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ORIGINAL ARTICLE

Induced systemic resistance to wheat take-all disease by probiotic bacteria

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Abstract

In this study, the effect of six commercial biocontrol strains, *Bacillus pumilus* INR7, *B. megaterium* P2, *B. subtilis* GB03, *B. subtilis* S, *B. subtilis* AS and *B. subtilis* BS and four indigenous strains *Achromobacter* sp. B124, *Pseudomonas geniculate* B19, *Serratia marcescens* B29 and *B. simplex* B21 and two plant defense inducers, methyl salicylate (Me-SA) and methyl jasmonate (Me-JA) were assessed on suppression of wheat take-all disease. Treatments were applied either as soil drench or sprayed on shoots. In the soil drench method, the highest disease suppression was achieved in treatment with strains INR7, GB03, B19 and AS along with two chemical inducers. *Bacillus subtilis* S, as the worst treatment, suppressed take-all severity up to 56%. Both chemical inducers and bacterial strains AS and P2 exhibited the highest effect on suppression of take-all disease in the shoot spray method. *Bacillus subtilis* S suppressed the disease severity up to 49% and was again the worst strain. The efficacy of strains GB03 and B19 decreased significantly in the shoot spray method compared to the soil drench application method. Our results showed that most treatments had the same effect on take-all disease when they were applied as soil drench or sprayed on aerial parts. This means that induction of plant defense was the main mechanism in suppressing take-all disease by the given rhizobacteria. It also revealed that plant growth was reduced when it was treated with chemical inducers. In contrast, rhizobacteria not only suppressed the disease, but also increased plant growth.

Keywords: methyl jasmonate, methyl salicylate, rhizobacteria, soil drench, wheat

Introduction

Wheat take-all caused by *Gaeumannomyces tritici* (J. Walker) Hern.-Restr. & Crous is the most important soil-borne disease which in some cases caused 80% damage to wheat yield (Cook 2003). Several strategies such as pH control, fertilizer application, crop rotation and fumigation have been introduced for take-all control (Kwak and Weller 2013). However, these methods are costly and only partially reduce the disease. Interestingly, the wheat monoculture makes the soil suppressive to the disease, a so-called "take-all decline" phenomenon. It has been found that take-all decline develops because during monoculture the population of 2,4-DAPG producing *Pseudomonas fluorescens* increases (Shirzad *et al.* 2012; Kwak and Weller 2013). In addition to fluorescent pseudomonads, *Bacillus* strains also contributed to controlling the disease, for example, *B. cereus* A47 and *B. subtilis* B908 were effective in the control of cereal take-all (Ryder *et al.* 1998). Soil treatment by *B. pumilus* 7KM not only inhibited the take-all severity up to 52% but also significantly increased the shoot and root dry weights (Sari *et al.* 2007). The endophytic strain *B. subtilis* E1R-j suppressed take-all by 61.9% under field conditions (Liu *et al.* 2009).

Plant growth promoting rhizobacteria (PGPR) exploit different mechanisms and metabolites to communicate with host plants (Sharifi *et al.* 2010; Karnwal 2017; Lemanceau *et al.* 2017; Sharifi and Ryu 2017). They modulate the plant hormones and signaling

pathways to improve plant growth and defense against pest and pathogens (Chung *et al.* 2016; Sharifi *et al.* 2017). Several bacterial determinants are involved in plant-bacteria communication (Djavaheri *et al.* 2012; Weller *et al.* 2012; Deori *et al.* 2018). Among them, bacterial volatile compounds (BVCs) play important roles in modulating plant physiology. BVCs such as indole, acetoin and butanediol modulate signaling pathways involved in plant growth and nutrition efficiency as well as defense signaling networks (Ryu *et al.* 2003; Bailly *et al.* 2014). Furthermore, plants also exploit volatile organic compounds such as Me-SA, Me-JA, indole, linalool and β-caryophyllene in intra- and inter-species communication with neighboring plants (Sharifi *et al.* 2018). There are examples of inducing systemic resistance against plant pathogens on monocot plants by means of plant and bacterial volatiles (Desmond *et al.* 2006; Cortes-Barco *et al.* 2010). Thus, volatile compounds can potentially be applied on seeds or by spraying plant leaves under field conditions.

This study was designed to first, compare the induction of systemic resistance by bacterial strains with chemical inducers and second, to check the possibility of their application during the crop growing season by spray application. The fitness cost of induced systemic resistance was evaluated by recording plant growth factors.

