Plant Physiology and Biochemistry 141 (2019) 142–153

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

Induction of essential oil production in *Mentha* x *piperita* by plant growth promoting bacteria was correlated with an increase in jasmonate and salicylate levels and a higher density of glandular trichomes

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ARTICLE INFO

Keywords:
Plant growth promoting bacteria
Mentha x piperita
Jasmonic acid
Salicylic acid
Essential oil
Glandular trichome

ABSTRACT

Plant growth promoting bacteria (PGPB) are agriculturally important soil bacteria that increase plant growth. We subjected peppermint to inoculation with three species of PGPB. After inoculation, the plants were sprayed with methyl jasmonate solution (MeJA) or SA (salicylic acid). Then, the plants were harvested and the plant growth parameters, trichome density, EO content and endogenous phytohormones were measured. Shoot fresh weight was reduced in plants inoculated and treated with MeJA whereas EO content varied depending on the MeJA concentration applied. Plants inoculated and treated with MeJA 2 mM showed the maximum increase in EO production, revealing a synergism between PGPB and MeJA. SA treatments also enhanced EO yield. The increased growth and EO production observed upon PGPB application were at least partly due to an increase in the JA and SA concentrations in the plant, as well as to an associated rise in the glandular trichome density.

1. Introduction

Plant growth promoting bacteria (PGPB) comprise a diverse group of soil bacteria that stimulate plant growth and development by direct or indirect mechanisms (Vessey, 2003; Glick, 2012; Olanrewaju et al., 2017). In *direct promotion*, PGPB may provide the host plant with synthesized compounds; facilitate the uptake of nutrients; fix atmospheric nitrogen; solubilize minerals such as phosphorus; produce siderophores that solubilize and sequester iron; synthesize phytohormones, including auxins, cytokinins, and gibberellins, which enhance various stages of plant growth; or synthesize enzymes that modulate plant growth and development (Lucy et al., 2004; Gray and Smith, 2005; Glick, 2012; Etesami and Maheshwari, 2018). In *indirect promotion*, PGPB decrease pathogen infestation by inducing systemic resistance (ISR), thereby reducing phytotoxic microbial communities (Kloepper, 1993; Niranjan et al., 2006; van Loon, 2007; Etesami and Maheshwari, 2018). The protection given to the plant by PGPB is associated with the jasmonate and ethylene produced by the plant (Pieterse et al., 2014). However, several PGPB can trigger the salicylic acid (SA)-dependent SAR pathway by producing SA at the root surface (Pieterse et al., 2014).

PGPB can also enhance plant growth and secondary metabolic production in aromatic plants. Inoculation of PGPB on sweet marjoram, Italian oregano, sweet basil, and wild marigold increased essential oil (EO) yield by varying degrees, depending on the inoculated strain (Banchio et al., 2009, 2010; Cappellari et al., 2013). However, the understanding of how these rhizobacteria can produce this response in aromatic plants remains unclear.

The production of EO takes place under diverse physiological, biochemical, metabolic and genetic factors, which are often difficult to separate from each other. Moreover, geographical, seasonal, developmental and organ variations are all involved (Hassiotis et al., 2014), along with anatomical and hormonal factors. The EO yield of aromatic plants is often strongly correlated with the total number and distribution of glandular trichomes, which are the structures in which oil components are synthesized and stored (Lange et al., 2011; Lange and Turner, 2013). In addition, plant growth regulators have been found to favorably influence the yield and quality of EO. For example, jasmonic acid (JA), which controls the production of a number of secondary metabolites including terpenoids, upregulates the genes and enzymes of secondary metabolite biosynthetic pathways (Howe, 2001; Maes et al., 2011; Dutta and Khurana, 2015; Wasternack and Song, 2016; Wasternack and Strnad, 2017).

Abbreviations: Plant growth promoting bacteria, (PGPB); essential oil, (EO); jasmonic acid, (JA); methyl jasmonate, (MeJA); salicylic acid, (SA)

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https://doi.org/10.1016/j.plaphy.2019.05.030
Received 13 March 2019; Received in revised form 28 May 2019; Accepted 28 May 2019

Table 1

Summary of the treatments applied to M. piperita plants and their respective abbreviations.

	0 mM MeJA	1 mM MeJA	2 mM MeJA	4 mM MeJA	1 mM SA	2 mM SA
Control (non-inoculated)	control	1 mM MeJA	2 mM MeJA	4 mM MeJA	1 mM SA	2 mM SA
Pseudomonas fluorescens WCS417r	WCS417r	1 mM MeJA + WCS417r	2 mM MeJA + WCS417r	4 mM MeJA + WCS417r	1 mM SA + WCS417r	2 mM SA + WCS417r
Bacillus subtilis GB03	GB03	1 mM MeJA + GB03	2 mM MeJA + GB03	4 mM MeJA + GB03	1 mM SA + GB03	2 mM SA + GB03
P. putida SJ04	SJ04	1 mM MeJA + SJ04	2 mM MeJA + SJ04	4 mM MeJA + SJ04	1 mM SA + SJ04	2 mM SA + SJ04

Peppermint (*Mentha* x *piperita*) is cultivated worldwide for the production of its EO. It is composed primarily of monoterpenes, and is one of the most important EO crops (Lawrence, 2007). *M. piperita* plants contain ~3% volatile oils, consisting of > 50 different compounds. The major EO components, which make up ~60% of the total oil volume, are 1,8-cineole, linalool, (−)-menthone, (−)-menthol, and (+)-pulegone. Peppermint leaves are used for teas and for flavoring foods and beverages, and its EO is also used in chewing gum, candy, toothpaste, mouthwash, aromatherapy, pharmaceuticals, antimicrobial agents and eco-friendly pesticides (MIRC, 2010). Previous studies have shown that inoculation of peppermint with PGPB increases the EO yield by increasing the glandular trichome density, as well as total chlorophyll content, shoot fresh weight and leaf area (Cappellari et al., 2015).To date, however, there is little detailed published information about how MeJA and SA signaling molecules influence the interaction between aromatic plants and rhizobacteria. Therefore, we conducted studies to determine the levels of endogenous phytohormones in inoculated peppermint plants. Following the observation that PGPB increased the JA and SA levels, we then investigated the effect of the exogenous application of JA and SA on plant development and secondary metabolite production in plants which had been previously inoculated with PGPB. In addition, we recorded the levels of endogenous phytohormones in plants exposed to JA and SA. The findings obtained from this study will help to improve plant growth parameters and secondary metabolite production for this crop.

2. Material and methods

2.1. Bacterial strains and culture conditions

The following three bacterial strains previously reported as PGPB were studied: *Pseudomonas fluorescens* WCS417r; *Bacillus subtilis* GB03 (Banchio et al., 2010); and *P. putida* SJ04 (a native fluorescent strain isolated from rhizospheric soil under a commercial crop of *Mentha* x *piperita* (San José) in Córdoba, Argentina, and demonstrated to have plant growth-promoting activity (GenBank KF312464.1)). Bacteria were grown on LB medium (Bertani, 1951) (10 g/L tryptone, 5 g/L yeast extract, 5 g/L NaCl) for routine use and maintained in nutrient broth with 15% glycerol at −80 °C for long-term storage.

Each bacterial culture was grown overnight at 30 °C and at 120 rpm until reaching the exponential phase, washed twice in 0.9% NaCl with centrifugation (4300 × *g*, 10 min, 4 °C), resuspended in sterile water, and adjusted to a final concentration of ~10^8 CFU/mL for use as inoculum.

