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ORIGINAL PAPER

Involvement of plant stress hormones in *Burkholderia phytofirmans*-induced shoot and root growth promotion

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Abstract Plant growth promoting bacteria (PGPB) enhance plant growth by often influencing plant hormone homeostasis. Inoculation of potato nodal explants with a known PGPB *B. phytofirmans* (strain PsJN) significantly enhanced shoot and root growth under gnotobiotic conditions. There was a proportionally higher increase in root than shoot biomass. The increases in shoot and root growth were assessed for association with endogenous levels of plant stress hormones, salicylic acid (SA), abscisic acid (ABA) and jasmonic acid (JA) using stable isotope dilution technique coupled with liquid chromatography–mass spectrometry. Inoculation of potato plants with PsJN caused about a 1.5-fold increase in shoot endogenous SA levels. However, shoot ABA levels were not affected, whereas shoot JA levels were not detectable. For roots, the PsJN inoculation caused almost a fourfold increase in endogenous SA levels, whereas increases in ABA and JA levels were about 1.5-fold. To test if the massive increases in SA levels following PsJN inoculation were directly related to observed shoot (about 1.5-fold) and especially root (almost threefold) growth increases, a range of exogenous SA concentrations were applied to control and PsJN-inoculated plants. Applied SA similarly inhibited root growth of control and PsJN-inoculated plants, whereas a 10 µM concentration inhibited shoot growth of PsJN-inoculated, but not control plants. It is thus concluded that while PGPB can modify *in planta* biosynthesis of several plant stress hormones, it is unlikely that changes in endogenous levels of these hormones are directly related to the observed plant growth increases.

Keywords *Burkholderia phytofirmans* strain PsJN · *Solanum tuberosum* L. · Shoot and root biomass · Salicylic acid · Abscisic acid · Jasmonic acid

Introduction

Plant growth and development can be influenced by many factors, including plant growth-promoting bacteria (PGPB). These are naturally occurring soil bacteria that colonize plant rhizosphere and/or plant tissues, and often cause an increase in plant growth (Gamalero and Glick 2011). The PGPB-mediated increase in plant growth can occur via increases in nitrogen acquisition or production of plant hormones, or both (Gamalero and Glick 2011; Kurepin et al. 2014). *Burkholderia* spp. have been shown to act as PGPB (Frommel et al. 1991; Mitter et al. 2013; Ali et al. 2013). *B. phytofirmans* strain PsJN was first isolated from surface-sterilized *Glomus vesiculiferum*-infected onion roots and has been reported to increase growth of potato, tomato and grapevine plants (Frommel et al. 1991; Nowak et al. 1997; Pillay and Nowak 1997; Bensalim et al. 1998; Ait Barka et al. 2000, 2002; Compant et al. 2005; Sessitsch et al. 2005). These growth increases caused by inoculation with PGPB can likely be attributed to PGPB induction of plant hormone production, as shoot and root changes in endogenous gibberellin (GA), cytokinin (CK) and auxin (indole-3-acetic acid [IAA]) levels have been reported (Lazarovits and Nowak 1997; Zuniga et al. 2013; Naveed et al. 2014; Kurepin et al. 2015).

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In addition to GAs, CKs and IAA (Kurepin et al. 2015), Forchetti et al. (2007) reported that PGPB can also produce abscisic acid (ABA), a hormone regulating plant water balance and often inhibiting plant growth (Assmann 2010), and jasmonic acid (JA), a plant hormone mainly involved in the induction of defense mechanism in response to insect infestation (Howe 2010). Furthermore, PGPB, as other bacteria, can also modify plant salicylic acid (SA) levels and thus serve as a biocontrol agents protecting plants against pathogen-induced diseases and pests (Ramamoorthy et al. 2001). Salicylic acid is known for its involvement in the plant defense mechanism in response to pathogen inoculation (Delaney 2010). Inoculation of tomato plants with *B. phytofirmans* strain PsJN increased their resistance to verticillium wilt—likely via induction of tomato's defense responses via increases in SA levels (Sharma and Novak 1998). Inoculation of Arabidopsis with PGPR from *Bacillus* spp. caused increased plant growth, higher endogenous SA accumulation in shoots and enhanced resistance to a pathogen, *Xanthomonas campestris* (Domenech et al. 2007). In grapevine cell suspension culture, both endophytic *B. phytofirmans* strain PsJN and non-host bacterium *Pseudomonas syringae* pv. *pisi* induced similar increases in endogenous SA levels, but only the non-host bacterium caused cell death as the defense response triggered by PsJN was significantly weaker than that of *P. syringae* (Bordeic et al. 2011).

