Interactive potential of *Pseudomonas* species with plants

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ABSTRACT

Pseudomonas species or pseudomonads are known for their metabolic and ubiquitous diversity which enables them to survive in extreme conditions such as in marine and terrestrial environments as well as in association with flora and fauna. The sequenced genomes of many strains of *Pseudomonas* spp. show their vast repertoire of biotechnological applicability potential with respect to their genetic makeup and also exhibit industrially important applications due to physicochemical tolerances to extreme conditions (such as temperature, pH, and toxic chemicals and solvents). The best studied species include opportunistic human and plant pathogens, soil bacteria, and the plant growth-promoting pseudomonads. *Pseudomonas* species also are plant-commensals known for exhibiting effective antimicrobial activities and enabling plants to retrieve key nutrients. Hence, studying *Pseudomonas* with respect to its various characteristics in response to plant interactions is a far more important subject to be studied for their effective applications. In this review, the Pseudomonads have been analyzed extensively for their genome; biomolecules produced and plant beneficial activities. Thus, the present work helps future endeavors for Pseudomonad research by streamlining the areas.

1. INTRODUCTION

Understanding of the beneficial activity and diversity of plant-bacterial association is important for maintenance and sustainable agriculture in agricultural-ecosystems [1-3]. The plant growth promoting rhizobacteria colonize the rhizosphere rapidly, suppress soil-borne pathogen at the root surface, and stimulate plant growth [4-7].

Since the dawn of agriculture, humans have been battling against plant diseases and pests which were greatly helped by the invention and deployment of chemical pesticides use which enhanced crop production increasing the need for persistent disease management strategies in 20th century. Although chemicals are available for plant-pest and disease-management, no alternatives are available for pest resistance for pesticides. The environmental, health, and safety concerns of these chemical products have increased the need for search for alternatives to control plant diseases and pests [8,10].

One group of bacteria that have become a focal point for research on biocontrol of plant diseases is the genus *Pseudomonas* (ubiquitous Gram-negative rod shaped gamma-proteobacteria possessing polar flagella) [13,51]. Their physiological and ecological diversity reported globally (which can extended to genetic level) are known for their

secondary metabolite production which are applicable for integrated biocontrol of plant diseases [18-20]. The genome size of *Pseudomonas* species typically varies from 4.6 to 7.1 Mb having G+C content of 57.8 to 66.6% with 4237–6396 predicted genes [21]. Using multi-locus sequencing techniques, genus *Pseudomonas,* currently, possesses more than 100 species with further groups and sub-groups [3,22,24,26]. The details of pseudomonads whose genome has been elucidated are discussed in Table 1.

Genus *Pseudomonas* are ecologically significant and the most heterogeneous group termed as pseudomonads are characterized by the presence of a complex enzymatic system and elevated metabolic versatility. With simple nutritional requirements *Pseudomonas* spp. are found in nature, from industrial equipment, oils-pills, aseptic solutions, cosmetics, medical products, and clinical instruments [29]. Certain they are known to be pathogens or carriers for plants and human infections, while others strains and species exhibit biocontrol and bioremediation activities [14,18]. They have also been reported for their ability to produce effective biosurfactants [31] and efficient remediation capabilities [33,35].

Fluorescent pseudomonads are visually distinguishable than other species in the genus due to their water-soluble fluorescent pigment production. Root associated pseudomonads in rhizosphere (which is a zone of high microbial activity) enhances and acts in the management of plant health [20,24,25]. They are known to act as both plant pathogens (*Pseudomonas syringae*) and plant growth promoters (fluorescent pseudomonads) and fight the phytopathogens [22,26,27]. They are known to be rapid root

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Table 1: Genome studies of Pseudomonads

