Chapter 8
Microbial Elicitors for Priming Plant Defense Mechanisms

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Abstract Some microrganisms have evolved to be associated with plants, receiving nutrients from plants, and helping plants to fight pathogens by producing microbial elicitors, which are compounds that trigger plant defenses. Elicitors are thus safe compounds that can replace harmful pesticides for a sustainable agriculture. Here we review plant immunity and microbial elicitors with focus on antibiotics, volatile organic compounds, siderophores, antimicrobials, enzymes, salicylic acid, methyl salicylate, benzoic acid, benzothiadiazole and chitosan.

Keywords Plants · Microbes · Pathogen · Immunity · Defence · R genes · Metabolites · Antibiotics · Siderophores

Abbreviations

PRR	Pattern-recognition receptors
MAMP	Microbe-Associated Molecular Pattern
DAMP	Damage-associated molecular patterns
MTI	MAMP triggered immunity
RLP	Receptor-like proteins

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8.1 Introduction

While the demand for food increases exponentially, crop productivity gets relentlessly haunted by an increased number of biotic and abiotic stress combinations generally associated with global warming (Schlenker and Roberts 2009; Challinor et al. 2014; Zhao et al. 2017; Mehta et al. 2019, 2020). Abiotic stress conditions like drought, salinity, low and high-temperature etc. also influence the biotic stress factors (microbes, insects, weeds, and phytopathogens) (Seherm and Coakley 2003; McDonald et al. 2009; Ziska et al. 2010; Peters et al. 2014) (Fig. 8.1). These stress conditions likewise influence the interactions between plants and microbes present in their rhizosphere which built up quite a long time ago. The more fascinating fact is that these plants are established on land with the help of symbiotic fungal associations. It suggests that plants are invariably exposed to microbes via associations since their first existence on land, and these disagreements between microbes and plants resulted in mutative coexistence cycles which further shaped their habitats, lifecycles, distribution, and genomes of both organisms.

Based on their nature, these microbes are either beneficial or harmful to the plants. The harmful microbes act as pathogens and delimit productivity by causing a large number of diseases in multiple crops (Lamichhane and Venturi 2015; Rahman et al. 2019; Singh et al. 2019). It is supported by the fact that these biotic

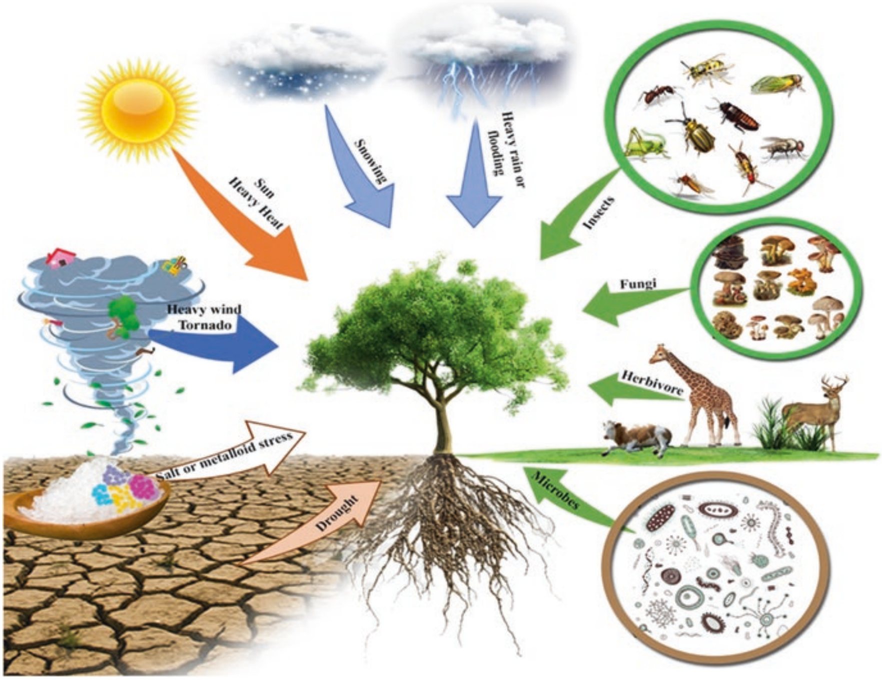

Fig. 8.1 Abiotic and biotic stresses which reduce plant productivity

Table 8.1 Characteristic features of necrotrophs and biotrophs

Features	Necrotrophs	Biotrophs
Uptake of nutrients	From dead plant cells	From live cells
Type of pathogen	Opportunistic (non-obligate)	Specialized (obligate)
Death of host cell	Rapid	Not rapid and induce hypersensitive cell death in incompatible interactions
Mode of entry	Enter through wounds or natural openings thus considered as unspecialized	Specialized entry via direct (mechanical) entry or through natural openings
Secretion of lytic enzymes	Cell-wall degrading enzymes and toxins	Few lytic enzymes or toxins
Systemic	Seldom	Often
Host range	Wide	Narrow
Survival on host	As saprotrophs	On host or as dormant propagules
Host preference	Weak, young, or damaged plants	Plants of all ages
Control	By quantitative resistance genes	By specific (gene-for-gene) Resistance genes
Growth within-host	Intercellular and intracellular through dead cells	Intercellular
Defense pathways of plants against pathogens	Jasmonate and ethylene-dependent	Salicylate-dependent
Examples	*Botrytis cinerea* – Grey mold, *Pythium ultimum* – Damping-off in seedling	*Uromyces fabea* – Rust, *Ustilago maydis* – Maize smut

