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Elicitors of plant immunity triggered by beneficial bacteria

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Abstract

The molecular basis of plant immunity triggered by microbial pathogens is being well characterized as a complex sequential process leading to the activation of defense responses at the infection site, but which may also be systemically expressed in all organs, a phenomenon also known as systemic acquired resistance. Some plant-associated and beneficial bacteria are also able to stimulate their host to mount defenses against pathogen ingress via the phenotypically similar, induced systemic resistance phenomenon. Induced systemic resistance resembles systemic acquired resistance considering its mechanistic principle as it successively involves recognition at the plant cell surface, stimulation of early cellular immune-related events, systemic signaling via a fine-tuned hormonal cross-talk and activation of defense mechanisms. It thus represents an indirect but efficient mechanism by which beneficial bacteria with biocontrol potential improve the capacity of plants to restrict pathogen invasion. However, according to our current vision, induced systemic resistance is specific considering some molecular aspects underpinning these different steps. Here we overview the chemical diversity of compounds that have been identified as induced systemic resistance elicitors and thereby illustrating the diversity of plants species that are responsive as well as the range of pathogens ~~from the micro- and mesofauna~~ that can be controlled via this phenomenon. We also point out the need for further investigations allowing better understanding how these elicitors are sensed by the host and the diversity and nature of the stimulated defense mechanisms.

Introduction

Some bacteria isolated from the root microbiome have been selected for their remarkable beneficial effect provided to their host plant and are referred to as Plant Growth-Promoting Rhizobacteria (PGPR) (Backer et al., 2018; Singh et al., 2019). These PGPR favor plant growth notably by facilitating nutrient availability and modulating the host's hormonal balance but also display plant protective activity toward pathogen ingress. This biocontrol potential relies on several traits including the ability to efficiently compete for space and nutrients with pathogens, a strong direct antagonistic activity based on secretion of low-size antimicrobials or hydrolytic enzymes and the capacity to stimulate Induced Systemic Resistance (ISR)~~, a systemically expressed resistance state that renders the host less susceptible to subsequent infection~~ (Pieterse et al., 2014; ~~Backer et al., 2018;~~ Köhl et al., 2019). ISR is a systemically expressed resistance state that renders the host less susceptible to subsequent infection, and it is of great interest from an agronomical perspective because ~~it is~~ effective against a broad spectrum of microbial pathogens, nematodes, and insects (Pieterse et al., 2014; Grady et al., 2016; Rashid and Chung, 2017; Mhatre et al., 2018). Phenotypically, ISR resembles the systemic acquired resistance (SAR) mounted upon pathogen perception, which culminates from a complex immune-related process. At the front line, molecular features of invading microbes are detected with high specificity and sensitivity in the apoplast by a range of plasma membrane-anchored immune sensors referred to as pattern recognition receptors (PRR). These PRRs bind precise structural motifs (epitopes) of larger (macro)molecules retaining important functions for microbial fitness and thus widely conserved across species and termed microbe-associated molecular patterns (MAMPs). Some of the best described MAMPs from bacterial pathogens are flg22, a 22 amino acids portion of the flagellin protein, elf18 which is the epitope of the elongation factor EF-Tu~~, and~~ surface-exposed lipopolysaccharides (LipidA), and peptidoglycan (sugar backbone) (Schellenberger et al., 2019). The binding of MAMP by PRR initiates within minutes early immune-related events in responsive cells such as ion fluxes, oxidative burst, and phosphorylation cascade. Furthermore, defense mechanisms *sensu stricto* such as cell wall reinforcement and production of antimicrobial enzymes and secondary metabolites, referred to as phytoalexins, are stimulated (Piasecka et al., 2015). This PRR-mediated immune response (pattern triggered immunity, PTI) is robust as it can detect MAMPs at nanomolar concentrations leading to fast and strong defensive responses (high transcriptional activation) but associated with growth-defense tradeoffs that reduce plant fitness (Huot et al., 2014). However, adapted pathogens use protein effectors injected into host cells to dampen PTI and subvert this first line of immune reaction. In turn, plants have evolved intracellular sensors called R (resistance)

65 proteins, which interfere with these effectors leading to the effector-triggered type of immunity
66 (ETI) which may, like PTI, lead to SAR- (Kanyuka and Rudd 2019; Schellenberger et al., 2019).

67 Due to the conserved nature of MAMPs, the plant's receptor equipment would enable detection not
68 only of pathogenic bacteria, but also of beneficials such as rhizobial symbiots and root-associated
69 epiphytic PGPR (Zipfel and Oldroyd, 2017). These beneficial microbes have thus to evade (by
70 hiding or changing their MAMPs) or suppress (by secreting effectors that interfere with immune
71 responses and signaling) PTI in order to establish a mutualistic relationship with their host (Stringlis
72 et al., 2018; Yu et al., 2019). This has been recently illustrated with the *Pseudomonas simiae* strain
73 WCS417 first detected as a pathogen via its flg22 epitope, but which then strongly attenuates the
74 host immune response presumably via T3SS-mediated delivery of effectors (Berendsen et al., 2015;
75 Stringlis et al., 2019). Subversion of host immune reaction allows PGPR to sustainably colonize the
76 rhizoplane and establish threshold populations necessary for providing beneficial functions
77 including priming of ISR triggering via the secretion of other elicitors not related to MAMPs.

