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Evaluation of systemic acquired resistance inducers for control of *Phytophthora capsici* on squash

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ABSTRACT

Phytophthora blight induced by *Phytophthora capsici* is a major constraint in vegetable production worldwide. Limited information is available regarding potential systemic acquired resistance (SAR) inducers that may provide protection of squash (*Cucurbita pepo*) plants against the disease and the direct effect of the products on the pathogen. In this study, the effect of DL-3-aminobutyric acid (BABA), 2,6-dichloroisonicotinic acid (INA), Saver (a.i. salicylic acid), Syrup (nutrient supplement), and acibenzolar-*S*-methyl (ASM) on mycelial growth, zoospore germination and sporangium production of *P. capsici* was evaluated. The products were tested in *in vitro* studies at concentrations ranging from 25 to 2000 $\mu g\,ml^{-1}$. Mycelial growth and zoospore germination were generally not significantly affected by BABA and ASM and sporangium production was not significantly affected by BABA. INA and Saver reduced mycelial growth and sporangium production significantly at 100 $\mu g\,ml^{-1}$ or higher concentrations and zoospore germination at 500 and 1000 $\mu g\,ml^{-1}$. In greenhouse studies, all the products applied as a soil drench or foliar spray at 25 or 50 $\mu g\,ml^{-1}$ significantly reduced disease severity on squash, compared with the pathogen-only control, and zoospores at a concentration of 10^3 spores ml^{-1} were used to inoculate the leaves. INA, BABA, and ASM also reduced disease significantly when zoospores at 10^3 spores ml^{-1} were used to inoculate the root. The results indicated that most of the SAR inducers did not inhibit the growth of the pathogen at concentrations generally recommended for use but had the potential to suppress the disease on squash significantly.

1. Introduction

Phytophthora blight caused by *Phytophthora capsici* is a devastating disease and a major constraint in the production of cucurbits, peppers, tomatoes, and several other vegetable crops throughout the world. The pathogen causes plant wilt, root rot, crown rot, seedling damping-off, leaf and stem blight, and fruit rot and results in significant yield and quality loss (Erwin and Ribeiro, 1996). The efficacy of current strategies for management of this disease is limited. No single fungicide has consistently and effectively suppressed losses related to *P. capsici* epidemics. While fungicides containing the active ingredient mefenoxam provide some level of control of *P. capsici*, mefenoxam-resistant strains of *P. capsici* have developed that challenge the usefulness of this compound (Gevens et al., 2007; Lamour and Hausbeck, 2000; Mathis, 1999). On squash (*Cucurbita pepo*), cultivars with resistance to this disease are not available. Due to its destructive nature and lack of efficient control measures, development of alternative or complementary approaches for management of this disease is highly desirable.

A control practice that has shown promise for plant disease management is the use of systemically induced plant resistance. The plant possesses a range of defences that can be activated to protect it from diseases. This defence response, termed systemic acquired resistance, can be localized at the site of application of an inducer and can also be transmitted systemically to other plant tissues (Kessmann et al., 1994). Systemic acquired resistance (SAR) inducers can be chemical compounds, metabolic substances of the host plant, or microorganisms, which induce plant resistance through activation of a plant's signalling pathways such as the salicylic acid pathway (Achuo et al., 2004; Métraux et al., 1990).

A number of SAR inducers have been evaluated for control of different plant diseases. For example, salicylic acid was shown to induce resistance to Cucumber mosaic virus (CMV) in squash and tobacco (Mayers et al., 2005). 2,6-Dichloroisonicotinic acid (INA) was effective against a wide range of pathogens and was mediated

