Bacterial endophytes from arid land plants regulate endogenous hormone content and promote growth in crop plants: an example of Sphingomonas sp. and Serratia marcescens

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INTRODUCTION

Endophytic microorganisms (bacteria) belong to a key class of plant symbionts that live inside plant tissues but do not cause disease in the host. These endophytic microorganisms are associated with the plant throughout the plant’s life, starting from seed germination to fruit development. They can be present in the rhizosphere (roots), phylloplane (in leaves), lamosphere caulosphere (in stems), and anthosphere (in flowers) according to Clay and Holah (1999), Lindow and Brandl (2003), Saikkonen et al. (2004), and Sessitsch et al. (2012). Bacterial and fungal endophytes have unique roles in plants. They provide alternative resources or facilitate the distribution or production of biologically active metabolites, such as enzymes, biofunctional chemicals, phytohormones, nutrients, and minerals (Schulz et al. 2002). In contrast, the host plant provides nutrients and a protective sanctuary for reproduction inside plant tissues without compromising its own growth resources (Khan et al. 2015).

Endophytic bacterial strains have been isolated and identified from various crop plants such as pea (Pisum sativum), tomato (Lycopersicum esculentum), corn (Zea mays), wheat (Triticum aestivum), oat (Avena sativa), canola (Brassica napus), barley (Hordeum vulgare), radish (Raphanus sativus), soybean (Glycine max), potato (Solanum tuberosum), lettuce (Lactuca sativa), and cucumber (Cucumis sativa). Adding to these, various other medicinally important plants that grow in arid regions have also been used to isolate and identify their associated bacterial endophytes. Some previous studies have evaluated medicinal plants such as Gynura procumbens (Bhore et al. 2010), Piper nigrum L. (Aravind et al. 2009), Trifolium repens, (Burch & Sarathchandra 2006), Artemisia annua (Li et al. 2012), Tridax procumbens (Preveena & Bhore 2013), and Tephrosia apollinea (Khan et al. 2014). Some novel strains belong to the genera Arthrobacter, Actinobacter, Aeromonas, Agrobacterium, Alkaligenes, Bacillus, Azospirillum, Enterobacter, Flavobacterium Pseudomonas, Acinetobacter, Azotobacter, Beijerinckia, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Rhizobium, and Serratia, were isolated from these medicinal plants (Gray and Smith 2014). However, few studies have examined bacterial endophytes in important arid land plants.

Endophytes always play an important role in ecological adaptation of host plant particularly in harsh environment due to its influencing role in conferring plant fitness (Achatz et al. 2010; Khan et al. 2013). Several mechanisms as described...
earlier have been attributed for this ability and thus shape the host plant resistance against biotic and abiotic stress with improved physiological characteristics. Owing to these characteristics, Strobel et al. (2004) hypothesized that the plants living in unique environment would be the better source for the isolation of novel endophytes. Keeping in view this hypothesis, several studies have been conducted on endophytic bacteria and fungi isolated from desert or arid land plants and exploited for growth promotion in crop plants (Achatz et al. 2010; Khan et al. 2014). Achatz et al. (2010) inoculated *Fusarium graminearum* diseased or healthy barley plants with fungal endophyte *Piriformospora indica* explored in Indian Thar desert. The endophytic inoculation caused rapid growth and development with more yield and higher number of tillers in both diseased and healthy barley plants. Inoculation of bacterial endophyte could also improve crop plant growth characteristics and the same have been reported in tomato inoculated with bacterial endophyte isolated from extreme arid land plants (Khan et al. 2014). The investigation of possible growth-promoting biologically active metabolites revealed the production of indole acetic acid (IAA) (Sirrenberg et al. 2007; Achatz et al. 2010; Khan et al. 2014) and gibberellins (GAs) (Khan et al. 2014) by endophytes used in these experiments. Furthermore, the same endophytes inoculation significantly modulated major phytohormones of these crop plants (Schäfer et al. 2009; Khan et al. 2013, 2014). Therefore, in the present study, we isolated, identified, and characterized endophytes from arid land plants. The isolated strains were inoculated into soybean plants and their effects on the growth and endogenous phytohormone (GAs, abscisic acid (ABA), and jasmonic acid (JA)) regulation were evaluated.