The increase in endogenous SA levels following plant inoculation with a pathogen can also have a negative effect on plant physiology, metabolism and reproductive development (Delaney 2010). This is supported by studies where exogenous SA supplied at concentrations above physiological levels inhibited plant growth (Schettel and Balke 1983), likely via stomatal closure (Larque-Saavedra 1979) and a decrease in chlorophyll accumulation, and the rate of photosynthesis (Hayat et al. 2010). However, when applied at or near physiological concentrations, exogenous SA can increase growth of plants subjected to various abiotic stresses (Hayat et al. 2010). Furthermore, multiple abiotic stresses increase endogenous SA production (Kurepin et al. 2013).

Here, the growth-promotive abilities of *B. phytofirmans* strain PsJN were tested in agar-grown potato nodal explants. The accumulation of endogenous levels of plant stress hormones, SA, ABA and JA in both shoot and root tissues was assessed to test the effect of PGPB inoculation on biosynthesis of these hormones *in planta*, and to evaluate their potential roles in PGPB-mediated shoot and root growth promotion. Since promotion of shoot and root growth typically involves increases in endogenous production of plant growth hormones, such as GAs, IAA and CKs, it was hypothesised that inoculation of potato nodal explants with PsJN will reduce the production of at least ABA and JA, whereas the potential increase in SA production may not be large enough to cause a plant growth-inhibiting effect.

Materials and methods

Bacterium strain and growth condition, and plant inoculation

Burkholderia phytofirmans strain PsJN was obtained from the collection of Dr. George Lazarovits and maintained as described in Kurepin et al. (2015).

Generation and maintenance of plant materials

Potato plantlets (cv. Kennebec) were grown from nodal explants as described in Kurepin et al. (2015). PsJN-inoculated and un-inoculated control plants were harvested 7 and 21 days after PsJN inoculation and fresh biomass measured before the tissue was stored at −80 °C for future plant hormone identification and quantification analysis.

Endogenous plant hormone analysis

For analysis of endogenous SA, ABA and JA levels, shoot and root tissues were separately collected from potato plantlets and immediately frozen in liquid N_2, and stored at −80 °C freezer until extraction. Extraction consisted of grinding frozen samples (0.5 to 2.0 g fresh weight [FW]) in a mortar and pestle with liquid N_2, followed by use of MeOH–H_2O–HOAc (90:9:1, v/v/v) as an extraction solvent. At this stage, 200 ng of $^2H_6$-SA (2-Hydroxybenzoic acid-d_6, dOC_6d_4COOd, CDN Isotopes, Quebec, Canada), 250 ng of $^2H_4$-ABA (PBI Institute, Saskatchewan, Canada) and 200 ng of d_5-JA (Jasmonic-d_5 Acid, 2,4,4-d_3; acetyl-2,2-d_2; CDN Isotopes, Quebec, Canada) were added to the 90 % (v/v) MeOH extract as quantitative internal standards. The extract was then dried in vacuo at 35 °C. The dried residue was reconstituted in 200 µL of 0.05 % (v/v) HOAc in H_2O–MeCN (85:15, v/v) and filtered with a 0.45 µm filter prior to the injection into the liquid chromatograph–mass spectrometer (LC–MS).