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by a salicylic acid-dependent process (Walters and Boyle, 2005). Bokshi et al. (2006) indicated that INA increased chitinase and peroxidase activities and reduced powdery mildew and downy mildew on leaves of melons. DL-3-aminobutyric acid (BABA) is a non-protein amino acid that appeared to enhance resistance in pepper against *P. capsici* and in tomato against late blight disease caused by *Phytophthora infestans* (Jeun et al., 2000; Lee et al., 2000). A BABA and mancozeb mixture exhibited a synergetic effect compared to the application of BABA or mancozeb alone in disease control (Baider and Cohen, 2003). Enhanced resistance by BABA in tomato against *P. infestans* was correlated with the accumulation of pathogenesis related proteins such as PR-1 chitinase, β-1,3-glucanase, and AP24 (Cohen et al., 1994; Jeun and Buchnauer, 2001). In recent years, a SAR inducer acibenzolar-*S*-methyl (ASM) had been studied for control of plant diseases. Application of ASM significantly reduced Phytophthora blight on pepper (Matheron and Porchas, 2000). ASM acts as a functional analog of salicylic acid in the SAR signalling pathway and enhanced expression of resistance related genes and accumulation of lignin and phenolic compounds. It also increased the activity of peroxidase, phenylalanine ammonia lyase, chalcone isomerise and reactive oxygen species (Benhamou and Nicole, 1999; Bokshi et al., 2003; Buzi et al., 2004; Malolepsza, 2006; Soylu et al., 2003). Integrated use of ASM and soil fumigation enhanced suppression of root-knot and bacterial wilt on tomato (Ji et al., 2007). Induced host resistance has the potential as an effective means for suppression of a number of diseases. However, the effect of SAR inducers on *P. capsici* and Phytophthora blight on squash has not been well documented.

This study was conducted to evaluate several SAR inducers to determine if they suppress the growth of *P. capsici in vitro* and disease development on squash. Identifying effective SAR inducers will not only provide an alternative means for control of Phytophthora blight on squash, but also provide new information to develop strategies integrating this technology with standard fungicides and other disease management approaches.

2. Materials and methods

2.1. SAR inducers

"Saver" is a product provided by Plant Food Systems, Inc. (Zellwood, FL, USA) that contains salicylic acid as the active ingredient. Maui liquid compost factor (LCF) "Syrup", provided by ABR, LLC (Puunene, HI, USA), contains a number of compounds including nitrogen (0.3%) and soluble potash (2.25%). Acibenzolar-*S*-methyl (ASM, Actigard 50WG) was provided by Syngenta Crop Protection (Greensboro, NC, USA). BABA (DL-3-aminobutyric acid) was purchased from Fluka (Buchs, Switzerland) and INA (2,6-dichloroisonicolinic acid) was purchased from Aldrich (Natick, MA, USA). Concentrations of Saver, ASM, BABA, and INA mentioned in this study are concentrations of active ingredients of the products.

2.2. Effect of SAR inducers on mycelial growth of P. capsici

A *P. capsici* strain isolated from squash in Tifton, GA, USA, was grown on V8 juice agar (V8 juice, 50 ml; $CaCO_3$, 2 g; agar, 17 g; distilled water, 950 ml) at 25 °C for 5 d. An agar plug (7 mm in diameter) was taken from the edge of the colony and placed at the centre of a potato dextrose agar (PDA) plate amended with each product at a final concentration of 0, 25, 50, 100, 500, 1000, and 2000 μg ml^{-1}. Triplicate plates were used for each concentration and the plates were incubated at 25 °C in the dark. Two perpendicular colony diameters were measured per plate 8 d after incubation and diameter of colonies was calculated for each concentration using the mean of the two perpendicular colony diameters (Keinath, 2007). The diameter of the agar plug was subtracted from the colony diameter for calculating diameter of colony. The experiments were conducted twice under the similar conditions.

2.3. Effect of SAR inducers on zoospore germination

Zoospores were produced using the methods described previously with minor modifications (Keinath, 2007). A 7-mm-diameter plug removed from the edge of an actively growing culture was placed on a V8 agar plate. The plates were incubated at 25 °C for 4 d with a 16-h photoperiod. The plates were flooded with 10 ml sterile distilled water, chilled at 4 °C for 45 min, and then held at 23–25 °C for 20 min to allow zoospore release. Five drops of zoospore suspensions were streaked on PDA amended with SAR inducers at concentrations of 0, 25, 100, 500, and 1000 μg ml^{-1}. The experiment was repeated twice with triplicate plates used for each