factors constrain the yield up to 26% globally. They invade the plants either through the leaf (stomata), stem (lenticels), and root surface directly or through injury. After the invasion, they employ a variety of strategies to impair plant growth. These pathogens are comprehensively divided into two types- necrotrophs (bacteria, fungi, insects, and also herbivorous animals), hemibiotrophs, and biotrophs (basically viruses). The former type kills their host and feeds on the dead material, unlike biotrophs that complete their life cycle in a living host. Being sessile by nature, the plants have evolved their immune system to prevent themselves from pathogens as they can't escape their enemy, unlike vertebrates. The characteristic features of necrotrophs and biotrophs are tabulated in Table 8.1.

8.2 Plant Immunity Against Harmful Microbes

An enormous set of pathogens have the potential to kill or damage plants and it goes on through the entire ecosystem. Plants utilize preformed defenses intended to avert pathogen and herbivore attacks. The first line of defense in plants is provided by the thick waxy or cuticular skin of the plant body along with the presence of antimicrobial products (Dangl and Jones 2001). Although pathogen finds a broad spectrum of strategy to invade. For the passive form of invasion, intercellular space like apoplast, stomata, hydathodes, lenticels, or local wounds are the frequent target, and in the active, plant-pathogen develop specialized organs like nematode and aphid have stylet, fungi have hyphae as well as haustoria (Jones and Dangl 2006). On successful plant invasion, the plants utilize their immune system consisting of mainly two interconnected tiers to fight against pathogens (Jones and Dangl 2006; Boller and Felix 2009; Thomma et al. 2011; Spoel and Dong 2012). One of these innate immunity strategies utilizes cell surface pattern-recognition receptors (PRRs) to perceive Microbe-Associated Molecular Patterns (MAMPs) and host-derived damage-associated molecular patterns (DAMPs) present in a large variety of microbes (Boller and Felix 2009). Receptor-like kinases and receptor-like proteins (RLPs) are the cell surface pattern-recognition receptors in plants. The canonical structure of receptor-like kinases has an extracellular domain to recognize ligands, an intracellular kinase domain with only one pass transmembrane domain (Couto and Zipfel 2016; Zipfel and Oldroyd 2017). Receptor-like proteins lack the kinase domain (Zipfel 2014; Couto and Zipfel 2016; Zipfel and Oldroyd 2017) (Fig. 8.2).

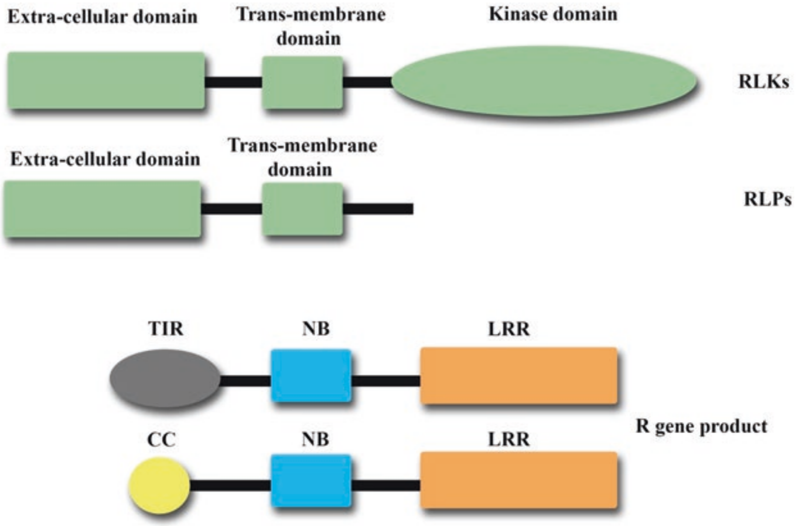

Fig. 8.2 Mechanism of plant immunity against harmful microbes. Receptor-like kinases (RLKs) and receptor-like proteins (RLPs) are potent membrane molecules to identify Microbe-Associated Molecular Patterns (MAMPs) and Pathogen-Associated Molecular Patterns (PAMPs). R gene products (NB-LRRs) recognize the released Avr factors from pathogens. *TIR* Toll-interleukin-1 receptor, *NB* Nucleotide-binding, *LRR* Leucine-rich repeat, *CC* Coiled coil, and *R gene* Resistance gene

Pattern-Recognition Receptors have a highly variable ligand recognition domain and thus recognizes a wide range of microbes. They along with their co-receptors (known to have the same extracellular domain as PRRs) triggers a signaling cascade to establish pattern-triggered immunity (Jones and Dangl 2006; Zipfel 2014). Microbe-Associated Molecular Patterns (MAMPs) are shared similar molecular patterns such as lipopolysaccharides, peptidoglycan, flagellin, etc. (Jones and Dangl 2006) which exist in pathogen cell wall or extremities to represent own group identity as well as potent virulence (Table 8.2). On the other hand, damage-associated molecular patterns (DAMPs) encourage the inflammatory responses by activating the PRRs (Table 8.3). They are endogenous molecules that are released from the stressed or dead cell eliciting the immune system activation (Gust et al. 2017). As, e.g., tomato systemin generated by the wound, influences the processing of prosystemin and it induces adjacent cells as well as vascular bundle elements to produce Jasmonic acid which finally activates the expression of proteinase inhibitor genes (Pearce et al. 1991).

