Introduction

In Chinese medicine, roots of *Astragalus mongholicus* are authorized as Astragali Radix (ie Huangqi in Chinese) and have been used as tonic and diuretic for thousands of years. At present, it is widely used in clinical practice for treating nephritis, diabetes and cancer, which is contributed by the host (ie commensal endophytes) or execute beneficial effects to the plant, such as protection against invading pathogens and herbivores, and plant growth-promotion (Pańka et al. 2013; Santhanam et al. 2015; Li et al. 2016). The mechanisms by which beneficial microbes support plant growth and health include increasing nutrient availability, improving soil structure, inducing plant defense mechanisms, producing antibiotics, outcompeting pathogens and providing growth-stimulating substances or enzymes. Their promotion on bioactive compound biosynthesis and accumulation has been explored in a few medical plants such as *Salvia miltiorrhiza*, *Atractylodes lancea* and *Artemisia annua* (Li et al. 2012; Ming et al. 2013; Yuan et al. 2016; Zhou et al. 2016). For *A. mongholicus* plants in Hunyuan, our previous work has revealed that their root microbiota was more complex and unique when compared to the specimens of the other production regions (Sun et al. 2017a). However, their potentials for improving the quality and production of the herb are underestimated.

On the other hand, some latent pathogens might inhabit inside the plant tissue and constitute the third group of endophytic consortia (Scortichini and Loreti 2007). Generally, they can have neutral or detrimental effects to the host under normal growth conditions, whereas they can be beneficial under more extreme conditions. This means that some members of endophytic consortia have dual roles as...
potential pathogens and as beneficial endophytes. The balance between these two states depends not only on the host genotype, but on locally occurring abiotic stress factors (Bacon et al. 2008). Although it is well accepted that increasing plant stress tolerance is associated with host antioxidative defense system (Devi et al. 2017; Hashem et al. 2018), strain-dependent regulation has also been indicated (Tamosiune et al. 2018). Hence, it is crucial to explore benefits of endophytic members on their hosts grown under stress conditions and to understand underlying antioxidative defense mechanism.

The species *Pseudomonas poae* was first reported on a strain isolated from the phyllosphere of *Poa* spp. (Behrendt et al. 2003). Endophytic *P. poae* JA01 show potential activities as biocontrol agents against phytopathogenic fungi in Ginseng (Cho et al. 2007). Its antagonistic effect on soilborne pathogen *Rhizoctonia solani* was then reported based on the work of *P. poae* strain RE*′*1-1-14 that was isolated from the internal part of sugar beet root (Zachow et al. 2008). Enhanced phosphate solubilization was detected when the strain was cultured at lower temperature (Vyas et al. 2009). Its plant growth promotion has been reported in sugar beet and lettuce plants (Zachow et al. 2010). A novel lipopeptide poeamide has been identified and is responsible for pathogen suppression and root colonization (Zachow et al. 2015). In addition, the species can be used as promising candidates for bioaugmentation (Rinland and Gomez 2015) and a bacterial consortium including *P. poae* could degrade cooking oil in wastewater (Nzila et al. 2017). However, no reports are available on the performance of *P. poae* under other stress conditions generated by environmental factors in medical plants.

The goal of the present work was to explore potentials of endophytic *P. poae* strain S61 on quality formation of *A. mongholicus* plant host. Firstly, in intro production of indoleacetic acid (IAA) was investigated in liquid medium containing variable levels of NaCl and PEG6000 or with different pH value. Based on the results, its beneficial effects on *A. mongholicus* plant growth and bioactive compound accumulation were explored as well as underlying antioxidative mechanism by pot experiment under drought stress. In our view, this was the first report on its limited beneficial effects in medical plants, which will be useful for understanding the quality formation of medical plants resulted from the interaction between host plant and endophytic bacteria.

