**Preussia** sp. BSL-10 producing nitric oxide, gibberellins, and indole acetic acid and improving rice plant growth

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**ABSTRACT**

*Preussia* sp. have been least known to improve plant growth and produce phytohormones. The current study investigated the production of nitric oxide (NO), indole-3-acetic acid (IAA), and gibberellins (GA₄, GA₇, GA₁₅, and GA₃₃) by a novel endophytic-fungal strain *Preussia* sp. BSL-10 using advanced chromatographic and spectroscopic techniques. Production of these phytohormones were validated by RT-PCR analysis, which indicated the expression of genes encoding tryptophan synthase (TRP), indole-3-acetamide hydrolase (IAMAH), tryptophan-2-monoxygenase (IAMAM), aldehyde dehydrogenase (ALD), GA₄₅ desaturase (DES), geranylgeranyldiphosphate synthase (GGS2), ent- desaturase oxidase (P450-4), GA₄₅₆ synthase (P450-1) and nitrite reductase (NIRK/NIRS), cytochrome P₄₅₀ (P450nor), nitrate reductase (NR), NOS-like (NOL), and nitric oxide reductase (QNOR/CNOR). In plant growth-promoting effects, the inoculation of *Preussia* sp. BSL-10 significantly increased the growth of dwarf mutant *Waito-C* and wild-type rice cultivars. In conclusion, utilizing new endophytic with the ability to produce NO, IAA, and gibberellins can be used to promote growth and yield of marginalized crops.

**Introduction**

Fungal endophytes live mutualistically in plant tissues without inducing any symptoms of disease (Schulz and Boyle 2005). After a long period of co-evolution, a mutually beneficial relationship has formed between endophytic fungi and their host plants. Host plants provide a habitat and access to the nutrients for endophytes, whereas the endophytes confer fitness and defense-related benefits to host plants (Khan et al. 2016b). The endophytic fungi induced growth-promoting benefits includes the increase in shoot and root biomass and resistance of host against abiotic stresses such as heat, drought, and salt and biotic stressors such as herbivores and pathogens (Redman et al. 2011). The crucial role of endophytic fungi in enhancing plant growth in a stressful environment has been demonstrated in *Sebacina vermifera*, *Piriformospora indica*, *Penicillium* spp., and *Colletotrichum* spp. (Redman et al. 2011; Khan et al. 2011; Khan et al. 2013; Khan et al. 2017).

The recognized benefits of endophytic fungi include their ability to produce biologically active metabolites and substances such as enzymes and secondary metabolites (Khan et al. 2015; Khan et al. 2016b). Endophytic fungi are known to produce biologically and physiologically active metabolites. These secondary metabolites range from various types of phenolic to hormone-like compounds such as auxins (including indole-3-acetic acid, IAA) and gibberellins (GAs) (Böhmke and Tudzynski 2009). GAs were first identified and isolated from a rice pathogenic fungus (*Fusarium fujikuroi*) as an active metabolite. GAs are synthesized from acetyl-coA through the mevalonic acid (MVA) pathway and then from isopentenyl diphosphate (IPP) (Böhmke et al. 2008).

Synthesis of IAA (indole-3-acetic acid) via the IAM (indole-3-acetamide) pathway has been reported in *Colletotrichum* sp. and *Fusarium* sp. (Robinson et al. 1998; Tsavkelova et al. 2012). In the IAM pathway, tryptophan is converted to IAM by tryptophan-2-monoxygenase (IAMAM), followed by further conversion of IAM to IAA by IAM hydrolase (IAMAH) (Tsavkelova et al. 2012). Very few classes of fungi have been known to produce nitric oxide (NO). NO, on the other hand, is a free radical gas that plays multiple important roles in cellular metabolism and stress signaling (Tsavkelova et al. 2012). In fungi such as *Aspergillus nidulans* and *Magnaporthe oryzae*, NO has been detected using a fluorescent indicator (Pengkit et al. 2016). However, compared to bacteria, the NO biosynthesis pathway in fungi is poorly defined (Tsavkelova et al. 2012).