Quantitative hormone analysis was accomplished on an Agilent Technologies 1260 Infinity HPLC system linked to an Agilent Technologies 6230 TOF MS. The MS was equipped with a electrospray ionization source (ESI). Negative ion mode was used for the analysis of SA, ABA and JA. A 100 µL aliquot was injected on a ZORBAX Eclipse Plus C18 column (1.8 µm, 3 × 100 mm; Agilent Technologies). Plant hormones were eluted with an increasing gradient of acetonitrile (solvent B) containing 0.05 % HCOOH and decreasing gradient of H_2O (solvent A) also containing 0.05 % formic acid at a flow rate of 0.25 mL min^{-1}. The LC binary pump conditions were 80 % A (time 0), 70 % A (time 2 min), 50 % A (time 4 min), 20 % A (time 8 min), hold at 0 % A at 10 and 12 min and back to 80 % A (time 15 min) for 5 min of

post-run. HPLC effluent was introduced into the electrospray source with gas temperature of 350 °C. The fragmentor voltage was 150 V and Vcap of 4000 V. Automated internal calibration was done using reference ion 121.0508. The quantification of target analytes was accomplished based on peak area for molecular ions of deuterated standards (SA—141; ABA—267; JA—213) and endogenous hormones (SA—137; ABA—263; JA—209).

Exogenous hormone applications

Exogenous SA (Sigma, Canada) was prepared with 95 % (v/v) EtOH at a final concentration of 0.1 % (v/v) in ddH_2O and applied at concentrations of 0.1, 1.0, 10 and 100 μM to either 20 mL of agar media (i.e. 27.6 ng, 276 ng, 2.76 μg or 27.6 μg of SA per plant at 35 °C after autoclaving) or directly to leaf buds (as 200 μL microdrops) of 1-week old seedlings. Two control solutions were tested with one containing 100 % ddH_20 and the other—0.1 % (v/v) EtOH in ddH_2O.

Statistical analysis

Each experiment was repeated three times with 10 plants per each treatment, and endogenous plant hormones were measured in tissue from three different experiments. Within each data set (fresh weight, individual hormone analysis), data were analyzed by *t* test and one-way ANOVA, followed by a Tukey's post hoc test ($P \leq 0.05$), using Sigma Plot version 12.

Results

Inoculation of potato plants with *B. phytofirmans* strain PsJN had no effect plant growth, shoot or root biomass, measured after 1-week period (Fig. 1a). However, PsJN inoculation caused more than doubling of total potato plant biomass after a 3-week period relative to the control plants: about a 1.5-fold increase in shoot fresh biomass and almost a threefold increase in root fresh biomass (Fig. 1b). Thus, PsJN inoculation re-allocated more growth to roots than shoot. While not evident at 1 week post inoculation (Fig. 1c), after 3 weeks the PsJN-induced allocation of more biomass towards roots resulted in 62:38 % shoot:root allocation relative to control plants where the allocation was 73:27 % (Fig. 1d). The higher biomass allocation towards roots 3 weeks after PsJN inoculation was due to increased development of lateral and adventitious roots relative to control plants (compare Fig. 1f with 1e).

The analysis of endogenous SA, ABA and JA levels in potato shoot and roots revealed that PsJN inoculation does affect the levels of these plant stress hormones (Fig. 2; Table 1). Plant endogenous SA levels, which were appreciably lower in roots than shoot at both time points (Figs. 2a, b), were not affected by the PsJN inoculation 1 week after (Fig. 2a). However, SA levels were increased by almost threefold 3 weeks after inoculation with about a 1.5-fold increase in shoot and almost a fourfold increase in roots (Fig. 2b). Similar trends were also observed when SA levels were expressed on a per gram dry weight basis (Table 1). One week after inoculation, there were no differences in endogenous ABA levels between control and PsJN-inoculated plants, or between shoot and root tissues of control or PsJN-inoculated plants (Fig. 2c). However, 3 weeks after inoculation, shoot ABA levels were fivefold to sixfold higher than root ABA levels in both control and inoculated plants (Fig. 2d). Biomass allocation to roots also increased 3 weeks post-inoculation for control and PsJN-inoculated plants (Fig. 1c, d). PsJN inoculation, 3 weeks after inoculation, had no effect on whole plant or shoot ABA content, but did increase ABA levels in roots by about 1.5-fold (Fig. 2d). However, 3 weeks after inoculation, root ABA levels, expressed on a per gram dry weight basis, were decreased by almost 1.5-fold by PsJN inoculation (Table 1). Endogenous JA levels were below detection limit in shoot and root tissues 1 week after inoculation (Fig. 2e), but were detectable in roots 3 weeks after inoculation (Fig. 2f). Thus, there was an increase in JA levels as plant matured. Similar increases in endogenous SA were also observed for potato plants as they matured (Fig. 2). PsJN inoculation resulted in about 1.5-fold higher root endogenous JA levels relative to roots of control plants (Fig. 2f). Similar trend was also observed when JA levels were expressed on a per gram dry weight basis (Table 1).