Strain	Source of isolation	References
P. aeruginosa 2192	Chronically-infected cystic fibrosis patient	
P. aeruginosa C3719	"Manchester epidemic strain" isolated from cystic fibrosis patient	Mathee *et al.*, (2008) [18]
P. aeruginosa LESB58	"Liverpool epidemic strain"isolated from cystic fibrosis patient	Winstanley *et al.*,(2009) [28]
P. aeruginosa PA14	Wound, from culture collection at University of California at Berkeley	Lee *et al.*, (2006) [29]
P. aeruginosa PAO1	Burn wound	Stover *et al.*, (2000) [30]
P. entomophila L48	Fruit or fruit fly	Vodovar *et al.*, [31]
P. fluorescens Pf-5	Soil	Paulsen *et al.*, (2005) [32]
P. fluorescens PfO-1	Soil	Silby *et al.*, (2009) [10]
P. fluorescens SBW25	Leaf of sugar beet	
P. putida KT2440	Cured strain lacking the TOL plasmid	Nelson *et al.*, (2002) [33]
P. putida W619	Endophytic strain isolated from poplar	Taghavi *et al.*, (2009) [34]
P. stutzeri A1501	Rice paddy soils	Yan *et al.*, (2008) [35]
P. syringae pv. *oryzae*	Rice	Reinhardt *et al.*, (2009) [36]
P. syringae pv. *phaseolica* 1448A	Bean	Joardar *et al.*, (2005) [37]
P. syringae pv. *syringae* B728a	Leaf of bean	Feil *et al.*, (2005) [38]
P. syringae pv. tomato DC3000	Tomato	Buell *et al.*, (2003) [39]
P. syringae pv. tomato T1	Tomato	Almeida *et al.*, [40]
P. protegens CHA0	Developmental stages of cabbage root fly	Flury *et al.* (2019) [41]
P. syringae pv. *syringae* B728	Common bean	Helmann *et al.* (2019) [42]
P. syringae pv. *actinidiae* (Psa)	Kiwi fruit plant	Donati *et al.* (2020) [43]
P. chlororaphis subsp. *aurantiaca* ARS-38	Cotton	Mehnaz *et al.* (2020) [44]
P. aeruginosa AJD 2	Monocropic cotton rhizosphere	Joshi and Chitanand (2020) [45]

colonizers directly or indirectly acting as plant growth promoter or plant pathogen [16,43].

The mechanism of action of the plant growth promoting pseudomonads by synthesis of various metabolites such as antimicrobial biomolecules (antibiotics) and volatiles such as hydrogen cyanide (HCN) [45], production of siderophore-nutrient competition (even iron), niche exclusion [47], and systemic resistance induction (ISR) [48,50,51]. The present review covers different aspects of plant growth promoting

bacterial (fluorescent pseudomonad) interaction with plants and rhizospheric microorganisms enhancing the disease resistance with agricultural and horticultural uses.

2. TAXONOMY

At present, the plant pathogenic *Pseudomonas* species are taxonomically restricted to specific group of organisms using rRNA gene analysis and about 21 plant associations are reported with 50 different pathogenic strains (termed pathovars or *pv*- a confusing concept of taxonomy) of *P. syringae*. The complete genomes of three important pathovars belonging to *P. syringae* have been sequenced. Host reactions to pathogen infections have been studied extensively because *P. syringae* pv. tomato could infect other model plants such as *Arabidopsis*. The common symptoms of plant pathogenic pseudomonads that cause various important diseases show cankers, galls, blights, soft rots, leaf, and stem spots. Other important virulence factors causing pathogenicity include type III secretion system, production of secondary metabolites (hormones, phytotoxins, pectolytic enzymes, exopolysaccharides, etc.), and ice nucleation activity. No single strategy has been effective against plant pathogenic pseudomonads and may need polyphasic strategies (combinations of physical, chemical, and biological strategies) [9]. For specific detection of plant pathogenic pseudomonads, tools of molecular biology are increasingly gaining diagnostic importance [20,27,52].

2.1. *P. syringae* Caused Symptoms on Plants

A variety of *P. syringae* pv. syringae symptoms on woody plants are dependent on the microbial strain, plant part infected, and the environment [53]. Disease symptoms of *P. syringae* infections are due to plant-microbe interactions involving molecular interactions modulated by biotic and abiotic conditions and hence the concept in *P. syringae* having continuum of potential pathogenesis with evolutionary significance [54]. Multiple symptoms can occur simultaneously on a single plant, such as (1) turning of brown to black coloration of flowers and/or flower buds, (2) buds-dead and dormant, (3) necrotic leaf spots, (4) discolored and/or blackened leaf veins and petioles (due to systemic invasion and infection), (5) fruit spots and blisters, (6) shoot-tip dieback (appearing as dead and blackened twig tissue extending to some distance from the tip), and (7) stem cankers: Bark depressions which darken with age [53,55]. The bacterium was found to have the ability to cause specific symptomology of each organ of the host plant and can form association with plant opening (such as stomata or trichomes, and wounds) resulting in apoplast infection. The pathogen could survive environmental in winter, wind dispersal, or even rain [56]. Causative agent of bacterial canker of Kiwi fruit – *P. syringae* pv. *actinidiae* (Psa) encodes three LuxR solos and no cognate LuxI. Thus, displaying a non-canonical quorum sensing system, *Psa* could perceive the acyl-homoserine lactones (AHLs) of neighboring bacteria and regulate its virulence in the host [57].