Materials and Methods

The microbial inocula

The strains used in this study (Table 1) were obtained from the Department of Plant Protection, College of Agriculture and Natural Resources, Razi University of Kermanshah. Strains *B. pumilus* INR7 and *B. subtilis* GB03 were kindly provided by Prof. Joseph Kloepper, Auburn University, USA. For bacterial inocula, a full loop of 48-hour culture of each strain from NA medium was transferred to flasks containing 100 ml of Nutrient Broth (NB) medium and then placed on a rotary shaker at 120 rpm for 48 h at 28°C. The bacterial cells were centrifuged at 6,000 rpm for 10 min and washed several times with a physiological serum solution (8 g · l^{-1} NaCl). The bacterial cells were re-suspended in 1% carboxymethylcellulose solution. To prepare the fungus inoculum, a wetted mixture of sawdust, wheat bran and perlite at a ratio of 2 : 1 : 1 (v/v/v) in 500-ml flasks, was autoclaved twice for 20 min for two consecutive days. The substrate was then inoculated with mycelium plugs from the periphery of fresh culture of *G. tritici*. The flasks were incubated at 25°C for 15 days.

Greenhouse experiment

In this experiment, the effects of 10 bacterial strains and two plant defense inducers on inhibiting wheat take-all were examined under greenhouse conditions. The treatments were applied in two different ways. In the first experiment, the bacterial strains and chemical inducers were added to the soil at sowing. In another experiment, after seedling growth, the treatments were sprayed on the leaves and the pathogenic fungus was inoculated into the soil after 48 h.

The seed and soil treatment bioassay

The wheat seed cultivar, Pishgham, was disinfected with 2.5% sodium hypochlorite for 3 min and washed three times with distilled water. The wheat seeds were immersed in suspensions of bacteria and shaken at 70 rpm for half an hour. Then, 10 seeds were planted in plastic pots (15 × 15 cm) containing autoclaved field soil and perlite (2 : 1). In the case of chemical inducers, 8 ml of 100 µM solution of Me-SA and Me-JA was added to the pot per kg of soil (Jeun *et al.* 2004).

Table 1. Bacterial strains used in this study

No.	Bacteria code	Providers	Scientific name
1	BS	Department Collection	*Bacillus subtilis*
2	B29	Department Collection	*Serratia marcescens*
3	B19	Department Collection	*Pseudomonas geniculata*
4	B21	Department Collection	*Bacillus simplex*
5	B124	Department Collection	*Achromobacter* sp.
6	INR7	Auborn University	*Bacillus pumilus*
7	GB03	Auborn University	*Bacillus subtilis*
8	S	Department Collection	*Bacillus subtilis*
9	P2	AgriLife India	*Bacillus megaterium*
10	AS	Shahid Beheshti University	*Bacillus subtilis*

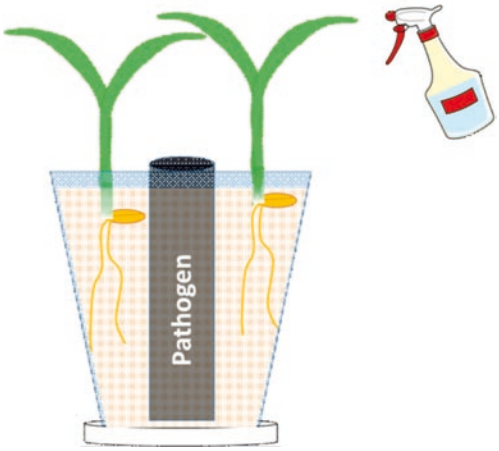

Fig. 1. Spray inoculation method to suppress take-all disease under greenhouse conditions

The foliar spray treatment bioassay

In this experiment, A 3-cm-diameter plastic tube was implanted in the center of each pot and un-inoculated seeds were sown in pots (Fig. 1). Two weeks after planting, plants were sprayed with 1×10^9 CFU · ml^{-1} of bacterial strains or 200 µM of Me-SA or Me-JA. After 48 h, the tube was removed from the soil and the hole was filled with the pathogen inoculum. The disease severity was assessed 50 days after planting. After washing both healthy and infected roots were counted and the percentage of infected roots was obtained (Mandal *et al.* 2009).

Data analysis

The data were subjected to analysis of variance in general linear model procedure (GLM) of SAS (SAS 9.1 SAS institute, Cary, NC). Mean comparisons were performed by Fisher protected least significance difference (FLSD) ($p < 0.05$). In all experiments, a completely randomized design was used with four replications.