**Materials and methods**

**Isolation and characterization of *P. poae* strain S61**

The strain S61 was isolated from the internal part of *A. mongholicus* plant roots in Hunyuan, Shanxi by the method of Sun et al. (2017). It contains ACC deaminase, as indicated by complete genome sequencing of *P. poae* RE*′*1-1-14 (Müller et al. 2013). After successively cultured in Luria–Bertani (LB) solid medium for five times, its colony forming unit appeared in light yellow, suggesting that it can stably produce pigment. In addition, the strain can synthesize indoleacetic acid (IAA) when cultured in LB liquid medium containing 1% tryptophan (Trp). The strain was maintained at −80°C in LB liquid medium supplemented with 20% (v/v) glycerol. At present, the strain has been stored at China General Microbiological Culture Collection Center (CGMCC No. 14946) (Beijing, China).

**Stress tolerance and the production of IAA**

Stress factors include salinity, desiccation and acidity. For salinity trial, 1%, 3%, 5% and 7% NaCl were respectively added into the LB liquid medium before inoculation. The normal medium was used as control. For acidity trial, the LB medium was adjusted to pH 5.0, 7.0 and 9.0 using HCl/NaOH. The tolerance of the strain to desiccation was examined in LB medium amended with 0%, 5%, 10%, 15% and 20% PEG6000. In addition, the medium was supplemented with 1% Trp and triplicates were applied for each trial. The trials were performed in 15 × 150 mm tubes containing 2 ml liquid medium and 1% initial inoculum was applied. The tubes were incubated at 28°C and shaked at 180 rpm until early log–arithmetic phase of the normal control. The absorbance at the wavelength 600 nm was measured using a spectrophotometer (Effendorf, Germany) to evaluate the strain growth performance. Afterwards, dynamic growth and production of IAA were quantified under 7% NaCl, 20% PEG6000 and pH 5.0. The quantification of IAA was performed by the spectrophotometric method described by Beffa et al. (1990).

**Inoculum preparation and seed treatment**

To prepare endophytic inoculant, after grown overnight the liquid culture of the strain S61 was centrifuged at 12,000 rpm for 10 min, then the pellets were washed with 300 mM MgCl2 for two times, finally resuspended in 300 mM MgCl2 and adjusted to an OD600 of 1.0 for immediately use.

Seeds of *A. mongholicus* were presented by Shanxi Beiyue God Qi (Hunyuan, Shanxi). In the lab, the seeds were firstly surface sterilized as follows: washed in 75% ethanol for 1 min with shaking and rinsed with distilled and autoclaved water three times; then sank in 5% sodium hypochlorite for 20 min, followed by rinsing with distilled and autoclaved water 5–6 times. The last wash was plated onto the LB solid medium and there should be no growth of microbes after cultured at 28°C for 72 h. The sterilized seeds were then incubated at 50°C in a water bath (HHS Type, Tianjinshi Huabei, Tianjin, China) for 10 min. After cooling down to room temperature, the seeds were incubated with *P. poae* strain S61 inoculant in a ratio of 1/5 (w/v) for 90 min.

Incubated seeds with the strain S61 were then germinated on wet sterile paper towels at 23°C under a day/night cycle: 16 h/8 h until the cotyledons were completely expanded. And light intensity ranged from 2000 to 3000 lux. Then uniformly sized seedlings were transferred into the pots containing sterilized sandy soil and vermiculite (v/v: 1/1) in a plant growth chamber (MLR-351, SANYO, Moriguchi, Japan) under the following conditions: 16 h, 23°C (day)/8 h, 16°C (night), 2000–5000 lux for 8 weeks. The sandy soil was collected from Hunyuan and irradiated at a dose of 10 KGY to kill microbes while the vermiculite was sterilized at 121°C for 20 min to exclude the effect of soil microbes on the seedling to exclude the interference of soil microbes. For each pot, 3–4 seedlings were planted and a routine watering was performed with sterile water once per week. The seedlings that were not incubated with the strain S61 were used as normal control and these treated with 300 mM MgCl2 alone were used as vehicle control.
Drought stress and collection of plant materials

After grown in plant growth chamber for 8 weeks, most seedlings had 5~6 true leaves. Again, uniformly sized seedlings were selected as raw materials for drought stress trial. For each trial group, the seedlings were randomly divided into two subgroups that were routinely watered with sterilized water and 20% PEG6000, respectively, for three weeks. The growth conditions were the same as described above. At the end, the aerial height, aboveground and belowground biomasses were first recorded. Then the 3rd to 5th leaves and root samples were individually collected, immediately frozen in liquid nitrogen and stored at −80 °C for further analysis.