Table 8.2 Common potent microbe-associated molecular patterns with their respective pattern recognition receptors

S. No.	Microbe associated molecular patterns	Origin	Family of pattern recognition receptors	Associated pattern recognition receptors	Plant species
1.	RaxX	*Xanthomonas oryzae pv. Oryzae*	LRR XII	XA21	*Oryza longistaminata*
2.	Flagellin	*Pseudomonas syringae pv. Tabaci*	LRR XII	FLS2	*Arabidopsis thaliana*
3.	csp22	*Staphylococcus aureus*	LRR XII	CORE	*S. lycopersicum*
4.	EF-Tu	*Escherichia coli*	LRR XII	EFR	*A. thaliana*
5.	Chitin	*Agaricus bisporus*	LysM	AtCERK1, AtLYK5	*A. thaliana*
6.	SnTox1	*Stagonospora nodorum*	WAK	Snn1/ TaWAK	*Triticum aestivum*
7.	Lipopolysaccharides	*P. fluorescens*	G-Lec	SD1–29/ LORE	*A. thaliana*
8.	Avr3/ Six1	*Fusarium oxysporum*	G-Lec	I-3	*S. lycopersicum*
9.	NLP	*Pythium aphanidermatum*	LRR	RLP23	*A. thaliana*
10.	Elicitin	*Phytophthora cryptogea*	LRR	RLP85/ ELRb	*S. microdontum*

Source: Google scholar-based literature survey 1995–2020. *LRR* Leucine-rich repeats, *WAK* Wall-associated kinase, *LysM* Lysine motif, *RLP* Receptor-like protein

Table 8.3 Potent damage-associated molecular patterns and respective host plants

Category	Potent Damage associated molecular patterns	Host plants
Protein	PAMP-induced secreted peptides	*Arabidopsis thaliana*
	Rapid alkalinization factors	*A. thaliana*
	AtPep1	*A. thaliana*
	High mobility group box 3	*A. thaliana*
Carbohydrate	Glucose (monosaccharide)	*Nicotiana tabacum*
	Sucrose (diholoside)	*A. thaliana*
	Trehalose (diholoside)	*A. thaliana*
	D-allose (monosaccharide)	*Oryza sativa*
Lipid	Hydroxystearic acid (cutin monomer)	*Hordeum vulgare*
Nucleotide	Extracellular ATP	*A. thaliana*

Source: Google scholar-based literature survey 1995–2020

After recognizing microbe-associated molecular patterns or damage-associated molecular patterns, pattern recognition receptor-dependent response triggers the downstream cell signaling to initiate the immune response (Schwessinger and Ronald 2012). The Pattern-recognition receptors have many kinds of an extracellular domain, *viz*., leucine-rich repeats, lectin, lysine motif, epidermal growth factor-like domains which are intended to provide a more significant range of ligand recognition. The co-receptors that form the complex to activate the different downstream signaling molecules namely Receptor-like proteins, receptor-like kinases, etc. also have a role in plant growth, abiotic stress, and mutualism with beneficial microbes. Finally, Calcium-dependent protein kinases, Mitogen-activated protein kinase cascades, reactive oxygen species production, and cellulose deposition get activated, which leads to modification in transcriptional products (Boutrot and Zipfel 2017).

Through evolution, microbes have developed a vast repertoire of effector molecules or elicitors for successful infection establishment in their hosts, while responsive plants persistently produce disease resistant R proteins to combat these effector molecules. As the elicitors enter into a plant cell through the type III secretion system (Finlay and Falkow 1997), their recognition in plants triggers the effector-triggered immunity (Jones and Dangl 2006; Spoel and Dong 2012). Most of the knowledge about the effectors and type III secretion system is based on the work conducted on *Pseudomonas syringae*, a highly diverse plant biotrophic pathogen (Baltrus et al. 2011). The pan-genome of *P. syringae* species complex from 494 strains was used to analyze type III secretory effector molecules, and a total 14, 613 putative type III secretory effectors were identified out of which 4636 were unique at the amino acid level (Dillon et al. 2019). To date, this vast repertoire of effector molecules constitutes 66 families. A particular strain from this complex typically expresses 15–30 effector molecules. These effector molecules are encoded by hrp/hrc (hypersensitive response and pathogenicity) genes and named Hop because of their ability to pass through the type III secretion system (Fig. 8.2).