The exogenous SA effect on shoot and root growth on potato plants was tested by using several SA concentrations, applied to agar and encompassing the physiological level in control and PsJN-inoculated plants (Fig. 3). For shoot growth of control plants, SA concentrations of 0.1, 1 and 10 μM had no effect on shoot biomass, whereas higher concentration of 100 μM inhibited shoot biomass accumulation (Fig. 3a). For root growth of control plants, even 0.1 μM SA inhibited root biomass accumulation which was further inhibited at 100 μM SA (Fig. 3b). For shoot growth of PsJN-inoculated plants, SA concentrations of 0.1 and 1 μM had no effect on shoot biomass, whereas higher concentrations, 10 and 100 μM, inhibited shoot biomass accumulation (Fig. 3a). For root growth of PsJN-inoculated plants, biomass accumulation was inhibited even at 0.1 μM SA and again at 100 μM, i.e. similarly to control plants (Fig. 3b). However, for both shoot and roots response to applied SA, PsJN-inoculated plants showed steeper inhibition of biomass accumulation to the same concentration of SA as was applied to control plants (Fig. 3).

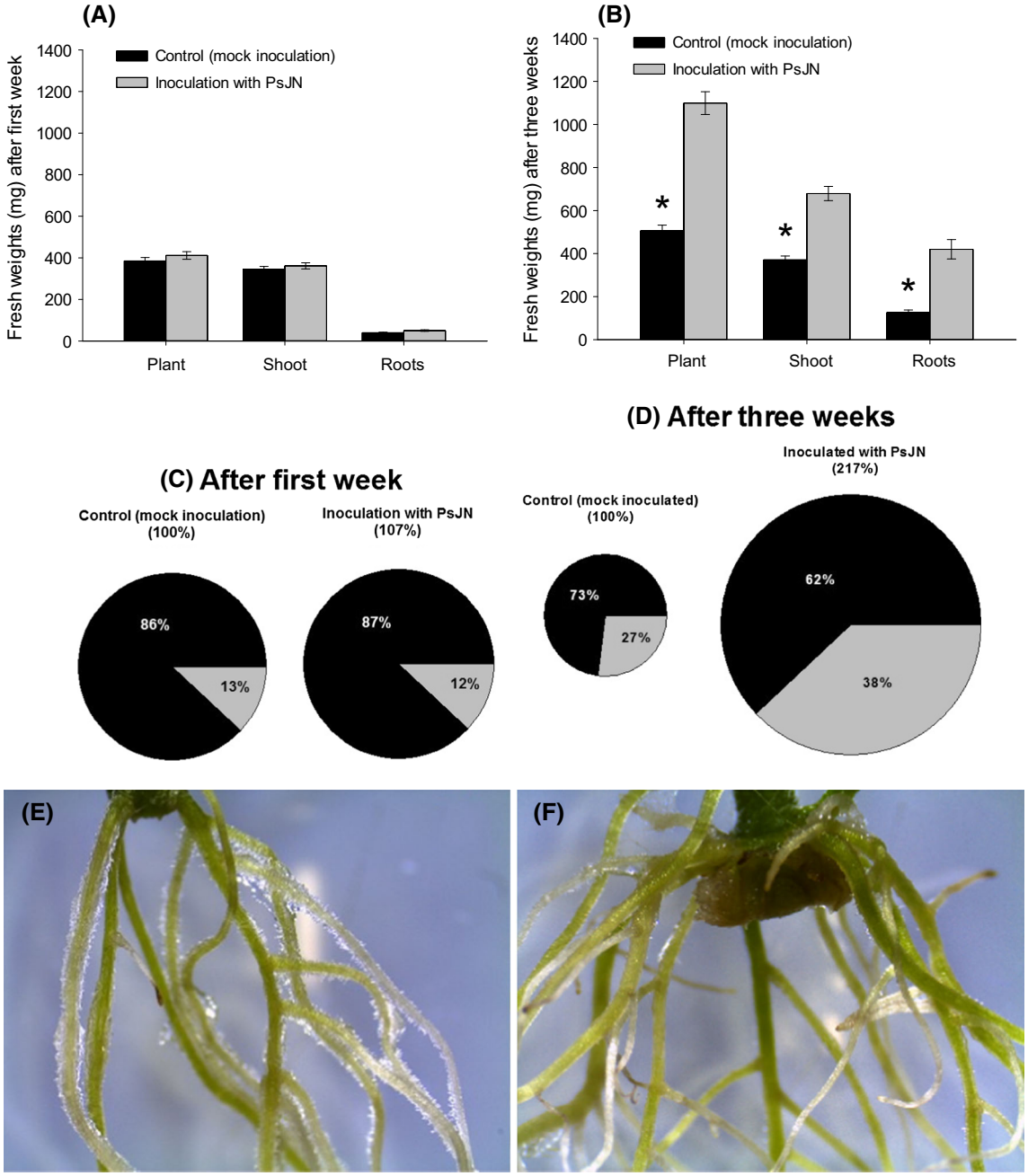