### Materials and methods

**Isolation and purification of bacterial endophytes from arid land plants**

Bacterial endophyte LK11 included in this study was previously isolated as described by Jasim et al. (2013) and Khan et al. (2014) from the leaves of *T. apollinaria* inhabiting the arid mountains under extreme water-deficient conditions (Ψ = −2.21 hPa) in Jabal Al-Akhdar, Sultanate of Oman. However, to isolate TP5, MPB5.3, S9, and TP1, leaf/root and stem samples free of any visible injury or disease spots were randomly collected with a sterilized knife from different *Moringa peregrina* plants (*n* = 9) at the same location. The plant parts were stored in ice box at temperature (0–6°C) in sterilized polythene zip-bags and transported to the laboratory. The collected plant parts were washed with running tap water and subsequently with autoclaved double-distilled water containing Tween-20 to remove attached dust and soil particles. Water was drained from washed plant parts and the samples were surface-sterilized with the disinfectant 2.5% sodium hypochlorite (30 min with shaking at 120 rpm) followed by 75% ethanol. The disinfectant was removed with autoclaved double-distilled water and the remaining few waters drops along with the sterilized tissues were imprinted onto Hagem medium. This was intended to validate our sterilization process and any kind of bacterial growth within 24 h suggested that the samples should be discarded because of ineffective surface sterilization (Jasim et al. 2013). The fragments of leaf/stem/root were ground to make fine pieces with an average size of 2.0 mm using a mortar and pestle. These samples were carefully spread on Hagem media (0.5% glucose, 0.05% KH₂PO₄, 0.05% MgSO₄·7H₂O, 0.05% NH₄Cl, 0.1% FeCl₃, 1.5% agar, 80 ppm fungicide; pH 5.6 ± 0.2) (Sheng et al. 2008). The bacterial endophyte in the form of emerging spots or layers from the leaves/stem/root pieces were picked with sterilized toothpicks. Further purification and growth were carried out on sterilized nutrient agar (NA) medium. From each petri dish, colonies were selected based on their growth, including growth time and morphology.

**Identification of plant growth-regulating substances in cell-free cultures**

After purification on NA medium, morphologically distinct strains were evaluated for the production of plant growth-regulating substances. Selected strains were cultured in 100 mL nutrient broth [gm/L, peptic digest of animal tissue 5.00, sodium chloride 5.00, beef extract 1.50, yeast extract 1.50, final pH (at 25°C), 7.4 ± 0.2] ± tryptophan at 28°C for 3 days with shaking (200 rpm) in the dark (Mergeay et al. 1985). The bacterial cultures were centrifuged at 2500 × g at 4°C for 15 min to separate the supernatant and cell pellets. The supernatant was passed through 0.45-µm cellulose acetate filter (DISMIC®; Friensenette ApS, Knebel, Denmark) to remove debris and then used for IAA analysis.

The presence of IAA was initially confirmed with the Salzkowski reagent (Patten and Glick 2002). A total volume of 2 mL from each supernatant of bacterial endophytes with and without tryptophan was added to 1 mL Salkowski’s reagent (50 mL 35% HClO₄, 1 mL 0.5 M FeCl₃) for 30 min in the dark. If IAA was present, the pink color intensity reading was taken at 530 nm (T60 UV VIS Spectrophotometer, Leicester, UK) and quantified using a calibration curve of IAA standard with linear regression analysis.

The exact determination of IAA in bacterial cell-free cultures (5 mL) with and without tryptophan was quantified by GC–MS/SIM (6890 N network GC system and 5973 network mass selective detector; Agilent Technologies, Palo Alto, CA, USA) as described by Ullah et al. (2013).

**Identification of phytohormones producing bacterial endophytes**

The findings for IAA in the culture broth of isolates were subsequently used for molecular identification. The identification was based on sequencing of partial 16S ribosomal RNA (rRNA). The standard procedures of Sambrook and Russel (2001) were followed to isolate total DNA, and the 16S rRNA gene was PCR-amplified using the 27F primer (5′-AGAGTTTGATCCTACGGACGCTAG-3′) and 1492R primer (5′-CGG (CT) TACCTGTTAGACCTT-3′), which were complementary to the 5′ and 3′ ends of the prokaryotic 16S rRNA, respectively.

