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Efficiency of Some Chemical Inducers on Chemotatic Movement of *Ralstonia solanacearum* towards Potato Root Exudates

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ABSTRACT

Motility is an important attribute to *Ralstonia solanacearum* to colonized potato (*Solanum tuberosum*) roots in soil. Quantitative and qualitative chemotaxis assays revealed that this bacterium is specifically attracted to diverse concentration of phenolics, organic and amino acids, sugars and other nutrients induced by microbes and especially to root exudates from the host plant around its root surface. Therefore, potato may secrete some compounds considered as chemotactic signals between potato roots and the pathogen in soil. The application of effective concentrations of different soil amendments resulted in significant changes in the chemical composition of root exudates in sterilized and non-sterilized sandy soil. These changes demonstrate an important role in the induced defense mechanism of systemic acquired resistance. The chemical change in root exudates may be responsible for breaking or cutting the chemical signals between potato roots and bacterial pathogenicity. So, both the percentage of infection and disease severity decreased. In control group, the root exudates collected after 40 days from potato cultivation were higher than those collected after 20 days showing significant differences in their composition.

Keywords: β-amino butyric acid, calcium oxide, potato, *Ralstonia solanacearum*, root exudates, salicylic acid, urea

INTRODUCTION

Bacterial wilt of potato is too serious to control. The causal agent, *Ralstonia solanacearum*, is a soil-borne Gram-negative bacterium that causes bacterial wilt in many crops (Hayward 2000; Horita and Tsuchiya 2002; Elphinstone 2005). Swimming motility makes an important quantitative contribution to bacterial wilt virulence in the early stages of host invasion and colonization (Tans-Kersten *et al*. 2001). The interaction between *R. solanacearum* and host roots results in surface colonization of two specific recognition sites; namely the elongation zone and axils of emerging secondary roots. The elongation zone is the major zone of plant root exudation and is commonly colonized by numerous microorganisms in the rhizosphere (Rovira 1973; Hirsch *et al.* 2003). It seems that colonization by *R. solanacearum*, which occurs at exudation sites along the root system, is the result of chemotaxis by the microorganism (Vasse *et al*. 1995; Yao and Allen 2006). Control methods are not effective and such conventional methods based on culturing bacteria isolated from plant tissue or soils on selective media are time consuming. Therefore, researchers are striving to develop novel methods to control this pathogen. Recently, the use of soil amendments such as β-amino butyric acid (β-ABA), salicylic acid (SA), and CaO + urea used as abiotic inducers have potential uses as tools to control harmful pathogens in potato (Zimmerli *et al.* 2008; Afrozet *et al.* 2009; Messiha *et al*. 2009; Emara *et al*. 2010).

Even though plants are sessile, they communicate extensively using secondary metabolites to express messages (Degenhardt *et al*. 2003; Dicke and Hilker 2003; Shim *et al*. 2004). Root exudates are compounds released into the surrounding medium by healthy and intact plant roots (Kalburtj and Mosjidi 1993). Such compounds secreted by plant roots play an important role as chemical attractants and repellants in the rhizosphere (Estabrook and Yoder 1998; Bais 2001). Root exudates may act as messengers that communicate and initiate biological and physical interactions between roots and soil organisms (de Weert *et al.* 2002; Greer-Phillips *et al.* 2004; Terry *et al.* 2005). Root-microbe communication can either be positive (symbiotic) or negative agent to the plant including interactions with parasitic plants, pathogenic bacteria, fungi, and insects (Ryan and Delhaize 2001). Molecules exuded by plant roots are thought to act as signals to influence the ability of microbial strains to survive in the rhizosphere and to colonize the roots (Brencic and Winans 2005; Yao and Allen 2006). The selection of specific rhizosphere populations may be mediated by responses to signals from different plant species.

In contrast, the defense mechanism of unprotected root cells that are under continual attack by pathogenic microorganisms is mediated by secretion of phytoalexins, defense proteins, and other unknown chemicals until now (Flores *et al*. 1999). One of the most remarkable metabolic features of plant roots is the ability to secrete a vast array of compounds into the rhizosphere, with nearly 5 to 21% of all photosynthetically fixed carbon that is being transferred to the rhizosphere through root exudates. Compounds such as amino and organic acids, sugars, phenolics, and various other secondary metabolites are believed to represent the majority of root exudates. In this study, we describe the chemotaxis behavior of *R. solanacearum* which was attracted to various chemicals of plant root exudates and to plant roots themselves. Specific tactic responses varied according to *R. solanacearum* from different hosts and different treatments.