2.2. The *Pseudomonas fluorescens* Group

Many strains of pseudomonads are fluorescent made up of seven subgroups and around 50 studied strains and species. They are common surface-microflora of virtually all plant tissues, along with many other natural habitats. Some of these plant associated strains are excellent promoters of plant growth and antagonists of plant pathogens. These strains have been enhanced as commercial products of plant growth promotion and agricultural bio-control agents (biofertilizers and biopesticides) [3,26].

Fluorescent pseudomonads produce phytohormones – indole acetic acid (IAA), gibberlins, cytokinins, and ethylene production inhibitors, helping in increasing the plant root absorptive surface for nutrient and water uptake [11]. They can act directly on the nutritional status and thus growth and physiology of plant they colonize. *P. fluorescens* having aminocyclopropane-1-carboxylic acid- or ACC-deaminase activity [18,58] is important as it controls the quantity of plant ACC deaminase left for ethylene biosynthesis [59]. When checked using *in vitro* plate assays of the fluorescent strain, *P. aeruginosa* PJHU15 was found to be positive for the production of IAA and phosphate solubilization [60,61]. This fluorescent *P. aeruginosa* was used in consortium with *Trichoderma harzianum* and *Bacillus subtilis* leading to improvement of plant health inducing the systemic resistance and proteome-level changes when challenged with *Sclerotinia sclerotiorum* [3,48,59,62,63]. The consortium was also modulated for nutritional and antioxidant quality of pericarps of pea seeds [64]. Mutualistic, host associated bacteria were checked on model plant *Arabidopsis* against *P. fluorescens* and here, commensal and pathogenic lifestyles of these host-associated bacteria convergently lost and gained in multi-lineage homologous recombination further constituting the early step of bacterial differentiation into pathogenic and commensal lifestyles [65].

A significant group of players in crop growth, yield, and maintenance having capability, as phosphate solubilizing and biocontrol agents are termed as plant growth promoting rhizobacteria (PGPR). *Pseudomonads* possess many PGPR traits such as (i) rapid growth *in vitro* and provision for mass production; (ii) utilize seed and root exudates rapidly; (iii) colonize and dominate the rhizosphere, spermosphere, and even in the interior of plants; (iv) bioactive metabolite production (volatiles, siderophores, growth promoting substances, and antibiotics); (v) environmental stress resistance, and (vi) compete aggressively with other microorganisms. They are also responsible for the innate suppressiveness of some soils to pathogens [3,53,61,66-68]. The pseudomonads exhibited spatial separation from the pathogen on the above ground plant parts, either in the stem [69] or on the leaf surface [70]. Pseudomonads which have been reported to possess PGPR traits are discussed in Table 2.

Pseudomonas brassicacearum, a harmless commensal and a member of *Pseudomonas fluorescence* group containing more than 51 species, is known for its plant growth promotion (PGP) and biocontrol activities. It is also closely related to *P. corrugata*, an opportunistic phytopathogen [71].

3. PLANT DISEASE PROTECTION

3.1. Antibiosis

Fluorescent pseudomonads are known producers of variety of antibiotics and act as biocontrol agents [3,17,24,46,71]. The biocontrol agents produced by fluorescent pseudomonads include pyocyanin [17], pyrrolnitrin [73], phenazine-1-carboxylic acid [29], 2,4-diacetylphloroglucinol (Phl), and pyoluteorin [74]. *P. fluorescens* SF4c produces more than one functional bacteriocin (such as S-type bacteriocin and phage-tail-like bacteriocin-Tailocins) by their regulator PrtR gene [75]. Flury *et al*. (2019) showed the role of insects such as cabbage root fly, *Delia radicum* in different developmental stages by harboring persistant root-colonizing *P. protegens* CHA0 as dispersal agents to new host plants [76].

3.2. Toxic Products (HCN Production)

Fluorescent pseudomonads have been long known for their production of HCN in disease suppression [77,78]. The rate of HCN production

has been reported to be relative to the plant species and its root exudates which show in reciprocation, beneficial effect on the growth of plant [79]. Some of these act as biocontrol by producing HCN have also been reported for their ability to induce plant resistance against phytopathogenic fungal diseases [80,81], for example, in wheat [82]. Ferramola *et al*. (2020) used the *Larrea divaricata* Cav. (jarilla) proteins to induce the antibody production and used the cross-reactivity of antibodies produced against nosocomial pathogen *Pseudomonas aeruginosa* [83].