Results

Soil treatment bioassay

Analysis of the results showed that all treatments were able to significantly suppress the disease severity ($p < 0.0001$, df = 13, F = 60.89) (Fig. 2). In the plants treated with the strain *B. pumilus* INR7 and the chemical inducer Me-JA, no symptoms of necrosis were observed on the root. The treatments *B. pumilus* INR7, Me-JA, Me-SA, *B. subtilis* GB03, *P. geniculata* B19, and *B. subtilis* AS were the best treatments of this experiment. Other strains also were able to significantly reduce the disease severity. Compared to the control, the lowest suppression level of the disease was recorded in *B. subtilis* S, which suppressed disease severity by 56%.

The pathogen reduced the mean shoot dry weight by 35% (Table 2). The soil treatment with two defense inducer compounds, Me-JA and Me-SA, did not improve plant growth. In contrast, all bacterial strains significantly improved the shoot dry weight in comparison to the infected control and were in the same statistical group as the healthy control ($p < 0.0001$, df = 13, F = 6.65). No significant differences were observed between the strains. It was also determined that the pathogen reduced the root dry weight by about 40%. The bacterial strain *B. subtilis* AS was effective in reducing the disease but did not show

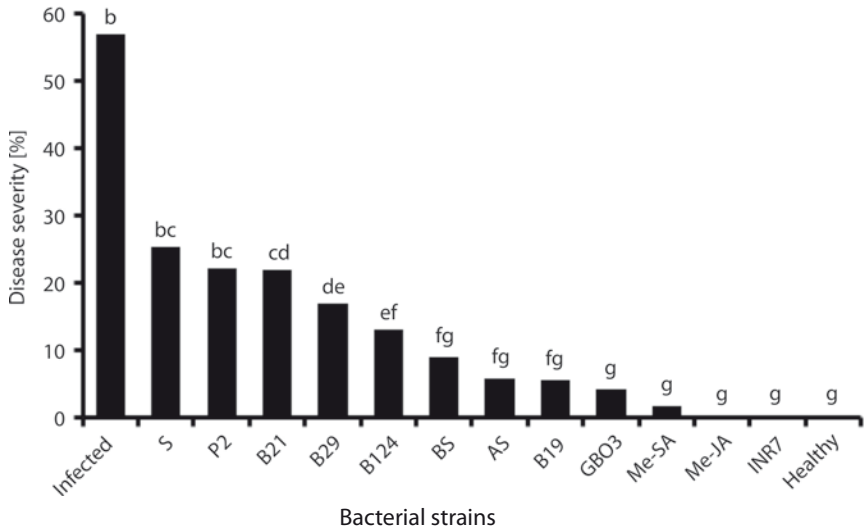

Fig. 2. Suppression of take-all disease by bacterial strains and plant defense inducers in the soil treatment test. The means comparison was performed by least significant difference (LSD) at 5% probability level. The means that have a common statistical letter do not differ significantly

Table 2. The effect of bacterial strains and plant defense inducers on plant growth factors in soil and spray treatment experiments

Treatments	Soil treatment			Spray treatment		
	SDW	RDW	SN	SDW	RDW	SN
Bacillus subtilis BS	4.47 a	1.65 a	44.72 b	4.29 a	1.81 ab	47.5 a
Serratia marcescens B29	4.28 a	1.57 a	38.85 bcd	3.73 abc	1.21 cd	28.2 cd
Pseudomonas geniculata B19	4.18 a	1.58 a	27.65 de	3.20 bcd	1.83 ab	24.42 de
Bacillus simplex B21	3.94 a	1.36 ab	28.87 cde	2.60 d	0.96 d	29.92 bcd
Achromobacter sp. B124	4.16 a	1.46 ab	43.35 bc	3.69 abc	1.20 cd	45.20 ab
Bacillus pumilus INR7	4.47 a	1.41 ab	29.92 b-e	3.93 ab	1.82 ab	33.85 a-d
Bacillus subtilis GB03	4.44 a	1.99 a	29.65 b-e	2.83 cd	1.90 a	38.85 a-d
Bacillus subtilis S	4.12 a	1.85 a	59.17 a	3.80 ab	1.53 abc	43.60 abc
Bacillus megaterium P2	3.90 ab	1.49 ab	20.55 ef	2.85 cd	1.06 cd	29.52 cd
Bacillus subtilis AS	4.32 a	0.79 b	41.52 bcd	3.86 ab	1.82 ab	41.65 abc
Methyl salicylate	3.21 bc	1.33 ab	2.77 g	2.86 cd	1.16 cd	13.60 e
Methyl jasmonate	2.99 c	1.34 ab	8.75 fg	3.36 bcd	1.08 cd	29.97 bcd
Healthy control	3.90 ab	1.21 ab	19.45 ef	2.92 cd	1.31 bcd	30.80 bcd
Infected control	2.53 c	0.73 b	9.55 fg	2.59 d	0.99 d	13.05 e