Fig. 1 Fresh weights (mg) of potato seedlings one (**a**) and three (**b**) weeks after mock (control, *black areas*) or *B. phytofirmans* strain PsJN (*grey areas*) inoculation. Plant shoot/root fresh mass growth allocations (%) one (**c**) and three (**d**) weeks after inoculation. Photographs of roots of control (**e**) and PsJN-inoculated (**f**) seedlings 3 weeks after inoculation. The *error bars* represent one SE of the mean. *Asterisk sign* indicates significant ($P \leq 0.05$) difference between control and PsJN-inoculated seedlings based on a *t* test

It is also possible that the effect of exogenous SA can depend on the application site. For example, application of 1 and 5 mM SA to roots of soybean plants showed dose-dependent inhibition of nodule number and dry weight per plant (Lian et al. 2000). In contrast, application of SA to the leaf of soybean plants (as a 1 mM "soak") significantly increased nodule number and dry weight per plant (Lian et al. 2000). Thus, application of exogenous SA to shoot tissues of potato seedlings may have an opposite (positive) effect on growth. This hypothesis was tested by brushing the same SA concentrations on potato leaves following the PsJN-inoculation. While higher doses of SA had lower inhibitory effect on plant growth compared to the application of SA to agar, they were still inhibitory and none of the lower doses increased growth of control or PsJN-inoculated plants (data not shown).