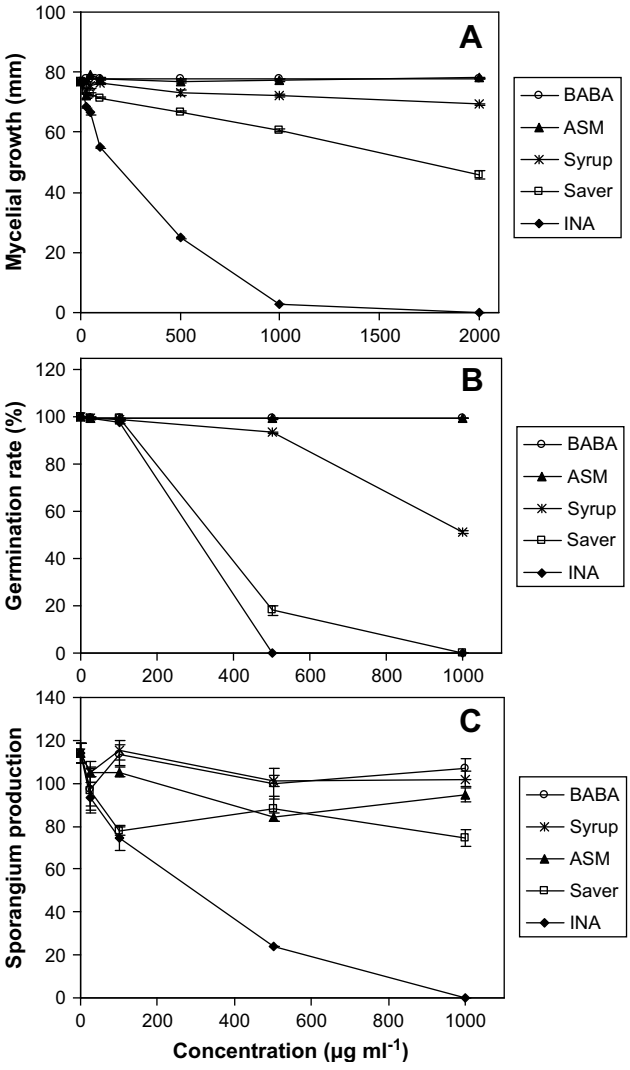

Fig. 1. Effect of different concentrations of SAR inducers on mycelial growth, zoospore germination and sporangium production of *P. capsici*. (A) Colony diameter (mm) of *P. capsici* on PDA amended with SAR inducers 8 d after incubation. (B) Zoospore germination rate (%) of *P. capsici* on PDA amended with SAR inducers 2 h after incubation. (C) Sporangium production (mean number per field under microscope) of *P. capsici* at different concentrations of SAR inducers 2 d after incubation. Data are means of two repeated experiments. The bar on each point represents the standard error of the mean and bars with length less than the diameters of the data points are not visible.

Table 1
Relationship between concentrations of SAR inducers and growth of *Phytophthora capsici*.

Product[a]	Mycelial growth			Zoospore germination			Sporangium production		
	Intercept	Slope	*P*	Intercept	Slope	*P*	Intercept	Slope	*P*
BABA	76.4	0.0009	0.17	99.7	−0.0001	0.67	107.2	−0.003	0.63
ASM	76.4	0.0009	0.17	99.7	−0.0002	0.50	106.7	−0.02	0.007
Syrup	76.2	−0.004	<0.0001	103.7	−0.046	<0.0001	111.1	−0.01	0.012
Saver	74.3	−0.01	<0.0001	99.5	−0.11	<0.0001	98.0	−0.02	0.012
INA	62.4	−0.04	<0.0001	97.0	−0.12	<0.0001	95.7	−0.11	<0.0001

[a] The SAR inducers were used at 0, 25, 50, 100, 500, 1000, and 2000 μg ml^{-1} for mycelial growth and 0, 25, 100, 500, and 1000 μg ml^{-1} for zoospore germination and sporangium production.

concentration in each experiment. The plates were incubated at 23–25 °C for 2 h and germinated and non-germinated zoospores were counted for 100 zoospores on each plate under a stereomicroscope at 100× magnification. The relative rate of germinated zoospores was calculated by dividing the number of germinated zoospores per 100 zoospores on SAR inducer amended medium by the number of germinated zoospores per 100 zoospores on non-amended medium as described previously (Keinath, 2007).