2.2. Greenhouse experiments

Peppermint plantlets were obtained by an in vitro micropropagation technique using young shoots of *M.* x *piperita* plants grown in the Traslasierra Valley (Córdoba Province, Argentina), as described by Cappellari et al. (2013). Rooting plantlets were transplanted directly (one per pot) in plastic pots (diameter 12 cm, depth 22 cm) containing vermiculite. To carry out the experiment, the following procedure was observed: plants were first inoculated with 1000 μL bacterial suspension as described above, with sterile water being applied to the control seedlings. After 7 days of inoculation, plants were sprayed until run-off with 1, 2 or 4 mM methyl jasmonate solution (MeJA) (Sigma-Aldrich, 1% methanol in water, v/v) or 1, 2 mM SA solution (1% ethanol in water, v/v). Then, the plants were left to dry for 30–60 min. For the phytohormone control treatments, a solution of the solvent used was applied. After phytohormone or control treatments, plants were transferred to a climate chamber with the phytohormone treatments being spatially separated from other treatments because MeJA is very volatile.

Plants were grown in a growth chamber under controlled conditions of light (16/8-h light/dark cycle), temperature (22 ± 2 °C) and relative humidity (~70%), and received Hoagland's nutrient medium (20 mL/pot) twice a week (Cappellari et al., 2013).

After 14 days of applied phytohormone treatments, the plants were removed from their pots and their roots were washed to remove vermiculite. Experiments were performed under non-sterile conditions and replicated 3 times (10 pots per treatment). The different experimental treatments are summarized in Table 1.

2.3. Phytohormone analysis

The phytohormone analysis was based on a procedure by Schmidt et al. (2011). Approximately 0.10 g of ground lyophilized plant material was homogenized in 1 ml of methanol spiked with 40 ng of $[^2H_2]$JA, 40 ng $[^2H_4]$SA, 40 ng $[^2H_6]$ABA and 8 ng ofJA-$[^{13}C_6]$Ile by shaking for 60 min. Homogenates were centrifuged at 20,000 g for 20 min at 4 °C, the methanol phase was collected, and the homogenate was re-extracted with1.0 ml methanol. The organic phases were then combined and the samples evaporated to dryness in a vacuum concentrator at 30 °C. The dry residue was reconstituted in 0.5 ml of 70% (v/v) methanol/water, and analyzed by LC-MS/MS.

Chromatography was performed on an Agilent 1200 HPLC system (Agilent), and separation was achieved on an XDB C18 column (1.8 μm, 50 mm × 4.6 mm; Agilent Technologies). The mobile phase, comprising of solvent A (0.05% formic acid) and solvent B (acetonitrile), was used in a gradient of 0–0.5 min, 5% B; 0.5–9.5 min, 0–58% B; 9.5–9.52 min, 58–100% B; 9.52–11 min, 100% B; 11–11.1 min, 5% B and 11.1–14 min, 5% B with a flow rate of 1.1 ml/min. The column temperature was maintained at 25 °C, and an injection volume of 2 μl was used for all samples. An API 5000 tandem mass spectrometer (AB Sciex) equipped with a turbospray ion source was operated in the negative ionization mode. The ion spray voltage was maintained at −4500 V, and the turbo gas temperature was set at 700 °C. Nebulizing gas was set at 60 psi, curtain gas at 25 psi, heating gas at 60 psi and collision gas at 7 psi.

Multiple reaction monitoring (MRM) was used to monitor analyte parent ion-to-product ion formation (DP, declustering potential; EP, entrance potential; CE, collision energy; CXP, collision cell exit potential): *m/z* 141/97 (DP -35, EP -8, CE -22, CXP 0) for $[^2H_4]$SA; 137/93 (DP -35, EP -8, CE -22, CXP 0) for SA; 213/59 (DP -35, EP -9, CE -24, CXP 0) for $[^2H_2]$JA; 209/59 (DP -35, EP -9, CE -24, CXP 0) for JA; 269/159 (DP -35, EP -12, CE -22, CXP -2) for $[^2H_6]$ABA; 263/153 (DP -35, EP -12, CE -22, CXP -2) for ABA; 328/136 (DP -50, EP -4, CE -30, CXP -4) for JA-$[^{13}C_6]$Ile; 322/130 (DP -50, EP -4, CE -30, CXP -4) for JA-Ile; 291/165 (DP -45, EP -12, CE -24, CXP -2) for OPDA. Data analysis was performed using Analyst Software 1.6 Build 3773 (AB Sciex), and JA, JA-Ile, ABA and SA were quantified according to the labeled standard compounds.

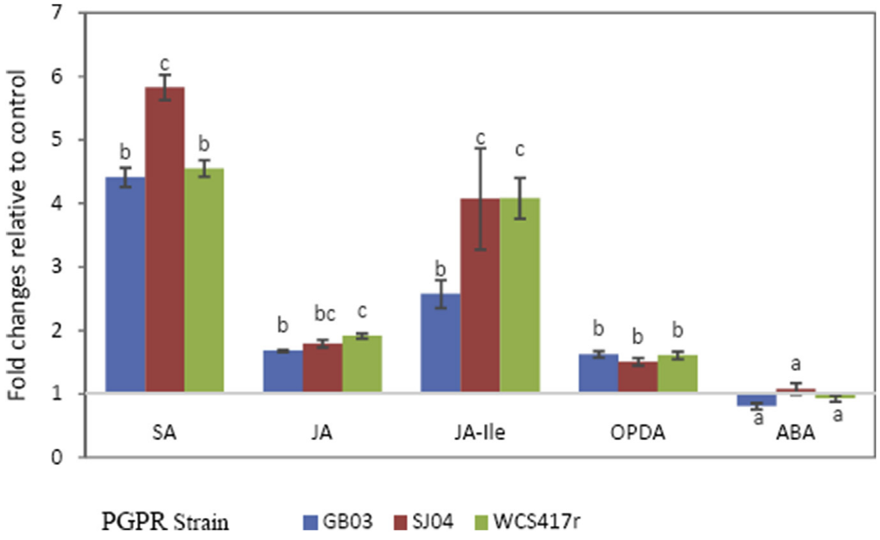

Fig. 1. Inoculation with different PGPB strains increased the endogenous concentrations of the phytohormones JA and SA in *M.* x *piperita*.Values are fold changes relative to the control. Different letters above bars indicate significant differences according to Fisher's LSD test ($p < 0.05$). The letter "a" indicates similar to the control. Different letters above bars indicate significant differences according to Fisher's LSD test ($p < 0.05$). Native values are given in Supplementary Table 1.

2.4. *Extraction of essential oil (EO)*

Shoot samples were individually weighed and subjected to hydrodistillation in a Clevenger-like apparatus for 40 min. The volatile fraction was collected in dichloromethane, and β-pinene (1 μL in 50 μL ethanol) was added as an internal standard.

The EO compound identification was performed using a PerkinElmer Q-700 gas chromatograph (GC) equipped with a CBP-1 capillary column (30 m × 0.25 mm, film thickness 0.25 μm) and a mass selective detector. The analytical conditions used were: injector temperature 250 °C; detector temperature 270 °C; oven temperature programmed from 60 °C (3 min) to 240 °C at 4°/min; carrier gas = helium, at a constant flow rate of 0.9 mL/min; source 70 eV. The oil components were identified based on mass spectral and retention time data and compared to standard compounds (Banchio et al., 2010). For quantification, GC analysis was performed using a Shimadzu GC-RIA gas chromatograph fitted with a 30 m × 0.25 mm fused silica capillary column coated with Supelco wax 10 (film thickness 0.25 μm). The GC operating conditions were: injector and detector temperatures 250 °C; oven temperature programmed from 60 °C (3 min) to 240 °C at 4°/min; detector = FID; carrier gas = nitrogen, at a constant flow rate of 0.9 mL/min. Flame ionization detector (FID) response factors for the major monoterpenes of the EO are essentially equivalent (differences < 5%), so the area of each peak was referenced directly to the internal standard for quantification.

