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SHORT COMMUNICATION

Medicinal plants with phytotoxic activity harbour endophytic bacteria with plant growth inhibitory properties

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Abstract
The cultivable endophytic bacteria associated with two medicinal plants *Hypericum perforatum* L. and *Ziziphora capitata* L. contrasting with phytotoxic activity were investigated. The phytotoxic activity of plant extracts, and bacterial metabolites on seed germination and seedling growth of tomato were evaluated. In comparison to Z. *capitata*, the extract of *H. perforatum* contains a higher content of phenolic compounds. The crude extract of *H. perforatum* inhibited germination of seeds and seedling growth of tomato, whereas *Z. capitata* extracts only slightly reduced these parameters. Interestingly, almost half of the endophytes associated with *H. perforatum* had an inhibitory effect on plant growth, whereas rarely any plant inhibitory effect was found among isolates from Z. *capitata*. All bacterial isolates from *Z. capitata* were able to stimulate plant growth, by 35–80%. In contrast, only five isolates from *H. perforatum* caused significant improvement in plant growth (22–46%). The results showed that medicinal plants with higher phytotoxic activity were colonized with endophytic bacteria which inhibit plant growth and development. These findings indicate that plant phytochemical constituents and activity determine the physiological properties of their endophytes.

Keywords Medicinal plant · Phenolic compound · Endophytes · Plant growth · Phytotoxicity

Introduction

Medicinal plants synthesize various biologically active compounds such as alkaloids, flavonoids, saponins, phenolics, tannins, essential oils, and other compounds and show wide range of biological activity (Puupponen-Pimiä et al. 2001; Varsha et al. 2013; Vashist and Sharma 2013). Several secondary metabolites in plants can act as allelochemicals to other plants, stimulating or inhibiting their growth and development. There are several reports on the bio-insecticidal and plant growth stimulating effects of plant extracts from certain herbal plants (Jbilou et al. 2008; Ma et al. 2012). Earlier, Angelini et al. (2003) found that essential oils of medicinal plants may pose inhibitory effects on growth of other plants by releasing allelopathic substances. Ali et al. (2010) reported that allelopathic compounds in plants such as polyphenols inhibit seed germination and plant growth. The composition of plant secondary metabolites is strongly affected by the endophytic microbes associated with the host plant (Brader et al. 2014; Chaparro et al. 2014; Hashem et al. 2016; Egamberdieva et al. 2016). The endophytes that colonise inside plant tissues produce various metabolites and stimulate plant growth and protect host plant from soil borne pathogens (Egamberdieva et al. 2016, 2017a, b, 2018). They produce various biological active metabolites including phytohormones, enzymes, antifungal compounds, and volatile organic compounds (Davis et al. 2013; Cho et al. 2015). Bioactive secondary metabolites produced by endophytes may also assist the plants in chemical defence (Ji et al. 2009). According to the host-endophyte coevolution hypothesis, chemical compounds synthesized by plants resemble those with the endophytic metabolites (Kumar et al. 2012; Rai et al. 2014). The root-associated bacteria with antifungal activity were reported from medicinal plants *Matricaria chamomilla* L., and *Calendula officinalis*, known with antibacterial activity (Köberl et al.

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2013). Goryluk et al. (2009) observed higher proportion of antagonistic endophytes associated with *Chelidonium majus* L., which has antimicrobial activity (Baker and Satish 2013).

Although the inhibitory or stimulatory effect of medicinal plants extracts on plant growth is known, there is little information concerning the plant growth traits of their associated endophytes. In this study, we compared the effect of medicinal plant extract and metabolites of their endophytic bacteria on the seed germination and seedling growth. Also we have evaluated the effect of bacterial inoculants on growth of tomato in pot experiments.

Materials and methods

Plants and endophytic bacteria

Two plant species *H. perforatum* and *Z. capitata* were collected during the summer from Chatkal Biosphere Reserve of Uzbekistan. The dried aerial parts were powdered and extracted with 50 ml of methanol for 24 h in the dark at room temperature. After evaporation in a rotary vacuum evaporator at 40 °C, the extract was re-suspended in dimethyl sulfoxide (DMSO) and was filtered through Whatman No. 1 paper.