78 Here we provide an updated overview of those PGPR determinants responsible for ISR elicitation
79 that are in most cases small-size compounds secreted by the colonizing bacteria even if some
80 proteins isolated from *Brevibacillus laterosporus*, *B. amyloliquefaciens*, and *Saccharothrix*
81 *yanglingensis* have also been recently proposed as bacterial triggers (Table 1)(Wang et al., 2015;
82 Wang et al., 2016; Zhang et al., 2018). We highlight their chemical diversity and structure- and
83 dose-dependent activity but only refer to compounds that have been tested in pure (proven) form at
84 biologically relevant concentrations and/or via specifically suppressed mutants and for which the
85 ability to stimulate systemic resistance was clearly demonstrated to be independent from direct
86 antimicrobial effect.

87

PGPR metabolites identified as elicitors of plant systemic resistance

Acyl-homoserine lactones

90 Many Gram-negative bacteria produce N-acyl-homoserine lactones (AHLs) as quorum-sensing
91 molecules involved in cell-to-cell communication in order to monitor their behavior according to
92 population density. Some AHLs are not only the mean of communication between bacterial cells,
93 but also may be used as signal in inter-kingdom interaction and act as plant growth promoting
94 compounds and/or as immunity elicitors (reviewed in Schikora et al., 2016). A first study showed,
95 by using an AHL-suppressed mutant of *Serratia liquefaciens* MG1, that induced resistance in

96 tomato towards *Alternaria alternata* by this strain is AHL-dependent (Schuhegger et al., 2006).

97 Several works performed with purified molecules further revealed that AHL bioactivity is structure-

98 dependent. AHLs with short length acyl chains have been mostly demonstrated to promote plant

99 growth, whereas AHLs with longer fatty acid (C12, C14) are better described as elicitors of

100 resistance (Schenk et al., 2012; Zarkani et al., 2013; Schikora et al., 2016). The long-chain N-3-oxo-

101 tetradecanoyl-L-homoserine lactone (oxo-C14-HSL; Figure 1.1) has been amply demonstrated for

102 immunity elicitation in many pathosystems. Upon treatment at 6 µM, oxo-C14-HSL successfully

103 induced systemic resistance against biotrophs (*Blumeria graminis* f. sp. *hordei*, *Puccinia hordei*,

104 *Golovinomyces orontii*) and hemibiotroph (*P. syringae* DC3000) in barley and Arabidopsis, but not

105 against the necrotrophs *Botrytis cinerea* and *Plectosphaerella cucumerina* BMM (Schikora et al.,

106 2011; Schenk et al., 2012; Wehner et al., 2019). ISR-eliciting activity of oxo-C14-HSL was also

107 observed in wheat and tomato against *Puccinia graminis* f. sp. *tritici* and *Phytophthora infestans*,

108 respectively (Hernández-Reyes et al., 2014). Collectively, these data indicate that the plant

109 defensive response triggered by the same oxo-C14-HSL molecule may not be efficient in enhancing

110 resistance against phytopathogens with necrotrophic lifestyle.

111

Cyclic lipopeptides

113 Rhizobacterial cyclic lipopeptides (CLPs) are multifunctional secondary metabolites involved in

114 developmental processes such as motility and biofilm formation and in biocontrol primarily based

115 on their antimicrobial activity (Ongena and Jacques, 2008; Guedens and Martins, 2018). However,

116 some CLPs secreted by beneficial bacilli and pseudomonads have emerged as an important category

117 of plant immunity elicitors as well. ~~The heptapeptide S~~surfactin is a heptapeptide occurring as a mix

118 of naturally co-produced homologues varying in the length of the fatty acid chain (Figure 1.2)~~., and~~

119 ~~it~~This CLP is among the *Bacillus* ~~CLP~~ compounds best described as trigger of systemic resistance.