Chemical analysis

For quantification of astragaloside IV, ononin and calycosin-7-glucoside, 0.15 g of individual root specimen was firstly ground into a fine powder with liquid nitrogen then extracted with 30 volume of 70% ethanol (chromatographic grade, v/w) containing 4% ammonium hydroxide in an ultrasonic bath for 60 min. Subsequently, root extract was concentrated by MTN-2800W Pressure Blowing Concentrator (Automatic Science, Tianjing, China) and dissolved in methanol of chromatographic grade after being centrifuged at 8000 g for 5 min to remove residue. Finally, the solution was adjusted to 2 mL. Extract of 5 μL was injected into a Agilent-1290 UHPLC (Agilent, America) coupled with AB SCIEX 3200 QTRAP-MS (ABI, America) in multi-reaction monitoring mode, m/z: 786.1 ([M + H]+) → 473.4 ([M–C$_5$H$_9$O$_4$–H$_2$O–C$_6$H$_10$O$_5$–H]+) for quantification of astragaloside IV. Chromatography was performed at 0.2 mL/min (flow rate) and 40°C (column temperature) and ZORBAX Eclipse Plus C18 (2.1 × 50 mm, 1.8 μm) column was used. Gradient elution was carried out with 0.1% formic acid (A) – acetonitrile (B) as mobile phase and programmed condition was as follows, 0~3 min, 85%→40% A; 3~4 min, 40%→20% A; 4~5 min, 20%→40% A; 5~7 min, 40%→85% A; 7~9 min, 85% A. Corresponding standard was brought from Shanghai Yongheng (Shanghai, China).

For quantification of ononin and calycosin-7-glucoside, 5 μL of extracts was injected into a RIGOL L-3000 Autosampling HPLC System (Puyuanjingdian, Beijing, China) and the separation was performed by the gradient elution program described in Pharmacopoeia of the People’s Republic of China (Chinese Pharmacopoeia Commission 2015). And the chemical standards were bought from Jiangxi Bencao Tiangong (Nanchang, China). For leaf chlorophylls, the quantification was performed by a spectrophotometric method of Sun et al. (2017). In order to determine malondialdehyde (MDA) content, TBA method was applied using a commercial assay kit (Cat. No, A003-1) that was bought from Nanjing Jiancheng (Nanjing, China).

Data analysis

For each experiment, the results were presented as the mean ± standard deviation (SD) of data from at least triplicates. Statistical evaluation was performed using one-way ANOVA, followed by Tukey’s multiple-comparison test. All the statistical analyses were performed using the software GraphPad Prism 7.01 (California, USA), a P-value of <.05 was considered as significant difference.

Results

Stress tolerance and production of indoleacetic acid (IAA) of P. Poae strain S61

Drought and salt stress are the two major kind of abiotic stress throughout the world. In addition, soil acidity is an extended edaphic condition in cultivable lands over the entire globe, and is also accepted as a major limited factor for legume productivity (von Uexküll and Mutert 1995) while a primary analysis showed that soil pH of the production area Hunyuan of Astragal Radix was ranged from 8.05~8.26 (supplemental Table S1). Thus, the growth performance P. Poae strain S61 was firstly investigated under different stress levels of salinity, desiccation and acidity and presented in Figure 1. Specifically, the strain was able to grow in the liquid medium ranged from pH 5.0–9.0, but the biomass at pH 5.0 was significantly reduced relative to the biomass at the other pH values examined (Figure 1(a)). As indicated in Figure 1(b), the strain was able to grow in the medium containing up to 7% NaCl and the adding of 2% NaCl exhibited improved growth performance. The influence of PEG6000 was presented in Figure 1(c), demonstrating that the strain S61 could tolerate the desiccation regime of 20% PEG6000 and adding less than 5% PEG6000 into the culture medium had no significant inhibitory effect on the strain growth.