The endophytic bacteria were isolated from *H. perforatum* and *Z. capitata* and identified in a previous study (Egamberdieva et al. 2016). Fifteen endophytic bacteria were obtained from *H. perforatum*, and thirteen bacterial endophytes from *Z. capitata* and used for the experiments (Table 2). Bacterial strains were cultured in Tryptic Soy Broth (TSB) medium (50 ml) for 3 days at 28 °C and bacterial cells were separated by centrifugation (10,000×*g* for 10 min). The supernatant was used to study the effect on seed germination.

Determination of phenolic content

The Folin–Ciocalteu colorimetric method (Slinkard and Singleton 1977) was used to determine total phenolic contents of plant extracts by using a calibration curve obtained with gallic acid (Merck, Germany) as a standard. The total phenolic content in plant extracts was indicated in mg/g of extract. For each sample, three replicate assays were performed and the absorbance value was measured at 765 nm using an UV 1601 spectrophotometer (Shimadzu Corporation, Japan).

Phytotoxic activity of plant extract and bacterial metabolites

The phytotoxic activity of crude extracts from *H. perforatum* and *Z. capitata* on seed germination and seedling growth of tomato (*Solanum lycopersicum* L.) were studied at 10 mg/ml concentration. The bacterial metabolites, that were obtained after growth in TSB were also checked. Tomato seeds (Enza Zaden, The Netherlands) were surface-sterilized by stirring in a flask with 5% sodium hypochlorite (NaClO) for 3 min, and 70% ethanol for 3 min, and rinsed with sterile water. Thirty uniformly sterile seeds were placed in 60 mm Petri dishes on Whatman No. 2 filter paper that were moistened with 5 ml of plant extract solution (10 mg/ml) and bacterial culture supernatant in separate sets. Control Petri dishes were maintained using only sterile water. Sterile TSB was also tested for its effect on seed germination. Petri dishes were sealed with parafilm (Sigma-Aldrich, UK) to avoid moisture loss and kept in a plant growth chamber with a 16 h light period at 24 °C and an 8 h dark period at 16 °C. After 3 and 5 days, the number of germinated seeds and the lengths of roots and shoots of seedlings (> 0.2 mm) were measured and recorded.

The effect of bacterial inoculants on plant growth

The effect of endophytic bacteria on growth of tomato (*S. lycopersicum*. cv. Bella, The Netherlands) was performed in plastic pots filled with 200 g potting soil. Chemical properties of soils were: Nitrogen—250 mg/l, Phosphorus 120 mg/l, Potassium—700 mg/l, pH 6.0, Floragard GmbH, Germany). The bacterial strains were grown in TSB for 48 h at 28 °C and 1 ml of each culture was pelleted by centrifugation and suspended with phosphate buffered saline at a bacterial density of 10^7 CFU/ml. Tomato seeds were surface-sterilized, germinated and inoculated with bacterial suspension and grown under greenhouse conditions for 1 month (temperature day 24 °C, night 16 °C; humidity 50–60%, day length 12 h). The dry weights of whole plants were determined.

Statistical analyses

The univariate and multivariate ANOVA (SPSS 15.0 for Windows) for the data sets were used for comparisons between treatments. The mean comparisons were conducted using Tukey's test at $P < 0.05$.

Results

Phenolic content of plant extracts

The total phenol contents of *H. perforatum* and *Z. capitata* are shown in Table 1. The extract of the *H. perforatum* exhibited a higher phenolic content with values of 61.6 mg Gallic acid equivalent (GAE)/g extract compared to *Z. capitata* (17.0 mg GAE/g extract).

Phytotoxic activity of plant extracts and bacterial metabolites

The result showed that the germination rate and seedling growth of tomato plants were affected by the crude plant extracts of *H. perforatum* and *Z. capitata*. The seed germination of tomato treated with methanol extract of *H. perforatum* was decreased by 15%, whereas only a slight decrease (0.8%) was observed with *Z. capitata* extracts. Furthermore, the extract of *H. perforatum* reduced roots and shoot growth of tomato seedlings (Table 1). Compared to a shoot length of 2.61 cm and a root length of 4.35 cm in the control, the crude extract of *H. perforatum* reduced the mean length of shoot to 1.81 cm (by 31%) and root to 3.11 cm (by 29%). In contrast, the extract of *Z. capitata* showed lower inhibitory effects on shoot (18%) and root growth (15%) of tomato seedlings compared to control seedlings.