Similar phytohormones have been recognized for their potent role in plant growth and yield. The biosynthesis pathways of these metabolites have been elucidated in some genera of Nectriaceae, but none have been reported for Sporormiaceae genera. We recently isolated a novel fungal strain, *Preussia* sp. BSL10, from a desert woodland tree, *Boswellia sacra*. *Preussia* sp. (Sporormiaceae) is distributed in soil, wood, and plant debris, and they are common across Mediterranean habitats (Arenal et al. 2007). Recently, some isolates of this genus have been found to produce chemical compounds (Mapperson et al. 2014); however, nothing is known about the production of phytohormones and their...
biosynthesis-related genes of these compounds in *Preussia* spp. Studies based on the draft genomes (Khan et al. 2016b) and an examination of growth-promoting functions (Khan et al. 2016a) have further increased our interest in investigating the potential of *Preussia* sp. BSL-10 to produce phytohormones, viz. GAs, IAA, and NO, and related biosynthesis genes. This is the first ever such investigation on any strain from *Preussia* genus.

**Materials and methods**

**Growth conditions and characterization of Preussia sp. BSL-10**

Previously, the endophytic fungus *Preussia* sp. BSL-10 (Gene Bank accession number KR231682), isolated from a frankincense tree (Khan et al., 2016a), was grown in Czapek growth medium (1% glucose, 1% peptone, 0.05% KCl, 0.05% MgSO<sub>4</sub> 7H<sub>2</sub>O, and 0.001% FeSO<sub>4</sub> 7H<sub>2</sub>O; 80 ppm streptomycin, pH 7.3 ± 0.2; 2 L; autoclaved for 15 min at 121°C) for 14 days. The culture collection is deposited at Landcare Research (Manaaki, Whenua, New Zealand; ICMP 21146; Khan et al., 2016b). The fungal culture was centrifuged at 10,000 × g and 4°C, and the supernatant was filtered through a sterilized 0.45-µm cellulose acetate filter for quantification of GAs, IAA, and NO, whereas the fungal cells were used for RT–PCR analysis.

**Extraction and quantification of phytohormones from pure culture of Preussia sp. BSL-10**

Extraction and quantification of GAs produced by *Preussia* sp. in its culture broth was carried out according to Lee protocol (Lee et al. 1998). Briefly, filtrate from a 14-day-old culture of the fungal isolate was supplemented with [2H₂]GA protocol (Lee et al. 1998). Briefly, filtrate from a 14-day-old culture broth was carried out according to Lee protocol (Lee et al. 1998). The fungal culture was centrifuged at (18000 × g) for 15 min at 4°C for 14 days. The culture collection is deposited at Landcare Research (Manaaki, Whenua, New Zealand; ICMP 21146; Khan et al., 2016b). The fungal culture was centrifuged at 10,000 × g and 4°C, and the supernatant was filtered through a sterilized 0.45-µm cellulose acetate filter for quantification of GAs, IAA, and NO, whereas the fungal cells were used for RT–PCR analysis.