2.4. Effect of SAR inducers on sporangium formation

The fungus was grown on V8 agar plates wrapped with parafilm at 25 °C for 4 d in the dark. Five 10-mm-diameter plugs removed from the edge of an actively growing culture were placed with the mycelium side up in a Petri dish containing sterilized distilled water amended with the compounds at final concentrations of 0, 25, 100, 500, and 1000 μg ml^{-1}. Five Petri dishes were used for each concentration and the Petri dishes, not wrapped with parafilm, were incubated at 23–25 °C under continuous light. After 48 h agar plugs were stained and fixed with acid fuchsin in 85% lactic acid. The number of sporangia on two microscopic fields of each agar plug was counted under a stereomicroscope at 100× magnification. The experiment was repeated one more time under the same conditions.

2.5. Application of SAR inducers in greenhouse

Seeds of yellow squash (cv. Destiny) were grown in 10-cm pots containing a potting mix (Miracle-Gro Lawn Products, Inc., Marysville, OH, USA) in the greenhouse (27 ± 2 °C) for a week. The seedlings were treated with the SAR inducers by applying 25 ml of solution at 25 or 50 μg ml^{-1} into each pot as a soil drench. The pots were arranged in randomized complete blocks (RCB) with four replicates and three plants in each replicate. Six days later the plants were treated with the compounds at the same concentrations by spraying 60 ml of solution onto 12 plants using a hand held garden sprayer. Three additional foliar applications of the compounds were made in the greenhouse once a week after pathogen inoculation.

2.6. Application of inoculum in greenhouse studies

Zoospores were produced as described earlier and immobilized by vortex and the concentrations of zoospore suspensions were adjusted to 10^3 and 10^4 zoospores ml^{-1}. Plants were inoculated 5 d after the first foliar application of SAR inducers. The plants were maintained in a moisture chamber with a relative humidity > 95% for 24 h prior to inoculation. For leaf inoculation, a drop of 50 μl of zoospore suspension was placed near the midrib on the first true leaf of the seedlings. For root inoculation in separate experiments, 5 ml of zoospore suspension was applied to the soil surface near the plant. Non-inoculated plants were treated with the same amount of sterile distilled water. Plants were maintained in the moisture chamber for 24 h after inoculation and then kept in the greenhouse. The experiments were repeated one more time under the same conditions.

2.7. Evaluation of disease and data analysis

In leaf inoculation experiments, disease severity was measured once a week using the following scale: 0 = no disease, 1 = small necrotic lesion on the leaf, 2 = large lesion on the leaf, 3 = leaf blight and petiole necrosis, 4 = leaf blight, petiole necrosis and stem lesions, and 5 = dead plant. In root inoculation experiments, soil was washed off the roots under running tap water and disease on roots was evaluated according to the following scale: 0 = no disease, 1 = 1–50% of root affected, 2 = more than 50% of roots affected, 3 = root rot and crown rot (lesion does not reach 1 cm in height from stem base), 4 = root rot and crown rot (lesion reaches 1 cm or greater in height from stem base), and 5 = dead plant. Plant height and fresh weight were measured at the end of the experiments. Disease data were analysed using the ANOVA or GLM procedures of the Statistical