Many effectors from its pangenome are also known as ‘Avr’ because of their discovery in the post-genomic era as avirulence phenotype (Lindeberg et al. 2005). These effector molecules were analyzed in the context of their role in the two-grade innate immunity of plants. According to this model, primarily the immunity elicited by bacterial flagellin, lipopolysaccharide, peptidoglycan, and elongation factor Tu which is commonly known as Pattern-triggered immunity was suppressed by these effector molecules secreted by bacteria. Later, these molecules are perceived by resistance (R) proteins, the second grade of innate immunity familiarized as Effector-triggered immunity (Jones and Dangl 2006). The resistance (R) proteins are characterized by nucleotide-binding site leucine-rich repeats through which they recognize and bind to the effector molecules released by microbes resulting in Effector-triggered immunity response. Sometimes Effector-triggered immunity induced response is called hypersensitive response where programmed cell death occurs eventually. This kind of immune is very effective on biotrophs as their association is within the cell. Pathogenic type III secretory effectors are like ‘double-edged swords’, as on one hand, they trigger Effector-triggered immunity response and on the other, they suppress Effector-triggered immunity response (Hou et al. 2011).

Local cellular responses are delivered throughout the system to generate a large scale of resistance toward similar infections as well as secondary infections. The Effector-triggered immunity response also instigates the synthesis of small, low-molecular-weight, mobile, immune signaling molecules like salicylic acid, glycerol-3-phosphate which are then transported from the site of infection where they were synthesized to the site of non-infection, to prevent the healthy plant tissues from infection (Spoel and Dong 2012; Fu and Dong 2013). After perceiving these immune signaling molecules, uninfected tissue accumulates Salicylic acid resulting in massive transcriptional programming. This instigated immune signaling is known as systemic induced signaling (Spoel and Dong 2012; Fu and Dong 2013) (Fig. 8.3).

Recent studies suggested that plant symbionts and pathogens take advantage of comparable molecular strategies to conquer the defense reactions of plants. The Microbe Associated Molecular Patterns/Pattern Recognition Receptor system also takes part in harmonious reciprocity with symbiotic microbes. This proposes the role of beneficial microbes for disease tolerance against pathogens employing the innate immune system of plants (Hacquard et al. 2017).

8.3 Beneficial Microbes and Their Metabolites

The ecosystem of the soil is one of the most complex and multifarious ecosystems of the earth which is inhabited by a wide range of organisms from fungi, arthropods, nematodes to bacteria (Venturi and Keel 2016). Bacterial diversity is lower in the