**Plant growth-promoting potential with mutant and normal rice cultivars**

The plant growth-promoting potential role of *Preussia* sp. BSL-10 was examined in the GA mutant biosynthesis mutant Waito-C and GA normal biosynthesis pathway ‘Jin so mi’ rice cultivars. Before germination, the seeds were thoroughly sterilized with 2.5% sodium hypochlorite, followed by 75% ethanol for 30 s, and then rinsed with autoclaved double-distilled water 5 times. The sterilized seeds were held at 28°C for 4 days in an incubator to ensure complete and equally germinated seeds. The Waito-C seeds were further treated with uniconazol (20 ppm) to further suppress the GA biosynthesis pathway of the rice and help to reveal any growth-promoting effects of endophyte (Khan et al. 2011). The germinated seeds were transferred to sterilized pots filled with an autoclaved sand nutrient medium containing perlite (11%), cocopeat (68%), and zeolite (8%) with the following macronutrient composition: NO₃⁻, 0.205 mg g⁻¹; NH₄⁺, 0.09 mg g⁻¹; P₂O₅, 0.35 mg g⁻¹; and K₂O, 0.1 mg g⁻¹ (Punong Co. Ltd, Korea). Plants were incubated in a growth chamber (day/night cycle: 12 h at 20°C and 12 h at 18°C; relative humidity 60–70%; light intensity 1000 µmol m⁻² s⁻¹) from sodium lamps) for further growth (Shahzad, Khan, et al. 2017). At the two-leaf stage, 20 mL pure culture of *Preussia* sp. BSL-10 was applied to each plant, whereas control plants were treated with fungal free culture. Each treatment had 21 rice plants which were repeated 3 times. After 7 days of treatment, growth responses, including shoot length and root length (cm), plant fresh and dry weight (digital balance, AR2140, OHAS, NJ, USA), and chlorophyll content (SPAD-502, Konica Minolta, Japan), were recorded and compared with control plants.

**Statistical analysis**

In the current study, all phytohormones and NO data were collected from triplicate experiments. The collected data...
Results

**GA production and biosynthesis-related gene expression**

In the current study, the endophytic fungus *Preussia* sp. BSL-10 was grown in Czapek growth medium for 14 days, and the pure culture was used for GAs production. The results showed that *Preussia* sp. BSL-10 was found to produce GAs viz. (GA4 [0.27 ± 0.02 ng/mL], GA7 [0.4 ± 0.01 ng/mL], GA15 [1.35 ± 0.03 ng/mL], and GA53 [4.19 ± 0.09 ng/mL]) (Figure 1). In our analysis, we did not detect GA14, GA12, and GA3, the main GA products in *Gibberella fujikuroi* and *Penicillium* spp. This was validated by examining the expression of biosynthesis-related genes using RT–PCR. In the case of GA biosynthesis, we analyzed geranylgeranyl-diphosphate synthase (GGS2), GA4 desaturase (DES), ent-desaturase oxidase (P450-4), GA14 synthase (P450-1), GA20-oxidase (P450-2), expression, whereas *ALD* was less highly expressed (Figure 2).

Table 1. Primers used for expression of various transcripts related to phytohormonal production of *Preussia* sp BSL-10 using real-time RT–PCR.

| Function          | Primer | Gene name              | Sequence                  |
|-------------------|--------|------------------------|---------------------------|
| Nitric oxide (NO) | QNOR   | nitric oxide reductase  | F-GGC CAT CAG GGA TAC GA  |
|                   | CNOR   | nitric oxide reductase  | R-ACCAAAGATGCGACACCCACCA  |
|                   | NOL2   | NOS-like               | R-GAA TTC CTA GAG CAD CC  |
|                   | NOL1   | NOS-like               | R-GAA ACC CCA CAC GGC TGC |
|                   | GSP1   | cytochrome P450        | F-CTG CGA TGA TGC TCT ATT TAA AAA |
|                   | NGSP   | cytochrome P450        | R-CCA TCG TGA ACT GCA TTC CT |
|                   | NIRK   | nitrite reductase      | F-CCT TGT ACC AAG GGT TAG TGC |
| Indole acetic (IAA)| RF13   |                        | F-GCA AGA AA GG TAC AAA ACT |
|                   | ALD    | aldehyde dehydrogenase | F-GGA AGA TCT TGC AGC AGG TG |
|                   | TRP    | tryptophan synthase    | R-TGG ACT GTA GCA CCC TTC TT |
|                   | IAAM   | tryptophan-2-monoxygenase| F-CAGGGAATGTGCAATGAGT |
|                   | IAAH   | Indole-3-acetamide hydrolase | R-TGA GTGACACTGGCCAG |
| Gibberellins (GA) | P450-4 | ent-desaturase oxidase | F-CCAACTCCTGGAGATCCTTGG |
|                   | P450-3 | C13- oxidase           | R-TGTCACAGAGCTGAAAACA |
|                   | CPSD   | Copalyldiphosphate/ent-kaurene synthase | F-CCAACTCCTGGAGATCCTTGG |
|                   | GSS2   | Geranylgeranyl-diphosphate synthase | R-TGTCACAGAGCTGAAAACA |
|                   | P450-1 | GA14 synthase          | F-CCAACTCCTGGAGATCCTTGG |
|                   | DES    | GA4 desaturase         | R-TGTCACAGAGCTGAAAACA |

were subjected to DMRT using SAS (version 9.2, USA), and graphs were drawn in GraphPad Prism (version 6, USA).