SDW – shoot dry weight; RDW – root dry weight; SN – spike number
The means comparison was performed by least significance difference (LSD) at 5% probability level. The means that have a common statistical letter do not differ significantly

a significant difference in the root dry weight compared to the infected control. In contrast, both Me-JA and Me-SA which had no significant effect on the shoot dry weight, significantly increased the root dry weight (Table 2). These compounds increased the root dry weight by 46 and 45%, respectively, compared to the infected control. The strain *B. subtilis* GB03 was the best treatment and increased root dry weight up to 2.7 times compared with the infected control. In addition to increasing the plant growth, the treatments used in this study also affected spike formation. Me-SA and Me-JA along with the infected control had the lowest spike numbers. The treatments *B. megaterium* P2, *P. geniculate* B19, *B. simplex* B21, *B. subtilis* GB03 and *B. pumilus* INR7 increased the spike number compared to the infected control, but no significant difference was observed when compared to the healthy control. Five other strains increased the spike number significantly over the healthy control (Table 2). About 60% of the wheat plants treated with the strain *B. subtilis* S, produced spike which was more than three times that of the healthy control.

Foliar spray treatment bioassay

With foliar spray, all the experimental treatments significantly suppressed disease severity. Disease severity in infected control was 37.73%. Two chemicals, Me-JA

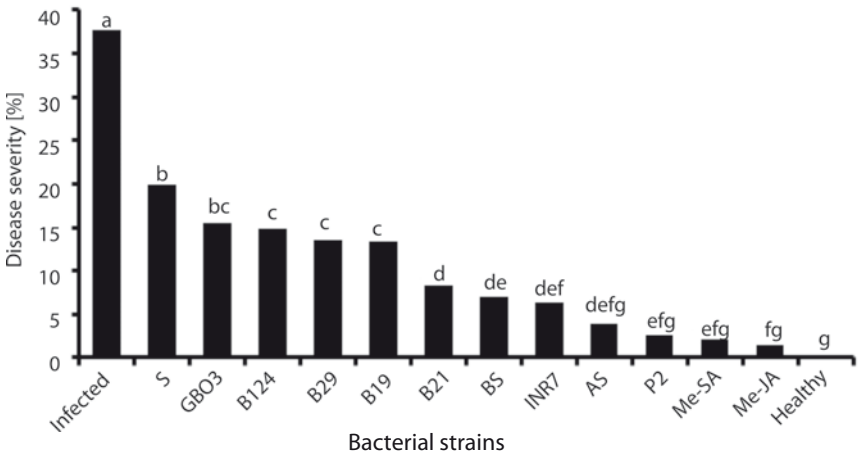

Fig. 3. Suppression of take-all disease by bacterial strains and plant defense inducers under greenhouse conditions. Treatments sprayed on aerial parts 2 weeks after sowing. Pathogens were applied 2 days post inoculation. The means comparison was performed by least significant difference (LSD) at 5% probality level

and Me-SA were among the best treatments. *Bacillus megaterium* P2 and *B. subtilis* AS also did not significantly differ from the plant defense inducer compounds and suppressed the disease by 93.1 and 89.6% in comparison to infected control, respectively (Fig. 3). Strains *B. pumilus* INR7 and *B. subtilis* BS with averages of 83.1 and 82.35, respectively, had a good effect on disease suppression. Strain *B. subtilis* S was the weakest treatment and suppressed disease severity by 47.2% compared to infected control. In this experiment, although all strains significantly suppressed the severity of the disease, the order of effect was not the same as the soil treatment bioassay. The treatment *B. megaterium* P2, which was a weak treatment in the soil application test, controlled the disease better with spray application. In contrast, the efficiency of strains *B. pumilus* INR7 and *B. subtilis* GB03 were reduced in spray application. However, a slight difference was observed between application methods in other treatments.