120 When applied as pure compound ~~(mix of naturally co-produced homologues varying in the length~~

121 ~~of the fatty acid chain) at~~ on the root~~s~~ ~~level and~~. in micromolar amounts (5-10 µM), surfactin ~~was~~

122 demonstrated to induce ISR in bean, tomato, tobacco, against *B. cinerea,* in melon against

123 *Podosphaera fusca*, and peanut ~~infected by *B. cinerea, Podosphaera fusca,* and~~ against *Sclerotium*

124 *rolfsii*~~, respectively~~ (Ongena et al., 2007; García-Gutiérrez et al., 2012; Cawoy et al., 2014;

125 Rodríguez et al., 2018). The structure of this CLP may strongly impact its elicitor activity as

126 observed on tobacco cells. Linear and/or methylated derivatives are much less efficient and only

127 homologues with long C14 and C15 acyl chain~~s length~~ are active at inducing early immune-related

events, unlike C12 and C13 (Jourdan et al., 2009; Henry et al., 2011). Despite its high bioactivity on dicot plant roots, surfactin shows low competence in mounting immunity when applied on dicots leaves or monocots roots (Yamamoto et al., 2014; Rahman et al., 2015; Mejri et al., 2018). Induction of systemic resistance and/or plant defenses by other CLPs produced by biocontrol bacilli has also been occasionally reported. In tomato and grapevine, fengycin triggered ISR against *B. cinerea* and *Plasmopara viticola* (Farzand et al., 2019; Li et al., 2019), while CLPs from the iturin group (Figure 1.3) were shown to have a similar role in strawberry (Yamamoto et al., 2015), cotton (Han et al., 2015), grapevine (Farace et al., 2015) and Arabidopsis (Wu et al., 2018). Additionally illustrating the dependence of between CLP-mediated ISR on the plant organ, iturin showed bioactivity on roots at concentration of 50 µM, whereas it was active already at 1-10 µM when applied on leaves (Yamamoto et al., 2014; Kawagoe et al., 2015; Han et al., 2015; Park et al., 2016). The activation of defense genes in Arabidopsis by iturin foliar treatment was also dependent on the molecule's structure, *i.e.* cyclization and/or length of the b-hydroxy fatty acid chain (Kawagoe et al., 2015).

Several studies have also reported the involvement of *Pseudomonas* sp. CLPs in plant resistance stimulation on various pathosystems. Massetolide A was the first reported for its resistance-inducing activity in tomato against *P. infestans* (Tran et al., 2007). Recent works conducted with *Pseudomonas* sp. strain CMR12a revealed that two other types of CLPs, sessilin and orfamide (Figure 1.4 and 1.5, respectively) are involved in ISR-triggering albeit differently according to the pathosystem tested. Works combining the use of biosynthesis mutants and CLP extracts showed that both sessilin and orfamide are determinants of ISR in bean against *Rhizoctonia solani*, but that a balanced production is needed for optimal effect. These two compounds are indeed active at precise range of concentrations from 0.001 to 0.1 µM for pure orfamide, and 0.001 and 0.01 mg/L for sessilin as crude extract (Olorunleke et al., 2015; Ma et al., 2016). In monocots, such as rice, *Pseudomonas* CLP structure is crucial in determining elicitor effect on a given pathosystem. For example, orfamide applied at 25 µM was identified as elicitor inducing resistance to *Cochliobolus miyabeanus*, but it is not active against *Magnaporthe oryzae* (Ma et al., 2017). Nevertheless, CLPs such as WLIP, lokisin, and entolysin were recently described to successfully induce resistance towards this last pathogen, confirming elicitor specificity for certain pathosystems (Omoboye et al., 2019).

Rhamnolipids

Rhamnolipids (RLs) are amphiphilic glycolipids produced by various species including pathogenic isolates, but also some plant beneficial *Pseudomonas* and *Burkholderia* species (Abdel-Mawgoud et al., 2010; Perneel et al., 2008). They are essential for bacterial surface motility and biofilm development (Chrzanowski et al., 2012; Vatsa et al., 2010). Mono- and di-RLs (Figure 1.6) tested as pure compounds have been shown to elicit plant defense responses and to induce resistance against various pathogens in grapevine, Arabidopsis, and in *Brassica napus* using a wide range of concentrations from approximately 10 up to 300 µM (Varnier et al., 2009; Sanchez et al., 2012; Monnier et al., 2018; 2020).

N-alkylated benzylamine derivative

Although its function for bacterial life is not clear, an N-alkylated benzylamine derivative (NABD; Figure 1.7) produced by *P. putida* BTP1, was identified as elicitor (Ongena et al., 2005). Treatment of bean and cucumber roots with pure NABD at low micromolar concentration elicited similar protective effect compared to living cells. On the other hand, while in tomato, the pure elicitor induced a lower protective effect than observed with the producing strain, suggesting the synthesis of an additional ISR determinant in that case (Ongena et al., 2008).

Siderophores

To ensure their growth in iron-limited environments, microorganisms have evolved powerful Fe^{3+}-acquisition systems based on the secretion of high-affinity iron-chelating molecules termed siderophores. PGPR siderophores are also known to antagonize pathogen populations by decreasing iron amounts in soil, resulting in competition for this essential element (Kramer et al., 2020). However, some siderophores also act as plant immunity elicitors and pyoverdines (also referred to as pseudobactines; Figure 1.8) produced by various fluorescent pseudomonads were, in the 90's, among the first PGPR metabolites proposed as ISR elicitors. Their key role in systemic resistance induction was notably shown for *P. fluorescens* CHA0 on tobacco infected by *Tobacco necrosis virus*, and in the protection provided by *P. fluorescens* WCS374 to radish against Fusarium wilt (Maurhofer et al., 1994; Leeman et al., 1996). These chromopeptides were further described as inducers of resistance in various plant species such as bean, tomato, Arabidopsis, tobacco, eucalyptus and rice against a range of microbial pathogens (Meziane et al., 2005; Ran et al., 2005;

190 De Vleesschauwer et al., 2008). In addition to pyoverdine, *P. aeruginosa* 7NSK2 also forms the

191 chelating agent pyochelin (Figure 1.9) ~~as chelating agent~~ and its precursor salicylic acid (SA).