As described above, the stress conditions including pH 5.0, 7% NaCl and 20% PEG6000 were nearly to the limitations that the strain was able to survive. The growth performance and IAA production of the strain were dynamically tracked under these extreme conditions and presented in Figure 2. When cultured in the medium with pH value 5.0, the strain exhibited a similar growth pattern to the control, suggesting that the medium pH slightly inhibited the strain growth.

Figure 1. The growth performance of P. Poae strain S61 under stress conditions. Absorbance at the wavelength 600 nm of the culture was respectively obtained by adjusting the medium acidity to variable values (a) and by adding different concentrations of NaCl (b) and PEG6000 (c) to the medium.
Growth-promoting effect of P. poae strain S61 on A. mongolicus seedlings under drought stress

Drought is one of the most significant abiotic stresses that affect plant growth and secondary metabolism. For medical plants, they need to cope with adverse environmental and edaphic conditions exerted by their habitats, from which their growth, development and defense suffer. As the most natural inhabitants of diverse environments, endophytic consortia play key roles in amelioration of host abiotic stresses (Dupont et al. 2015). As shown in Figure 2, the adding of 20% PEG6000 severely inhibited the strain growth but induced relatively higher IAA production, suggesting that P. poae S61 was more robust and endurable to drought stress than salt stress. Thus, plant growth promotion of the strain was firstly explored in A. mongolicus seedlings by pouring 20% PEG6000. The result was listed in Figure 3, showing that the aboveground biomass (Figure 3(b)) was significantly decreased upon individual treatment of PEG6000 and the combination with the strain inoculation when compared with P. poae strain S61 inoculation alone. Although no significant difference in the aerial height or shoot biomass was observed between the trials and normal control, significant reduction in the combined trial of 20% PEG6000 and the strain inoculation was observed relative to the inoculation alone (Figure 3(a,b)). On the other hand, the combination of 20% PEG6000 with the inoculation significantly increased the root biomass (Figure 3(c)) and root shoot ratio (Figure 3(d)), especially the latter index when compared to the treatment of 20% PEG6000 and the strain inoculation alone as well as the normal control. The result also indicated that the inoculation alone had the lowest root shoot ratio. Altogether, plant growth promotion of endophytic P. poae S61 was executed only when the seedlings grew under drought stress and focused on the belowground part.

As sessile organisms, plants have to tradeoff limited metabolic resources to grow or defend. Under stressed conditions, investment into defense leads to reduced growth (Wasternack 2017). As chlorophylls are essential components of photosynthetic system and derived from diterpenoids, impact on the seedling leaf chlorophylls was investigated and presented in Figure 4. Relative to the normal and vehicle controls, the combination of PEG6000 with P. poae S61 inoculation significantly decreased chlorophyll a content (Figure 4(a)). Meanwhile, individual application of PEG6000 and P. poae S61 inoculation kept chlorophyll a content at the same scale to the normal and vehicle controls. The figure also denoted that the combination of MgCl2 with 20% PEG6000 obviously increased chlorophyll a when compared to the normal control. A similar influence on chlorophyll b was observed (Figure 4(b)). Taken together, the inoculation of P. poae S61 significantly reduced the contents of chlorophyll a and b in A. mongolicus seedlings under drought stress, suggesting that the strain has no benefits on the biosynthesis of essential chlorophylls in challenging environment.

Enhanced accumulations of bioactive compounds in the seedling roots obtained by the combination application of PEG6000 with P. poae S61 inoculation