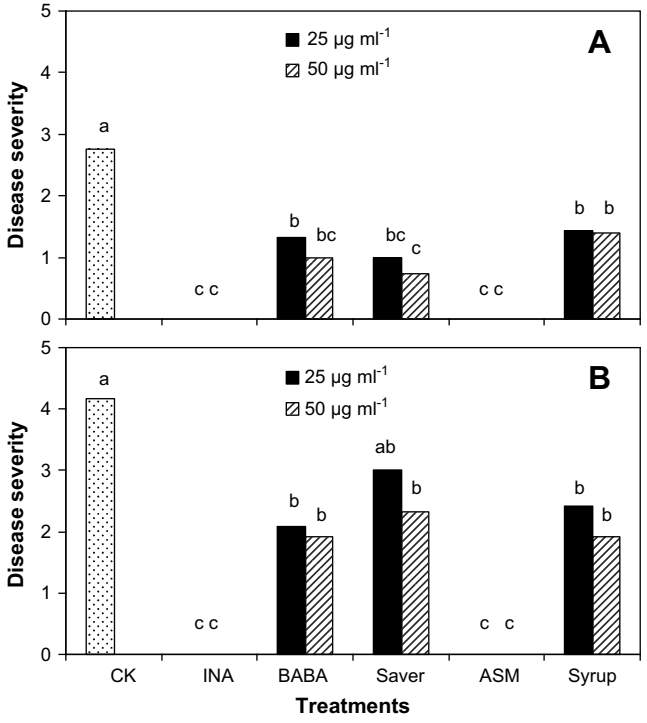

Fig. 2. Inoculation of squash leaves with *P. capsici* to evaluate effect of SAR inducers on Phytophthora blight in greenhouse studies. The SAR inducers were applied at 25 and 50 μg ml^{-1} and zoospore suspensions at concentrations of 10^3 zoospores ml^{-1} (A) or 10^4 zoospores ml^{-1} (B) were used to inoculate the leaves. Data are means of two repeated experiments. Same letter indicates no significant difference according to the least significant difference test at $P = 0.05$.

Analysis System (SAS Institute, Cary, NC). Orthogonal contrasts and least significant difference were used to compare the means. Mycelial growth, zoospore germination, sporangium production and plant growth data were analyzed using the GLM procedures and linear regression analysis (PROC REG) in SAS.

3. Results

3.1. Effect of SAR inducers on mycelial growth, zoospore germination and sporangium production

Mycelial growth of *P. capsici* was generally not inhibited by BABA and ASM at all the concentrations used (Fig. 1, Table 1). Syrup reduced mycelial growth at a concentration of 500 μg ml^{-1} or higher and Saver inhibited mycelial growth at 100 μg ml^{-1} or higher concentrations. Reduction of mycelial growth was significantly correlated with increasing concentrations of INA which significantly inhibited mycelial growth at all concentrations (Fig. 1, Table 1). Zoospore germination was not affected by BABA and ASM (Fig. 1, Table 1). Syrup, Saver and INA inhibited zoospore germination significantly at 500 and 1000 μg ml^{-1}. Sporangium production was generally not significantly affected by BABA (Fig. 1, Table 1). ASM reduced sporangium production at 500 and 1000 μg ml^{-1}. Saver reduced sporangium production significantly at 100 μg ml^{-1} or higher concentrations. Reduction of sporangium production was significantly correlated with increasing concentrations of INA (Fig. 1, Table 1).

3.2. Reduction of disease severity by SAR inducers

All the products applied at 25 or 50 μg ml^{-1} as a soil drench and foliar spray significantly reduced disease severity on squash, compared with the pathogen-only control, and zoospores at a concentration of 10^3 spores ml^{-1} were used to inoculate the leaves (Fig. 2). When zoospores were used at a concentration of 10^4 spores ml^{-1} all the products, except Saver at 25 μg ml^{-1}, reduced disease significantly. No Phytophthora blight symptom was observed when the plants were treated with INA or ASM (Fig. 2). Plants that died of Phytophthora blight ranged from 0 to 50% when zoospores at a concentration of 10^3 spores ml^{-1} were used and 0–83.3% when zoospores at 10^4 spores ml^{-1} were used as inoculum.

INA, BABA, and ASM reduced disease significantly when applied as a foliar spray and root drench and zoospores at 10^3 spores ml^{-1} were used to inoculate the root (Fig. 3). INA and ASM also reduced disease when zoospores at 10^4 spores ml^{-1} were used as inoculum. Plants that died of Phytophthora blight ranged from 0 to 75% when zoospores at a concentration of 10^3 spores ml^{-1} were used and 0–100% when zoospores at 10^4 spores ml^{-1} were used as inoculum.

