzymes, which cause cell collapse in powdery mildew cells (Bélanger et al. 2012). Some fungi release protease enzymes such as *Pochonia chlamydosporia*, which causes infection in eggs of the nematodes (Escudero et al. 2016). Rust pathogens *Puccinia violae* and *Puccinia striiformis* f. sp. *tritici* were tested with more than 30 hyperparasitic fungal species, including *Cladosporium uredinicola* and *Alternaria alternata*, respectively, and positive results were obtained (Zheng et al. 2017). Köhl et al. (2019) reviewed that *Alternaria alternata* had the capability to penetrate the urediniospore of wheat rust fungus by germ tubes; the urediniospores were completely collapsed and lost their ability to germinate. In an

experiment, it was reported that the urediniospores treated with *A. alternata* pustules had reduced ability to germinate up to 25% as compared to untreated urediniospores pustules (80%) (Zheng et al. 2017). In *Trichoderma*, parasitism was observed most frequently against *Pythium myriotylum* and *Macrophomina phaseolina* (Kubicek et al. 2001). *Trichoderma* and *Clonostachy* are the most studied mycoparasites, and members belonging to these genera have a wide and varied plant pathogenic host range. These antagonistic isolates form different structures by which they attach to the host and cause infection and death of their hosts by producing cell wall degrading enzymes (Karlsson et al. 2017; Nygren et al. 2018). The synthesis of cell wall degrading substances is not constitutive. The synthesis of enzymes is triggered upon host recognition. Host contain some specific types of molecules on their surface (lectins or secondary metabolites), and these molecules trigger specific types of signaling pathways (G-protein signaling cAMP pathway, and MAPK cascades) (Zhai et al. 2017; Karlsson et al. 2017; Zehra et al. 2015; Meena et al. 2017e, f). Signaling pathways lead to upregulation and transcription of certain genes known as “molecular weapons” including lytic enzymes, which attack and cause lysis of the host. In *Trichoderma*, there are two types of mycoparasitism-related gene families, namely *ech42* and *prb1*, which are overexpressed throughout mycoparasitism (Barbara et al. 2011). Mycoparasitism (*Trichoderma*) first release lytic enzymes; as a result, some oligosaccharides are secreted from the host that are identified by receptors and trigger increased synthesis of lytic enzymes (Karlsson et al. 2017; Meena et al. 2016a, b). This increased level of lytic enzymes results in increased permeability, degradation, and death of the host plant. These types of collaborative transcriptional results were also reported by Reithner et al. (2011) in *Trichoderma atroviride* in response to *B. cinerea* and *Phytophthora capsici*. In *Metschnikowia fructicola*, induced chitinase activity was observed to be regulated by *MfChi* gene due to close contact with the cell wall of yeast *Monilinia fructicola* (Banani et al. 2015). The same type of result was also observed with *Pichia pastoris* when used against *Monilinia fructicola* and *Monilinia laxa* that cause postharvest disease in peach fruits (Dukare et al. 2019).

6.2.3.3 Competition

Competition is a mechanism in which two or more organisms utilize the same type of nutrition or space or both for their survival; therefore, the interaction becomes competitive. The microbial bioagents exploit the nutrients, prevent the pathogen growth and proliferation, and reduce the virulence of the pathogen. For a microbe to thrive in the phyllosphere or rhizosphere, it must be able to make use of accessible nutrients in the form of leachates and exudates or senescent tissue. In rhizosphere, plants release different photosynthates, which are a great source of nutrients (specific sugars, organic acids, and amino acids) for microbes; therefore, the rhizosphere works as a niche. High availability of carbon (40%) around the root surface attracts

different microbes. Microbial bioagents compete with pathogens for nutrients and protect the host from disease occurrence (Degenhardt et al. 2003). This type of approach has been observed in different pathogens such as *Pythium* and *Fusarium*; these are soil-borne pathogens and cause infection by mycelial penetration. *Enterobacter cloacae* act as a microbial bioagent against *Pythium ultimum* by increasing catabolism of nutrients (van Dijk and Nelson 2000; Kageyama and Nelson 2003). Some microbial bioagents, namely *Pseudomonas fluorescense*, chelate iron, which is essential for *Fusarium oxysporum*, whereas *Chryseobacterium* sp. WR21 exploits root exudates and competes with *Ralstonia solanacearum* (Huang et al. 2017). Moreover, antagonistic fungus *Pichia guilliermondii* was found to show competition against certain known pathogenic fungi isolated from wounds of fruit such as apple, namely *Penicillium expansum*, *Penicillium digitatum*, *Colletotrichum* spp. or *B. cinerea*, and *Aureobasidium pullulans* (Spadaro and Droby 2016). It was reported that microbes compete for nitrogen sources in a carbohydrate-rich environment. Besides nitrogen, they also compete for iron because it is a limiting factor for microbial growth and also has low solubility, thus playing a vital role in antagonistic activity such as competition (Spadaro and Droby 2016). Microorganisms have the ability to produce a variety of siderophores, which are low-molecular-weight chelating compounds with a great affinity for iron (van Loon 2000). Pathogenic strains use the chelating compounds to accumulate the ions, and they can be used as microbial bioagents for disease suppression through competition with pathogenic strains that produce siderophores but with low affinity (van Loon 2000; Lugtenberg and Kamilova 2009). *Pseudomonas* spp. have shown siderophore-facilitated iron competition with pathogenic populations present in rhizospheres and reduced their number in soil (Raaijmakers et al. 1995). Fungal antagonists such as *Trichoderma asperellum* and *Metschnikowia pulcherrima* produce iron-binding siderophores and control the growth of *Fusarium* and *A. alternata*, *B. cinerea*, and *P. expansum*, respectively (Saravanakumar et al. 2008; Segarra et al. 2010).