**NO production and related genes in *Preussia* sp. BSL-10**

Using a Griess reagent system, we found that *Preussia* sp. BSL-10 also produces 1.87 ± 0.04 µM NO (Figure 1). The expression of biosynthesis-related genes also confirmed this. NO biosynthetic genes, viz., *P450nor* (GSP, NGSP), NOL (Real), QNOR, CNOR, and NIRK were highly expressed in *Preussia* sp. BSL-10 (Figure 2).

**Plant growth-promoting activity of *Preussia* sp. BSL-10**

To confirm the phytohormones production ability and possible beneficial effects of *Preussia* sp. BSL-10, we applied the pure culture to the dwarf GA mutant *Waito-C* and normal 'jin so mi' rice cultivars and compared with control. Any traces of phytohormones in the culture will be evidenced with the increase in shoot length of dwarf mutant *Waito-C*. The results confirmed the beneficial effect of *Preussia* sp. BSL-10 on both GA biosynthesis mutant *Waito-C* and...
GA biosynthesis normal ‘Jin so mi’ rice cultivars (Figure 3, Table 2). Preussia sp. BSL-10 inoculation into GA biosynthesis mutant Waito-C cultivars significantly increased shoot length (88.15%), root length (179.37%), seedling fresh weight (116.6%), seedling dry weight (36.76%) and chlorophyll contents (215.79%), as compared to fungal free non-inoculated plants (Figure 3, Table 2). Results of Preussia sp. BSL-10 inoculation in the normal ‘Jin so mi’ cultivar were similar, showing a similar trend of significantly increased shoot length (49.96%), root length (119%), seedling fresh weight (60.37%), seedling dry weight (70.09%), and chlorophyll contents (96.16%), as compared to non-inoculated control plants (Figure 3 and Table 2).

Discussion

GAs production has long been recognized as a feature of the fungal microsphere, whereas such production by endophytes has only recently been elucidated (Khan et al. 2015). This feature has been well accepted in recent studies that GAs producing fungal endophytes are more beneficial to host than non-producers. GA4 and GA7 are physiologically active GAs known to significantly increase plant growth and development (Bömke and Tudzynski 2009; Khan et al. 2015). This is in conformity with the previous reports as well. Studies such as by Waqas et al. (2012) reported that the fungal endophyte Penicillium sp. produce GA1 (5.33 ng mL$^{-1}$), GA3 (3.42 ng mL$^{-1}$). In addition, endophyte from Phoma glomerata was found to produce active GA1 (8.720 ng mL$^{-1}$), GA3 (2.42 ng mL$^{-1}$), and GA4 (0.220 ng mL$^{-1}$) as revealed by Hamayun et al. (2010). Furthermore, Penicillium fumiculosum, Aspergillus fumigatus sp. LH02 (Khan et al. 2011), P. spadiceum AGH786 (Hamayun et al. 2017), and Aspergillus clavatus Y2H0002 (You et al. 2015) have been recently revealed to produce various kinds of gibberellins in their growth cultures.