3.3. Niche Domination (by Competing for Nutrients Available at Root Niches)

Plant exudates dictate the plant dependent rhizosphere microflora. The surface surrounding rhizosphere acts as carbon sink [3,49,83] providing various nutrients (including important elements, water, and other secondary metabolites such as antimicrobials, enzymes, vitamins, mucilage, and plant growth regulators). Thus resulting in influx of diversity of micro- and macro-organisms (pathogens included) at the rhizosphere site and resulting in competition for nutrients and consequently at this niche. The fast adaptability of fluorescent pseudomonads and other beneficial microorganisms (PGPR) to such condition make them effective competitors against pathogens. Most of these PGPR are flagellated and respond with chemotactic responses for plant exudates reaching root surfaces faster than others [26,84].

Many pseudomonads such as *P. psychrotolerans* CS51 and *P. aeruginosa* AJD 2 have been studied recently for their genome-wide ability to encode PGP traits [86,87]. Singh et al. (2019) have compiled an excellent overview of different PGPR strains of *Pseudomonas* spp. and their mediated tolerance responses for different heavy metals [89].

3.4. Cellular Communication

Cellular communication or quorum sensing (QS) within the spatially structured *P. fluorescens* rhizospheres communities was found to be possible. QS signaling is dependent on cell density, their spatial distribution and mass transfer [91]. *N*-acyl homoserine lactone (AHL) based QS signaling molecules is predominantly seen among Gram-negative bacteria. *Pseudomonad* motility on semi-solid surfaces is mediated by type IV pili and peritrichous flagella [53,93] and Pyoverdine seems to be playing a major role in this locomotion as the mutations in pvdQ (which codes for stages of pyoverdine biosynthesis) resulted in bacterial motility loss [95].

3.5. Pseudomonas spp. Producing Rhamnolipids

The rhamnolipids are a group of biosurfactants and their production is regulated by the QS molecules. These biosurfactants (Rhamnolipids) have some extreme properties such as antimicrobial properties (antibacterial, antifungal, and antiviral) [72,90,91]. These surfactants are important in cell-to-cell interaction (or Quorum sensing), bacterial cell motility, cellular differentiation, and water channels formation these are the characteristics of the *Pseudomonas* biofilm. In comparison to the chemical surfactants, biological biosurfactants are more valuable for the environment and different industrial uses [97,101,103]. Rhamnolipids are widely used in agriculture, pharmaceutical, pesticide removal, improvement in oil recovery, household cleaning, and food industry. *P. aeruginosa* rhamnolipid shows the wide range of the bacteria such as *A. faecalis*, *E. coli*, *Micrococcus luteus*, *Mycobacterium phlei*, *Serratia Marcescens,* and *S. epidermidis*. *P. aeruginosa* rhamnolipids are also show the antifungal activity against the *Aspergillus niger*, *Aureobasidium pullulans*, *Chaetomium globosum,* and *Penicillium*