The effect of bacterial culture supernatants on the seed germination and seedling growth showed that eight bacterial isolates from *H. perforatum* inhibited seed germination of tomato (Table 2). The highest inhibitory activity was observed with *A. piechaudii* S7a, *A. piechaudii* S7, *Achromobacter* sp. 14 and *Pseudomonas koreensis* S25. Most of the bacterial isolates from *Z. capitata* did not show strong inhibitory activity on seed germination, only isolates *A. piechaudii* M41, *Achromobacter* sp. M19, and *A. spanius* M8 inhibited seed germination of tomato (Table 2).

The effect of bacterial inoculants on plant growth

Fifteen endophytic bacteria isolated from *H. perforatum* and thirteen bacterial endophytes from *Z. capitata* were tested for their effect on growth of tomato. All bacterial isolates from *Z. capitata* which contains low phenolic compounds were able to stimulate plant growth. Of these six isolates, *A. piechaudii* M6, *A. piechaudii* M31, *A. piechaudii* M24, *Bacillus cereus* M14, *Enterobacter cloacae* M20a, *E. cloacae* M17 showed a *s*ignificant ($P < 0.05$) increase in plant dry biomass (between 35 and 80%) (Fig. 1). In contrast, only five isolates from *H. perforatum* (containing higher phenolic compounds), i.e., *Arthrobacter crystallopoietes* S1, *Bacillus* sp. S2, *Pseudomonas kilonensis* S3, *Pantoea agglomerans* S22, and *Stenotrophomonas* sp. S9 stimulated plant growth significantly (between 22 and 46%) (Fig. 2). On the other hand nine bacterial isolates inhibited plant growth. *A. piechaudii* S7a showed highest phytotoxic activity compared to other bacterial isolates.

Discussion

In our experiments, the crude extract of *H. perforatum* inhibited both the germination of seeds and the growth of tomato seedlings, whereas *Z. capitata* extracts slightly reduced these parameters. Similar to our findings, Fritz et al. (2007) also found a reduction of *Lactuca sativa* seedling growth by crude extracts of *Hypericum* species. In a previous report, Ali et al. (2010) found that plants producing allelopathic substances can pose inhibitory effects on the growth of other plants. Allelopathic compounds in plants such as polyphenols have been reported to inhibit both germination and plant growth (Dall'Agnol et al. 2003). In our study, a higher phenolic content in plant extract of *H. perforatum* was observed compared to *Z. capitata*, which may be responsible for the inhibition of tomato seed germination. A high phenolic compound content in *H. perforatum* was also reported by Oztürk et al. (2009). Similarly, Fritz et al. (2007) reported high levels of total phenolic compounds in the crude extracts of *H. polyanthemum* and *H. myrianthum* and suggested that these compounds play a role in the inhibition of plant growth.

Table 1 Phytotoxic activity and contents of total phenols of extracts obtained from *Hypericum perforatum* and *Ziziphora capitata*

Plant species	Total phenol content	Phytotoxicity (on tomato), %		
	mg (GAE)/g extract	Seeds germination[a]	Root length[b]	Shoot length[b]
Hypericum perforatum	61.6	85	28.5	30.6
Ziziphora capitata	17.0	92	17.6	15.1

[a]% of germinated tomato seeds

[b]% of inhibition of tomato shoot and root length; (Control: seeds germination—100%, length of shoot 2.61 cm, length of root 4.35 cm as 100%)

Table 2 Phytotoxic activity of bacterial culture supernatant on tomato seeds germination and seedlings growth

Plant	Isolate	Bacteria	Seeds germination (petri plates)[a]	Seedling growth[b]		HCN[c]
				Root	Shoot	
Hypericum perforatum	S1	*Arthrobacter crystallopoietes*	100	0	0	+
	S22a	*Achromobacter piechaudii*	89	25	29	–
	S7a	*Achromobacter piechaudii*	83	35	36	+
	S7	*Achromobacter piechaudii*	85	29	33	–
	S23	*Achromobacter spanius*	98	5	6	–
	S14	*Achromobacter* sp.	89	27	25	+
	S2	*Bacillus* sp.	100	0	0	–
	S40	*Bacillus cereus*	96	7	7	+
	S4	*Erwinia persicina*	94	9	7	+
	S25	*Pseudomonas koreensis*	86	31	34	–
	S24	*Pseudomonas* sp.	100	0	0	–
	S3	*Pseudomonas kilonensis*	100	0	0	–
	S22	*Pantoea agglomerans*	100	0	0	–
	S26	*Serratia liquefaciens*	100	3	3	+
	S9	*Stenotrophomonas* sp.	100	0	0	+
Ziziphora capitata	M11	*Achromobacter piechaudii*	100	0	0	–
	M6	*Achromobacter piechaudii*	100	0	0	–
	M31	*Achromobacter piechaudii*	100	0	0	–
	M24	*Achromobacter piechaudii*	100	0	0	–
	M41	*Achromobacter piechaudii*	93	11	9	–
	M19	*Achromobacter* sp.	89	19	21	–
	M18	*Achromobacter spanius*	89	22	17	–
	M19a	*Bacillus altitudinis*	100	0	0	–
	M14	*Bacillus cereus*	100	0	0	–
	M20	*Enterobacter cloacae*	100	0	0	–
	M17	*Enterobacter* sp.	100	0	0	–
	M13	*Pantoea agglomerans*	100	0	0	–
	M6a	*Pseudomonas kilonensis*	100	0	0	–