The BLAST search program and EzTaxon-e were used to identify similar reference sequence homologues to the nucleotide sequences of bacterial isolates in this study. The most similar reference sequences with the highest homology and query coverage and the lowest E values were selected and aligned by ClustalW using MEGA version 6.0 software. *Pseudomonas alcaliphila* and *P. putida* were used as outgroups during neighbor-joining tree generation using the same software. TP1, MPB5.3, S9, Tp5, and LK11 showed
the highest similarity for the subclade of Serratia sp., Bacillus subtilis subsp. Subtilis, B. subtilis subsp. Subtilis, B. subtilis, and Sphingomonas sp., respectively. These similar bacteria showed 44%, 100%, 65%, and 100% bootstrap support, respectively, when bootstrap 1000 replications was analyzed for statistical support of the nodes in the phylogenetic tree. The 16S rRNA gene region sequences of isolates TP1, MPB5.3, S9, TP5, and LK11 were submitted to NCBI GenBank under accession numbers KX822701, KX822702, KX822703, KX822704, and KF515708, respectively.

**Endophytes–crop plant interaction study under controlled greenhouse conditions**

Disease- and damage-free healthy soybean seeds (G. max L. var. Tae Kwang) from the Soybean Genetic Resource Center (Kyungpook National University) with 6% moisture content and 95% germination rate were used in this study. For surface sterilization, seeds were treated with the disinfectant 2.5% sodium hypochlorite for 30 min, followed by thorough rinsing with autoclaved double-distilled water. Seedlings of equal size are very important for minimizing experimental error and therefore the seeds were germinated (10 days, 28°C and relative humidity of 60%) in germination trays to obtain uniform plants. The sterilized germination tray and pots were filled with horticulture soil that had been autoclaved (121°C, 15 psi for 15 min) three times and had the following nutrient composition of peat moss (10–15%), perlite (35–40%), coco peat (45–50%), zeolite (6–8%), and NH₄NO₃ ~0.09 mg/g; NO₃~0.205 mg/g; P₂O₅ ~0.35 mg/g; and K₂O ~0.1 mg/g to prepare the microbe-free condition. Randomly selected uniform seedlings were planted (VI stage) with one plant in each round plastic pot (10 × 9 cm) for 21 days; bases were used to prevent contamination through the leaching of irrigation water. The experimental treatments were as follows: (1) control soybeans without microbial cells and (2) soybean with bacterial endophyte (LK11, TP5, MPB-5.3, S9, or TP1) inoculation. During the experiment, plants were exposed to the following environmental conditions: 14 h at 28°C/10 h day/night cycle at 25°C and 60–70% relative humidity. For irrigation, distilled water was applied as needed with care to prevent leaching. However, irrigation was suspended one day before in designated plants for treatments with endophytic application to enhance the inoculation. Bacterial endophytes cells dissolved in 35 mL sterilized double-distilled water were applied three times to ensure complete infection in the first treatment at the time of transplantation and two times consecutively at 1-week intervals. Endophytes cells were collected as described above. The harvested cells were then washed with 0.8% NaCl solution and dissolved in autoclaved double-distilled water adjusted to an optical density of OD = 0.5. The following plant physiological parameters were analyzed: chlorophyll contents (SPAD-502 Minolta, Tokyo, Japan), shoot length, root length, and fresh weight at the time of harvest. For dry weight data, representative soybean plants were randomly collected separately divided into stems and roots for drying in an oven at 70°C for 72 h. For hormonal analysis, the plants were immediately stored in liquid nitrogen and then freeze-dried for 1 week (Virtis Freeze Dryer, Gardiner, NY, USA).

**Quantification of endogenous GAs, ABA, and JA**

A protocol established by Lee et al. (1998) as previously described in Waqas et al. (2014) was used to extract and quantify, respectively, GAs in freeze-dried samples of soybean plants using gas chromatography with a mass spectrometer (6890N network GC system, and 5973 network mass selective detector; Agilent Technologies). The data were calculated in nanogram per gram of freeze-dried weight of plant samples.

The contents of the plant growth-regulating hormone ABA were determined in freeze-dried biomass of non-inoculated and inoculated plants according to the method of Qi et al. (1998) with GC-MS SIM. For quantification, Lab-Base (ThermoQuest, Manchester, UK) data system software was used to monitor the responses to ions of m/z 162 and 190 for Me-ABA and 166 and 194 for Me-[2H₆]-ABA.

For endogenous JA content, the plant extracts obtained as described by McCloud and Baldwin (1997) were analyzed by GC-MS SIM. The quantification of GAs, ABA, and JA was based on the average of three replicates per treatment and repeated three times.