Table 2: Pseudomonads as PGPR and plant responses

Bacteria	Enzymatic activity	Host plant	Plant responses	References
P. polymyxa	Indole-3-acetic acid	Wheat grass	Increased growth over uninoculated Control	Holl *et al.*, (1988) [69]
P. putida	ACC deaminase	Tomato	Inoculated tomato seed increased plant resistance in 55 days to nine consecutive days of flooding and increased resistance to salinity	Grichko and Glick, (2001) [94]
P. asplenii	ACC deaminase	Rape seeds	Significant increase in fresh and dry weight and biomass yield	Reed and Glick, (2005) [95]
P. putida	Indole-3-acetic acid	Canola	Two–threefold increases in the length of seedling roots	Ahmad, Ahmad and Khan, (2005) [96]
P. fluorescens	ACC deaminase	Maize	Increased root length and fresh weight under saline conditions	Kausar and Shahzad, (2006) [97]
P. fragi	Hydrogen cyanide	Wheat seedlings	Significantly increases the germination percentage, germination rate, plant biomass and nutrient uptake	Selvakumar *et al.*, (2008) [98]
P. fluorescens	ACC deaminase	Groundnut plants	Improved the saline resistance and yield	
P. putida UW4	Indole-3-acetic acid and ACC deaminase	Canola	Under saline conditions, protected the seedling of canola from growth inhibition	Siddikee *et al.*, (2010) [99]
P. aeruginosa	Hydrogen cyanide	Wheat	Control fungus diseases and enhance defense against phyto-pathogen	Rana *et al.*, (2011) [100]
P. chlororaphis	Siderophore production	Maize	Increased root shoot biomass and seed germination rate	Hayat, Ahmed and Sheirdil, (2012) [101]
P. fluorescens Psd	Tryptophan Monooxygenase	Sorghum (var. *Sudex chari*)	Increased root shoot biomass and seed germination rate	Kochar, Upadhyay and Srivastava, (2011) [102]
P. fluorescens EBC191	Indoleacetonitrilase, Nitrile hydrolase	NA	NA	Kiziak *et al.*, (2005) [103]
Pseudomonas sp. K-9	Phenylacetaldoxime Dehydratase	NA	NA	Kato and Asano, (2005) [104]
P. putida WCS358	Cell envelope components Flagella	Arabidopsis	Inducement of systemic resistance	Meziane *et al.*, (2005) [57]
P. fluorescens WCS374	Lipopolysaccharides	Radish	Inducement of systemic resistance	Leeman *et al.*, (1995) [105]
P. fluorescens WCS417	Lipopolysaccharides	Arabidopsis Carnation Radish	Inducement of systemic resistance	Van Peer and Schippers, (1992); Leeman *et al.*, (1995); Van Wees *et al.*, (1997) [105–107]
P. putida WCS358	LPS or pseudobactin	Arabidopsis Bean Tomato	Inducement of systemic resistance	Meziane *et al.*, (2005) [57]
P. putida BTP1	Iron-regulated metabolites N-alkylated benzylamine Derivative	Bean	Inducement of systemic resistance	Ongena *et al.*, (2005) [108]
P. fluorescens CHA0 *P. fluorescens* WCS374 *P. putida* WCS358 *P. putida* WCS358 *P. putida* WCS358 *P. putida* WCS358	Pseudobactin siderophore	Tobacco Radish Arabidopsis Bean Eucalyptus Tomato	Inducement of systemic resistance	Maurhofer *et al.*, (1994); Leeman *et al.*, (1996); Meziane *et al.*, (2005); Ran *et al.*, (2005) [57,63,84,109]
P. aeruginosa 7NSK2 *P.aeruginosa* 7NSK2 *P. fluorescens* P3 pchBA	Salicylic acid	Bean Tobacco Tobacco	Inducement of systemic resistance and root exudates	Maurhofer *et al.*, (1994); De Meyer and Höfte, (1997); De Meyer, Audenaert and Höfte, (1999) [84,110,111]
P. putida WCS358	Cell envelope components Flagella	*Arabidopsis*	Inducement of systemic resistance	Meziane *et al.*, (2005) [57]
P. fluorescens WCS374	Lipopolysaccharides	Radish	Inducement of systemic resistance	Leeman *et al.*, (1995) [105]
P. fluorescens WCS417	Lipopolysaccharides	*Arabidopsis* Carnation	Inducement of systemic resistance	Van Peer and Schippers, (1992) Leeman *et al.*, (1996); Van Wees *et al.*, (1997) [106,107,109]

(*Contd...*)

Table 2: (*Continued*)

Bacteria	Enzymatic activity	Host plant	Plant responses	References
P. aeruginosa 7NSK2	Pyocyanin and pyochelin (and/or salicylic acid)	Tomato	Inducement of systemic resistance	Audenaert *et al.*, (2002) [112]
P. fluorescens WCS374	Unknown	Radish	Inducement of systemic resistance	Leeman *et al.*, (1996) [109]
P. fluorescens WCS417	Unknown	Radish	Inducement of systemic resistance	Iavicoli *et al.*, (2003) [113]
P. fluorescens CHA0	Antibiotics 2,4-Diacetyl- phloroglucinol	*Arabidopsis* Tomato	Disease suppression	Siddiqui and Shaukat, (2003) [114]
P. fluorescens Q2-87	2,4-Diacetyl phloroglucinol	*Arabidopsis*	Inducement of systemic resistance	Weller *et al.*, (2004) [115]
P. putida KT2440	Indole compounds, Siderophore synthesis, and phosphate solubilization	Soybean and Corn	Induced systemic resistance in response to certain foliar pathogens	Costa-Gutierrez *et al.* (2020) [116]
P. chlororaphis subsp., *aurantiaca* ARS-38	Production of indole acetic acid, hydrogen cyanide, lahorenoic acid, phenazines (lipopeptide), and a hydroxamate-type siderophore	Wheat	Increased root and shoot dry weights in wheat seedling growth	Mehnaz *et al.* (2020) [44]
P. psychrotolerans CS51	Auxin biosynthesis, nitrate and nitrite ammonification, phosphate-specific transport system, and the sulfate transport system	Cucumber	Endogenous indole-3-acetic acid (IAA) and gibberellins (GAs) resulting in enhanced cucumber growth (root shoot length) and increased the heavy metal tolerance	Kang *et al.* (2020) [85]
P. syringae pv. tomato (*Pst*) DC3000	Pathogencity	*Arabidopsi thaliana*	Cation-Chloride Co-Transporter 1 (CCC1)	Han *et al.* (2020) [117]

chrysogenum [76,78,93,118]. Rhamnolipids are also shows the antiviral activity against TMT and Potato X virus [97].