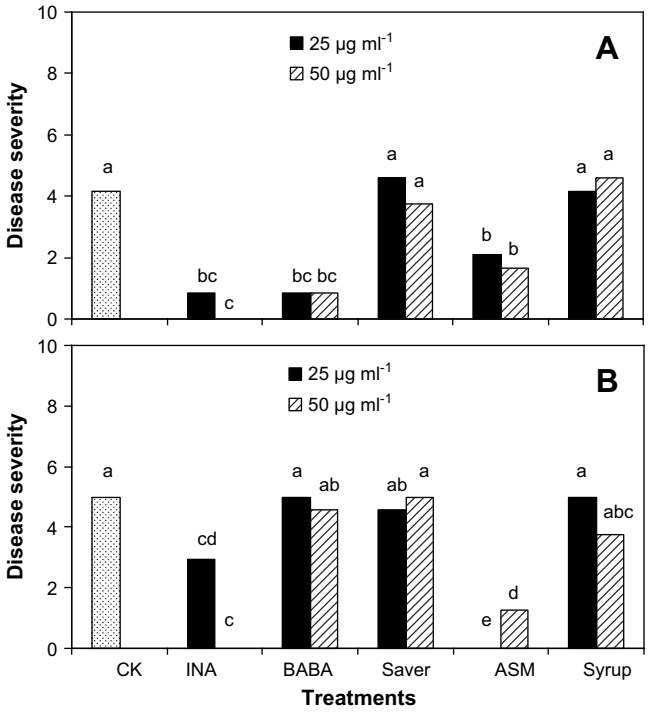

Fig. 3. Inoculation of squash roots with *P. capsici* to evaluate effect of SAR inducers on Phytophthora blight in greenhouse studies. The SAR inducers were applied at 25 and 50 μg ml^{-1} and zoospore suspensions at concentrations of 10^3 zoospores ml^{-1} (A) or 10^4 zoospores ml^{-1} (B) were used to inoculate the root. Data are means of two repeated experiments. Same letter indicates no significant difference according to the least significant difference test at $P = 0.05$.

3.3. Effect of SAR inducers on plant growth

All the plants that survived were sampled and plant fresh weight and height were measured. Weight and height of the surviving seedlings treated with Syrup, Saver, BABA, ASM, and INA