**Statistical procedures for data analysis**

To compare the plant growth-regulating effects of bacterial endophytes on soybean plants, the present study was conducted in a completely randomized design. Each treatment was replicated 25 times, and the whole experiment was independently repeated three times. The treatment effects on different plant growth parameters were derived by calculating the mean ± standard deviation using GraphPad Prism (Ver 6.0; GraphPad Software, La Jolla, CA, USA) and subsequent comparisons were conducted using Duncan’s multiple range tests at P < 0.05 (SAS, Inc., Cary, NC, USA).

**Results and discussion**

**Isolation, selection, and molecular identification of bacterial endophytes from arid plants**

The isolation and selection of the plant growth-promoting bacterial endophyte strain LK11 were previously reported by Khan et al. (2014). However, TP5, MPB5.3, S9, and TP1 were also isolated from the organs of plants native to the arid area with extreme low soil moisture content. Final selection of these bacterial endophytes among the total obtained isolates was conducted according to morphological criteria described by Tehler (1995) and Khan et al. (2014). All bacterial endophytes similar in apparent morphological traits were combined for comparison. A single isolate from each group was picked to analyze IAA production and then subsequently molecularly identified before further experimentation.

IAA released in cell-free cultures by endophytes was initially detected by the Salkowski test, and those containing IAA were subjected to quantification by GC-MS SIM. Three endophytes, LK11, MPB5.3, and TP1, produced IAA; 12.31 ± 0.45, 6.8 ± 0.59, and 10.5 ± 1.02 μM/mL, respectively.

BLASTn searching of EzTaxon and NCBI based on PCR amplification and sequencing of the 16S rRNA gene region was conducted to identify IAA-producing and IAA-non-producing bacterial endophytic isolates at the molecular level. The BLASTn search identified isolates with 100% homology to their respective species and showed the TP5, S9 as B. subtilis; MPB as Bacillus sp.; LK11 as Sphingomonas sp. and TP1 as Serratia sp. Detailed phylogenetic analysis (MEGA 6.0) using maximum parsimony (MP) and the
neighbour-joining method was performed to determine the exact positions of the bacterial endophytes (Figure 1). To obtain consensus trees based on both methods, the respective sequences of the 16S rRNA gene region showing similarity to our endophytic isolates were aligned at 1000 bootstrap replications. Hence, the performance of phylogenetic analysis further confirmed the molecular identification of the bacterial endophytes strains.

In the present study, we isolated and identified *B. subtilis; Bacillus* sp., *Sphingomonas* sp., and *Serratia* sp. Among the isolated strains, endophytic bacteria *Sphingomonas* sp. LK11 is a novel strain. *Sphingomonas* belongs to a group of gram-negative bacteria producing yellow-pigmented colonies and is present in a diverse range of environments. The bacterium is metabolically versatile, as it can utilize a wide range of naturally occurring compounds as well as some types of environmental contaminants (Miyauchi et al. 1998; Aylward et al. 2013; Puškárová et al. 2013). *Sphingomonas* sp. has recently been shown to help in the degradation of persistent metabolites in the environment (Puškárová et al. 2013). *Sphingomonas* sp. was found to contain genes responsible for carbazole degradation. Additionally, it can regulate certain classes of pesticides such as dibenzo-p-dioxins and remediate heavy metals (Puškárová et al. 2013). *Sphingomonas* sp. has recently been shown to help in the degradation of persistent metabolites in the environment (Puškárová et al. 2013). *Sphingomonas* sp. has recently been shown to help in the degradation of persistent metabolites in the environment (Puškárová et al. 2013). *Sphingomonas* sp. has recently been shown to help in the degradation of persistent metabolites in the environment (Puškárová et al. 2013). *Sphingomonas* sp. has recently been shown to help in the degradation of persistent metabolites in the environment (Puškárová et al. 2013).

In addition to LK11, *Bacillus* sp. or *B. subtilis* have been identified in various plant and crop species (Gagne-Bourque et al. 2016). *Bacillus* is among the most common taxa of isolated endophytes, and has been shown to possess dominant prospects of plant growth promotion. *Bacillus* species are well known to improve plant growth and biomass and their secondary metabolites have been widely examined (Bacon et al. 2015; Müller et al. 2015).