In Chinese pharmacopoeia, calycosin-7-O-glucoside and astragaloside IV are authorized as isolavone and saponin indicators for quality evaluation of Astragali Radix, respectively. They are also major bioactive compounds contained in the herb (Zhang et al. 2014; Ju et al. 2018). In addition, ononin shares the same precursor formononetin with calycosin-7-glucoside and is another bioactive isolavone widely distributed in legumes (Pan et al. 2007; Luo et al. 2018). Thus, the contents of ononin, calycosin-7-O-glucoside and astragaloside IV were determined in the seedling roots upon individual treatment of P. poae S61 inoculation and PEG6000 and their combination (Figure 5). It demonstrated that the contents of calycosin-7-glucoside and ononin were significantly decreased upon individual treatment of NaCl and PEG6000. The adding of which consistently had higher IAA levels than the addition of 7% NaCl. The figure also indicated that the IAA level reached the peak at the incubation time point 17 h regardless of the stress factor, coinciding with the maximum biomass at the time point. Since the production of IAA is very important of the stress factor, coinciding with the maximum biomass at the incubation time point 17 h, an improved growth performance was observed when the strain was cultured in the medium containing 7% NaCl. Dynamic production of IAA under extreme stresses was presented in Figure 2(b). It showed that the IAA production performed similar patterns to corresponding biomass that was obtained under the same stressed conditions excluding 20% PEG6000, the adding of which consistently had higher IAA levels than the addition of 7% NaCl. The strain S61 was more robust upon treatment of 7% NaCl. The result was listed in Figure 3, showing that the aboveground biomass (Figure 3(b)) was significantly decreased upon individual treatment of 20% PEG6000 and the strain inoculation as well as the normal control. The result also indicated that the inoculation alone had the lowest shoot biomass. Altogether, plant growth promotion of endophytic P. poae S61 was executed only when the seedlings grew under drought stress and focused on the belowground part.

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increased by the combination trail of 20% PEG6000 with P. poae S61 inoculation relative to the normal control. Meanwhile, the individual treatment of PEG6000 or the strain inoculation exhibited no obvious promoting effect on root accumulation of calycosin-7-O-glucoside. Conversely, P. poae strain S61 inoculation alone significantly decreased calycosin-7-O-glucoside content, suggesting that the promoting effect of P. poae S61 was executed only when the seedlings grew under drought stress condition. For astragaloside IV, the combined treatment of PEG6000 with the strain S61 inoculation resulted in a much lower concentration when compared with the other trials and controls, indicating that the promotion of P. poae strain S61 was not associated with saponin compounds under drought stress. On the contrary, the vehicle control roots contained significantly higher astragaloside IV content than the normal control, suggesting that the treatment of MgCl2 was beneficial to astragaloside IV accumulation in the seedling roots under a routine watering management. Altogether, beneficial effect of P. poae S61 was mainly concentrated on root accumulation of isoflavone compounds in A. mongolicus seedlings under drought-stressed condition.

Figure 3. Effects of P. poae S61 inoculation, PEG6000 and their combination on A. mongolicus seedling growth. Note: The seedling growth performance was evaluated by follow parameters: the aerial height (a), aboveground biomass (b), belowground biomass (c) and the root shoot ratio (d). NC, MgCl2 and S61 represented the normal control, vehicle controls and P. poae strain S61 inoculation alone, respectively. The groups of 20%PEG6000, 20%PEG6000&MgCl2 and 20% PEG6000&S61 represented individual application of PEG6000 and combinations of PEG6000 with MgCl2 and S61, respectively. The different letters above the bar indicate significant differences between the groups.

Figure 4. Effects of P. poae S61 inoculation, PEG6000 and their combination on chlorophyll a (a) and b (b) contents in A. mongolicus seedling leaves. Details of the groups and the letters above the bars were in line with Figure 3.
Effects of P. poae S61 inoculation, PEG6000 and their combination on malondialdehyde (MDA) content

Under drought stress conditions, plants produce excessive reaction oxygen species (ROS), thus result in an imbalance between ROS productivity and the ability to detoxify the reactive intermediates or to repair the resulting damage (Storz and Imalay 1999). And the damage caused by ROS can be evaluated by the lipid peroxidation of cellular membranes, using MDA as a chemical index of the process (Chugh et al. 2011). In order to understand underlying mechanism associated, MDA content in the seedling leaves and roots was determined and presented in Figure 6. Relative to the normal control, individual application of 20% PEG6000 slightly enhanced the leaf MDA level but had no significant effect on root MDA. On the contrary, the combination of 20% PEG6000 with the strain inoculation and the inoculation alone resulted in significantly higher MDA level in the leaves (Figure 6(a)) and significantly decreased MDA concentration in the roots (Figure 6(b)). Meanwhile, the seedling roots from a combined trial of 20%PEG6000 with MgCl2 contained much lower MDA content. The result also demonstrated that the combination of 20% PEG6000 with the strain inoculation kept root MDA level at a moderate scale, which was higher than the combined application of 20% PEG6000 with MgCl2. Relatively, P. poae inoculation increased the leaf MDA content but decreased the root MDA to a moderate level, which was regardless of the drought stress, suggesting that the endophytic strain S61 might protect the medicinal part from the lipid peroxidation of cellular membranes in this herbal plant.