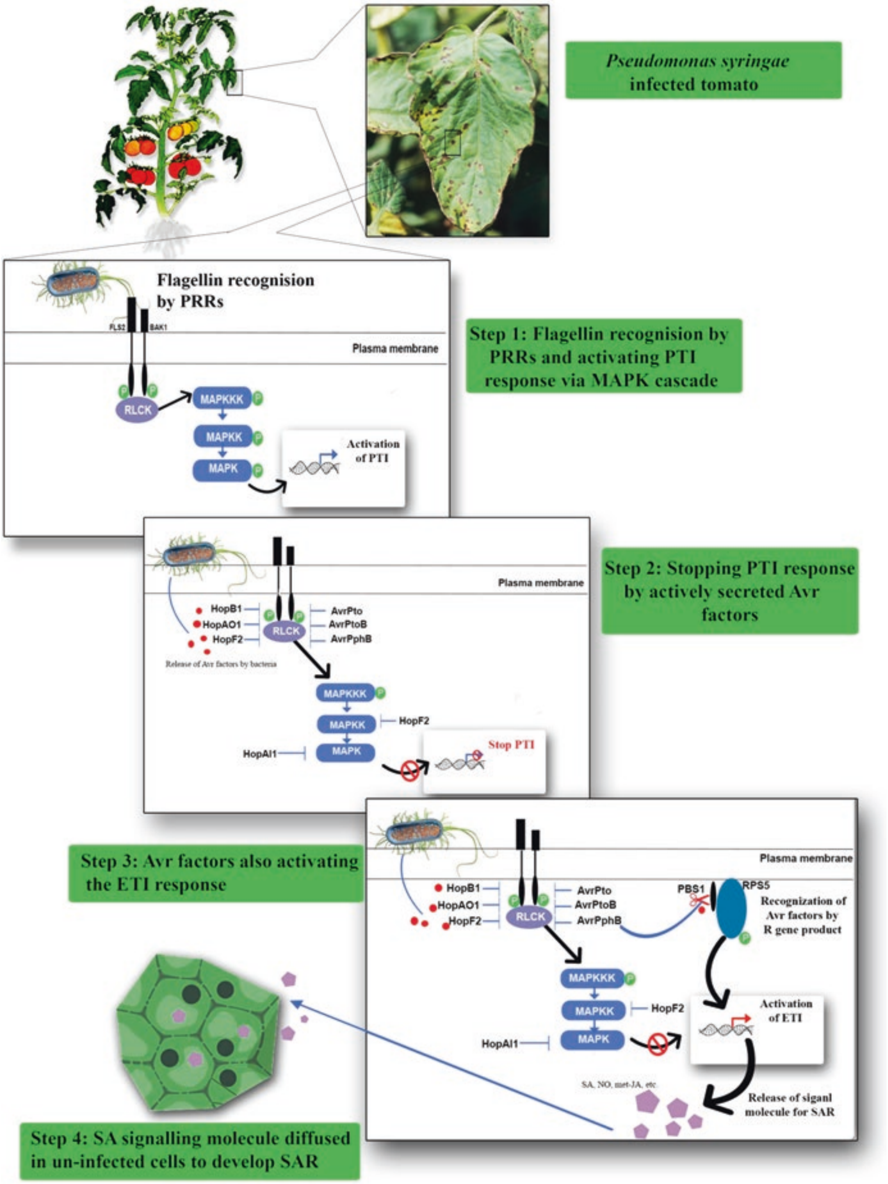

Fig. 8.3 Down-stream signaling in tomato upon recognition of *Pseudomonas syringae* flagellin

rhizosphere but has increased abundance and activity. These bacteria in the rhizosphere are under the selective pressure of plants suggesting a correlation between plant-derived metabolites and microbial metabolites. Through such association, mutual relationships are established between plants and microbes which are essential for root-root interactions, nutrient availability, amassing of microorganisms, and biofilm formation of soil microbes (Mommer et al. 2016; Rosier et al. 2016; Sasse et al. 2018), as well as inhibition of phytopathogens (Bertin et al. 2003; Li et al. 2013).

Based on their effects on plants, plant-associated microbial communities are classified into three categories such as beneficial, deleterious, and neuter. Microbes that play a role in plant growth, nutrient uptake, defense, resistance, and development during stress and normal circumstances are known as plant growth-promoting microbes. The typical plant growth-promoting microbes in the rhizosphere are *Paenibacillus, Burkholderia, Pseudomonas, Bacillus, Acinetobacter, Arthrobacter,* and *Arthrobacter* (Finkel et al. 2017; Sasse et al. 2018; Zhang et al. 2017). These bacteria secrete molecules to establish an association with plants which triggers specific changes in the transcriptome of plants. These plant growth-promoting microbes can produce phytohormones like auxins, abscisic acid, cytokinins, salicylic acid, gibberellins, and jasmonic acid (Fahad et al. 2015).

Additionally, antibiotics, siderophores, antimicrobials, enzymes, volatile organic compounds, and many more helps in priming defense mechanisms in plants. All these metabolites secreted by microbes are known as “elicitors”. “Elicitors can be defined as small molecules secreted under stress which induces biosynthesis of specific molecules having an essential role in the adaptations of plants to a stress condition” (Radman et al. 2003). The role of these elicitors for plant growth promotion and ISR priming has been extensively studied for decades, and these are promising substitutes for herbicides, fertilizers, and pesticides (Kloepper et al. 2004; Gupta et al. 2015). Below, we look at the elicitors secreted by plant growth-promoting microbes which are of paramount importance in priming induced systemic resistance in plants against phytopathogens.

8.3.1 Antibiotics

The utmost important mechanism employed by plant growth-promoting microbes to hamper the negative impact of plant pathogens is the biosynthesis of a wide range of antibiotics (Couillerot et al. 2009; Raaijmakers and Mazzola 2012). However, the host range of these antibiotics varies and is also dependent on different field conditions. A large range of bacterial antibiotics have been derived from genera *Bacillus* includes zwittermycin-A (Silo-Suh et al. 1994), kanosamine (Milner et al. 1996), Bacillomycin (Volpon et al. 1999) and Plipastatins A and B (Volpon et al. 2000). On the other hand, *Pseudomonas* include cepafungins (Shoji et al. 1989), pseudomonic acid (Fuller et al. 1971), 2,4 Diacetyl phloroglucinol (Shanahan et al. 1992), pyoluteorin (Howell and Stipanovic 1980), oomycinA (Kim et al. 2000), phenazine-1-carboxylic acid (Pierson III and Pierson 1996), butyrolactones (Thrane et al. 2000), rhamnolipids, viscosinamide (Nielsen et al. 1999), cepaciamide A (Howie and

Suslow 1991), ecomycins (Jiao et al. 1996), azomycin (Shoji et al. 1989), and karalicin which is an anti-viral antibiotic (Lampis et al. 1996).

These metabolites serve as antioxidant, antimicrobial, phytotoxic, antiviral anti-helminthic, insect and mammalian antifeedant, cytotoxic, and plant growth-promoting activity agents and are best studied in disease management. For example, a novel antibiotic secreted by *B. cereus* UW85 is Zwittermicin A, which is highly active against Oomycetes, algal protists and moderately active against a vast range of gram-negative bacteria and fungi and few gram-positive bacteria. When it is combined with another antibiotic, kanosamine secreted by the same organism they act synergistically against *E. coli* (Laura et al. 1998). *P. flouorescens* produce 2,4 Diacetyl phloroglucinol which inhibits *Sclerotium rolfsii* – a soil-borne pathogen (Asadhi et al. 2013). It also secretes another antimicrobial compound, phenazine-1-carboxylic acid (Lohitha et al. 2016) which is responsible for oxidation-reduction reactions as well as amassing of superoxides in target cells and is efficacious in wheat disease caused by *G. graminis* var. *tritici* and *S. rolfsii*, resulting in stem rot in groundnut.