Potato cv 'Spunta' is the most sensitive plant to *R. solanacearum*, and showed the highest infection percentage and disease severity among different potato genotypes (Ata 2008). So, it was selected to evaluate the decrease in pathogenicity of *R. solanacearum* to potato plants by evaluating the biochemical changes associated with the possible induced resistance in root exudates.

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MATERIALS AND METHODS

Potato tubers and sowing

1. Collection of root exudates

Firstly, different potato tubers (*Solanum tuberosum*) obtained from MABA Co., Giza, Egypt were superficially sterilized by immersing in 0.1% sodium hypochlorite solution for 10 min and then washed in sterile distilled water (SDW). After that sterilized potato tubers were placed in trays at room temperature in the dark to stimulate germination within a period of 2-3 weeks. Tuber pieces contained one or more sprout(s) were cut from germinated tubers and left for 48 h for callus formation. Experiments were set up in a glasshouse (Potato Brown Rot Project, Central Administration of Plant Quarantine, Dokki, Egypt). Each sprout was planted in a 25-cm vessel (1.5-L capacity) containing sterilized and non-sterilized sandy soil (non-infested and infested with *R. solanacearum*). Sterilized sandy soil was steam autoclave (2 h at 121°C and 1.5 atm). Every vessel has an opened end closed with 0.2-µm Millipore filter paper at 25°C in the first growth stage and at 22°C until the end of the experiment with 75-80% relative humidity (RH).

2. Inoculation of soil

Potato was planted in sterilized and non-sterilized sandy soil (non-infested and infested with *R. solanacearum*) and each group was six-replicated. After 48 h from culture on nutrient agar media, a suspension of *R. solanacearum* was prepared in SDW and adjusted to an optical density of 600 nm (OD_{600}) = 0.3 (approximately 6×10^8 CFU/ml). Inocula and soil were mixed thoroughly in a ratio of 1: 10 (v/v) and placed in polyethylene bags, then incubated at 30°C. One tenth-strength sterile Hoagland's nutrient solution was added to each vessel during the experimental period. Potato root exudates were separately collected after 20 days and 40 days from planting under septic condition by flooding irrigation of potato plant roots with SDW, which was received in 1-L conical flask and left overnight. The collected root exudates were filter-sterilized under vacuum suction apparatus (0.22-µm filter, Millipore; Pall, Life sciences, USA) and stored at -20°C in the dark until use. The chemical composition for each treatment was analyzed in Gas Chromatography mass detector (Hewlett Packard, USA) in Biotechnology Lab, Agriculture Research Centre. The condition used in this assay was as follows: Column: DB-5 (30 cm × 0.25 mm, 1.0 mm); P/N: 122-5533; Oven condition: (I) 35°C for 9 min, (II) 35-40°C for 10min, (III) 40°C for 30 min, (IV) 40-150°C for 15 min, (V) 150°C for 5 min; Injector: splitless at 200°C; Volume: 1 µl.

3. The effect of abiotic elicitor on causative agent of potato brown rot

Another experiment was conducted at the same conditions as previously mentioned for potato (*S. tuberosum*) commercial cultivar 'Spunta' (15-20-day old seedlings) where the abiotic elicitors (salicylic acid, β–amino-butyric acid), and calcium oxide + urea) were used. After 20 and 40 days from soil infestation, potato root exudates were collected to monitor the changes in their chemical composition.

RESULTS

Root exudates of 'Spunta' at different conditions

Table 1 indicates that in soil infested with *R. solanacearum* previously sterilized, the potato plant roots secrete more various exudates than those secreted in non-infested soil. This is because potato root exudates act as chemical signals in contact with *R. solanacearum* responding to its root colonization. The composition of root exudates collected after 20 days from potato cultivation showed variation in different conditions; sterilized and non-sterilized sandy soil (non-infested and infested with *R. solanacearum*). This variation in composition illustrated that 'Spunta' cultivar cultivated in a soil previously sterilized but infested with *R. solanacearum* secrete wide variety of root exudates that differed from those secreted in (sterilized soil) non-infested soil. Generally, the amount of compounds found in root exudates in infested soil is more than that found in non-infested soil (**Table 1**).