6.2.3.4 Production of Antimicrobial Compounds

Active microbes and the produced allelochemicals as secondary metabolites are potent options for treating plant diseases (Puopolo et al. 2018; Zhao et al. 2021). The most common mechanism associated with biocontrol activity is the production of antibiotics. Besides that, many biocontrol strains produce antifungal enzymes like β -1,3-glucanases, chitinases, proteases, or lipases that are involved in fungal cell wall lysis, produce siderophores, and chelate iron in the rhizosphere, thus inhibiting the proliferation of pathogens (Bais et al. 2004; Latz et al. 2018; Köhl et al. 2019; Pirttilä et al. 2021).

6.2.3.5 Antibiotics

Antibiotics are small, heterogenous molecular compounds, which can inhibit the growth of pathogens at low concentrations (Huang et al. 2021). The general mechanism of antibiotic action is cell wall synthesis inhibition, disruption of cell membrane structure and function, nucleic acids structure and function inhibition, and blocking of key metabolic pathways (Wu et al. 2021). Some antibiotic-producing strains among rhizobacteria are *Bacillus* sp. producing surfactin and iturin A, *Pseudomonas* spp. producing phenazine derivatives, *Erwinia* sp. producing herbicolin A, *Agrobacterium* sp. producing agrocin 84, etc. (Viswanathan and Samiyappan 1999; Compant et al. 2005a, b; Sonigra and Meena 2021).

6.2.3.6 Siderophores

Iron is a trace element that affects the growth, germination, and virulence of a pathogen and hence the development of the pathogen (Spadaro and Droby 2016; Chen et al. 2020; Huang et al. 2021). The bacterial siderophores compete for zinc, copper, manganese, and most importantly iron. These BCA limit the availability of iron in the soil by solubilization and the competitive acquisition of Fe^{3+} and subsequently inhibit the plant pathogen by limiting their growth (Leong 1986; Loper and Henkels 1997; Chin-A-Woeng et al. 2003; Haas and Défago 2005; Ab Rahman et al. 2018). Bacteria produce many types of siderophores, for example, catecholate, carboxylate, hydroxamate, and salicylate (Rajkumar et al. 2010; Kumari et al. 2018a, b). Dual inoculation of *Pseudomonas koreensis* and *B. subtilis* strains have been proved to have antagonistic activity and produce siderophore in controlling *Cephalosporium maydis* in maize plants (Ghazy and El-Nahrawy 2021). *Paenibacillus polymyxa*, a siderophore producer, has been proved as a growth promoter of *Lilium lancifolium* and showed antifungal activity against *Botryosphaeria dothidea*, *F. oxysporum*, *Fusarium fujikuroi*, and *B. cinerea* (Khan et al. 2020).

6.2.3.7 Volatile Organic Compounds (VOCs)

VOCs are low-molecular-weight compounds that, under low normal atmospheric temperature and pressure, can evaporate below 300 Da (Vespermann et al. 2007). The main composition of VOC mixture is alcohols, esters, aldehydes, terpenes, aliphatic and aromatic hydrocarbons, nitrides, and sulfides, which exhibit strong antimicrobial effects (Strobel 2011; Lemfack et al. 2018; Huang et al. 2021). Delgado et al. (2021) developed a new consortium PUCV-VBL, composed of *Hanseniaspora osmophila* and *Gluconobacter cerinus*, to control fungal rots in the grapes. The VOCs produced by this consortium showed 86% mycelial inhibition against *B. cinerea*.

6.2.3.8 Lytic Enzymes

Microbial enzymes assist microbes in reproducing in a particular niche and function as biocatalysts for key biochemical reactions (Chaudhari and Patel 2021). The microbes extracellularly produce hydrolytic enzymes to prevent potential plant pathogens (Umer et al. 2021). The antagonists release various enzymes, such as lipase, cellulases, chitinases, xylanases, mannanases, laminarinase, chitosanase, glucose oxidase, protease, and betaglucosidases for biocontrol activity (Picard et al. 2000). Two novel *Bacillus* strains (*simplex* and *subtilis* species) have been found to produce lytic enzymes (protease and β -glucanase), which aided in the biofungicidal activity against *Zymoseptoria tritici* causing *Septoria tritici* blotch of wheat (Allioui et al. 2021).

6.3 Conclusion

During the past few years, beneficial plant microbes have received attention as a substitute for chemical fertilizers because of their sustainable plant protection property. The microbial bioagents produce different elicitors and MAMPs, which trigger induced systemic resistance. A distinctive feature of ISR-eliciting microbial bioagents is local suppression of root immune response in a cell-type specific manner. The studies of root cell-type-specific metabolome and transcriptome profiles in response to microbial bioagents will aid in providing information to develop consistent and reliable methods of crop production. Agrochemicals pose a danger to the health of living beings and the environment due to their toxicity, while elicitors have no adverse effects and leave no residues. The isolation of novel microbial bioagents with high effectiveness against plant pathogens is important and essential. The microbial bioagents with synergistic action against plant pathogens may provide desirable results.

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AZ and PS: Provided the general concept; validation; writing – review & editing.

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