4. INFLUENCE OF *PSEUDOMONAS* SPECIES

Among the various rhizobacteria, *Pseudomonas* spp., are aggressive rhizospheres and rhizoplane colonizers of different crop plants [47] with broad spectrum of antagonistic activity against plant pathogens [79,80,82,119,120]. The primary biocontrol mechanism of many pseudomonads includes the production of metabolites such as HCN, antibiotics, and siderophores [95]. The beneficial effect on dry mass of plant shoot was more evident with HCN producing *Pseudomonas* strains [110], especially *P. aeruginosa*, a PGPR has been found to be an effective biocontrol agent of root pathogens [15,81]. Many pseudomonads have been reported for such abilities such as control of damping off of cotton seedlings caused by *R. solani* using the antibiotic produced by the *P. fluorescens* [81] and *Septoria tritici* (*Mycosphaerella graminicola*) suppressed by *P. aeruginosa* strain leci [111]. The siderophore producing pseudomonads with mixtures of *Bradyrhizobium japonicum* strain USDA 110 improved nodulation [3,87,124]. *P. fluorescens* CHAO, isolated in Switzerland, has been the most highly studied pseudomonad capable of producing different bioactive compounds (such as IAA, siderophores, antibiotics, and HCN) making it the best PGPR so far [89,125].

Plants can be protected from various pests and diseases by the strains of *pseudomonads* which induce systemic resistance or ISR [3,24,115-117]. The enhancement of plant defensive capacity due to specific chemical and biotic stimuli is called induced resistance [95]. It was found that PGPR especially fluorescent pseudomonads induced systemic resistance (ISR) leading to plant disease suppression [68,69]. Pseudomonads beneficial to plants are studied in Table 3.

Costa-Gutierrez *et al*. (2020) showed the ISR of soybean and corn against certain foliar pathogens due to root-colonizing non-pathogenic *P. putida* KT2440 [118]. Gislason and de Kievit (2020) studied all the

21 sequenced genomes of *P. brassicacearum* and *P. corrugata* clade for PGP, biocontrol activities, and pathogenicity. They reported the extreme similarity among these two groups of beneficial and harmful bacteria. The bacterial ability to manipulate plant immune system to form harmful/harmless associations, the physiological and genotypic state of the host plant, and other stressors (biotic/abiotic) contribute to the plant-microbe interactions and results [71]. The strain *P. putida* KT2440 was found to be excellent root colonizer of agronomical important crops with ability to activate the ISR against certain plant pathogens [118].

Azelaic acid, a dicarboxylic acid is shown to play the *Arabidopsis* plant signaling specifically promoting the resistance priming by salicylic acid (SA) as a part of plant immunity against *Pseudomonas nitroreducens* DSM 9128 [119].

4.1. Lipopolysaccharides

Many reports suggested that pathogenic bacterial cell surface components such as the lipopolysaccharides can induce resistance (ISR) as reported in *P. fluorescens* inducement of carnation plants against *Fusarium oxysporum* f. sp. *dianthi* infections [53]. The LPS of *P. fluorescens* strains was demonstrated to be of important in ISR against wilt of radish caused by *F. oxysporum* f. sp. *raphanin* [120]. However, redundancy of ISR triggering traits in *P. fluorescens* strains was reported for the suppression of *Fusarium* wilt in radish [121]. In *A. thaliana*, application of isolated LPS of *P. fluorescens* and *P. putida* has been reported to be involved in ISR against *P. syringae* pv. tomato, triggering ISR which was further found to be having redundancy in ISR triggering traits in these strains [12,58,122]. A mutant of *P. fluorescens* strains lacking the 0-antigen no longer triggered ISR and the iron-regulated elicitor of ISR in BTP1 (an *N* alkylatedbenzylamine derivative) in bean and tomato [58]. Pseudobactin mediated ISR was effective against *Tobacco necrosis virus* in tobacco with reduction in numbers of viral lesions and lesion diameter in comparison to pseudobactin-negative mutant of *P. fluorescens* CHA0 [123].