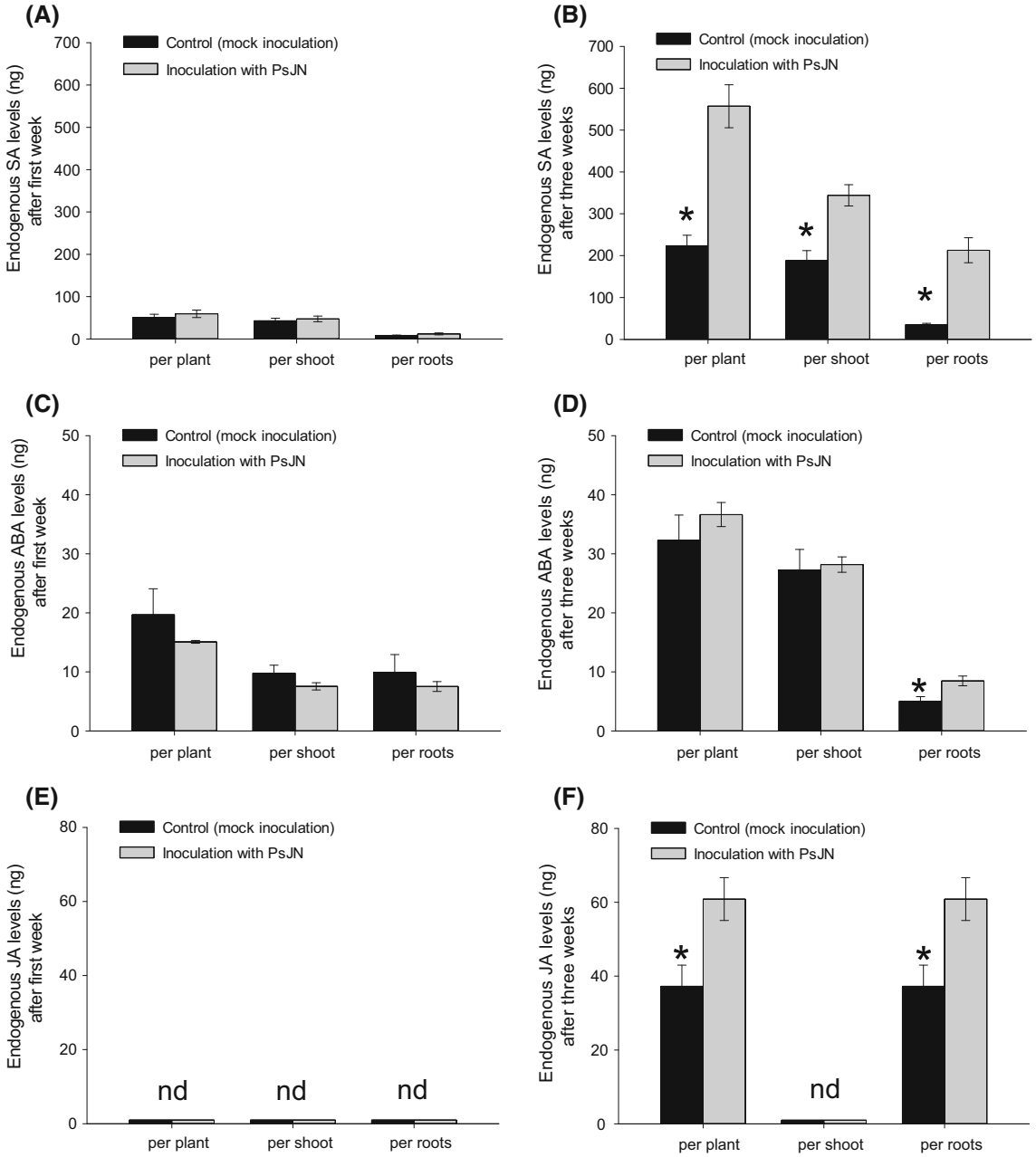

Fig. 2 Endogenous SA, ABA and JA levels (ng) of potato seedlings one (**a**, **c** and **e**, respectively) and three (**b**, **d** and **f**, respectively) weeks after mock (control, *black bars*) or *B. phytofirmans* strain PsJN (grey bars) inoculation. The *error bars* represent one SE of the mean. *Asterisk sign* indicates significant ($P \leq 0.05$) difference between control and PsJN-inoculated seedlings based on a *t* test

Discussion

Inoculation of potato plants with PsJN strain caused significant plant growth increases after a period of 3 weeks. Higher biomass increases were found in roots as PsJN inoculation resulted in more lateral and adventitious root development, and thus the higher allocation of biomass to roots than shoots compared with the control plants (Fig. 1). The PsJN-induced growth promotion of potato plants and PsJN inoculation effect on *in planta* changes in the biosynthesis of plant growth hormones have been reported (Kurepin et al. 2015). The increases in shoot growth were positively correlated with increases in endogenous IAA and GA_1 levels, whereas increases in root growth were positively correlated with endogenous increases in IAA and a bioactive CK, *trans*-zeatin, levels (Kurepin et al. 2015). The growth of shoot tissues is positively regulated by multiple plant growth hormones (Kurepin and Pharis 2014), but increases in plant SA,

Table 1 Shoot and root endogenous levels (ng gDW^{-1}) of plant hormones one and 3 weeks after mock or PsJN inoculation of in vitro grown potato plantlets