[a]% of germinated tomato seeds

[b]% of inhibition of tomato shoot and root length (0—means no inhibition); (Control: seeds germination—100%, length of shoot 2.42 cm, length of root 4.21 cm as 100%)

[c]Egamberdieva et al. (2016)

Tian et al. (2011) observed a small amount of polyphenolic compounds in different *Ziziphora* species.

It has been reported that volatile metabolites released by bacteria play a major role in diverse plant microbe interactions (Schmidt et al. 2015; Kai et al. 2016). Interestingly, in our study almost half of the endophytes associated with *H. perforatum* had an inhibitory effect on plant growth while minimal or no inhibitory effect was found by isolates from Z. *capitata*. Moreover, bacteria isolated from *Z. capitata* and *H. perforatum* were tested for their phytotoxic activities. The results showed that the supernatant of eight isolates from *H. perforatum* inhibited seed germination and seedling growth of tomato. Similarly, Tabatabaei et al. (2016) observed an inhibition of seed germination and seedling growth of durum wheat by *Pseudomonas* sp. UW3, *P. fluorescent* 550, and *Pseudomonas* sp. 57. In earlier studies, Brimecombe et al. (2007) and McPhail et al. (2010) also observed an inhibition of plant growth by plant-associated bacteria. Several bacterial metabolites such as phytotoxins, cyanide and non-volatile compound can inhibit plant growth (Banowetz et al. 2008). In present study seven isolates from *H. perforatum* produced HCN whereas such activity was not found in any isolates from *Z. capitata* (Table 2). In earlier work, Kremer and Souissi (2001) found that 32% of bacteria from a collection of over 2000 isolates, synthesized HCN and showed inhibition of lettuce and barnyard grass. In other study, Banowetz et al. (2008) observed an inhibition of *Poa annua* seeds by *P. fluorescens* WH6 due to the production of 4-formylaminooxyvinylglycine. There are many reports on the stimulatory effect of root-associated bacteria as well