Table 3: Plant beneficial pseudomonads

Strain	Origin/ Plant protection	Plant-beneficial traits documented	Reference
DR54	Sugarbeet	Viscosinamide, chitinase	Sanguin *et al.*, (2008) [131]
F113	Sugarbeet	DAPG, HCN, pyoverdine, ACC deaminase, T3SS	Moënne-Loccoz *et al.*, (1998) [132]
KD	Wheat	T3SS, HCN, pyoverdine	Rezzonico *et al.*, (2007) [133]
Pf29A	Wheat	Pathogen growth inhibition, ISR	Barret *et al.*,(2009) (Barret *et al.* 2009) [134]
Q2-87	Wheat	DAPG, HCN, ACC deaminase	Weller, (2007) [135]
Q8r1-96	Wheat	DAPG	Mavrodi *et al.*, (2006) [136]
SBW25	Sugar beet	T3SS, competition, pyoverdine	Sanguin *et al.*, (2008) [131]
WCS365	Potato	ISR, siderophore, competition, T3SS	de Weert *et al.*, (2002) [83]
WCS374	Potato	ISR, pseudoverdine, pseudomonine, salicylate, T3SS	Pieterse *et al.*, (2003) [48]
Pseudomonas spp.	Arabidopsis and Potato	Phenazine-production and Rhizosphere colonization	Zboralski *et al.* (2020) [137]
2P24	Wheat	DAPG, HCN, pyoverdine	Sanguin *et al.*, (2008) [131]
2-79	Wheat	Phenazine-1-carboxylate, pyoverdine, anthranalate, T3SS	Cook *et al.*, (1995) [138]
CHA0	Tobacco	DAPG, HCN, ISR, pyoluteorin, pyoverdine, salicylate, pyrrolnitrin, ISR	Haas and Défago, (2005) [139]
Pf-5	Cotton	Pyoluteorin, pyrrolnitrin, DAPG, HCN, pyoverdine	Loper, Kobayashi and Paulsen, (2007) [140]
LBUM677	Soybean, Canola and Corn gromwell	Increase in plant biomass, total oil content and lipid composition	Jiménez *et al.* (2020) [141]
KT2440	Soybean and Corn	Seed germination, root and stem length increment under saline conditions	Costa-Gutierrez *et al.* (2020) [116]

Fluorescent pseudomonads with biocontrol capability (Production of DAPG: 2,4-diacetylphloroglucinol, ACC: 1-aminocyclopropane-1-carboxylate, ISR: Induced systemic resistance, HCN: hydrogen)
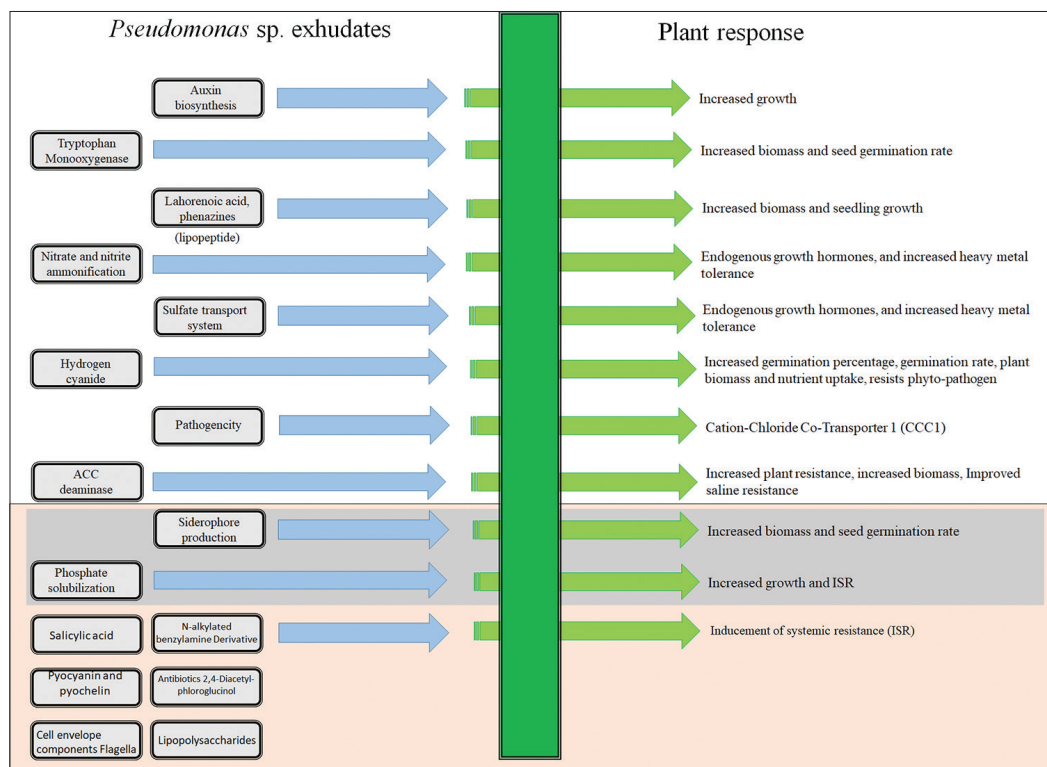