One week after inoculation	Shoot tissue		Root tissue	
	Control	PsJN	Control	PsJN
SA levels	180 ± 16	246 ± 28	53 ± 3.9	112 ± 27
ABA levels	41 ± 3.6	40 ± 5.0	63 ± 17	67 ± 6.6
JA levels	nd	nd	nd	nd
Three weeks after inoculation	Shoot tissue		Root tissue	
	Control	PsJN	Control	PsJN
SA levels	351 ± 23*	606 ± 33	190 ± 18*	396 ± 18
ABA levels	51 ± 3.3	50 ± 1.2	27 ± 2.9*	16 ± 0.2
JA levels	nd	nd	240 ± 46*	556 ± 101

The hormone levels are expressed as mean values ± SE (n = 3). Data labeled with an asterisk (*) are significantly different between treatments within a plant tissue ($P = 0.05$)

nd not detected

ABA and JA production are typically associated with decreases in shoot growth (Delaney 2010; Assmann 2010; Howe 2010). The development of lateral and adventitious roots is regulated by temporal and localized action of several plant hormone classes, including auxins and CKs, by triggering localized changes in ethylene production (De Klerk et al. 1999; Kurepin et al. 2011). The roles of SA, ABA and JA in lateral and adventitious root growth and formation are less clear (Kurepin et al. 2011).

The most substantial effect of PsJN inoculation was on endogenous SA levels: about 1.5-fold increase in shoot and almost fourfold increase in roots. Application of SA at low doses can promote shoot growth, especially for abiotically stressed plants (Hayat et al. 2010). Furthermore, inoculation of drought-stressed sunflower plants with PGPB *Bacillus pumilus* enhanced plant growth and this was associated with higher accumulation of shoot SA levels (Forchetti et al. 2010). Therefore, the PGPB-mediated increase in shoot SA levels may not result in shoot growth inhibition. Application studies with a range of SA concentrations did not result in shoot growth promotion of control or PsJN inoculated plants. Furthermore, at one concentration, 10 μM, applied SA inhibited shoot growth of PsJN-inoculated plants, whereas shoot growth of control plants was not affected. It is thus concluded that PsJN-mediated increases in endogenous shoot SA levels are likely not involved in shoot growth promotion. In most literature examples where exogenous SA caused plant growth promotion, the plants were subjected to various abiotic stresses and therefore the SA action was "stress-alleviating" rather than "growth-promoting" (Kurepin et al. 2013). Further, although numerous abiotic stresses can increase endogenous SA levels: high and low temperatures (Scott et al. 2004; Wang et al. 2005), drought and flooding (Kurepin et al. 2013), high light irradiance, low red to far-red (R/FR) ratio (Kurepin et al. 2010, 2012) and UV light (Yalpani et al. 1994), these increases are not always associated with growth promotion as discussed in Kurepin et al. (2013).

The highest increase in endogenous SA levels in response to a PsJN inoculation was in roots. Salicylic acid involvement in the promotion of root growth was reported for mung bean (Li 1995), soybean (Gutierrez-Coronado et al. 1998) and Mexican marigold (Sandoval-Yapiz 2004) plants. Further, Kling and Meyer (1983) reported that a combination of applied auxin and 0.1 mM SA increased adventitious root formation and also stimulated root growth in cuttings of mung bean, silver maple and paperbark maple, and the combined effect of auxin and SA was higher than auxin alone. Thus, PsJN-mediated increase in root SA levels could be responsible for root growth increases. Furthermore, since it is know that inoculation of potato plants with PsJN increases IAA levels in roots (Kurepin et al. 2015), the endogenous SA increase may interact with increased IAA levels to stimulate root growth. However, application of SA at a range of concentrations had no effect on root growth of control or PsJN inoculated plants. Therefore, it cannot be established that PGPB-induced increases in SA levels are responsible for root growth increases.

Inoculation of potato plants with PsJN increased root JA levels, whereas shoot JA levels were not detected. Jasmonic acid may play a role in lateral and adventitious root development (Kurepin et al. 2011). For example, JA was shown to stimulate adventitious root formation in in mung bean (Zimmerman and Vick 1983) and potato stem cuttings (Ravnikar and Gogala 1990; Ravnikar et al. 1992). Furthermore, JA applied with auxins enhanced adventitious rooting of tobacco thin cell layers (Fattorini et al. 2009). Thus, the PsJN-induced increase in root JA levels could be related to increases in root growth and development, but further research is required to establish endogenous JA role in lateral and adventitious root formation.