**Role of bacterial endophytes in soybean growth and biometric analysis**

The plant growth-promoting behavior of phytohormones producing bacterial endophytes obtained from plants inhabiting arid regions was physiologically determined in soybean. Biometric analysis of soybean plants in all treatments exhibited high growth promotion behavior of LK11 and TP1 followed by the remaining treatments and control plants (Figures 2 and 3(a)–(e)). Application of LK11 significantly promoted shoot/root length, fresh/dry weight, and chlorophyll contents followed by TP1 and MPB5.3 compared to the remaining treatments and control plants (Figure 3(a)–(c) and e). The shoot length of soybean was 11.33 ± 1.17 cm following treatment with LK11 and 9.40 ± 1.32 cm and 9.24 ± 1.13 cm following treatment with TP1 and MPB5.3, respectively, compared to the control (7.423 ± 1.74 cm). The same positive effect was found for fresh/dry weight in soybean plants treated with LK11 (3.89 ± 0.14 g/0.42 ± 0.017 g), followed by TP1 (3.75 ± 0.15 g/0.37 ± 0.01 g) and MPB5.3 (3.57 ± 0.15 g/0.36 ± 0.03 g). However, for root length, TP1 (34.22 ± 3.64 cm),...
LK11 (35.20 ± 2.99 cm), MPB5.3 (32.78 ± 3.39 cm), and S9 (33.08 ± 3.74 cm) showed significant effects compared to the control (29.69 ± 4.24 cm). Determination of the SPAD value indicated that chlorophyll contents were significantly higher in plants inoculated with LK11, TP1, and MPB5.3 followed by control and S9. 

*Sphingomonas* sp. LK11 was previously reported to improve the growth of tomato plants during salinity stress (Khan et al. 2014). This was also attributed to its ability to produce phytohormones such as GA and IAA (Halo et al. 2015). A similar role was also identified in the present study, as LK11 has significantly increased the plant growth attributes of soybean plants compared to the other strains and non-inoculated control plants. This further suggests the potent role of this strain in explicit multi-host growth ameliorations, i.e. previously for tomato and in the present study for soybean. The present results also indicate that LK11 can be used as an inoculant for a wide variety of crops.

In addition to LK11, among other strains, *S. marcescens* improved the growth of soybean plants. In a previous study, Khan et al. (2015) showed that a strain of *Serratia* sp. isolated from *Solanum nigrum* relieved heavy metal stress in *S. nigrum* by improving biomass and decreasing stress indicators. The proposed mechanisms for plant growth promotion include IAA synthesis and phosphate solubilization (Kang et al. 2015; Khan et al. 2015). Information on *Serratia* strains imparting plant growth and stress tolerance have been thoroughly described by Kang et al. (2015). This is largely because most studies concentrated on understanding the mechanisms that elicit plant growth-promoting effects (Dimkpa et al. 2009). Utilizing endophytic bacteria residing inside the tissues of arid land plants can reveal broader roles in not only improving plant growth but also enhancing the tolerance of the host plant to a variety of abiotic stresses.

**Relative quantification of GAs, ABA, and JA in soybean with bioactive bacterial endophytes interaction**

Relative quantification of GAs, ABA, and JA was determined in the most bioactive bacterial endophyte-treated plants (LK11, TP1) and compared with the control in order to understand hormonal regulation during mutual interaction. LK11-treated plants showed the highest levels of GA4 and GA7 as compared to that of TP1 and control plants (Table 1). Moreover, there was no significant difference in GA4 and GA7 between TP1 and the control, except for GA12, which was higher in TP1. No GA9, GA20, or GA53 were detected in control plants. GA20 and GA53 were significantly

| Treatments | GA4 (ng/g D.W.) | GA7 (ng/g D.W.) | GA12 (ng/g D.W.) | GA3 (ng/g D.W.) | GA7 (ng/g D.W.) | GA3 (ng/g D.W.) | Total GAs |
|------------|----------------|----------------|-----------------|----------------|----------------|----------------|-----------|
| Control    | 94.66 ± 0.87b  | 18.39 ± 0.79b  | 0.71 ± 0.06c    | ND             | ND             | ND             | 113.76    |
| LK11       | 106.85 ± 0.46a | 21.56 ± 0.26a  | 1.57 ± 0.22b    | 3.51 ± 0.10a   | 0.49 ± 0.13b   | 21.45 ± 0.46b  | 155.43    |
| TP1        | 91.09 ± 0.97c  | 19.18 ± 0.22b  | 2.14 ± 0.06a    | ND             | 0.82 ± 0.05a   | 33.74 ± 0.26a  | 146.94    |