8.3.2 Siderophores

Iron is of paramount importance in the photosynthetic system of plants due to being an essential molecule of chlorophyll. However, its soluble concentration in soil is deficient and its insoluble form (ferric, Fe^{3+} hydroxides) is not readily available for plants and microbes (Saha et al. 2013). To find the key to this issue, some plants, fungi, and bacteria secrete iron-binding molecules of low molecular weight (~400–1000 Da) known as “siderophores” the chelating agents for iron (DalCorso et al. 2013; Saha et al. 2013). These molecules have a surprisingly high affinity for iron and thus scavenge it from the soil.

When iron gets bound to the siderophore, it becomes solubilized and is recognized by receptors on the surface of plants or microbes from where it gets internalized followed by reduction to ferrous state (Fe^{2+}). For the most part, siderophores of plant growth-promoting microbes have a higher affinity for iron than plants and fungi (Saha et al. 2012, 2013). They behave as transport vehicles of iron and common iron-binding molecules and include catechols, hydroxamic acid, and hydroxylic acid. In addition to priming growth, siderophores also help to dampen phytopathogens (Tank et al. 2012). For instance, *B. subtilis* secreted siderophores had similar disease suppression activity in chickpea against dry root rot causing fungi (Patil et al. 2014).

8.3.3 Microbial Volatile Organic Compounds

Volatile organic compounds, as the name suggests are organic molecules having high vapor pressure at room temperature. They are products of metabolic pathways and occurs as a composite aggregation of low-molecular-weight compounds that are having an affinity for lipids and are now termed as "volatile" because of their complex nature (Maffei et al. 2011). These are accountable for communication between various organisms like plants and their pathogens, plant growth-promoting microorganisms, and plants (Maffei 2010; Maffei et al. 2011; Garbeva et al. 2014; Lemfack et al. 2014; Kanchiswamy et al. 2015). Due to their volatile nature, they can easily move from the point of their synthesis to the point of their action, thus acting as communication molecules among organisms (Maffei et al. 2011). Volatile organic compounds released by microbes are commonly termed as microbial volatile organic compounds.

These volatile organic compounds serve chemical windows through which information is allowed to leave (Liang et al. 2008). To name a few; furfurals, camphor, acetaldehyde, methanol, geosmin, butanoic acid, 5-hydroxy methylfurfural, camphene are the most commonly secreted molecules (Li et al. 2004; Müller et al. 2004; Leff and Fierer 2008; Gray et al. 2010; Ramirez et al. 2010; Wenke et al. 2010; Perl et al. 2011; Jünger et al. 2012; Sundberg et al. 2013). Among all metabolites secreted by beneficial microbes, volatile organic compounds form the successful primary defense system in plants against phytopathogens along with promoting plant growth (Ryu et al. 2004; Beneduzi et al. 2012; Song and Ryu 2013). For instance, the mycelial growth of *Rhizoctonia solani* has been reported to be inhibited by microbial volatile organic compounds (Kai et al. 2007). In vitro, volatile organic compounds – 2,4decadienal, n-hexadecanoic acid, oleic acid, and diethyl phthalate secreted from *Paenibacillus* spp. and *Bacillus* suppresses the disease activities of *Ascochyta cutrillina, Alternaria brassicae* and *Alternaria solani* (Han et al. 2016).

In addition to all these, many beneficial microbes secrete enzymes like chitinase, glucanases, amylases, and lipases which also aids in the growth, development, and elicitation of defense mechanisms in plants against phytopathogens (Bull et al. 2002; Saraf et al. 2014). Plant receptors recognize lipopolysaccharides, flagellin, and elicitors from both phytopathogens and plant growth-promoting microorganisms in the same manner, and in response, microbe-associated molecular pattern-triggered immunity is activated in both cases but somehow this response does not ward off beneficial microbes or plant growth-promoting microorganisms, the reason is still unknown (Van Wees et al. 2008). Table 8.4 elucidates the various microbes and their respective elicitors in various plant species and Fig. 8.4 depicts the interaction between phytometabolites and microbial metabolites which includes beneficial as well as infectious interactions. Table 8.5 provides insight into the role of the elicitors and their mode of action in plant defense mechanisms.