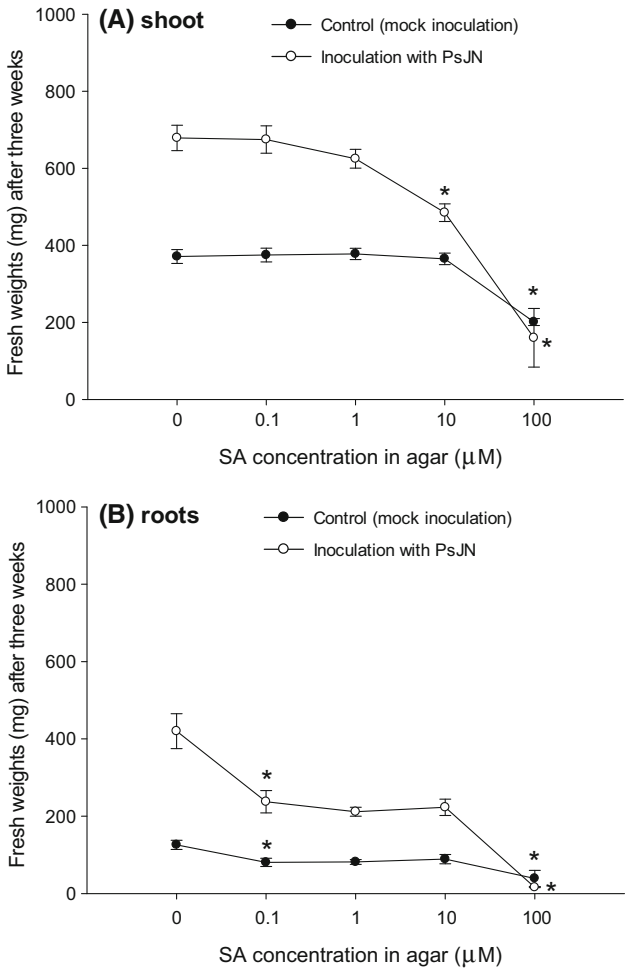

Fig. 3 Shoot (**a**) and root (**b**) fresh weights potato 3 weeks after mock (control, *black circles*) or *B. phytofirmans* strain PsJN (*grey circles*) inoculation. The seedlings were grown with different concentrations of exogenous SA in agar: 0, 0.1, 1, 10 and 100 µM. The *error bars* represent one SE of the mean. *Asterisk sign* indicates significant ($P \leq 0.05$) difference between various exogenous SA concentrations for each of control and inoculated tissues based on an ANOVA and Tukey's post hoc test

Inoculation of plants with a PGPB typically reduces ABA biosynthesis as a necessary step for improved plant pathogen resistance (Mauch-Mani and Mauch 2005). Furthermore, a PGPB (*Bacillus subtilis* GB03) inoculation can promote Arabidopsis shoot growth, enhance photosynthetic efficiency and chlorophyll content, while inhibiting ABA biosynthesis (Zhang et al. 2008). Inoculation of potato plants with PsJN had no effect on shoot ABA levels. However, there was about 1.5-fold increase in total root ABA levels in PsJN-inoculated plants, whereas on a per root weight basis, there was almost 1.5-fold decrease. Abscisic acid appears to be a negative regulator of root development (Brady et al. 2003). For example, in Arabidopsis seedlings, exogenously applied ABA significantly inhibited primary and lateral root development (Beaudoin et al. 2000; De Smet et al. 2003). It is therefore unlikely that the observed increases in root total ABA levels of PsJN-inoculated plants could be responsible for increased lateral and adventitious root development. Thus, it is the distribution of endogenous ABA in root tissues, lower in PsJN-inoculated than in control plants, which could be a contributing factor for observed increases in root growth.

In conclusion, based on the results presented here and previously (Kurepin et al. 2015), inoculation of plants with PGPB does cause changes in endogenous levels of multiple plant growth and stress hormones. However, these endogenous changes, as demonstrated here for SA, do not appear to be directly involved in the increased allocation of shoot to root biomass. Further research is required to understand the hormonal mechanism employed by PGPB to stimulate plant growth increases.

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