Infection with the pathogenic fungus caused a 21% reduction in shoot dry weight. The *B. subtilis* GB03, *B. megaterium* P2, Me-SA, *P. geniculate* B19 and Me-JA treatments did not have a significant effect on the dry weight of the plants compared with the infected control (Table 2). In contrast, the *B. subtilis* BS, *B. pumilus* INR7, *B. subtilis* AS and *B. subtilis* S treatments increased plant growth significantly, which was statistically even higher than the healthy control ($p = 0.0002$, $df = 13$, $F = 5.15$). The shoot dry weight in *B. subtilis* BS was 1.6 fold more than the infected control and 1.4 fold more than the healthy control. *Bacillus subtilis* GB03, *P. geniculata* B19, B. *pumilus* INR7, *B. subtilis* AS, *B. subtilis* BS and *B. subtilis* S significantly improved root growth compared with the infected control. *Bacillus subtilis* GB03 increased root dry weight in comparison with the infected control by 1.99 fold and compared with the healthy control by 1.44 fold (Table 2). Results also showed that only 13% of the infected control plants produced spikes compared to about 30% in healthy control. The treatments Me-SA and *P. geniculate* B19 did not show a significant difference with the infected control. The highest number of spikes was 47% and was related to strain *B. subtilis* BS. Strain *B. subtilis* S, which had the greatest effect on spike numbers in the soil application, could also be considered as a top strain in the foliar spray. In general, strain *B. subtilis* BS was not only an effective strain in controlling the disease but also could significantly increase growth traits and the number of spikes of the plant.

Discussion

In this study, the effect of several bacterial strains, mainly related to *Bacillus* spp., were assessed for biological control of wheat take-all disease. Me-SA and Me-JA, as elicitors of SA and JA/ET signaling pathways, were also included as references. Treatments were applied either as soil drench or as foliar spray to check induced systemic resistance mechanisms. Foliar spray treatment had some potential advantages over seed and soil treatments. Wheat seeds are normally disinfected with fungicides and the possibility of adverse effects of these pesticides on the bacterial population exists. For example, it has been reported that fungicide Benomyl has a harmful effect on N-stabilizing bacteria (Handelsman and Stabb 1996). The disinfection of potato pods with Mancozeb affected *P. fluorescens* and *P. putida* populations, negatively (Zablotowicz *et al.* 1991). Also, adapted indigenous microorganisms are in strong competition with the microbial inoculant in the rhizosphere, while the microbial population of the phyllosopheric region is much lower which allows easier establishment of the introduced bacteria (Beneduzi *et al.* 2012).

Data analysis revealed that inducing systemic resistance is a predominant mechanism in most bacterial strains such as *B. subtilis* AS, *B. subtilis* BS and *Serratia marcescens* B29. In other strains, induction of resistance was also dominant in controlling the disease. *Bacillus pumilus* INR7 causes complete suppression of the disease in the soil treatment, while it causes 83% disease suppression compared to the infected control with spray treatment. Perhaps the effect of this strain on the soil treatment can be attributed to the rhizosphere behavior of this strain. This strain had no inhibitory effect on the pathogens under *in vitro* condition (Kloepper *et al.* 2004) but suppressed the disease caused by *Ralstonia solanacearum* and *X. axonopodis* pv. *vesicatoria* by 72 and 52%, respectively, under greenhouse conditions (Yi *et al.* 2013).

Bacillus subtilis GB03, as an active ingredient of Kodiak®, suppressed the take-all disease by 58% with foliar spray treatment and suppressed the disease by 92% in the soil treatment. This indicates that the mentioned rhizospheric strain has the potential for low survival under phyllosophere conditions, or that this strain may, in addition to resistance induction, use a direct mechanism for inhibiting the pathogen. This strain has the high ability to colonize monocot roots and produce an itorin antibiotic that is effective against a wide range of fungi (Brannen and Kenney 1997). However, one of the main mechanisms for controlling the pathogens in this strain is inducing plant defense by producing volatile compounds (Ryu *et al.* 2004; Sharifi and Ryu 2016).

According to our results, Me-SA in the soil and foliar spray treatments inhibited 96% and 94% of the disease, respectively. Me-JA showed almost the same ability in suppression of take-all disease. However, it is known that Me-SA activates the SA pathway which

is effective against biotrophs, and Me-JA activates the JA/ET pathway against necrotrophs (Pieterse *et al.* 2009). As a general rule, these two pathways negatively affect each other; the phenomenon called cross-talk (Moon and Park 2016). Recently, it has been shown that for the pathogens with hemibiotrophic behavior, the time-dependent resistance pathway is expressed to control the pathogen. In the first few hours of infection, when the pathogen is conquering the host tissues and the necrotrophic phase has not begun, the SA pathway is activated. By entering the necrotrophic phase, the JA pathway is activated and effectively inhibits the pathogen. Some resistance inducer agents can stimulate and activate the pathway based on the pathogenicity of the pathogen (Martínez-Medina *et al.* 2017).