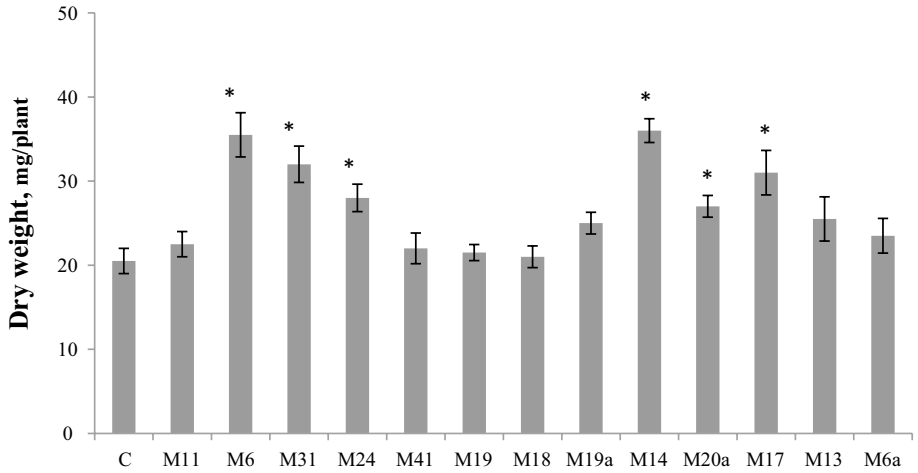

Fig. 1 The effect of seedling inoculation with endophytic strains isolated from *Z. capitata* on dry weight of tomato. (*Achromobacter piechaudii* M11, *A. piechaudii* M6, *A. piechaudii* M31, *A. piechaudii* M24, *A. piechaudii* M41, *Achromobacter* sp. M19, *Achromobacter spanius* M18, *Bacillus altitudinis* M19a, *Bacillus cereus* M14, *Enterobacter cloacae* M20a, *E. cloacae* M17, *Pantoea agglomerans* M13, *Pseudomonas kilonensis* M6a) Columns represent means for six seedlings (N = 6) with error bars showing standard error. Columns marked with an asterisk differed significantly from uninoculated plants at $P < 0.05$

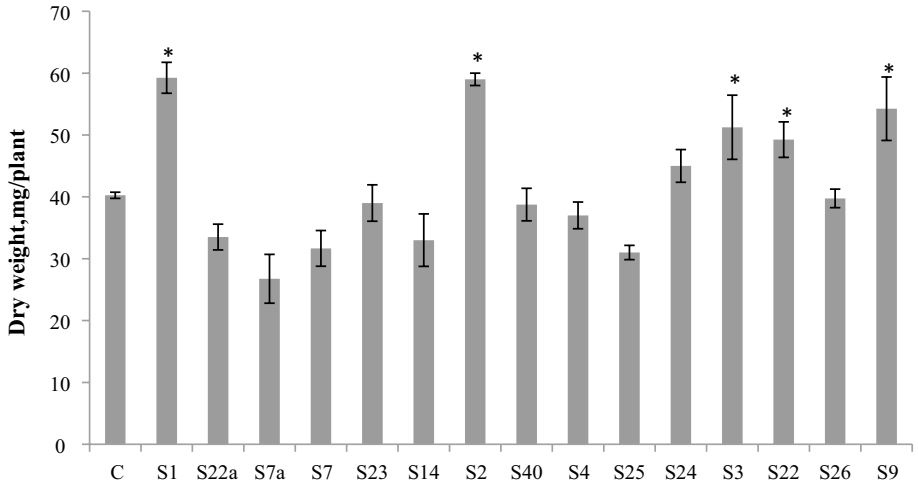

Fig. 2 The effect of seedling inoculation with endophytic strains isolated from *H. perforatum* on dry weight of tomato. (*Arthrobacter crystallopoietes* S1, *Achromobacter piechaudii* S22a, *A. piechaudii* S7a, *A. piechaudii* S7, *Achromobacter spanius* S23, *A. spanius* S14, *Bacillus* sp. S2, *Bacillus cereus* S40, *Erwinia persicina* S4, *Pseudomonas koreensis* S25, *Pseudomonas* sp. S24, *Pseudomonas kilonensis* S3, *Pantoea agglomerans* S22, *Serratia liquefaciens* S26, *Stenotrophomonas* sp. S9). Columns represent means for six seedlings (N = 6) with error bars showing standard error. Columns marked with an asterisk differed significantly from uninoculated plants at $P < 0.05$

(Egamberdieva et al. 2013, Cho et al. 2015). We have also observed plant growth stimulation of tomato by bacterial strains. The most interesting finding in this study was that the majority of bacterial isolates from *H. perforatum* showed phytotoxic activity on seed germination and seedling growth. Phytotoxic activity of *H. perforatum* plant extracts was also observed in this study. In contrast, we found only a few endophytes from *Z. capitata* inhibited seed germination and seedling growth of tomato. Furthermore, plant extracts of *Z. capitata* also did not show phytotoxic activity against seed germination and seedling growth. The potential of secondary metabolite production by endophytic bacteria, and their biological activity especially those exclusive to their host plants was reported in earlier studies (Mehanni and Safwat 2010; Kusari et al. 2012). Endophytic bacteria that colonize internal plant tissue and able to synthesize plant beneficial metabolites which improve nutrient mobilization and uptake are expected to play a significant role in low-input sustainable agriculture (Arora et al. 2018).

Conclusion

The results of present study showed that medicinal plants with high phytotoxic activity are colonized internally by higher percentage of bacteria with plant inhibiting properties. These findings indicate that biological activity of bacteria that colonize the interior of both below- and aboveground tissues are closely linked to host plant activities. Therefore, selecting the host plant without signs of phytotoxicity is the first prerequisite for isolation and screening of promising endophytic bacteria as plant growth stimulators and biocontrol agents.

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