192 When tested on pathosystem grapevine/*B. cinerea*, SA produced by *P. aeruginosa* 7NSK2 was

193 crucial for ~~7NSK2 to~~ mount**ing the plant** immunity (De Meyer et al., 1999; Verhagen et al., 2010).

194 However, for ISR stimulated in tomato by the same strain, an important role for SA could not be

195 excluded, but probably combined with the action of other metabolites including pyochelin which

196 may somehow also retain some eliciting activity (Audenaert et al., 2002).

197

Elicitors with antibiotic function

199 To ensure fitness in the competitive rhizosphere niche, PGPR produce a wide range of secondary

200 metabolites best identified for their antimicrobial function such as non-ribosomal peptides,

201 polyketides, bacteriocins, terpenes, phenazines, quinolones, or rhamnolipids (Raaijmakers and

202 Mazzola, 2012; Zhao and Kuipers, 2016; Tracanna et al., 2017). Interestingly, some of these

203 antibiotics were also shown to act as signal for ISR stimulation at similar concentrations, making

204 them promising tools for biocontrol with dual action on pathogen populations (Kenawy et al.,

205 2019). One such antibiotic ~~is~~ 2,4-diacetyl phloroglucinol (Figure 1.10), formed by *P. fluorescens*, is

206 triggering~~triggers~~ resistance in Arabidopsis against various pathogens, such as *Peronospora*

207 *parasitica*, *P. syringae* pv. *tomato*, and *B. cinerea,* upon application at relatively high 10-100 µM

208 concentrations (Iavicoli et al., 2003; Weller et al., 2012; Chae et al., 2020). 2,4-diacetyl

209 phloroglucinol can also induce resistance against nematodes as shown with *P. protegens* CHA0 for

210 the reduction of infection caused by *Meloidogyne javanica* on tomato roots (Siddiqui and Shaukat

211 2003). Besides, other *Pseudomonas* antibiotics of the phenazine-type were also reported to induce

212 resistance. N~~n~~otably phenazine-1-carboxamide (Figure 1.11) in rice towards *M. oryzae* at 0.1 - 1

213 µM, in bean towards *R. solani*, and pyocyanin produced by *P. aeruginosa* 7NSK2 in the

214 pathosystem tomato/*B. cinerea* (Audenaert et al., 2002; D'aes et al., 2011; Ma et al., 2016).

215

Volatile organic compounds

217 Most of the well-characterized PGPR elicitors are soluble compounds, but some volatile organic

218 compounds (VOCs) were a**s well**~~lso~~ reported to induce systemic resistance in the host plant,

219 showing that these metabolites can also act as infochemicals involved in inter-kingdom

220 communication (Kai et al., 2016). The most studied VOC immunity elicitor is 2,3-butanediol (2,3-

221 BD; Figure 1.12) produced from glucose in the central metabolism (Yang et al., 2013). ~~Firstly, i~~Its

222 bioactivity was first assessed on Arabidopsis by application on roots, where *B. subtilis* GB03

223 induced resistance against *Erwinia carotovora* subsp. *carotovora*, while mutants deprived in 2,3-

224 BD or its precursor acetoin production were inactive (Ryu et al., 2004). Bioactivity, when treated on

225 roots in relatively high mM concentrations, was demonstrated as well in the pathosystems

226 maize/*Setosphaeria turcica*, tobacco/*Erwinia carotovora*, and in pepper against multiple viruses

227 (Table 1), where the immunity eliciting ability was structure-dependent. Namely, among the three

228 forms, 2R,3R-BD (R), 2S,3S-BD (S) and 2R,3S-BD (meso), the S form is the least active

229 (D'Alessandro et al., 2014; Han et al., 2006; Kong et al., 2018). However, on pepper against

230 *Xanthomonas axonopodis* pv. *vesicatoria*, another VOC 3-pentanol (10 µM, 1 mM; Figure 1.13)

231 showed higher activity than 2,3-BD (Choi et al., 2014). Beside 3-pentanol, long-chain VOCs

232 tridecane and hexadecane (Figure 1.14 and 15, respectively) showed ~~as well bioactivity~~bioactivity

233 as well at µM (100) concentration (Lee et al., 2012; Park et al., 2013).