Notes: Control = plants treated with water; LK11 = plants inoculated with *Sphingomonas* sp.; TP1 = plants inoculated with *Serratia marcescens*; ND = not detected; ng/g D.W. = nano gram per gram of plant dry weight; Total GAs = across the rows sum of the bioactive and inactive gibberellins detected in particular treatment. Mean ± SD of bioactive/non-active GAs detected and quantified in bacterial endophytes inoculated and non-inoculated soybean plants; different letters in a column indicate significant difference at p = 0.05 by Duncan’s multiple range test.
higher in TP1 compared to in LK11; GA9 was detected only in LK11-treated plants.

One of the major defence hormones, JA, was present at lower levels in bacterial endophytic-treated plants than in controls (Figure 4). In this experiment, bacterial endophyte LK11-treated plants showed significantly lower levels of JA (50.07 ± 4.50 ng/g D.W.) compared to controls (93.90 ± 0.53 ng/g D.W.). In contrast, ABA was significantly higher following bacterial endophyte treatments, and plants exposed to LK11 presented significantly higher contents of ABA (457.30 ± 7.41 ng/g D.W.), followed by TP1-treated plants (398.55 ± 8.33 ng/g D.W.) compared to controls (205.93 ± 8.74 ng/g D.W.) (Figure 5).

Endophytic microorganisms were recently shown to influence various plant physiological characteristics by either increasing their concentrations in specific plant parts or by decreasing to avoid utilizing energy resources for growth or stress (Khan et al. 2014; Santoyo et al. 2016). In the present study, LK11 application significantly increased the contents of physiologically active GA4 and GA7, contributing to the larger shoot length of the soybean plants. A similar previous study by Kang et al. (2012) showed that inoculation with *Pro-micromonospora* sp. SE188 significantly up-regulated the non-C-13 hydroxylation GA biosynthesis pathway (GA12 → GA24 → GA3 → GA4 → GA34) in tomato plants compared to control plants. This was correlated with the ability of SE188 to produce GAs and solubilize phosphate.

In the present study, ABA levels were significantly increased in LK11 compared to endophytic treatments. ABA induces symptoms of stress such as stomatal closure;
Figure 5. ABA contents in non-inoculated and inoculated soybean plants with IAA producing LK11 and TP1. The column bars with errors represent the mean ± SD and different letters represent significant differences at p = 0.05 by Duncan’s multiple range test. Control = plants treated with water; LK11 = plants inoculated with Sphingomonas sp.; TP1 = plants inoculated with Serratia marcescens. ABA in soybean plants was determined (ng/g D.W. = nano gram per gram of plant dry weight) in triplicate.

however, increased ABA levels can also decrease transpiration during inoculation. Sherameti et al. (2008) showed that during endophytic association, endogenous ABA levels were generally increased in Arabidopsis plants. A similar correlation was observed for Arabidopsis plant inoculated with Azospirillum brasilense sp. 245 (Cohen et al. 2008), which showed a significantly higher ABA level upon inoculation. However, this up- and down-regulation can vary among different plants and different species and should be analyzed at the molecular level.

In addition to ABA, JA is an endogenous plant hormone that plays an essential role in regulating herbivory and pathogenesis. In the present study, we found that JA was significantly lower following LK11 inoculation compared to controls. This is also correlated with plant growth, as control plants showed lower growth in the presence of high JA, and LK11 showed high plant growth at lower levels of JA. Similar results were reported by Kang et al. (2012, 2014, 2015), where the authors found that inoculation of the plant growth-promoting bacteria Promicromonospora sp. SE188, Burkholderia cepacia SE4, Acinetobacter calcoaceticus SE370, and Serratia nematophila PEJ1011 increased the growth of horticulture crops plant (i.e. cucumber, pepper) by regulating the endogenous hormones GA, ABA, JA, and salicylic acid.

Conclusion

In conclusion, we showed that arid land plants can act as hosts for beneficial endophytes. Utilizing such plants and their traits may improve plant growth and development. In the present study, among five strains, LK11 showed the highest potential for improving soybean plant growth compared to other strains. Inoculation with this strain improved physiology and growth.

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