Discussion

It is well known that plants accumulate higher contents of secondary metabolites under drought stress. However, higher concentrations of secondary metabolites do not equate with their enhanced biosynthesis and accumulation in some cases. When drought-stressed plants exhibit reduced growth rate, they usually have lower biomass than the well-watered counterparts. In case of a similar biosynthetic rate of secondary metabolites, the concentrations of secondary metabolites will be enhanced due to lower biomass in drought-stressed plants (Paulsen and Selmar 2016). Hence, impact on the biomass and secondary metabolite content should be considered together in drought-stressed plants. In the current study, individual application of 20% PEG6000 and P. poae S61 incubation exerted no beneficial effect on the belowground biomass, calycosin-7-O-glucoside or ononin accumulation in the root tissue but their combination worked. The promoting effect was further confirmed by significant increase in the amounts of calycosin-7-glucoside and ononin in the seedling roots (see supplemental Figure S1), demonstrating that endophytic bacterium P. Poae S61 promoted their accumulations in the roots only when the seedlings grew under drought-stressed condition. In addition, our work showed that all the trials had no promoting effect on astragaloside IV accumulation in the seedling roots excluding the vehicle control (ie MgCl2). After 10 days of UV-B treatment, calycosin-7-O-glucoside accumulation was significantly enhanced in A. mongholicus plant roots (Liu et al. 2018). In addition, low temperature stress could induce calycosin-7-O-glucoside accumulation in different tissues of...
A. mongholicus seedlings (Pan et al. 2007); ononin accumulation in the root tissue was improved in A. mongholicus plants under moderate salt stress (Liu et al. 2016). Thus, our work provided new evidence that endophytic bacteria residing in A. mongholicus roots might play key roles in A. mongholicus plant growth and root accumulation of bioactive isoflavones, especially under drought stress.

In A. lancea, application of endophytic bacterium P. fluorescens increased oxygenous sesquiterpenoid content and diversity by triggering ROSs but kept the host MDA at the same level to the control, which was verified by the application of hydrogen peroxide and singlet oxygen (Zhou et al. 2016). Under mild drought treatment (10% PEG6000), fungal incubation of endophytic Acremonium strictum increased leaf MDA content of A. lancea plantlets to a moderate level, coinciding with obviously increased root shoot ratio and root fresh weigh, while no incubation contained much higher MDA content (Yang et al. 2014). Armada et al. (2016) draw a similar conclusion in Lavandula dentata by dual inoculation of AMF and Bacillus thuringiensis. In the current study, the combined trial of PEG6000 with P. poae S61 inoculation kept A. mongholicus seedling root MDA at a moderate scale but significantly enhanced leaf MDA level, demonstrating that the strain was able to alleviate root oxidative stress to some extent. Meanwhile, P. poae S61 inoculation enhanced A. mongholicus seedling root biomass and root shoot ratio under drought stress conditions. Taken improved accumulations of calycosin-7-O-glucoside and ononin into accounts in the roots, it was assumed that the promoting effect of endophytic P. poae S61 should be focused on the medicinal part of A. mongholicus by triggering shoot oxidative stress under drought-stressed conditions. And increased lipid peroxidation in the seedling leaves should be involved in the process. Further investigation should be done to understand the strain’s beneficial effects assigned to the host plant growth and accumulation of bioactive isoflavones as well as underlying mechanism.

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References
Armada E, Probanza A, Roldán A, Axcón R. 2016. Native plant growth promoting bacteria Bacillus thuringiensis and mixed or individual mycorrhizal species improved drought tolerance and oxidative metabolism in Lavandula dentata plants. J Plant Physiol. 192:1–12.

Auyeung KK, Han QB, Ko JK. 2016. Astragalus membranaceus: a review of its protection against inflammation and gastrointestinal cancers. Am J Chin Med. 44:1–22.