234

Molecular basis of plant immunization: PGPR vs. MAMP elicitors

236 The potential of PGPR to induce plant immunity ~~thus~~ mainly relies on the secretion of a range of

237 structurally diverse low-molecular weight metabolites. However, the molecular mechanisms driving

238 recognition of these elicitors at the plant cell surface are poorly understood. By contrast with

239 MAMPs from pathogens, there is no indication so far for specific PRRs involved in the perception

240 of PGPR elicitors. They activate immune responses only at relatively high µM concentrations

241 compared to MAMPs, suggesting that they are not sensed via high-affinity receptors. CLPs are

242 known to promptly insert into biological membranes causing defects, pore formation and cell lysis

243 in a range of (micro)organisms (Balleza et al., 2019). Furthermore,~~Based on the fact that the~~

244 immune response triggered by the *Bacillus* CLP surfactin was fully conserved in protease-treated

245 tobacco cells, and~~that~~ successive applications do not lead to some refractory state due to the

246 saturation of high-affinity binding sites (as receptors). Based on these and the fact that ~~and that it~~

247 surfactin readily interact with sphingolipid-enriched microdomains in the plasma membrane, it was

248 suggested that this CLP is ~~also~~ perceived by plant cells via a lipid-mediated process. This is

249 supported by the strong structure-dependent activity showing that only long fatty acid chain

250 homologues are active at triggering early immune-related events in tobacco cells because they

251 should display stronger interaction with lipid bilayers (Jourdan et al., 2009; Henry et al., 2011).

252 Rhamnolipids also readily fit into plant lipid-based bilayer models. ~~and it was t~~ Therefore, it was

253 proposed that by inserting into plasma membranes, these compounds provoke subtle changes in

lipid dynamics that could be related to plant defense induction (Monnier et al., 2019; Schellenberger et al., 2019). As other alkyl-chain containing elicitors, AHLs could also be perceived by plant cells via a receptor-independent but lipid-mediated process, by analogy with data recently obtained on mammalian cells (Schikora et al., 2016; Song et al., 2018). It may explain why a given compound does not act at the same level on different targets, considering that the lipid composition in the plasma membrane differs according to the plant species/ organs.

The way PGPR elicitors are perceived at the plasma membrane level is not clear, but there is still a clear convergence between PGPR-triggered immunity and pathogen-induced PTI in the early steps of downstream signaling. The best studied PGPR elicitors induce similar early immune events as observed upon pathogen perception, such as oxidative burst, ion fluxes, and phosphorylation cascade (Jourdan et al., 2009; Schikora et al. 2011; Cho et al., 2013; Cawoy et al., 2014; Rahman et al., 2015; Farace et al., 2015). DThat said, while detection of MAMPs from pathogens leads to a fast and strong defensive response, but alsoleading to a costly reduction of the plant growth and fitness (Huot et al., 2014)., On the other hand, PGPR and/or their elicitors usually prime the host to stimulate defense mechanisms but only after pathogen challenge as observed upon treatment with surfactin, AHLs, or with bacteria producing NADB or pyoverdines (De Vleesschauwer et al., 2008; Mariutto et al., 2011; Cawoy et al., 2014; Debois et al., 2015; Schikora et al., 2016). Again by contrast with PTI, PGPR elicitor-priming is not associated with major transcriptional reprogramming until the pathogen is detected and does not involve fitness costs but still prepares the plant for mounting a robust defense (Martinez-Medina et al., 2016; Mauch-Mani et al., 2017). Globally, the defense mechanisms restricting pathogen ingress that are stimulated by beneficial bacteria or their elicitors resemble those observed upon pathogen MAMP perception. It notably means up-regulation of genes involved in the synthesis of antimicrobial enzymes/proteins or metabolites and in hormone signaling. Higher expression of Such genes such are pathogenesis-related, lipoxygenase, plant defensin factor, and phenylalanine ammonia lyase, is often reported in elicitor pretreated plants after pathogen infection.pathogenesis- related (PR) proteins genes involved in chitinase, glucanase, thaumatin, defensin and thionin production, JA/ET-inducible plant defensin factor (PDF1.2), lipoxygenase (LOX) that stimulates the oxylipin pathway generating a wide array of biologically active secondary metabolites, and phenylalanine ammonia lyase (PAL) that plays a crucial role in the phenylpropanoid pathway leading to synthesis of the precursors of lignins, flavanoids, and coumarins, serving as weapons against pathogens (Ongena et al., 2007; García-Gutiérrez et al., 2012; Zarkani et al., 2013; Song et al., 2015; Park et al., 2016; Yi et al., 2016; Kong et al., 2018; Song et al., 2019). Besides, PGPR elicitors also trigger stomatal closure and enhance cell wall reinforcement which serves as a structural barrier to pathogen invasion via callose

288 deposition or accumulation of phenolic compounds and lignin (De Vleesschauwer et al., 2006;
289 García-Gutiérrez et al., 2012; Schenk et al., 2014; Rodríguez et al., 2018).