Table 8.4 Microbial elicitors that instigate systemic resistance in plants

Plants	Microbes	Organic substance	Phytopathogen	References
Arabidopsis	2,4-diacetylphoroglucinol	*Peronospora parasitica*	*P. fluorescens*	Iavicoli et al. (2003)
	B. subtilis GB03, *B. amyloliquefaciens* IN937a	Volatile compounds	*Erwinia carotovora*	Ryu et al. (2004)
	B. subtilis	Surfactin	*P. Syringae*	Bais et al. (2004)
	Transgenic *Arabidopsis*	PevD1 protein	*B. cinerea, P. syringae* pv. Tomato	Liu et al. (2016)
	B. Amyloliquefaciens UCMB5113	Fengycins	*Alternaria brassicicola*	Asari et al. (2017)
	Saccharothrix yanglingensis Hhs.015	BAR11 protein	*P. Syringae* pv. Tomato DC3000	Zhang et al. (2018)
Bt cotton	*Penicillium chrysogenum*	Dry mycelium	*Fusarium oxysporum, Verticillium dahlia*	Chen et al. (2006)
Cotton	*E. coli* (recombinant)	PevD1 protein	*Verticillium dahliae*	Bu et al. (2014)
Tobacco	*E. coli, Alternaria tenuissima*	PeaT1	*Tobacco mosaic virus*	Zhang et al. (2011)
	Alternaria tenuissima	Hrip1	*Tobacco mosaic virus*	Kulye et al. (2012)
	B. subtilis 985, *B. amyloliquefaciens* 5499	Surfactin lipopeptide	*Botrytis cinerea*	Cawoy et al. (2014)
	B. subtilis	Culture supernatant	*Tobacco mosaic virus, Ralstonia solanacearum, Phytophthora parasitica*	Chang et al. (2015)
	Bacillus sp. SJ	Volatile compounds	*Rhizoctonia solani, Phytophthora nicotianae*	Kim et al. (2015)
	B. subtilis SYST2	Albuterol, 1,3-propanediol	*Ralstonia solanacearum* TBBS1	Tahir et al. (2017)
Rice	*E. coli* (recombinant)	MoHrip1	*Magnaporthe oryzae*	Chen et al. (2012)
	Pseudomonas protegens CHAO	Orfamide A	*Cochliobolus miyabeanus*	Ma et al. (2017)
Soybean	*B. amyloliquefaciens* MEP(2)18 and ARP(2)3	Surfactin, Fengycins	*Sclerotinina scleriotorum*	Alvarez et al. (2012)
Bean	*Pseudomonas sp.* CMR12a	Phenazines, sessilins	*Rhizoctonia* web blight	Ma et al. (2016)
Cucurbits	*B. subtilis UMAF6639*	Iturin and fengycin	*Podosphaera fusca* (cucurbit powdery mildew)	García-Gutiérrez et al. (2013)

(continued)

Table 8.4 (continued)

Plants	Microbes	Organic substance	Phytopathogen	References
Grapevine	*B. subtilis*	Surfactin, mycosubtilin	*B. cinerea*	Farace et al. (2015)
Tea	*P. fluorescens* RRLJ134, *P. aeruginosa* RRLJ04	Phenazine analogues	*Fomes lamoensis, Ustulina zonata*	Mishra et al. (2014)
Tomato	*Trichoderma virens, Trichoderma atroviride*	SM1 (small protein1) and EPl1 proteins (eliciting plant response-like protein)	*Alternaria solani, B. cinerea, P. syringae* pv. Tomato (Pst DC3000)	Salas-Marina et al. (2015)
	B. fortis IAGS 162	Phenylacetic acid	*Fusarium oxysporum* f.sp. *lycopersici*	Akram et al. (2016)
	P. aeruginosa PM12	3-Hydroxy-5-methoxy benzene methanol	*Fusarium oxysporum*	Fatima and Anjum (2017)
Maize	*B. Amyloliquefaciens, B. subtilis*	Iturin A, Fengycin, Bacillomycin	*Fusarium moniliforme*	Gond et al. (2015)
	B. subtilis DZSY21	Lipopeptides	*Bipolaris maydis*	Ding et al. (2017)

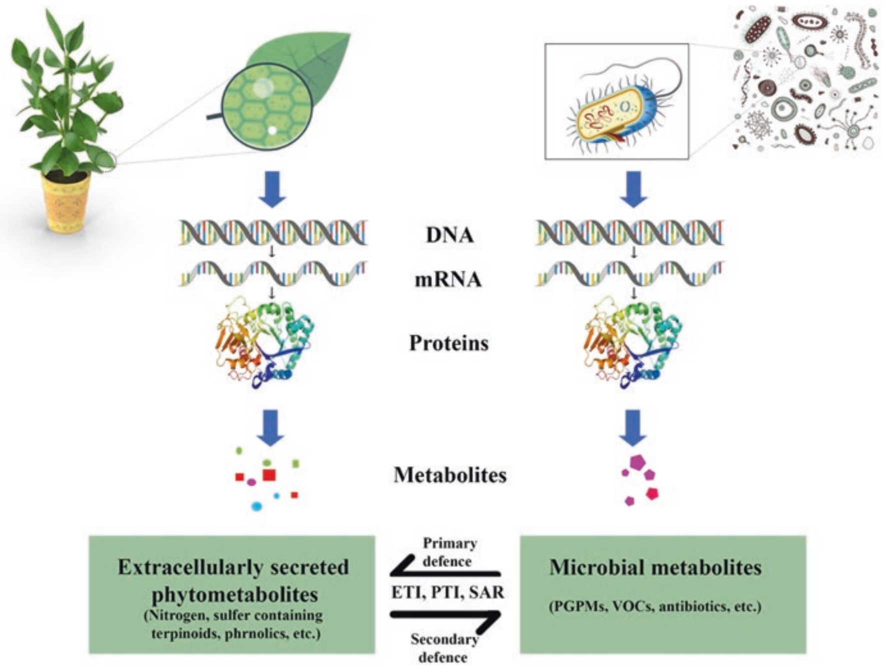

Fig. 8.4 Interaction of phytometabolites and microbial metabolites in the rhizosphere. *ETI* Effector-triggered immunity, *PTI* Pattern-triggered immunity, *SAR* Systemic acquired resistance, *PGPM* plant growth-promoting microorganism, *VOCs* Volatile organic compounds