The root exudates collected after 40 days from potato cultivation was higher and revealed a more significant difference in its composition than those collected after 20 days. So, the concentration of phenolics and organic acid such as ethanethioc acid s-tetradecyl ester, cyclotetradecane, hexadeconic acid methyl ester (34.3, 32.1 and 24.6%, respectively) showed a high concentration in potato root exudates, which cultivated in infested sterilized soil collected after 20 days from potato plantation. In sterilized, non-infested soil, potato roots secreted haxanoic acid and hexanoic acid methyl ester at a high concentration (37.8 and 8.25%, respectively). Potato root exudates after 40 days in infested sterilized soil contained compounds such as diisooctyl phthalate with the highest concentration 60.61%, while that cultivated in non infested soil phthalic acid diisobutyl ester secreted with concentration 36.76%. In non-sterilized soil infested with *R. solanacearum* root exudates of 'Spunta' contained compounds such as diisooctyl phthalate with highest concentration 52.93), whereas in non-infested soil, root exudates of 'Spunta' contained diisooctyl phthalate (30.61%).

Chemical analysis of root exudates of 'Spunta' after different soil amendments

Table 2 indicates that application of salicylic acid to soil cultivated with potato plants and infested with *R. Solanacearum* is able to change the chemical composition of root exudates and concentration of compounds related to phenolics, organic acids were increased. These compounds such as diisooctyl phthalate, octanoic acid triglyceride, dicyclohexyl phthalate and dodecenyl succinic anhydride appeared in root exudates with concentrations of 26.94, 17.4, 14.12 and 11.75%, respectively. When the soil amended with β-amino butyric acid, 'Spunta' root exudates contained 1-octadecanol, 8-octadecanoic acid methyl ester, *trans*-phytol, gamma-aminobutyric at 30.34, 18.01, 15.9 and 12.04%, respectively. However, root exudates in soil amended with CaO + urea showed 6-phenyl-dodecane, *p*-chloro-m-xylenol and 2-phenyl-dodecane at 25.08, 23.29 and 15.82%, respectively.

DISCUSSION

Motility is an important factor for *R. solanacearum* to colonized potato roots in soil, resulting in moving the bacteria towards nutrient-rich regions (Chet and Mitchell 1976). One of the most nutrient-abundant regions of the soil is the root surface of actively growing plants which continuously secreted amino acids, sugars, and other nutrients induced by microbes. Chemo-attractive forces of these exudates increased with time; that increase was higher at 40 days than that was after 20 days. This is due to the amount of root exudates content of phenolics, organic acid, and amino acid increased with time and acted as chemo-attractive signals between potato roots and *R. solanacearum* (Bais *et al.* 2004).

Potato plants depend on the ability of roots to communicate with microbes. However, *R. solanacearum* abundant is dependent on its associations with potato plants that often are regulated by root exudates. A chemotactic response towards root-secreted phenolic compounds, organic acids, and amino acids is the first step in root colonization (Zheng and Sinclair 1996). The motility required for *R. solanacearum* to colonize potato roots is driven by root exudate-influenced chemotaxis (de Weert *et al.* 2002).

Table 1 Chemical analysis of root exudates of potato plants in different type of soil after 20 and 40 days after potato plantation.