290

Discussion

292

293 From an agronomic perspective, ISR triggered by PGPR is interesting since the phenomenon is
294 considered to provide long-lasting and broad-spectrum protection without causing growth cost and
295 is not *a priori* conducive for development of resistance in pathogens (Köhl et al., 2019). However,
296 the success of PGPR as stimulators of plant defenses is so far rather limited due to a range of
297 factors. Theseis includes our global lack of knowledge about the nature and mode of action of their
298 elicitors. Indeed, ISR determinants were identified mainly from a limited number of species
299 (*Pseudomonas* spp. and *Bacillus* spp.), leaving elicitors from many other PGPR to be discovered.
300 Moreover, in the last decades, tremendous advances have been done on understanding the basics of
301 MAMP perception during PTI, but the mechanistic of PGPR elicitor recognition at theby plant
302 plasma membrane level cells and the molecular events underlying PGPR-induced priming remain
303 largely obscure. As the lipid phase is suspected to act as docking platform for some of these
304 elicitors, experimental biophysics and *in silico* dynamic modeling using appropriate biomimetic
305 vesicles represent interesting approaches to get further insights into the physico-chemical basis of
306 the interactions (Deleu et al., 2014; Balleza et al., 2019; Nishimura and Matsumori 2020). More
307 research It would help to explain why some compounds are only efficient on specific plants/tissues
308 according to the nature and proportions of lipids in their domain-structured plasma membranes
309 (Gronnier et al., 2018)., triggering resistance against a broad range but not all pathogens. Also, the
310 variety of pathosystems tested so far is still limited and additional research on agriculturally
311 important crops and pathogens is needed in order to better appreciate their potential at a larger
312 market scale.
313 Furthermore, PGPR elicitors in most instances are active at micromolar doses but, however only in
314 a few studies it was demonstratedsuggest that quantities produced by bacteria *in planta* are
315 sufficient to locally reach such threshold around the roots (D'Alessandro et al., 2014; Debois et al.,
316 2015). Determining the amounts of elicitors produced by PGPR under natural conditions is still
317 important, but not an easy task. It would require optimal extraction from rhizosphere samples and
318 the most-advanced MS-based metabolomics allowing high sensitivity for their detection and
319 quantification. Also, the impacts of environmental factors may affect ISR efficiency (Williams et al,
320 2018), but their impact on the production of elicitors by PGPR remains poorly appreciated. Low

temperature, acidic pH or poor oxygen availability are among the rhizosphere specific abiotic parameters that affect bacterial physiology and which may also modulate the production of secondary metabolites including elicitors as reported for Bacillus lipopeptides (Pertot et al., 2013; Zhao and Kuipers, 2016; Fahim et al., 2012). Biotic factors such as and biotic factors (interactions with other microbial species of the rhizosphere soil microbiome or, chemical cross-talk with the host plant) that , may also influencemodulate theelicitore production of under natural conditions these ISR determinants (Debois et al., 2015; Wu et al., 2015; Venturi and Keel, 2016; Andrić et al., 2020). under natural conditions are largely unknown and A better evaluation of the impact of all these factors deserve further investigations and is necessary if we want to better understand and anticipate inconsistencies in PGPR efficacy observed in the PGPR performance when appliedupon application in theunder field conditions.

Integrating all this missing information should also lead to more rationally determinedefine the range of pathosystems, and environmental conditions in which PGPR-based bioproducts would be the bestmost efficient. An alternative is to make from these bacterial immunogenic compounds microbial-derived products for the phytosanitary market provided that they can be mass produced and formulated in cost-effective industrial processes. This is feasible for some metabolites with high production rate in bioreactors, such as *Bacillus* lipopeptides (Zannoto et al., 2019; Brück et al., 2020), but the dose and structure dependent activity should guideimposes a rational selection of the strain, optimization of culture conditions and extensive testing in field experiments in comparison with chemical products.

356

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772 **Figure and Table Legends**

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774 **Figure 1. Chemical structures of PGPR produced ISR elicitors.** 1.N-3-oxo-tetradecanoyl-L-
775 homoserine lactone; 2. Surfactin; 3. Iturin; 4. Sessilin; 5. Orfamide; 6. Rhamnolipid, L-
776 rhamnosyl-3-hydroxydecanoyl-3-hydroxydecanoic acid; 7. N,N-dimethyl-N- tetradecyl-N-
777 benzylammonium; 8. Pyoverdine; 9. Pyochelin; 10. 2,4-diacetyl phloroglucinol; 11. phenazine-
778 1-carboxamide; 12. 2,3-butanediol; 13. 3-pentanol; 14. Tridecane; 15. Hexadecane

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781 **Table 1. PGPR produced elicitors of systemic resistance**

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Elicitor	Strain	Plant	Pathogen	Method	Reference
Acyl-homoserine lactones					