Table 8.5 Role of elicitors in plant defense mechanisms

Plants	Elicitors/ inducers	Phytopathogens	Mode of action of elicitors/ inducers	References
Tobacco	PeBA1 protein	*Tobacco mosaic virus, B. Cinerea*	Induction of defense responsive genes to produce salicylic acid, phenyl ammonia-lyase, jasmonic acid, H_2O_2, and phenolic compounds	Wang et al. (2016)
	3-Acetonyl-3-hydroxyoxindole (AHO)	Tomato spotted wilt virus	Two differentially expressed genes (PR1 and PR10) were activated for the synthesis of phytometabolites like propanoid, sesquiterpenoid and triterpenoid to protect the wax and cuticle of plants	Chen et al. (2017)
	PevD1	*Verticillium dahlia, tobacco mosaic virus, P. syringae* pv. Tabaci	Interacts with Nbnrp1 to regulate PevD1	Liang et al. (2018)
Tobacco, *Arabidopsis*	Benzoyl salicylic acid	*Tobacco mosaic virus*	WRKY transcription factors, hypersensitive response molecule, mitogen-activated protein kinase as well as NPR1 genes were activated	Kamatham et al. (2016)
Tomato	Benzothiadiazole	Tomato spotted wilt virus and citrus exocortis viroid	Activates salicylic acid signaling pathways of plants	López-Gresa et al. (2016)
	N-decanoyl-homoserine lactone	*Botrytis cinerea*	Induction of jasmonic acid synthesis pathway	Hu et al. (2018)
Sunflower	Benzothiadiazole	*Sclerotinia sclerotiorum*	Hinders growth of fungal hyphae and increase the formation of mycorrhizae in the plant roots	Bán et al. (2017)
Whitebark pine	Methyl jasmonate	*Cronartium ribicola,* mountain pine beetle, *Dendroctonus ponderosae*	Reprogram of defensive genes	Liu et al. (2017)
Cassava	Salicylic acid or methyl jasmonate	*Xanthomonas axonopodis* pv. Manihotis	Elevates the defense action	Yoodee et al. (2018)

Note: *PeBA*1 protein elicitor from *Bacillus amyloliquefaciens* NC6, *NPR*1 Nonexpressor of Pathogenesis-Related Genes 1, *Nbnrp*1 *Nicotiana benthamiana* Neuropilin-1 gene, *PevD*1 Proteinaceous elicitor secreted by *Verticillium dahliae*, *PR*1 Pathogenesis-related protein1, *PR*10 Pathogenesis related protein10

8.4 Conclusion

Thus, in the rhizosphere, plants along with all beneficial and pathogenic microbes are considered as a whole ecological community and referred to as “holobiont”. Plant pathogens are the necrotrophs, hemibiotrophs, and biotrophs had in due course of evolution helped the plant communities to advance their immune responses in one or the other way. The present strategies discussed above include Pattern recognition receptors to perceive Microbe associated molecular patterns and Damage associated molecular patterns to further elicit the downstream signaling cascade involving Calcium dependent protein kinases, Mitogen-activated protein kinase, etc. However, in terms of co-evolution, the microbes developed an enormous repertoire of effector molecules while plants in response co-evolved with disease resistance (R) proteins to counteract these effector molecules.

On the beneficial front or in other terms in a mutualistic way, plant growth-promoting microorganisms promote plant growth via establishing an association triggering the production of phytohormones like auxins, abscisic acid, cytokinins, salicylic acid, gibberellins, and jasmonic acid, antibiotics, siderophores, antimicrobials, enzymes, volatile organic compounds. For example, beneficial microorganisms or plant growth-promoting microorganisms dominated by *Bacillus* and *Pseudomonas* spp. lives in a symbiotic relationship with the plants for food and nutrients and inturn helps plants in their growth, development, and defense against phytopathogens. Plant Growth Promoting Microbes employ direct and indirect mechanisms to hamper the growth of phytopathogens. The direct mechanism involves inhibition of metabolism while the indirect mechanism involves competition against phytopathogens for the nutrients. The metabolism of phytopathogen was inhibited by various mechanisms including secretion of antibiotics (antimicrobial, antiviral, etc.). However, all these mechanisms to surpass, co-evolve, or to involve in symbiotic associations pave the way for further advancements in both the plants and the microbial genome in order to thrive at their utmost capabilities and in future years may evolve or co-evolve in a different mechanism as discussed above under the influence of selection pressure and can lead to different or novel mechanisms.

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