Bacon CW, Glenn AE, Yates IE. 2008. Fusarium verticillioides: managing the endophytic association with maize for reduced fumonisins accumulation. Toxin Rev. 27:411–446.

Beffa M, Martin HV, Pilet PE. 1990. In vitro oxidation of indoleacetic acid by soluble auxin-oxidases and peroxidases from maize roots. Plant Physiol. 94:485–491.

Behrendt U, Ulrich A, Schumann P. 2003. Fluorescent pseudomonads associated with the phyllosphere of grasses: Pseudomonas trivialis sp. nov. Pseudomonas poae sp. nov. and Pseudomonas ctenogelas sp. nov. Int J Syst Evol Microbiol. 53:1461–1469.

Bulgarelli D, Schlaepf K, Spaepen S, van Themaat EVL, Schulze-Lefert P. 2013. Structure and functions of the bacterial microbiota of plants. Annu Rev Plant Biol. 64:807–838.

Chinese Pharmacopoeia Commission. 2015. The Pharmacopoeia of the People’s Republic of China. Beijing: China Medical Science and Technology Press; p. 302–303.

Cho KM, Hong SY, Lee SM, Kim YH, Kahng GG, Lim YP, Kim H, Yun HD. 2007. Endophytic bacterial communities in ginseng and their antifungal activity against pathogens. Microb Ecol. 54:341–351.

Chugh V, Kaur N, Gupta AK. 2011. Evaluation of oxidative stress tolerance in maize (Zea mays L.) seedlings in response to drought. Indian J Biochem Biophys. 48:47–53.

Devi KA, Pandey G, Rawat AKS, Sharma GD, Pandey P. 2017. The endophytic symbiont Pseudomonas aeruginosa stimulates the antioxidant activity and growth of Achyranthes aspera L. Front Microbiol. 8:1897.

Dupont P, Eaton CJ, Wargent JJ, Fechtner S, Solomon P, Schmid J, Day RC, Scott B, Cox MP. 2015. Fungal endophyte infection of ryegrass reprograms host metabolism and alters development. New Phytol. 208:1227–1240.

Hashem A, Alqarawi AA, Radakrishnan R, Al-Arjani AF, Aldehaish HA, Egamberdieva D, Allah EFA. 2018. Arbuscular mycorrhizal fungi regulate the oxidative system, hormones and ionic equilibrium to trigger salt stress tolerance in Cucumis sativus L. Saudi J Biol Sci. 25:1102–1114.
Ju Y, Su Y, Chen Q, Ma K, Ji T, Wang Z, Li W, Li W. 2018. Protective effects of astragaloside IV on endoplasmic reticulum stress-induced renal tubular epithelial cells apoptosis in type 2 diabetic nephropathy rats. Biomed Pharmacother. 109:84–92.

Li J, Zhao GZ, Varma A, Qin S, Xiong Z, Huang HY, Zhu WY, Zhao LX, Xu LH, Zhang S, Li WJ. 2012. An endophytic pseudonocarcidiaspecies induces the production of artemisinin in *Artemisia annua*. PLoS ONE. 7:e51410.

Li L, Zheng S, Brinckman JA, Fu J, Zeng R, Huang L, Chen SC. 2017. Chemical and genetic diversity of *Astragalus mongholicus* grown in different eco-climatic regions. PLoS ONE. 12:e0184791.

Li X, Geng X, Xie R, Fu L, Jiang J, Gao L, Sun J. 2016. The endophytic bacteria isolated from elephant grass (*Pennisetum purpureum Schumach*) promote plant growth and enhance salt tolerance of Hybrid Pennisetum. Biotechnol Biofuels. 9:190.

Liu Y, Liu J, Wang Y, Abozeid A, Tian DM, Zhang XN, Tang ZH. 2018. Simultaneous determination of six active metabolites in *Astragalus mongholicus* (Fisch.) Bge. under salt stress by ultra-pressure liquid chromatography with tandem mass spectrometry. Springerplus. 5:927.

Luo LY, Fan MX, Zhao HY, Li MX, Wu X, Gao WY. 2018. Characterization of root-associated bacteria from onion waste produced in South Buenos Aires province, Argentina. World J Microbiol Biotechnol. 34:497–507.