2.5. *Glandular trichome density*

A layer of acrylic (synthetic nail coating) was brushed onto the adaxial and abaxial surfaces of the leaf, left to dried for a few seconds, and then carefully peeled off and mounted for microscopy in glycerol/distilled water 1:10 (D'Ambriogio de Argüeso, 1986). Six leaf blades were processed for each treatment.

The glandular trichome density (number per mm^2) was calculated from three microscope fields chosen at random for each leaf epidermis. Histological preparations of the trichomes were assessed using a standard Zeiss model 16 microscope, and photomicrographs were taken with a Zeiss Axiophot microscope equipped with image capture and digitization (AxioVision 4.3, with an AxioCamHRc camera at 200 × magnification). Trichomes were counted using the Image J program for image analysis, and their frequency was calculated as described previously by Cappellari et al., (2015). Density was expressed as the ratio of the mean number of trichomes per leaf pair and the corresponding leaf area.

2.6. *Plant growth parameters*

Once the plants were harvested, the growth parameters (shoot length, leaf number, branch number, shoot fresh weight) were measured.

2.7. *Statistical analyses*

Data were pooled and subjected to an analysis of variance (ANOVA) followed by a comparison of multiple treatment levels with controls using Fisher's post hoc LSD (least significant difference) test. Differences between means were considered to be significant for p values < 0.05. The Infostat software program, version 2008 (Group Infostat, Universidad Nacional de Córdoba, Argentina) was used for all statistical analyses.

3. Results

3.1. *PGPB inoculation increased endogenous levels of JA and SA*

The phytohormone content (ABA, JA, JA-ile, OPDA and SA) in inoculated *M. piperita* was determined by using the LC-MS/MS technique. Plants inoculated with PGPB revealed an important change in endogenous phytohormones, with plants inoculated with some PGPB strains showing a 4–5-fold increase in SA levels compared to uninoculated controls, and an almost 6-fold increase being observed for SJO4 ($p < 0.05$)(Fig. 1). A similar trend for the three strains was observed for JA, with plants inoculated with WCS417r showing a 2-fold increase ($p < 0.05$) compared to controls. The levels of 12-oxo-phytodienoic acid (OPDA), a biosynthetic precursor of JA, were slightly less boosted than JA, but the level of the isoleucine conjugate (JA-Ile), considered to be the bioactive form of jasmonate, rose more than JA, by approximately 2.5–4-fold compared to controls, with this increase being more evident for the Pseudomonas strains. However, no difference in ABA levels was detected in inoculated plants with respect to controls ($p > 0.05$). The above results are expressed just as "fold changes" in order to facilitate their interpretation, with the statistics being obtained from an analysis of the native data (shown in Supplementary Table 1).

3.2. *Exogenous JA and SA increased essential oil content*

As we had now shown that PGPB increased the endogenous levels of SA and JA, we directly tested the effects of these hormones on EO content both with and without PGPB inoculation. The gas

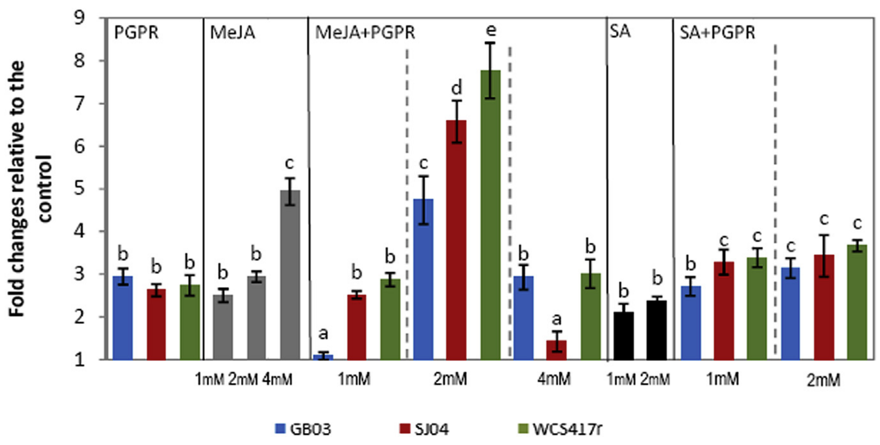

Fig. 2. Inoculation with PGPB and hormone treatments increased essential oil concentration in shoots of *M.* x *piperita* plants. Values are fold changes relative to the control. Different letters above bars indicate significant differences according to Fisher's LSD test ($p < 0.05$). The letter "a" indicates similar to the control. Three different ANOVA analyses were performed (*a)* PGPB- *b)* MeJA + PGPB- *c)* SA + PGPB). The letter "a" indicates similar to the control. Native values are given in supplementary table 2, 3 and 4.

chromatographic (GC) analysis of EO revealed that spraying with methyl jasmonate (MeJA) boosted the EO yield. In addition, plants treated with 1 or 2 mM MeJA increased their EO yield approximately three-fold with respect to the control (similar to that of PGPB) ($p < 0.05$) (Fig. 2), while using 4 mM MeJA led to a five-fold increase. After spraying with SA, the EO yield rose approximately two-fold in comparison to the control, similar to the increase observed in PGPB-inoculated plants. As the control with solvent for MeJA did not differ statistically from the control ($p > 0.05$), this is not shown in the figures.

The response of plants treated with PGPB in addition to MeJA depended on the concentration of MeJA applied. The strongest effect was observed when plants were treated with 2 mM, with an increase of nearly 8-fold being observed compared to controls without MeJA or PGPB, which was also much greater than that observed for either treatment alone. Plants treated with 2 mM MeJA + WCS417r revealed the greatest effect, followed by SJ04 (~7 times) and then WCS417r (~5 times).

In plants inoculated with PGPB and then sprayed with 1 mM or 4 MeJA, the EO yield was similar to that in plants which had only been inoculated (Fig. 2). Only in the plants treated with 1 mM MeJA + GB03 and 4 mM MeJA + SJ04 was the EO content similar to that of control plants, and this was less than that in inoculated plants. The EO yield of plants treated with PGPB in addition to SA at 1 and 2 mM concentrations showed an increase of approximately three-fold in comparison to untreated uninoculated controls, but this was generally higher than for either treatment alone (Fig. 2), irrespective of the inoculated strain. The control with solvent for SA did not differ statistically from the control ($p > 0.05$), therefore this is not shown in the figures. In Supplementary Table 2, the native data is shown.

3.3. *JA and SA increased the peltate glandular trichome density by up to 2-fold*

To determine which factors contributed to the increase in essential oil content, we measured the density of the glandular trichomes, which are the structures that synthesize and store monoterpene-rich essential oil. Single glandular capitate trichomes and peltate glandular trichomes were present on the adaxial and abaxial leaf surfaces, with a small capitate glandular trichome consisting of a globose unicellular head attached to the leaf by a two- or three-celled uniseriate stalk. The peltate glandular trichomes consisted of a large eight-celled head with an enlarged secretory cavity attached to a one-celled short stalk, with these trichomes being present on both surfaces of plants, but with their density being higher on the abaxial surface.

PGPB alone induced a 20–25% rise in the peltate glandular trichome density on both surfaces (Table 2), and spraying with MeJA significantly increased the peltate trichome density on the adaxial surface ($p < 0.05$), which was approximately two-fold higher than the control (Tables 2 and 2). On the abaxial surface, MeJA treatment produced the same trend, with the number of peltate trichomes increasing by approximately 50% on plants sprayed with respect to control or PGPB-inoculated plants (Fig. 3). MeJA spraying and PGPB inoculation resulted in the highest densities, especially in plants inoculated with SJ04 and WCS417r and sprayed with 4 mM MeJA. SA applications led to an significantly increased density of peltate trichomes on the adaxial (Table 4) and abaxial surfaces (Fig. 3) compared to control or PGPB-inoculated plants, with plants treated with 2 mM and inoculated with GB03 and WCS417r producing the highest increase in the number of peltate trichomes. As the control with solvent for MeJA and SA did not differ statistically from the control ($p > 0.05$), this is not shown in the figures. In Supplementary Table 3, the native data is shown.