Compounds	20 days				Compounds	40 days			
	Sterilized soil		Non sterilized soil			Sterilized soil		Non sterilized soil	
	Infested	Non infested	Infested	Non infested		Infested	Non infested	Infested	Non infested
4-methyl-2.6-bis(1,1-dimethylethyl)-phenol	8.6	0	0	0	2,6-dimethyl-3-(methoxymethyl)-*p*-benzoquinone	0	0	16.65	0
α-cadinol	4.6	0	0	0	Dimethoxy phenol	0		3.94	0
1H-indol-4-ol	14.1	0	0	0	L-lysine ethyl ester	0	0	5.22	0
14-β-H-pregna	14.8	0	2.32	1.85	Dihydropyran	0	0	4.82	0
1,2-benzenedicarboxylic acid, butyl octyl ester	18.8	0	0	0	3-phenylpropylamine	0	0	4.46	0
cyclotetradecane	32.1	0	0	0	hexadecanoic acid	0	14.3	4.69	0
hexadeconic acid, methyl ester	24.6	8.25	0	0	Heptacosane	0.61	0	0	0
7,9-di-tert-butyl-1-oxaspiro(4,5)deca-6,9-diene-2,8-dione	7.5	0	0	0	tricosane	0	0.16	0	0
2-butanone,4-(2-isopropyl-5-methyl-5-(2-methyl-5-oxocyclopentyl)	17.9	0	0	0	Eicosane	2.36	0.08	4.62	6.72
Dibutyl phthalate	8.5	0	9.41	0	palmitic acid, methyl ester	7.25	0.31	7.07	6.44
9,12-octadecadienoc acid (*z,z*)-methyl ester	8.6	0	0	0	Hexadecyl vinyl ether	0	0.21	0	4.32
6-octadecenoic acid, methyl ester	20.4	0	0	0	Dibutyl phthalate	0.85	0.19	4.14	4.16
methyl (*N*-salicyl)-3-amidepropanoyl)-aminoacetate	14.9	0	0	0	9-Octadecanoic acid methyl ester	9.64	0.8		1.58
Ethanethioc acid, s-tetradecyl ester	34.3	0	0	0	diisooctyl phthalate	60.61	13.66	52.93	30.61
hexanoic acid	0	37.8	0	0	Phthalic acid, diisobutyl ester	0	36.76	0	0
glycerine	0	2.97	0	0	4-methyl-2,6-di-*tert*-butylphenol	0.19	0	2.25	0
octanoic acid,1,2,3-propanetriylester	0	0	9.52	0	14-β-H-pregna	7.74	0	0	4.14
Glycerol tricaprylate	0	0	27.7	0	octacosane	3.25	0	0	3.79
1-Nonadecene (*cis*)1-Docosanol, acetateHentriacontane	0	0	3.26	8.25	Hebtamethylene di bromide	0	0	0	6.44
Docosane	0	0	1.54	0	2- tetradecanol	0	0	0	6.64
octadecane	0	0	0.71	0	7,9-di-*tert*-butyl-1-oxaspiro(4,5)deca-6,9-diene-2,8-dione	0	0	0	2.19
Cyclic tetramethylene sulfone	0	0	0	0.87	11-Octadecanoic acid, methylester (z)	0	0		6.76
Linoleic acid	0	0	0	0.85	Δ-Cadinene	0	0	7.54	0
2-Vinylnaphthalene	0	0	0	6.25	nonadecane	0	0	14.96	0
8-methoxy-1,3,4,5-tetrahydrobenz[cd] indole	0	0	0	3.17	Linoleic acid	0	0	1.76	0
Eugenol	0	0	8.33	0	2-methoxy-4-vinylphenol	0	0	23.44	0
2,4-di-*t*-butylphenol	0	0	12.85	0					
O-Menth-2-ene,4-isopropylidene-1-vinyl	0	0	12.4	0					
Benzyl benzoate	0	0	6.02	0					
Neophytadiene	0	0	0	8.71					

For potato plants cultivated in soil (non-sterilized soil) roots are in contact with the microbial rhizosphere in which root–microbe communications are continuous occurrence in this biologically active soil zone. Increasing evidence suggested that root exudates might initiate biological and physical interactions between roots and soil organisms. Rhizosphere interactions are based on complex exchanges that evolved around plant roots. The underground biological interactions that are driven by root exudates are more complex than those occurring above the soil surface (McCully 1999). These interactions include signal traffic between roots and soil microbes (Wo *et al*. 2002; Hirsch *et al*. 2003) and one-way signals that relate the nature of chemical and physical soil properties to the roots (Ryan and Delhaize 2001). Many of the processes mediated by roots in the rhizosphere such as the secretion of root exudates (Hawes *et al*. 2000). Root exudates play an active and relatively well-documented role in the regulation of symbiotic and protective interactions with microbes (Buee 2000; Hawes *et al*. 2000; Neumann and Martinoia 2002; Jones *et al*. 2003; Hirsch *et al.* 2003). So, this competition between soil microbes leads to root exudates that contained compounds less than those cultivated in non-sterilized soil infested with *R. solanacearum* in which pathogen bacteria are able to colonize its host roots (potato) through chemical signaling related to root exudates (deWeger *et al.* 1987), however, chemical composition of potato root exudates collected after 40 days showed a high content of different compounds related to chemical signals (**Table 1**). So, the attractive force of root exudates collected after 40 days from potato cultivation to *R. solanacearum* increased more than root exudates collected after 20 days.

Application of SA to soil cultivated with potato induced organic acid such as diisooctyl phthalate, octanoic acid triglyceride, dicyclohexyl phthalate and dodecenyl succinic anhydride appeared in root exudates with concentrations of 26.94, 17.4, 14.12 and 11.75%, respectively, which thought to play an important role in protecting potato roots from colonization by *R. solanacearum* (Raskin 1992). The chemical change in root exudates may be responsible for breaking or cutting the chemical signals between 'Spunta' roots and bacterial pathogenicity so that both percent of infection

Table 2 Chemical analysis of root exudates of 'Spunta' cultivar after soil amendments by salicylic acid (SA), butyric acid (BA), and CaO + urea.