Müller H, Zachow C, Alavi M, Tilcher R, Krempl PM, Thallinger GG, Nzila A, Thukair A, Sankara S, Razzak SA. 2017. Characterization of *Pseudomonas* sp. isolated from rice (Oryza sativa L.) grown in the *South Buenos Aires* province, Argentina. World J Microbiol Biotechnol. 31:487–497.

Santhanan R, Luu VT, Weinhold A, Goldberg J, Oh Y, Baldwin Ian T. 2015. Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. Proc Natl Acad Sci USA. 112:E5013–E5020.

Scortichini M, Loretì S. 2007. Occurrence of an endophytic, potentially pathogenic strain of *Pseudomonas syringae* in symptomless wild trees of *Corylus avellana L.* J Plant Pathol. 89:431–434.

Storz G, Imaly JA. 1999. Oxidative stress. Curr Opin Microbiol. 2:188–194.

Sun HF, Kang BL, Chai Z, Sun HH, Hu DZ, Gao JP, Feng QJ, Zhang CF, Cao QF, Guo LP. 2017. Characterization of root-associated micro-biota in medicinal plants *Astragalus membranaceus* and *Astragalus mongholicus*. Ann Microbiol. 67:587–599.

Sun HF, Kang BL, Kang LP, Guo LP, Sun HH, Gao JP. 2017. Involvement of C6-volatiles in quality formation of herbal medicine: a case study in *Astragalus membranaceus var. mongholicus*. J Appl Bot Food Qual. 90:214–223.

Tamošiūnė I, Staniūnas G, Haimi P, Stanys V, Rugienius R, Banulis D. 2018. Endophytic *Bacillus* and *Pseudomonas* spp. modulate apple shoot growth, cellular redox balance, and protein expression under in vitro conditions. Front Plant Sci. 9:889.

von Uexküll HR, Mutert E. 1995. Global extent, development and economic impact of acid soils. Plant Soil. 171:1–15.

Vyas P, Rahi P, Gulati A. 2009. Stress tolerance and genetic variability of phosphate-solubilizing fluorescent *Pseudomonas* from the cold deserts of the Trans-Himalayas. Microb Ecol. 58:425–434.

Wasternack C. 2017. A plant’s balance of growth and defense - revisited. New Phytol. 215:1291–1294.

Yang T, Ma S, Dai CC. 2014. Drought degree constrains the beneficial effects of a fungal endophyte on *Atractylodes lancea*. J Appl Microbiol. 117:1435–1449.

Yuan J, Sun K, Wang M, Dai CC. 2016. The mechanism of ethylene signaling induced by endophytic fungus *Glimianiella* sp. AL12 mediating sesquiterpenoids biosynthesis in *Atractylodes lancea*. Front Plant Sci. 7:361.

Zachow C, Fachi J, Cardinale M, Tilcher R, Berg G. 2010. Strain-specific colonization pattern of *Rhizoctonia* antagonists in the root system of *A. lancea*. FEMS Microbiol Ecol. 74:124–135.

Zachow C, Jahanshah G, de Bruin I, Song C, Ianni F, Pataj Z, Gerhardt H, Pianet I, Lämmerhofer M, Berg G, et al. 2015. The novel lipopeptide *P. aureofaciens* RE*’*1-1-14 is involved in pathogen suppression and root colonization. Mol Plant Microbe Interact. 28:800–810.

Zachow C, Tilcher R, Berg G. 2008. Sugar beet-associated bacterial and fungal communities show a high indigenous antagonistic potential against plant pathogens. Microb Ecol. 55:119–129.

Zhang W, Jiang S, Qian D, Shang EX, Duan JA. 2014. Analysis of interaction property of calycosin-7-O-β-D-glucoside with human gut microbiota. J Chromatogr B Analyt Technol Biomed Life Sci. 963:16–23.

Zhou JY, Yuan J, Li X, Ning YF, Dai CC. 2016. Endophytic bacterium-triggered reactive oxygen species directly increase oxygenous sesqui-terpenoid content and diversity in *Atractylodes lancea*. Appl Environ Microbiol. 82:1577–1585.