Table 2
Effects of inoculation with PGPB strains on the glandular trichome density of M. x piperita plants. Values are mean ± standard error (SE). Means followed by the same letter in a given column are not significantly different according to Fisher's LSD test ($p < 0.05$). Abbreviations for PGPB strains: G, strain GB03; S, strain SJ04; W, strain WCS417r.

	Adaxial face		*Abaxial face*
	peltate (number per mm^2)	capitate (number per mm^2)	capitate (number per mm^2)
Control	2.35 ± 0.09 a	2.31 ± 0.27 b	7.26 ± 0.47 a
G	3.09 ± 0.16b	2.08 ± 0.16 ab	6.78 ± 0.46 a
S	3.01 ± 0.26	1.98 ± 0.26 ab	6.28 ± 0.49 a
W	3.08 ± 0.15 b	1.54 ± 0.17a	6.39 ± 0.65 a

The density of capitate trichomes on the adaxial surface increased by up to 2-fold after MeJA or SA treatment in comparison to the control, but on the abaxial surface there was no significant change (Tables 3 and 4). PGPB inoculation did not usually significantly alter the density of capitate trichomes with respect to that of control plants (Table 2).

3.4. *Plant weight decreased after JA treatment, but increased after PGPB inoculation*

To determine whether the increase in EO content might be a consequence of alterations in plant growth, we also measured the effect of SA and JA treatments on various plant growth parameters. Spraying with MeJA led to a reduction in fresh weight; and the higher the concentration, the greater was the effect observed. Plants treated with 4 mM weighed on average 20% less than the unsprayed control (Fig. 4). On the other hand, the fresh weight of plants sprayed with SA did not differ from that of controls ($p < 0.05$) (Fig. 4). In contrast, plants inoculated with PGPB exhibited a significant increase in fresh weight of ~40% in comparison to controls ($p < 0.05$). When PGPB (irrespective of the strain evaluated) and MeJA spraying were combined, the PGPB

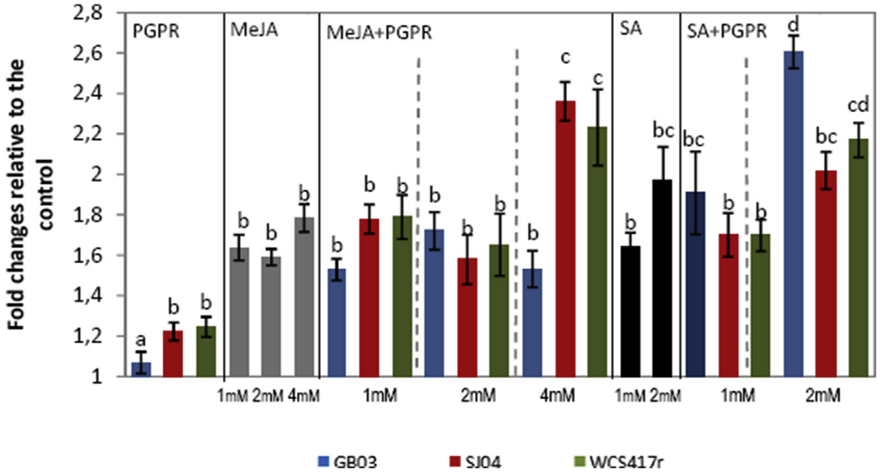

Fig. 3. Inoculation with PGPB and hormone treatments increased the density of peltate glandular trichomes on the abaxial (lower) surface of *M.* x *piperita* leaves. Values are fold changes relative to the control in units of trichomes per mm^2. Different letters above bars indicate significant differences according to Fisher's LSD test ($p < 0.05$). The letter "a" indicates similar to the control. Three different ANOVA analyses were performed (*a)* PGPB- *b)* MeJA + PGPB- *c)* SA + PGPB).Native values are given in supplementary table 2, 3 and 4.

Table 4
Effects of application of SA and PGPB inoculation on the glandular trichome density of *M.* x *piperita* plants. Values are mean ± standard error (SE). Means followed by the same letter in a given column are not significantly different according to Fisher's LSD test ($p < 0.05$).Abbreviations for PGPB strains: G, strain GB03; S, strain SJ04; W, strain WCS417r.

	Adaxial face		*Abaxial face*
	peltate (number per mm^2)	capitate (number per mm^2)	capitate (number per mm^2)
Control	2.29 ± 0.40 ab	2.50 ± 0.34abc	10.03 ± 0.72 ef
1 mM SA	3.62 ± 0.56 bc	3.54 ± 0.47 c	6.38 ± 0.74 cd
2 mM SA	4.80 ± 0.49 d	5.25 ± 0.88 d	12.56 ± 1.18 f
1 mM SA + G	4.37 ± 0.38 bcd	2.45 ± 0.32abc	5.58 ± 0.56 bcd
1 mM SA + S	4.05 ± 0.31bcd	2.01 ± 0.55 ab	5.84 ± 0.56 bcd
1 mM SA + W	4.80 ± 0.26 cd	2.22 ± 0.33abc	3.82 ± 0.71 ab
2 mM SA + G	5.74 ± 0.46 d	6.10 ± 0.33 d	4.38 ± 1.46 abc
2 mM SA + S	5.32 ± 0.45 d	2.93 ± 0.15bc	2.40 ± 0.12a
2 mM SA + W	4.71 ± 0.39 cd	5.52 ± 0.94 d	7.72 ± 0.63 de

increase canceled out most of the decrease in fresh weight due to MeJA, except at 4 mM. However, when PGPB and SA spraying were combined, there was a rise in fresh weight which was similar to the increase seen in plants that had been inoculated with PGPB alone ($p < 0.05$). Only plants inoculated with SJ04 and sprayed with 2 mM did not reveal any difference with controls. The control with solvent for MeJA and SA did not differ statistically from the control ($p > 0.05$), therefore this is not shown in the figures. In Supplementary Table 4, the native data is shown.

Although the number of leaves and branches in plants treated with MeJA and SA did not differ from those of control plants (Tables 6 and 7), the shoot length decreased significantly ($p < 0.05$) after MeJA treatment (by up to one-third), while after SA treatment an increase of up to one-quarter was recorded. After PGPB inoculation, neither leaf, nor branch number, nor shoot length differed from those of controls (Table 5). When PGPB inoculation and MeJA spraying were combined, the leaf and branch number were not affected, while shoot length was reduced for most combinations (Table 5). When PGPB inoculation and SA spraying were combined, leaf and branch number were again not affected, but as before, the shoot length increased for most combinations (Tables 6 and 7).

JA treatment modified the content of other phytohormones.

Spraying MeJA had a significant effect on SA levels, depending on the concentration applied. A concentration of 1 mM led to a reduction in SA by about a half in comparison to the control. However, although a concentration of 2 mM had no effect, a concentration of 4 mM increased SA by about 2-fold (Fig. 5). Related to this, inoculation with PGPB only changed this pattern slightly. Interestingly, compared to PGPB alone (Fig. 1), the levels of endogenous SA measured were always lower when MeJA was applied, regardless of the concentration.

As expected, the JA levels changed significantly ($p < 0.05$) when plants were sprayed with MeJA, with a higher MeJA application resulting in higher endogenous JA concentrations. PGPB inoculation modified these effects at 4 mM MeJA by reducing the endogenous JA levels by approximately 25% in plants sprayed only with 4 mM MeJA.

Table 3
Effects of application of MeJA and PGPB inoculation on the glandular trichome density of *M.*x *piperita* plants. Values are mean ± standard error (SE). Means followed by the same letter in a given column are not significantly different according to Fisher's LSD test ($p < 0.05$). Abbreviations for PGPB strains: G, strain GB03; S, strain SJ04; W, strain WCS417r.