Precise structure not defined	*Serratia liquefaciens* MG1	Tomato	*Alternaria alternata*	Mutant	Schuhegger et al., 2006
oxo-C14-HSL		Arabidopsis	*P. syringae* pv. *tomato* DC3000	Pure 6 µM	Schikora et al., 2011
			Golovinomyces orontii		
		Barley			
			Blumeria graminis f. sp. *hordei*		
		Arabidopsis	*P. syringae* pv *tomato* DC3000	Pure 6 µM	Schenk et al., 2012
	Sinorhizobium meliloti Rm2011	Arabidopsis	*P. syringae* pv *tomato*	Mutant	Zarkani et al., 2013
	Sinorhizobium meliloti	Barley	*Blumeria graminis* f. sp. *hordei*	Mutant	Hernández-Reyes et al., 2014
			Puccinia graminis f. sp. *tritici*		
		Wheat			
			Phytophthora infestans		
		Tomato			

Cyclic lipopeptides

Surfactin	*Bacillus subtilis* 168	Bean Tomato	*Botrytis cinerea*	Mutant, pure 5 µM	Ongena et al., 2007
	B. subtilis UMAF6639	Melon	*Podosphaera fusca*	Mutant, Mutant + pure, pure 10 µM	García-Gutiérrez et al., 2012
	B. amyloliquefaciens S499 / FZB42/ QST713, *B. subtilis* 98S/ BNO1, *Paenibacillus*	Tomato	*B. cinerea*	SRF-producing strains, pure 10 µM	Cawoy et al., 2014

	polymyxa 56				
	B. amyloliquefaciens S13-3	Strawberry	*Colletotrichum gloeosporioides*	Pure 50 µM	Yamamoto et al., 2014
	B. amyloliquefaciens FZB42-AK3	*Lolium perenne* L.	*Magnaporthe oryzae*	Semi-purified ~250, ~500 µM	Rahman et al., 2015
	B. subtilis	Peanut	*Sclerotium rolfsii*	Pure 5, 10 µM	Rodríguez et al., 2018
	B. amyloliquefaciens S499	Wheat	*Zymoseptoria tritici*	Pure 1, 10, 100 µM	Le Mire et al., 2018
	B. subtilis BBG131/ BBG125/ Bs2504	*idem*	*idem*	Pure surfactin +mycosubtilin 100 µM, 50/50	Mejri et al., 2018
Mycosubtilin	*idem*	*idem*	*idem*	Pure ~100 µM	*same study*
Fengycin	*B. amyloliquefaciens* FZB42	Tomato	*S. sclerotiorum*	Pure ~60 µM	Farzand et al., 2019
Iturin	*B. amyloliquefaciens* S13-3	Strawberry	*Colletotrichum gloeosporioides*	Pure 10µM	Yamamoto et al., 2014
	B. amyloliquefaciens 41B-1	Cotton	*Verticillium dahliae*	Pure 50 µM	Han et al., 2015
		Arabidopsis	*C. gloeosporioides*	Pure 10 µM	Kawagoe et al., 2015
	B. vallismortis EXTN-1	Chili pepper	*Phytophthora capsici*	Pure 1, 10 µM	Park et al., 2016
Massetolide A	*Pseudomonas fluorescens* SS101	Tomato	*P. infestans*	Mutant, pure ~ 45, 90 µM	Tran et al., 2007
Orfamide	*Pseudomonas* sp. CMR12a	*Brassica chinensis*	*R. solani* AG 2-1 *R. solani* AG 4-	Mutant	Olorunleke et al., 2015

		Bean	HGI		
	Pseudomonas sp. CMR12a	Bean	*R. solani* AG2-2	Mutant, pure 1 - 100 nM	Ma et al., 2016
	Pseudomonas sp. CMR12a	Rice	*Cochliobolus miyabeanus*	Mutant, pure 25 µM	Ma et al., 2017
Sessilin	*Pseudomonas* sp. CMR12a	Bean	*R. solani* AG 2-2 *R. solani* AG 4 - HGI	Mutant	D'aes et al., 2011
	Pseudomonas sp. CMR12a	*Brassica chinensis* Bean	*R. solani* AG 2-1 *R. solani* AG 4- HGI	Mutant	Olorunleke et al., 2015
	Pseudomonas sp. CMR12a	Bean	*R. solani AG2-2*	Mutant, crude extract 1, 10 µg/L	Ma et al., 2016
Lokisin	*Pseudomonas* sp. COR10	Rice	*M. oryzae*	Crude extract 25 µg/ml, one CLP-producing strains	Omoboye et al., 2019
WLIP	*Pseudomonas* sp. COW10	*idem*	*idem*	*Idem*	*same study*
Entolysin	*Pseudomonas* sp. COR5	*idem*	*idem*	*idem*	*same study*