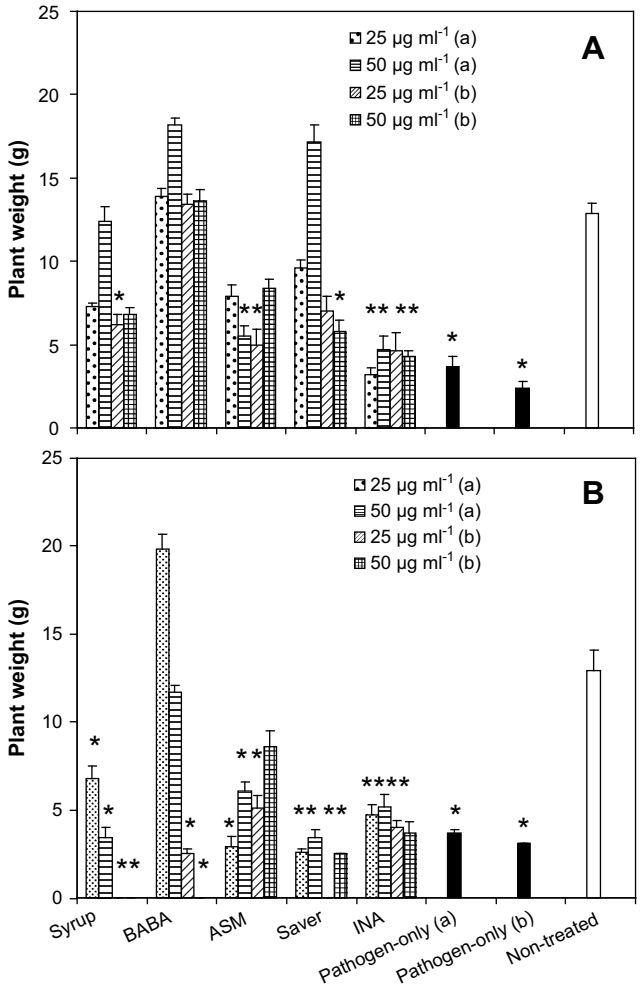

Fig. 4. Weight of surviving squash plants in greenhouse studies. The SAR inducers were applied at 25 and 50 μg ml^{-1} and zoospore suspensions at concentrations of 10^3 zoospores ml^{-1} (a) or 10^4 zoospores ml^{-1} (b) were used to inoculate the leaves (Fig. 4A) or roots (Fig. 4B). Data are means of two repeated experiments. The error bar represents the standard error of the mean. "*" above each bar indicates significant difference between the treatment and the non-treated control according to the least significant difference test at $P = 0.05$.

were either greater or not significantly different compared with the pathogen-only control (Figs. 4 and 5). Compared with the non-treated healthy control, plant growth was not affected by BABA when applied at either 25 or 50 μg ml^{-1} and zoospores at 10^3 spores ml^{-1} were used to inoculate the leaves or roots. Saver and Syrup applied at 25 or 50 μg ml^{-1} did not affect plant growth, compared with the non-treated healthy control, when zoospores at 10^3 spores ml^{-1} were used to inoculate the leaves (Figs. 4 and 5). No phytotoxicity was observed on the plants treated with the products except when ASM or INA was applied at 50 μg ml^{-1}. Weight and height of the non-treated healthy plants were significantly greater than the pathogen-only control, indicating the effect of the pathogen on plant growth.

4. Discussion

Several known SAR inducers including BABA, INA, salicylic acid and ASM were evaluated, which provided significant suppression of Phytophthora blight on squash. SAR inducers could be a promising component in developing effective integrated programs for managing this disease.