The treatment with resistance inducers had a negative effect on the host growth. The application of Me-JA reduced shoot dry weight in the soil application and foliar spraying treatments by 23 and 21%, respectively, compared to the healthy control. The application of Me-SA in the soil application and foliar spraying treatments also reduced root dry weight by 18 and 3%, respectively, compared to the healthy control. Increasing the expression of resistance genes is costly for the plant, which means that the expression of the defensive genes affects the plant's fitness negatively. The plant has limited resources and should use them purposefully and in accordance with the need and urgency (Heil 2002). Using chemical inducers such as salicylic acid, isonicotinic acid and benzothiadiazole has a negative effect on plant growth (Walters and Heil 2007). Therefore, application of plant defense inducers could be recommended based only on epidemiological data.

Inducing the resistance by PGPR and plant probiotic fungi increases PR proteins such as chitinases, glucanases, proteinase inhibitors and oxidative enzymes such as peroxidase, polyphenol oxidase and lipoxygenase just after pathogen challenge (Hoffland *et al.* 1997). Indeed, these agents sensitized the plant defense system to respond to pathogens stronger and faster, a phenomenon called plant defense priming (Kohler *et al.* 2002; Conrath *et al.* 2006). PGPR can improve plant defense without negative effects on it fitness (Sharifi and Ryu 2018).

In conclusion, some PGPR were able to significantly suppress take-all. In contrast to chemical defense inducers, PGPR did not show negative effects on plant growth. Therefore, the application of these strains under field conditions can be considered as a promising approach in controlling take-all disease. In addition to soil drench, foliar spray showed that PGPR and chemical defense inducers can be exploited to control take-all throughout the crop growing season. Often farmers seek products that prevent the disease from spreading after its appearance in the field. Most plant probiotic products are designed to be applied in the soil. However, it is necessary to develop bacterial formulations to be applied under phyllosphere conditions. Of course, suitable surfactant and UV protectant should be considered in developing these types of formulations. It is noteworthy that we used rhizobacteria in this work, but phyllosphere-dwelling bacteria are also a good source of biocontrol agents in screening plant defense inducer bacteria.

References

Bailly A., Groenhagen U., Schulz S., Geisler M., Eberl L., Weisskopf L. 2014. The inter-kingdom volatile signal indole promotes root development by interfering with auxin signalling. The Plant Journal 80 (5): 758–771. DOI: https://doi.org/10.1111/tpj.12666

Beneduzi A., Ambrosini A., Passaglia L.M. 2012. Plant growth-promoting rhizobacteria (PGPR): their potential as antagonists and biocontrol agents. Genetics and Molecular Biology 35 (4): 1044–1051. DOI: https://doi.org/10.1590/s1415-47572012000600020

Brannen P.M., Kenney D.S. 1997. Kodiak® – a successful biological-control product for suppression of soil-borne plant pathogens of cotton. Journal of Industrial Microbiology and Biotechnology 19 (3): 169–171. DOI: https://doi.org/10.1038/sj.jim.2900439

Chung J.H., Song G.C., Ryu C.M. 2016. Sweet scents from good bacteria: Case studies on bacterial volatile compounds for plant growth and immunity. Plant Molecular Biology 90 (6): 677–687. DOI: https://doi.org/10.1007/s11103-015-0344-8

Conrath U., Beckers G.J., Flors V., García-Agustín P., Jakab G., Mauch F., Newman M.-A., Pieterse C.M., Poinssot B., Pozo M.J. 2006. Priming: getting ready for battle. Molecular Plant-Microbe Interactions 19 (10): 1062–1071. DOI: https://doi.org/10.1094/mpmi-19-1062

Cook R.J. 2003. Take-all of wheat. Physiological and Molecular Plant Pathology 62: 73–86.

Cortes-Barco A., Hsiang T., Goodwin P. 2010. Induced systemic resistance against three foliar diseases of *Agrostis stolonifera* by (2R, 3R)-butanediol or an isoparaffin mixture. Annals of Applied Biology 157 (2): 179–189. DOI: https://doi.org/10.1111/j.1744-7348.2010.00417.x

Deori M., Jayamohan N.S., Kumudini B.S. 2018. Production, characterization and iron binding affinity of hydroxamate siderophores from rhizosphere associated fluorescent *Pseudomonas*. Journal of Plant Protection Research 58 (1): 36–43. DOI: https://doi.org/10.24425/119116

Desmond O.J., Edgar C.I., Manners J.M., Maclean D.J., Schenk P.M., Kazan K. 2006. Methyl jasmonate induced gene expression in wheat delays symptom development by the crown rot pathogen *Fusarium pseudograminearum*. Physiological and Molecular Plant Pathology 67 (3–5): 171–179. DOI: https://doi.org/10.1016/j.pmpp.2005.12.007