	Adaxial face		*Abaxial face*
	peltate (number per mm^2)	capitate (number per mm^2)	capitate (number per mm^2)
Control	2.20 ± 0.24 a	2.22 ± 0.34 ab	6.50 ± 0.40abc
1 mM MeJA	4.16 ± 0.20bc	3.18 ± 0.35bc	6.97 ± 0.39abc
2 mM MeJA	4.04 ± 0.17b	3.16 ± 0.30 b	9.78 ± 0.57d
4 mM MeJA	4.62 ± 0.25 bc	4.44 ± 0.75cd	8.66 ± 0.60 cd
1 mM MeJA + G	4.06 ± 0.19bc	3.16 ± 0.35bc	9.53 ± 0.71 d
1 mM MeJA + S	4.87 ± 0.40 bcd	2.50 ± 0.31 ab	7.10 ± 0.70abc
1 mM MeJA + W	3.99 ± 0.38b	2.22 ± 0.33 ab	6.95 ± 0.44abc
2 mM MeJA + G	5.69 ± 0.65 d	2.41 ± 0.53 ab	9.55 ± 0.51d
2 mM MeJA + S	4.93 ± 0.46 bcd	2.08 ± 0.14 ab	5.19 ± 0.52 a
2 mM MeJA + W	4.07 ± 0.24bc	2.02 ± 0.26 a	6.28 ± 0.36 ab
4 mM MeJA + G	5.85 ± 0.51 d	4.72 ± 0.57d	10.07 ± 1.00d
4 mM MeJA + S	7.20 ± 0.54e	6.22 ± 0.33e	15.45 ± 1.31e
4 mM MeJA + W	5.16 ± 0.50 cd	3.24 ± 0.29 bc	14.95 ± 1.38e

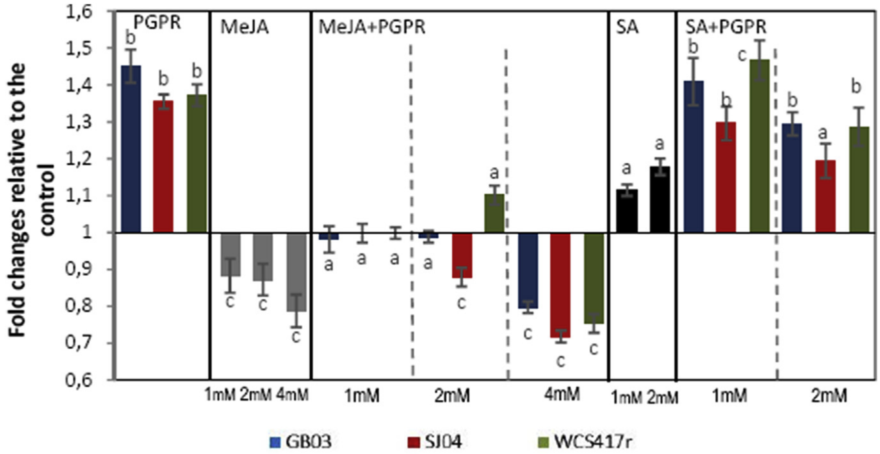

Fig. 4. Inoculation with PGPB and hormone treatments affected the fresh weight of *M.* x *piperita* plants. Values are fold changes relative to the control. Different letters above bars indicate significant differences according to Fisher's LSD test ($p < 0.05$). The letter "a" indicates similar to the control. (Three different ANOVA analyses were performed (*a)*PGPB- *b)*MeJA + PGPB- *c)* SA + PGPB). Native values are given in supplementary table 2, 3 and 4**.**

Table 6
Effects of application of MeJA and PGPB inoculation on growth parameters of *M.*x *piperita* plants. Values are mean ± standard error (SE. Means followed by the same letter in a given column are not significantly different according to Fisher's LSD test ($p < 0.05$). Abbreviations for PGPB strains: G, strain GB03; S, strain SJ04; W, strain WCS417r.

	Leaves (number)	Branches (number)	Shoot length (cm)
Control	19.33 ± 2.67 b	1.00 ± 0.00 a	9.07 ± 0.81ef
Control (for MeJAonly)	18.55 ± 0.65 ab	1.33 ± 0.33 a	9.25 ± 0.25 f
1 mM MeJA	15.33 ± 0.33 ab	1.00 ± 0.00 a	6.33 ± 0.17 abc
2 mM MeJA	14.67 ± 0.67 ab	1.00 ± 0.00 a	7.50 ± 0.29 c-f
4 mM MeJA	18.00 ± 1.15 ab	1.33 ± 0.33 a	6.03 ± 1.12 abc
1 mM MeJA + G	17.80 ± 2.89 ab	2.00 ± 0.55 a	6.10 ± 0.30 abc
1 mM MeJA + S	14.83 ± 0.40 ab	1.00 ± 0.00a	5.63 ± 0.85 abc
1 mM MeJA + W	18.75 ± 1.75 ab	2.00 ± 0.32 a	8.48 ± 0.13 def
2 mM MeJA + G	17.33 ± 1.45 ab	1.33 ± 0.33 a	7.17 ± 0.60 b-e
2 mM MeJA + S	14.50 ± 0.65 a	1.00 ± 0.00 a	5.25 ± 1.03 ab
2 mM MeJA + W	19.33 ± 1.76 b	1.33 ± 0.33 a	6.77 ± 0.96 a-d
4 mM MeJA + G	17.00 ± 1.53 ab	1.67 ± 0.67 a	6.03 ± 0.77 abc
4 mM MeJA + S	17.67 ± 2.33 ab	1.00 ± 0.00 a	4.67 ± 1.17 a
4 mM MeJA + W	16.00 ± 0.71 ab	2.33 ± 1.33 a	5.10 ± 0.97 ab

Table 7
Effects of application of SA and PGPB inoculation on growth parameters of *M.*x *piperita* plants. Values are mean ± standard error (SE). Means followed by the same letter in a given column are not significantly different according to Fisher's LSD test ($p < 0.05$). Abbreviations for PGPB strains: G, strain GB03; S, strain SJ04; W, strain WCS417r.

	Leaves (number)	Branches (number)	Shoot length (cm)
Control	22.75 ± 0.48 a	3.60 ± 0.75 a	7.94 ± 0.34 a
Control (for SA only)	23.75 ± 1.49 a	3.50 ± 0.65 a	8.23 ± 0.25 ab
1 mM SA	25.25 ± 0.48 a	2.60 ± 0.51 a	10.06 ± 0.68 bc
2 mM SA	25.25 ± 4.31 a	2.50 ± 0.87 a	10.18 ± 1.06 bc
1 mM SA + G	24.75 ± 0,75 a	3.00 ± 0.51 a	11.33 ± 0.82 c
1 mM SA + S	27.00 ± 2.08 a	4.40 ± 1.08 a	9.97 ± 0.28 bc
1 mM SA + W	23.00 ± 2.28 a	2.60 ± 0.51a	10.87 ± 0.41 c
2 mM SA + G	24.25 ± 1.70 a	2.50 ± 0.29 a	11.90 ± 1.20 c
2 mM SA + S	24.75 ± 1.89 a	3.75 ± 0.75 a	11.43 ± 0.89 c
2 mM SA + W	25.00 ± 2.77 a	2.80 ± 0.49 a	9.94 ± 0.76 bc

Table 5
Effects of inoculation with PGPB strains on growth parameters of *M.*x *piperita* plants (mean ± SE). Values are mean ± standard error (SE). Means followed by the same letter in a given column are not significantly different according to Fisher's LSD test ($p < 0.05$).Abbreviations for PGPB strains: G, strain GB03; S, strain SJ04; W, strain WCS417r.