Compounds	SA	BA	CaO + Urea
α- terpinolene	4.16	0	0
4-Methyl-2,6-di-*tert*-butylphenol	1.7	1.62	0.84
1-(4-Methylphenyl) cyclohexene	4.05	0	0
octanoic acid triglyceride	17.4	0	0
1-nonadecene	4.48	0	0
Hexadecanoic acid methyl ester	8.8	6	1.21
Dodecenyl succinic anhydride	11.75	0	0
Dibutyl phthalate	8.73	0	1.14
Ethyl n-heptadecanoate	2.94	0	0
14β-H-Pregnane	0.58	0.77	0
8-Octadecanoic acid, methyl ester	3.84	18.01	1.17
Stearyl acrylate	3.38	0	0
Dicyclohexyl phthalate	14.12	0	0
Diisooctyl phthalate	26.94	0	0
Phenyl-oxirane	0	0	2.28
2-methyl-2-isopentyl-1,3-dioxolane	0	0	2.46
2-Pyrrolidinone	0	0	5.66
3-Ethyl-2,4-dimethylpentane	0	0	6
Butanoic acid-3-methyl-pentyl ester	0	0	2.2
2-Methoxy-4-vinylphenol	0	1.39	3.18
Methyl 2-nonenoate	0	0	1.27
2,6 dimethoxy phenol	0	0	1.5
P-Chloro-m-xylenol	0	0	23.29
α-Citral	0	0	1.22
Epoxy-*trans*-linalooloxid	0	0	2.26
4,5-Dimethoxybenzocyclobutenol	0	0	4.31
trans-Phytol	0	15.9	11.19
Hexadecanoic acid	0	9.36	9.96
trans-3-Octen-2-one	0	0	6.21
Linoleic acid	0	1.92	1.63
2-phenyl-Dodecane	0	0	15.82
6-phenyl-Dodecane	0	0	25.08
4-phenyl-Dodecane	0	0	11.26
3-phenyl-Undecane	0	0	10.44
2-phenyl-Dodecane	0	0	9.47
Propyl pentanoate	0	1.04	0
γ- aminobutyric	0	12.04	0
2-Chloro-4-fluoro-benzenamine	0	4.28	0
α-Ethylpiperidine	0	6.16	0
2-(aminomethyl)-Piperidine	0	10.8	0
2,4-Di(1-phenylethyl)phenol	0	10.05	0
2-*cis*-6-*trans*-Farnesal	0	6.21	0
Pentadecanoic acid methyl ester	0	13.92	0
1-Nonadecene,5-eicosene,1doecene	0	11.85	0
1-Octadecanol	0	30.34	0
β-Gurjunene	0	2.28	0

and disease severity were decreased. In this regard, Yao and Allen (2006) and Afrozet *et al.* (2009) reported that root exudate is a mechanism through which a plant is able to regulate soil microbial community composition. Also, they stated that *R. solanacearum* actively attracted to root exudates from the host plant and that this pathogen depends on taxis to locate and colonize plant roots.

Also, DL-β-amino-*n*-butyric acid played an important role in inducing phytoalyxin accumulation (Hwang *et al.* 1997) which is considered as a specific mechanism of host defense. Such induction of butyric acid caused accumulation of pathogenesis-related protein before challenge (Hwang *et al*. 1997). The phenolic compounds were accumulated in the potato plant roots These compounds such as 1-octadecanol, 8-octadecanoic acid methyl ester, *trans*-phytol, γ-aminobutyric were consequently detected in 'Spunta' root exudates which are thought to have an active role in reducing the pathogenicity of *R. solancearum* to potato plants. By alteration in chemical composition of root exudates, *R. solancearum* can not find its way to colonize the roots of potato plants and that protecting potato plants from bacterial wilt infection.

In case of soil amended with calcium oxide + urea, the chemical composition of potato root exudates was different; 6-phenyl-dodecane, *p*-chloro-m-xylenol and 2-phenyl-dodecane. However, urea was responsible for accumulation of nitrite in soil. Accumulation of nitrite against time leads to a decrease in pH and nitrous acid, which considered as a non-ionized form of nitrite that accumulated in soil (Tenuta and Lazarovits 2002; Cohen *et al.* 2005). Increasing the pH may lead to alteration in chemical composition of potato root exudates. So, the chemical signal between *R. solanacearum* and potato root was cut and pathogenicity of bacteria decreased.

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