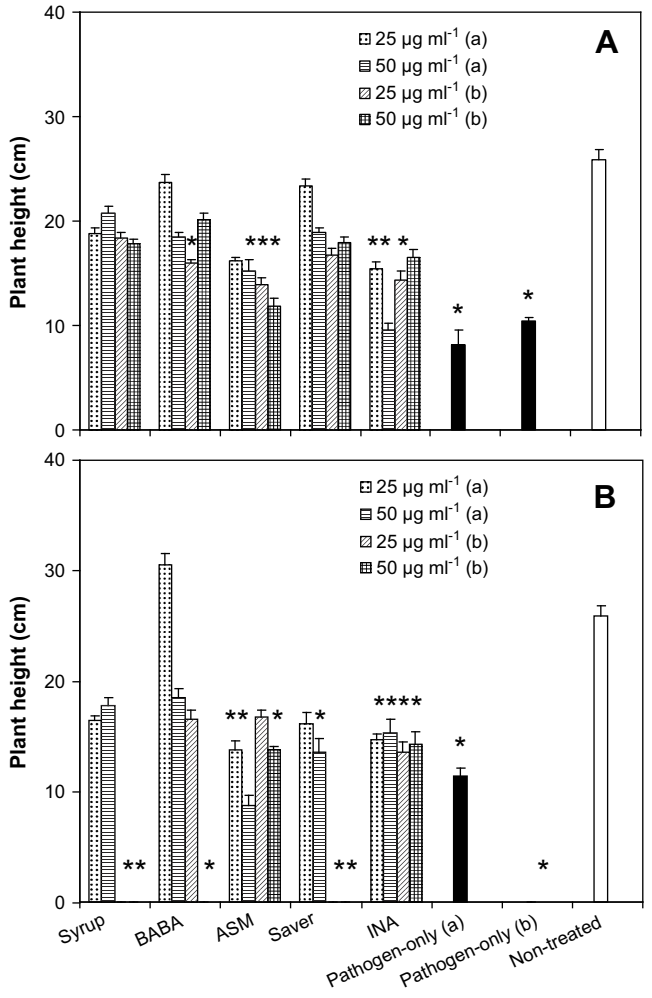

Fig. 5. Height of surviving squash plants in greenhouse studies. The SAR inducers were applied at 25 and 50 μg ml^{-1} and zoospore suspensions at concentrations of 10^3 zoospores ml^{-1} (a) or 10^4 zoospores ml^{-1} (b) were used to inoculate the leaves (Fig. 5A) or roots (Fig. 5B). Data are means of two repeated experiments. The error bar represents the standard error of the mean. "*" above each bar indicates significant difference between the treatment and the non-treated control according to the least significant difference test at $P = 0.05$.

Little was known about potential SAR inducers that could be used to reduce Phytophthora blight on squash. More information was available regarding the activity of these products in other plant disease systems. For instance, INA induced resistance against powdery mildew and downy mildew on leaves of melons (Bokshi et al., 2006) and BABA induced resistance against *Pseudocercospora cubensis* in cucumber (Baider and Cohen, 2003), *P. capsici* in pepper (Lee et al., 2000), *P. infestans* in tomato (Jeun et al., 2000), and *Peronospora parasitica* in cauliflower (Silue et al., 2002). While this study was not addressed to elucidate the physiological and biochemical mechanisms behind the reduction of Phytophthora blight on squash by the SAR inducers, this study provides information that these compounds reduce the disease on squash which has not been documented previously. The efficacy of these compounds in reducing the disease was more evident when squash plants were inoculated with lower zoospore concentrations. This is in agreement with previous studies that acibenzolar-*S*-methyl was effective in reducing bacterial wilt on tomato when lower concentrations of *Ralstonia solanacearum* were used to inoculate while not effective when higher concentrations of the pathogen were used (Pradhanang et al., 2005).

Assessment of direct inhibitory effect of the SAR inducers on mycelial growth, zoospore germination and sporangium production of *P. capsici* was not reported previously. However, Baider and Cohen (2003) indicated that BABA did not inhibit the growth of *P. infestans*. This is consistent with our study that mycelial growth, zoospore germination and sporangium production of *P. capsici* were not significantly inhibited by BABA. Salicylic acid was reported to inhibit mycelial growth and zoospore germination of *Pythium aphanidermatum* at high concentrations (Chen et al., 1999). Saver, which contains salicylic acid as its active ingredient, reduced *P. capsici* mycelial growth and sporangium formation at 100 μg ml^{-1} or higher concentrations and zoospore germination at 500 and 1000 μg ml^{-1}. Acibenzolar-*S*-methyl did not inhibit the growth of *P. capsici* except that sporangium production was reduced at 500 and 1000 μg ml^{-1}. INA reduced mycelium growth at all concentrations and sporangium production and zoospore germination at 100 μg ml^{-1} or higher. These results indicated that the SAR inducers, except INA, did not have a direct inhibitory effect on *P. capsici* when used at lower concentrations (25 and 50 μg ml^{-1}) that were in the range generally recommended for application. Plant growth in the BABA treatments appeared to be the best among those treated by the SAR inducers, which was consistently better than the pathogen-only control and not significantly different from the non-treated healthy control in most of the leaf/root inoculation and inoculum concentration combinations. Plant weight in most of the INA and acibenzolar-*S*-methyl treatments was significantly lower compared with that of BABA treatments.

This study indicated that some SAR inducers had the potential to provide significant suppression of Phytophthora blight on squash. This may offer an additional option to complement the use of chemical fungicides that directly inhibit the pathogen. Squash is one of the most susceptible vegetable crops to Phytophthora blight and lack of resistant squash cultivars and inadequate control efficacy of conventional fungicides make the management of this disease extremely challenging. Further studies to evaluate the efficacy of the SAR inducers under field conditions and incorporate promising ones into fungicide spray programs and other established practices will be meaningful in an attempt to reduce losses caused by the disease.

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