	Leaves (number)	Branches (number)	Shoot length (cm)
Control	19.33 ± 1.07 a	1.00 ± 0.00 a	9.07 ± 0.81 a
G	23.00 ± 1.53 b	2.33 ± 0.88 a	9.00 ± 1.04 a
S	21.67 ± 1.28 ab	1.33 ± 0.33 a	8.63 ± 0.52 a
W	20.33 ± 1.67 ab	1.67 ± 0.33 a	8.10 ± 0.97 a

Endogenous JA-Ile levels generally revealed the same increasing trend as JA ($p < 0.05$). Although the levels of the JA precursor OPDA were increased at 4 mM MeJA, there was little or no effect at lower MeJA treatment levels (Fig. 5). PGPB inoculation increased the effect of MeJA on OPDA, but only at 2 mM. Finally, the level of ABA increased significantly upon MeJA application, but only at 4 mM MeJA, and then only by about 25%.

3.5. SA treatment had little effect on the content of other phytohormones

Plants sprayed with 1 and 2 mM SA had significantly increased SA levels, as would be expected (Fig. 6). When combined with PGPB inoculation, there was a slight increase recorded in the SA levels after the 2 mM spraying treatment, compared to the treatment with no PGPB.

The amounts of the jasmonates, JA, JA-Ile and the jasmonate precursor OPDA were generally not affected by the application of SA, except for a 30–50% increase in OPDA in comparison to the unsprayed control (Fig. 6). PGPB inoculation combined with SA increased the JA content by approximately 1.4-fold upon 1 and 2 mM spraying, increased the JA-Ile content by approximately 3-fold upon 2 mM spraying, and resulted in differing effects on OPDA compared to plants treated with SA alone.

The level of ABA did not reveal any change in plants sprayed with 1 and 2 mM SA with respect to unsprayed controls (Fig. 6). In addition, PGPB inoculation combined with SA gave variable but only small changes in ABA content compared with controls treated with SA only.

4. Discussion

4.1. The induction of JA and SA by PGPB observed in peppermint

In order to try to gain a better understanding of how PGPB can cause an increase in the essential oil of peppermint and various other Lamiaceae and Asteraceae species, we measured changes in the plant defense hormones in peppermint leaves after inoculation with three different PGPB strains. The endogenous JA levels registered increases of approximately two-fold, and those of the JA-Ile levels of up to 4-fold, in inoculated plants compared to non-inoculated ones regardless of the strain used. Previous work on the mechanism of PGPB action has

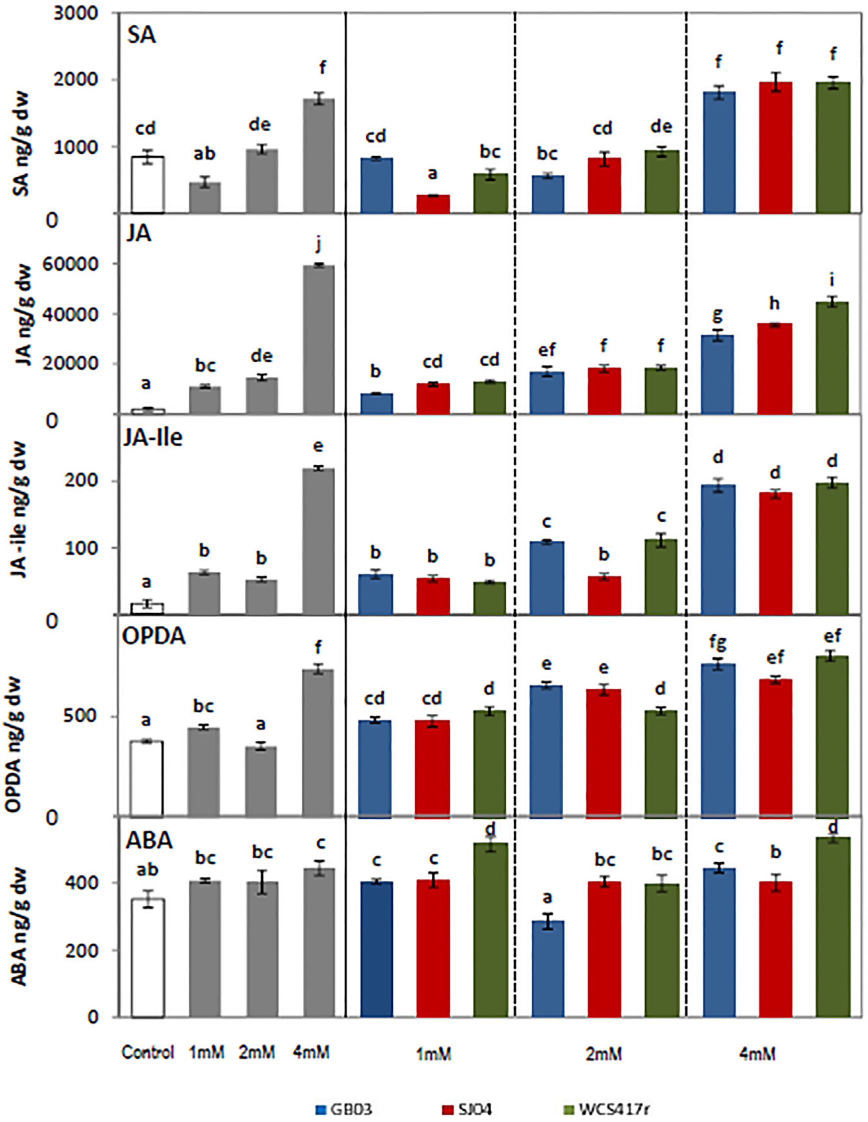

Fig. 5. Effect of MeJA treatment and PGPB inoculation on endogenous hormone levels in *M.* x *piperita*. Values are mean ± standard error (SE). Different letters above bars indicate significant differences according to Fisher's LSD test ($p < 0.05$).

focused on its role in triggering induced systemic resistance (ISR) to pathogens. However, the colonization of roots by PGPB is often not associated with an increase in the production of JA Pieterse et al., (2000). In fact, ISR appears to be based on a higher sensitivity rather than an increased production of this hormone (Pieterse et al., (2000), 2014). In contrast, we observed a significant increase in free jasmonic acid and the active form JA-Ile in *M. piperita* plants inoculated with different rhizobacteria strains.

We also measured a 4–5-fold increase in the defense hormone SA upon PGPB inoculation in *M.* x *piperita*. Earlier work on this topic had shown that PGPB effects, such as ISR, are not mediated by SA signaling. For example, whether Arabidopsis plants could or could not accumulate SA had no effect on the ISR induced by *Pseudomonas fluorescens*WCS417r, a strain also used in our study, and therefore ISR did not coincide with enhanced SA levels (van Wees et al., 1997; Pieterse et al., 2000, 2012). However, more recently several PGPB have been reported to trigger a rise in the endogenous level of salicylic acid in various parts of plants (Singh et al., 2003; Tjamos et al., 2005; van de Mortel et al., 2012; Li et al., 2015).While the induction of SA and JA by PGPB may have various benefits for their host plants, the increase of these two defense hormones suggests that plants may perceive these bacteria as a threat and thereby initiate a defensive response.

Several PGPB strains can also synthesize ABA (Sgroy et al., 2009; Salomon et al., 2014; Cohen et al., 2015), but the inoculation of peppermint with PGPB did not modify endogenous the ABA levels. In addition, no change in ABA content was observed in tomato plants inoculated with *Bacillus megaterium* (Porcel et al., 2014).

4.2. Both JA and SA stimulate the formation of essential oil of peppermint

Jasmonates are not only induced by PGPB in *M.* x *piperita*, but are at least partially responsible for PGPB-caused stimulation of the monoterpene-rich essential oil of this species. When we sprayed jasmonates in the form of MeJA on *M.* x *piperita* foliage, the essential oil content increased by up to 5-fold in a dose-dependent manner.