The current study suggests the existence of gibberellin biosynthesis where the end-product is GA4 not GA3 in Preussia sp. BSL-10. This finding is in contrary to the observation of Bömke et al. (2008) who showed that GA3 in Gibberella fujikuroi is the last step in biosynthesis. GA biosynthesis could occur as follows: ent-kaurenoic acid $\xrightarrow{}$ GA12 $\xrightarrow{}$ GA53 $\xrightarrow{}$ GA15 $\xrightarrow{}$ GA7 $\xrightarrow{}$ GA3. Bömke et al. (2008) suggested that GAs in fungi are synthesized from acetyl-CoA via the MVA pathway and are then converted to farnesyl diphosphate, which serves as an intermediate to form geranylgeranyl diphosphate (GGDP), ent-copalyl diphosphate (CDP), ent-kaurene, and ent-kaurenoic acid, leading to the production of GA12-aldehyde. GA12-aldehyde is 3b-hydroxylated to GA14-aldehyde and then oxidized to form GA14. The subsequent conversion of GA14 leads to desaturation of GA4, which lead to the formation of GA7 and then GA3. These results are the first to describe this production in Preussia sp. BSL-10 and Sporormiaceae. A similar GA gene cluster was also reported in Phaeosphaeria sp., G. fujikuroi, Fusarium proliferatum, and Penicillium sp.
proliferatum, Rhizoctonia sp., Tricholoma vaccinum, and Colletotrichum gloeosporioides have recognized IAA biosynthesis pathways (Tsavkelova et al. 2012; Luo et al. 2016).

The NO biosynthesis pathway comprises copper-containing nitrite reductase (NIRK, NIRS), a cytochrome P450 (P450nor), nitrate reductase (NR), NOS-like (NOL), and nitric oxide reductase (QNOR, CNOR) genes to reduce nitrite to nitrous oxide (N₂O) (Samalova et al. 2013). Results of previous studies support those found here, suggesting the existence of NO-related biosynthesis genes in fungi such as Magnaporthe oryzae (Samalova et al. 2013), Cylindrocarpon tonkinense, and Fusarium solani (Shoun et al. 2012). However, most of these fungi have been shown to cause disease in plants, whereas Preussia sp. BSL-10 shows a plant growth-promotion ability (Khan et al. 2016b). Endophytes with this potential may be an essential resource for obtaining exogenous nitrates.

Fungal endophytes are renowned plant symbionts (Khan et al. 2015; Tudzynski et al. 2016). The growth-promoting ability has often considered due to the potential of these endophytes producing various biologically active metabolites and enzymes (Yuan et al. 2010). Among these, GAs and Auxin have been reported to play vital roles in plant growth (Hamayun et al. 2010; Yuan et al. 2010). Although secondary metabolite production and the plant growth-promoting ability of Preussia spp. is very limited (Khan et al. 2016b). Furthermore, Preussia species are very unique, for instance, very few species have been reported as endophytes (Khan et al. 2016b). Previously Preussia sp. BSL-10 was reported as potential endophyte to produce glucosidases, phosphatases, and indole acetic acid that significantly promoted plant growth and development (Khan et al. 2016b). In the current study, we analyzed this Preussia sp. BSL-10 for the first time to produce NO, and gibberellins that enhance plant growth. The results are supported by the work of other researchers, who have reported on bioactive metabolite production from endophytic fungi that promotes plant growth (Castillo et al. 2015; Khan et al. 2015; Tudzynski et al. 2016).

### Conclusion

Phytohormones produced by fungal endophytes can play an important role in the growth and development of host plants. The current study concluded that isolation of novel Preussia sp. BSL-10 from frankincense tree can be an ideal potential for broader application, as this strain not only produce various GAs, IAA, and NO, but also possesses genes that encode
enzymes for this purpose. This is the first ever report on phytohormones viz. GAs, IAA, and NO production ability and their biosynthesis-related genes of novel fungal strain Preussia sp. BSL-10. These are ideal traits for a symbiotic microorganism, which could be used for large-scale phytohormone production, as well as field experiments on economically important crop plants. Moreover, both GA biosynthesis mutant and GA biosynthesis normal rice cultivars inoculated with Preussia sp. BSL-10 showed significantly increased shoot and root lengths, seedling fresh and dry weights, and chlorophyll contents, suggesting its benefits for the growth of crops in marginal environments.

Disclosure statement
No potential conflict of interest was reported by the authors.

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