Figure 1: *Pseudomonas* sp. - Plant interactions. The orange section shows the inducement of systemic resistance in plants and blue sections indicate the cation solubilisations

4.2. Iron-regulated Metabolites

Under iron limiting conditions, most aerobic and facultative anaerobic microorganisms (including fluorescent Pseudomonads) produce siderophores (low-molecular weight Fe^{3+} specific chelators). The siderophores sequester ferric ions and form ferrated siderophores which are, in turn, taken up by microbial cells through surface mediated uptake [124]. Siderophores have also been implicated in ISR in several systems like bacterial wilt suppression caused by *Ralstonia solanacearum* in *Eucalyptus urophylla* (due to *P. putida* siderophores) [64]. It was observed that bacterial SA production was not involved in ISR by PGPR as SA production was suppressed in the rhizosphere probably due to SA being a precursor of SA-containing siderophores such as "pseudomonine" in *P. fluorescens* [125] and "pyochelin" in *P. aeruginosa* [126] thus being utilized to extinction. SA has been reported for its complex ISR activity in tobacco, tomato and bean but was predominantly seen in mutant that can synthesize it but unable to incorporate it in pyochelin [110,127,144]. Many antibiotics are produced by the *Pseudomonas* spp. strains including 2,4-diacetylphloroglucinol (DAPG) and its role in ISR was recently demonstrated in *Arabidopsis*. Here, DAPG produced by *P. fluorescens* CHA0 elicited ISR against *Peronospora parasitica* [131]. In tomato, *P. fluorescens* CHA0 induced DAPG mediated ISR against the root-knot nematode *Meloidogyne javanica* (as DAPG-negative mutant was ineffective and restoration of effectiveness on mutant complementation) [132]. DAPG produced by *P. fluorescens* in *Arabidopsis* was also found to be effective for the ISR against *P. syringae* pv. *Tomato* [133]. The phenazine antibiotic pyocyanin produced by *P. aeruginosa* was found to be involved in ISR against *B. cinerea* in tomato [126].

The *Pseudomonas* spp. ability to induce plant responses are summarized in Figure 1. There is a need for model designing for understanding the microbe [134]. The ability of the bacterial genus in effectively establishing itself as plant pathogen and growth promoter has increased the value of studies in this regard. The future of this research relies on the development of effective microbial combinations and consortia providing a stable community which could work effectively against plant pathogens and improve the plant growth [111,129,146].

5. CONCLUSION

For understanding of this complex microorganism *Pseudomonas*, it is imperative to understand the mechanisms involved in plant growth promotion and different aspects of these interactions. The rhizospheric competence is a prerequisite for effective biocontrol applications, root-microbe, cell-to-cell and microbe-to-microbe interaction, while genetic and environmental factors affecting growth will help in elucidation of the mechanisms should be adopted. Thus, there is a need for designing different strategic approaches and constructing models to improve the efficiency of this bacterium. The discovery of strains from diverse ecological niches and targeting biosynthetic genes specifically may result with the identification of biomolecules and metabolites, detection of their mechanisms involved and may further increase the knowledge of the topic. Basic genetic engineering methods can be employed coupled with multiple modes of action. Exploration of molecular tools and techniques to study the interactions of fluorescent *Pseudomonads* with –plants and – pathogens by studying genome expression and proteome level changes during interactions can clarify the complex rhizosphere biodiversity. Thus, further studies should focus on the identification of genes and gene-products in *Pseudomonads* and plants that decide improved biocontrol and efficient colonization of rhizospheres. Further studies into ISR in fluorescent pseudomonads can open new horizons for research in signaling network and related mechanisms involved.

7. AUTHORS' CONTRIBUTIONS

SS and NY collected data and prepared the basic manuscript (given first and second authorship according to contribution) under the guidance of corresponding author AM who planned, corrected, and structured the manuscript.

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