Djavaheri M., Mercado-Blanco J., Versluis C., Meyer J.M., Van Loon L.C., Bakker P.A.H.M. 2012. Iron-regulated metabolites produced by *Pseudomonas fluorescens* WCS374r are not required for eliciting induced systemic resistance against *Pseudomonas syringae* pv. tomato in *Arabidopsis*. Microbiology Open 1: 311–325. DOI: https://doi.org/10.1002/mbo3.32

Handelsman J., Stabb E.V. 1996. Biocontrol of soilborne plant pathogens. The Plant Cell 8: 1855–1869. DOI: https://doi.org/10.1105/tpc.8.10.1855

Heil M. 2002. Ecological costs of induced resistance. Current Opinion in Plant Biology 5 (4): 345–350. DOI: https://doi.org/10.1016/s1369-5266(02)00267-4

Hoffland E., Bakker P.A.H.M., Van Loon L.C. 1997. Multiple diseaseprotection by rhizobacteria that induce systemic

resistance-reply. Phytopathology 87: 138. DOI: https://doi.org/10.1094/PHYTO.1997.87.2.138

Jeun Y.C., Park K.S., Kim C., Fowler W., Kloepper J. 2004. Cytological observations of cucumber plants during induced resistance elicited by rhizobacteria. Biological Control 29 (1): 34–42. DOI: https://doi.org/10.1016/s1049-9644-(03)00082-3

Karnwal A. 2017. Isolation and identification of plant growth promoting rhizobacteria from maize (*Zea mays* L.) rhizosphere and their plant growth promoting effect on rice (*Oryza sativa* L.). Journal of Plant Protection Research 57 (2): 144–151. DOI: https://doi.org/10.1515/jppr-2017-0020

Kloepper J.W., Ryu C.M., Zhang S. 2004. Induced systemic resistance and promotion of plant growth by *Bacillus* spp. Phytopathology 94 (11): 1259–1266. DOI: https://doi.org/10.1094/phyto.2004.94.11.1259

Kohler A., Schwindling S., Conrath U. 2002. Benzothiadiazole-induced priming for potentiated responses to pathogen infection, wounding, and infiltration of water into leaves requires the NPR1/NIM1 gene in *Arabidopsis*. Plant Physiology 128 (3): 1046–1056. DOI: https://doi.org/10.1104/pp.010744

Kwak Y.-S., Weller D.M. 2013. Take-all of wheat and natural disease suppression: a review. The Plant Pathology Journal 29 (2): 125–135. DOI: https://doi.org/10.5423/ppj.si.07.2012.0112

Lemanceau P., Barret M., Mazurier S., Mondy S., Pivato B., Fort T., Vacher C. 2017. Chapter five-plant communication with associated microbiota in the spermosphere, rhizosphere and phyllosphere. Advances in Botanical Research 82: 101–133. DOI: https://doi.org/10.1016/bs.abr.2016.10.007

Liu B., Qiao H., Huang L., Buchenauer H., Han Q., Kang Z., Gong Y. 2009. Biological control of take-all in wheat by endophytic *Bacillus subtilis* E1R-j and potential mode of action. Biological Control 49 (3): 277–285. DOI: https://doi.org/10.1016/j.biocontrol.2009.02.007

Mandal S., Mallick N., Mitra A. 2009. Salicylic acid-induced resistance to *Fusarium oxysporum* f. sp. *lycopersici* in tomato. Plant Physiology and Biochemistry 47 (7): 642–649. DOI: https://doi.org/10.1016/j.plaphy.2009.03.001

Martínez-Medina A., Fernandez I., Lok G.B., Pozo M.J., Pieterse C.M., van Wees S. 2017. Shifting from priming of salicylic acid-to jasmonic acid-regulated defences by *Trichoderma* protects tomato against the root knot nematode *Meloidogyne incognita*. New Phytologist 213 (3): 1363–1377. DOI: https://doi.org/10.1111/nph.14251

Moon Ju Y., Park J.M. 2016. Cross-talk in viral defense signaling in plants. Frontiers in Microbiology 7. DOI: https://doi.org/10.3389/fmicb.2016.02068

Pieterse C.M., Leon-Reyes A., van der Ent S., van Wees S.C. 2009. Networking by small-molecule hormones in plant immunity. Nature Chemical Biology 5 (5): 308–316. DOI: https://doi.org/10.1038/nchembio.164