The exogenous application of JA has long been known to increase secondary metabolites, including alkaloids, phenolics and terpenes in aromatic and medicinal plants (Gundlach et al., 1992; Patt et al., 2018; Wasternack and Strnad, 2017).Treatment with JA significantly increased the content of EO and its constituent monoterpenes, linalool, eugenol and limonene in the aromatic and medicinal plant *Ocimum basilicum* (basil), in which the monoterpenes accumulate in glandular trichomes (Zlotek et al., 2016). In conifers, the exogenous application of JA induced the accumulation of monoterpenes and diterpenes in the

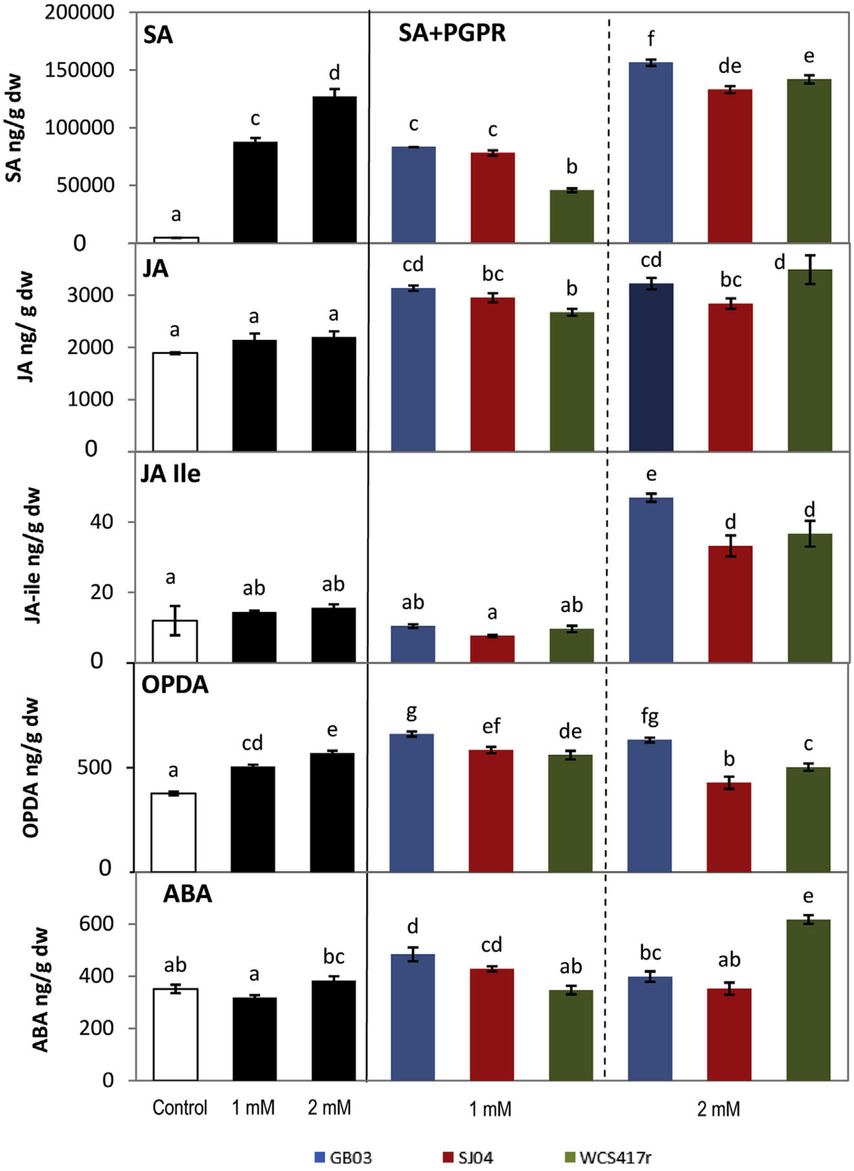

Fig. 6. Effect of SA treatment and PGPB inoculation on endogenous hormone levels in *M.* x *piperita*. Values are fold changes relative to the control. Different letters above bars indicate significant differences according to Fisher's LSD test ($p < 0.05$).

resin ducts of *Picea abies* stems (Schmidt et al., 2011). In contrast, treatment with JA did not produce a significant increase in terpenoids in eucalyptus leaves, which stores monoterpenes in secretory cavities (Henery et al., 2008). Treatment with JA also increased the transcript levels of the *LeMTS1* gene, which encodes a monoterpene synthase producing linalool located in the glandular trichomes of tomato plants (van Schie et al., 2007).

Other factors are also involved in stimulating EO content in addition to jasmonates, since when PGPB inoculation was combined with 2 mM MeJA treatment, the EO yield increased by up to 8-fold above that observed in untreated control plants (Fig. 2). In addition, this increase in EO was not necessarily correlated with the level of endogenous jasmonates measured. For example, plants sprayed with 4 mM MeJA either with and without PGPB inoculation had the highest of levels of jasmonates, but the highest EO yield was found in plants sprayed with 2 mM MeJA and inoculated with PGPB (compare Figs. 2 and 5).

The role of SA in the PGPB induction of EO was also confirmed by the EO increase recorded after SA spraying. Nevertheless, SA does not simply work through JA, as plants treated with 2 mM SA showed an increased EO without any rise in endogenous JA and JA-Ile levels. This result suggests that the biosynthesis of *M.* x *piperita* monoterpenes is both SA and JA dependent.

SA treatment is known to activate genes of the terpene metabolism. For example, genes from the chloroplastic MEP pathway, and also those from the cytosolic mevalonate pathway, have been shown to be transcriptionally upregulated by SA in the terpene-accumulating *Salvia miltiorhiza* and *Michelia chapensis*, respectively (Yan et al., 2009; Cao et al., 2012). Moreover, the expression of three prenyl transferases from the core terpenoid biosynthetic pathway has been shown to be upregulated by SA in different species (Kai et al., 2010; Shabani et al., 2010; Cao et al., 2012). Holm oaks fumigated with SA revealed higher monoterpene levels in leaves and also enhanced volatile monoterpene emission (Peñuelas et al., 2007). Furthermore, Zhang et al. (2013) reported that treatment of *Glycine* max with 1 mM SA induced transcription of a newly identified gene encoding a monoterpene synthase. Thus, although JA and SA are often thought to be antagonistic defense hormones that work in opposite ways (Nomura et al., 2005; Pietrese and Dicke, 2007), the formation of terpenes in *M.* x *piperita* appears to be a result of a cooperation between the two hormones.

It is important to take into account that the yield or chemical composition in aromatic plants is also significantly affected by numerous factors, including environment, physiology of the plant, agronomic management and genetic factors (Verpoorte et al., 2002), as well as the presence of other soil beneficial microorganisms such as arbuscular mycorrhizal (AM) fungi. Copetta et al. (2006) inoculated AM *Gigaspora rosea* fungus in cultivars of Ocimum basilicum, and observed increases in oil yield associated with a significantly larger number of peltate glandular trichomes. Similar results were also observed in *Mentha arvensis* cultivars inoculated with the fungus *Glomus fasciculatum* (Gupta et al., 2002).

4.3. JA and SA both stimulate an increased density of monoterpene-accumulating glandular trichomes

The EO content of peppermint leaves is closely correlated with the total number of glandular trichomes present (Turner et al., 2000; Lange et al., 2011; Lange and Turner, 2013). Thus, we measured the effect of PGPB and hormone treatments on the glandular trichome density. Although peppermint has both peltate and capitate glandular trichomes, only the peltate glandular trichomes accumulate monoterpenes. The density of both types was positively correlated with EO content, with PGPB inoculation resulting in an increase in glandular trichome density on the abaxial and adaxial surfaces, in agreement with previous observations (Cappellari et al., 2015). In the current study, we also showed that plants sprayed with MeJA, regardless of the concentration, exhibited an increase in the peltate glandular trichome density.