Rhamnolipids

	P. aeruginosa	Grapevine	*B. cinerea*	Pure ~150 µM	Varnier et al., 2009
	P. aeruginosa	Arabidopsis	*P. syringae* pv *tomato, Hyaloperonospora arabidopsidis, B. cinerea*	Pure ~300 µM	Sanchez et al., 2012
	P. aeruginosa	*Brassica napus*	*B. cinerea*	Pure 10, 100 µM	Monnier et al., 2018

N-alkylated benzylamine derivative

NABD	*P. putida* BTP1	Bean	*B. cinerea*	Mutant, pure 0.2 µM	Ongena et al., 2005
	P. putida BTP1	Bean Cucumber	*B. cinerea* *Colletotrichum lagenarium*	Pure 1 µM	Ongena et al., 2008

Siderophores

Pyoverdine	*P. fluorescens* CHA0	Tobacco	*Tobacco necrosis virus* (TNV)	Mutant	Maurhofer et al., 1994
	P. fluorescens WCS374	Radish	*Fusarium oxysporum* f. sp. *raphani*	Mutant, pure 70 µg/root	Leeman et al., 1996
	P. putida WCS358	Tomato Bean Arabidopsis	*Colletotrichum lindemuthianum* *B. cinerea* *P. syringae* pv. *tomato*	Mutant, Pure 3.02 µg pyoverdine/g soil	Meziane et al., 2005
	P. putida WCS358r	*Eucalyptus urophylla*	*Ralstonia solanacearum*	Mutant, pure 10–100 µg/ml	Ran et al., 2005
	P. fluorescens WCS374r	Rice	*M. oryzae*	Mutant, pure 70 µg per root	De Vleesschauwer et al., 2008
Salicylic acid	*P. aeruginosa 7NSK2*	Bean	*B. cinerea*	Pure 100 nM	De Meyer et al., 1999
	P. aeruginosa 7NSK2	Grapevine	*B. cinerea*	Mutant	Verhagen et al., 2009
Pyochelin +SA/pyoverdine	*P. aeruginosa 7NSK2*	Tomato	*B. cinerea*	Mutant	Audenaert et al., 2002

Elicitors with antibiotic function

DAPG	*P. fluorescens* CHA0	Tomato	*Meloidogyne javanica*	Mutant	Siddiqui and Shaukat, 2003
	P. fluorescens CHA0	Arabidopsis	*Peronospora parasitica*	Mutant, pure 10, 100 µM	Iavicoli et al., 2003
	P. fluorescens Q2-87	Arabidopsis	*P. syringae* pv. *tomato*	Mutant, pure 10 - 250 µM	Weller et al., 2012

		Arabidopsis	*P. syringae* pv. *tomato* *B. cinerea*	Pure 10, 100, 200 µM	Chae et al., 2020
Phenazine	*Pseudomonas* sp. CMR12a	Bean	*R. solani* AG 2-2 *R. solani* AG 4-HGI	Mutant	D'aes et al., 2011
	Pseudomonas sp. CMR12a	*Brassica chinensis* Bean	*R. solani* AG 2-1 *R. solani* AG 4-HGI.	Mutant	Olorunleke et al., 2015
	Pseudomonas sp. CMR12a	Rice Bean	*R. solani* AG2-2	Mutant pure 0.1, 1 µM	Ma et al., 2016

Volatile Organic Compounds

2,3-butanediol	*B. subtilis* GB03, *B. amyloliquefaciens* IN937a	Arabidopsis	*Erwinia carotovora* subsp. *carotovora*	Mutant	Ryu et al., 2004
	P. chlororaphis O6	Tobacco	*E. carotovora*	Pure 100 µg/root	Han et al., 2006
		Pepper	*Cucumber mosaic virus*, *Tobacco mosaic virus*, *Pepper mottle virus*, *Tomato yellow leaf curl virus*, *Tomato spotted wilt virus*	Pure 1, 5, 10 mM	Kong et al., 2018
	Enterobacter aerogenes	Maize	*Setosphaeria turcica*	Pure 22 mM	D'Alessandro et al., 2014
3-pentanol	*B. amyloliquefaciens* IN937a	Pepper	*Xanthomonas axonopodis* pv. *vesicatoria*	Pure 10 µM, 1 mM	Choi et al., 2014
	B. subtilis GB03	Arabidopsis	*P. syringae* pv. *tomato* DC3000	Pure 100 nM, 10 µM	Song et al., 2016
Tridecane	*Paenibacillus polymyxa* E681	Arabidopsis	*Pseudomonas syringae* pv. *maculicola* ES4326	Pure 100 µM	Lee et al., 2012
Hexadecane	*Paenibacillus polymyxa* E681	Arabidopsis	*P. syringae* pv *maculicola*, *Pectobacterium carotovorum*	Pure 1, 100 µM	Park et al., 2013

subsp. *carotovorum*

783   Abbreviations: oxo-C14-HSL: N,N-dimethyl-N- tetradecyl-N-benzylammonium; NABD: N,N-dimethyl-N-
784   tetradecyl-N-benzylammonium; DAPG: 2,4-diacetyl phloroglucinol
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