Ryder M.H., Yan Z., Terrace T.E., Rovira A.D., Tang W., Correll R.L. 1998. Use of strains of *Bacillus* isolated in China to suppress take-all and rhizoctonia root rot, and promote seedling growth of glasshouse-grown wheat in Australian soils. Soil Biology and Biochemistry 31 (1): 19–29. DOI: https://doi.org/10.1016/s0038-0717(98)00095-9

Ryu C.M., Farag M.A., Hu C.H., Reddy M.S., Kloepper J.W., Pare P.W. 2004. Bacterial volatiles induce systemic resistance in *Arabidopsis*. Plant Physiology 134 (3): 1017–1026. DOI: https://doi.org/10.1104/pp.103.026583

Ryu C.M., Farag M.A., Hu C.H., Reddy M.S., Wei H.X., Pare P.W., Kloepper J.W. 2003. Bacterial volatiles promote growth in *Arabidopsis*. Proceedings of the National Academy of Sciences of the USA 100 (8): 4927–4932. DOI: https://doi.org/10.1073/pnas.0730845100

Sari E., Etebarian H., Aminian H. 2007. The effects of *Bacillus pumilus*, isolated from wheat rhizosphere, on resistance in wheat seedling roots against the take-all fungus, *Gaeumannomyces graminis* var. *tritici*. Journal of Phytopathology 155 (11–12): 720–727. DOI: https://doi.org/10.1111/j.1439-0434.2007.01306.x

Sharifi R., Ahmadzadeh M., Sharifi-Tehrani A., Talebi-Jahromi K. 2010. Pyoverdine production in *Pseudomonas fluorescens* UTPF5 and its association with suppression of common bean damping off caused by *Rhizoctonia solani* (Kűhn). Journal of Plant Protection Research 50 (1): 72–78. DOI: https://doi.org/10.2478/v10045-010-0013-5

Sharifi R., Lee S.M., Ryu C.M. 2017. Microbe-induced plant volatiles. New Phytologist 218. DOI: https://doi.org/10.1111/nph.14955

Sharifi R., Ryu C.-M. 2016. Are bacterial volatile compounds poisonous odors to a fungal pathogen *Botrytis cinerea*, alarm signals to *Arabidopsis* seedlings for eliciting induced resistance, or both? Frontiers in Microbiology 7: 196. DOI: https://doi.org/10.3389/fmicb.2016.00196

Sharifi R., Ryu C.-M. 2018. Sniffing bacterial volatile compounds for healthier plants. Current Opinion in Plant Biology 44: 88–97. DOI: https://doi.org/10.1016/j.pbi.2018.03.004

Sharifi R., Ryu C.M. 2017. Chatting with a tiny belowground member of the holobiome: communication between plants and growth-promoting rhizobacteria. Advances in Botanical Research 82: 135–160. DOI: https://doi.org/10.1016/bs.abr.2016.09.002

Shirzad A., Pazhouhandeh M., Ahmadabadi M., Behboudi K. 2012. Analysis of cross-talk between *Trichoderma atroviride* and *Pseudomonas fluorescens*. Journal of Plant Pathology 94 (3): 621–628. DOI: http://dx.doi.org/10.4454/JPP.FA.2012.063

Walters D., Heil M. 2007. Costs and trade-offs associated with induced resistance. Physiological and Molecular Plant Pathology 71 (1–3): 3–17. DOI: https://doi.org/10.1016/j.pmpp.2007.09.008

Weller D.M., Mavrodi D.V., van Pelt J.A., Pieterse C.M., van Loon L.C., Bakker P.A. 2012. Induced systemic resistance in *Arabidopsis thaliana* against *Pseudomonas syringae* pv. *tomato* by 2,4-diacetylphloroglucinol-producing *Pseudomonas fluorescens*. Phytopathology 102 (4): 403–412. DOI: https://doi.org/10.1094/phyto-08-11-0222

Yi H.-S., Yang J.W., Ryu C.-M. 2013. ISR meets SAR outside: additive action of the endophyte *Bacillus pumilus* INR7 and the chemical inducer, benzothiadiazole, on induced resistance against bacterial spot in field-grown pepper. Frontiers in Plant Science 4: 122. DOI: https://doi.org/10.3389/fpls.2013.00122

Zablotowicz R.M., Tipping E.M., Lifshitz R., Kloepper J.W. 1991 Plant growth promotion mediated by bacterial rhizosphere colonizers. p. 315–326. In: "The Rhizosphere and Plant Growth" (Keister D.L., Cregan P.B., eds.). Beltsville Agricultural Research Center (BARC), Beltsville, Maryland, 386 pp. DOI: https://doi.org/10.1007/978-94-011-3336-4_70