JA has been previously associated with glandular trichome formation in tomato (Li et al., 2003; Maes and Goossens, 2010; Bosch et al., 2014). This is perhaps best seen in mutant lines with defects in JA biosynthesis, which have shown reductions in the number of glandular trichomes and in the terpene constituents synthesized and stored in these structures. In addition, the exogenous application of 7.5 mM MeJA to leaves of tomato plants led to an increase in the density of glandular trichomes in new leaves of tomato plants (Boughton et al., 2005). JA seems to stimulate both the initiation of glandular trichomes and their accumulation of EO. However, these two processes do not respond in identical ways to JA in *M.* x *piperita*. We observed the highest density of peltate glandular trichomes after treatment with PGPB inoculation and 4 mM MeJA (Fig. 3), with the highest level of EO accumulation being achieved with PGPB and 2 mM MeJA (Fig. 2).

Spraying with SA also significantly increased the number of peltate glandular trichomes on peppermint, suggesting that SA is also involved in the regulation of the formation of these structures. However, the glandular trichome density was similar in plants that were SA-sprayed or PGPB-inoculated, but when plants were 2 mM sprayed and inoculated the density increased significantly. Moreover, since plants treated with SA alone did not exhibit increased endogenous levels of JA or JA-Ile, the increased density of glandular trichomes is based on more than just JA. In a previous study, *Arabidopsis* plants exposed to exogenous SA had a lower number of non-glandular trichomes on their adaxial surface than control plants (Traw and Bergelson, 2003), but no information was given about SA or glandular trichomes.

4.4. The opposing effects of PGPB (positive) and JA (negative) on plant growth illustrate that PGPB does more than just trigger increased hormone levels

The ability of PGPB to enhance plant growth and development following inoculation, a property inherent in their name, has been reported for many plant species in addition to aromatic plants (Vessey, 2003; Gray and Smith, 2005; van Loon, 2007; Etesami and Maheshwari, 2018; Gouda et al., 2018). Yet, the reasons for this enhancement differ according to the plant, and may include both direct and indirect mechanisms (Glick, 1995). In aromatic plants, such as *Origanum majoricum*, *O. majorana*, *Tagetesminuta* and *M.* x *piperita,* the magnitude of growth promotion also depends on the strain of bacteria used for inoculation (Banchio et al., 2010; Cappellari et al., 2013), with various PGPB having been shown to produce auxins, cytokinins, gibberellins and volatile organic compounds in amounts that can promote plant development (Zahir et al., 2004; van Loon, 2007; Vespermann et al., 2007; Santoro et al., 2011).

The exogenous application of MeJA, in contrast, inhibited the growth of *M.* x *piperita* in a concentration-dependent manner. Moreover, the inhibition of plant growth after treatment with jasmonates has been reported in many plant species under different growing conditions (Baldwin, 1998; Zhang and Turner, 2008; Krzyzanowska et al., 2012; Heinrich et al., 2013; Shyu and Brutnell, 2015). The synthesis of JA has been determined to have an antagonistic effect on the biosynthesis and accumulation of gibberellins, leading to a delay in plant development (Yang et al., 2012; Heinrich et al., 2013; Shahzad et al., 2015). JA may also interfere negatively with the other hormones involved in the regulation of growth, such as auxin, brassinosteroids and cytokinins. In addition, JA has a negative effect on the progression of the cell cycle in cell cultures, particularly on mitosis (Noir et al., 2013).

The opposite effects of JA and PGPB on plant growth observed in this study indicate that PGPB do not act by merely inducing JA. In fact, plant growth and development are controlled by a balance among several hormones that interact in multiple ways (Grant and Jones, 2009; Depuydt and Hardtke, 2011). In our present study, while JA reduced the growth rate in peppermint plants by 25%, it stimulated EO accumulation by up to 3–5 fold.

The application of SA did not affect the growth of *M.* x *piperita* and did not override the growth influence of the PGPB. However, several studies have reported that SA or its methylated derivative, MeSA, positively affects plant development. Gutiérrez-Coronado et al. (1998), reported that SA treatment stimulated the development of soybean plants, and seeds of rice plants (*Oryza sativa*) treated with MeSA revealed a significant increase in the weight of both the stem and the root (Kalaivani et al., 2016).

4.5. JA induces SA in peppermint leaves, but not vice versa

Since both JA and SA appeared to be involved in PGPB stimulation of EO content in *M.* x *piperita*, we investigated whether either of these hormones was able to induce the other. When plants were treated with JA, the SA response varied. At 1 mM MeJA, the level of SA decreased by half, whereas at 2 mM MeJA it was not significantly altered. However, at 4 mMMeJA the SA level increased nearly 2-fold (Fig. 5). A decline in SA indicates an antagonism between these two hormones, a situation frequently described in the literature, with negative crosstalk between SA and JA first being described in tomato many years ago (Penacortes et al., 1993; Doares et al., 1995), More recently, this has been observed in many other dicots (Pieterse et al., 2012) and monocots (Tamaoki et al., 2013). On the other hand, the increase in SA with JA suggests the existence of synergistic effects between the JA and SA signaling pathways, as also previously reported (Schenk et al., 2000; Mur et al., 2006).

In contrast, when peppermint plants were treated with SA, the endogenous levels of JA and JA-Ile were not altered, but OPDA increased by up to 40%, suggesting that SA did not affect JA formation as in effector-triggered immunity against pathogens in Arabidopsis (Liu et al., 2016). The JA and SA pathways are connected by nodes of positive and negative crosstalk and interact in a complex manner (Schweiger et al., 2014). Therefore, it is not surprising that both antagonistic and synergistic interactions between the two hormones have been observed, depending on their concentrations (Mur et al., 2006).

5. Conclusions

The use of PGPB in agriculture is gaining importance and having an ever increasing role in crop-growing systems throughout the world.

PGPB are not only ecologically friendly, but are also cost-effective, reliable and durable.

In the present study, we showed that the endogenous levels of SA and JA increase after PGPB inoculation, suggesting that both phytohormones are involved in the signaling pathways elicited by rhizobacteria. PGPB inoculation has been shown to increase the EO yield in *M. piperita* plants (Cappellari et al., 2015), but the promotion of the growth and the increased EO production induced by PGPB cannot be replaced by the external application of phytohormones (as JA causes an increase in EO yield, but a decrease in growth). In the present study, we observed that in addition to inoculation, the external application of MeJA at 2 mM increased the EO production by up to 8-fold, indicating that there is synergy between PGPB and MeJA. Thus, from a biotechnological standpoint, our findings could be useful to help improve the production of EOs. Nevertheless, further studies are still required in order to determine the main molecular mechanisms driving the increase in essential oil after PGPB inoculation.

From a biotechnological point of view, the data obtained in the present investigation could be used in future to improve the production of EOs.

Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Funding

This study was supported by grants from the Secretaría de Ciencia y Técnica de la Universidad Nacional de Río Cuarto, the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), MinCyT Córdoba, the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) PICT 0636/14, Argentina, and financial support was given to EB from the Georg Förster Research Fellowship of the Alexander von Humboldt Foundation. EB is a Career Member of CONICET. LC and MVS received fellowships from CONICET- MinCyT.

Author contributions

LC and MVS performed the experiments; EB designed the research and analyzed the data. AS and JG were involved in data interpretation. EB, AS and JG wrote the manuscript. All authors read, revised and approved the final manuscript.

Acknowledgments

This study was supported by grants from the Secretaría de Ciencia y Técnica de la Universidad Nacional de Río Cuarto, the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), MinCyT Córdoba, and the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) PICT 0636-14, Argentina. EB obtained financial support from a Georg Forster-Research Fellowship of the Alexander von Humboldt Foundation. EB and WG are Career Members of CONICET. LC and MVS received fellowships from CONICET- MinCyT. The authors are grateful to Dr. Paul Hobson, native speaker, for editorial assistance.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.plaphy.2019.05.030.

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