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Priming by Low Abiotic Stress and DL-β-Aminobutyric Acid Compared to Acibenzolar-S- methyl to Control of Tomato Crown and Root Rot Disease

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HIGHLIGHTS

- BABA and salt stress combined enhanced tomato resistance to Fusarium wilt.
- High BABA doses alone outperformed treatments with BABA-ASM combinations.
- Disease severity on plants on which abiotic stress and BABA combination used was also lower than the control and BABA sprayed at 500 µg mL^{-1} to plants alone.

Abstract

Crown and root rot disease caused by *Fusarium oxysporum* f.sp. *radicis-lycopersici* (FORL) is a destructive pathogen on the seedling and mature tomato (*Lycopersicon esculentum* Mill) plants in greenhouses of Turkey. The synergistic effect of abiotic stress (100 m*M* NaCl) by known chemical defense inducers DL-β-Aminobutryric acid (BABA) to FORL was tested on tomato plants. The roots of plants were immersed into 125, and 500 µg mL^{-1} BABA or foliages of plants were separately sprayed by BABA (125, 500 µg mL^{-1}) before the plants were inoculated with fungal spore suspension by day 1 post treatment. Furthermore, in another study conducted on only by BABA and abiotic stress (foliar spray) resulted in remarkable plant disease resistance if the plants were detached into BABA (125 µg mL^{-1}) solution. This combination caused a positive effect on plants, which was comparable with the plants detached into the highest BABA concentration at 500 µg mL^{-1}. Disease severity of plants on which abiotic stress and BABA combination used was also lower than the control and BABA sprayed at 500 µg mL^{-1} to nontreated (control) plants alone until the 20th day post inoculation. Therefore, synergistic effect by salt stress and BABA can be suggested for plant resistance to FORL.

Keywords: Acibenzolar-S-methy; DL-β-Aminobutyric acid; *Fusarium oxysporum* f.sp. *radicis-lycopersici*; Priming; Salt stress

1. Introduction

Crown and root rot caused by *Fusarium oxysporum* f.sp. *radicis-lycopersici* (FORL) is the most frequently observed plant disease in Turkey's southwest tomato production areas and this pathogen especially infects

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tomato seedlings in the fields. Acibenzolar-S-methyl (ASM), also known as benzo-1,2,3-thiadiazole-7-carbothioic acid S-methyl ester or BTH, serves as a recognized functional analog of salicylic acid, eliciting resistance in numerous plant species against a broad spectrum of plant pathogens, particularly under controlled conditions (Dempsey et al. 1999; Thakur and Sohal 2013; Walters et al. 2013). Numerous studies have illustrated the ability of ASM to trigger plant defenses associated with systemic acquired resistance (SAR) (Baysal 2015; Bektas and Eulgem 2015; Durrant and Dong 2004; Ton and Mauch-Mani 2004). Moreover, this compound is commonly employed to chemically induce SAR in plant model systems, thereby facilitating the elucidation of the molecular network underlying SAR (Wang et al. 2006).

DL-β-Aminobutyric acid (BABA), is an analog of gamma aminobutyric acid (GABA) classified as a non-protein amino acid, possesses the capability to induce plants by the absence of expressed defenses. However, plants in this state exhibit enhanced responsiveness, reacting more swiftly and/or robustly to subsequent attacks compared to plants that have not undergone prior stress. The enhancement of resistance in plants mediated by BABA is referred as the primed state. Priming entails the transition of plants into an alarmed state of defense alertness, resulting in an enhancement of their defensive capabilities (Yang et al. 2001; Conrath et al. 2002; 2006). Priming offers an economical and effective defense against plant diseases, especially in areas experiencing considerable disease pressure (van Hulten et al. 2006). BABA has the capability to provide defense against a wide range of both biotic and abiotic stresses, including *Peronospora parasitica* in *Arabidopsis thaliana* L. (Zimmerli et al. 2000), *Sclerotinia sclerotiorum* in *Cynara cardunculus* L. (Marcucci et al. 2010), and *Bremia lactucae* in *Lactuca sativa* L. (Cohen et al. 2010; 2011). Additionally, it has been demonstrated that pre-treating Arabidopsis plants with BABA effectively primes them for abiotic stresses such as low temperatures, high temperatures, and elevated salt levels or drought conditions (Conrath et al. 2002).

In the previous studies of Baysal et al. (2003; 2005a), the effect of BABA and ASM on tomato seedlings has been shown in the control of *Clavibacter michiganensis* ssp. *michiganensis*. Also, the control of *Pseudomonas syringae* pv. *tomato* was observed in plants subjected to salinity-induced abiotic stress, even when treated with lower concentrations of BABA, as reported by Baysal et al. (2007).

The use of priming agents to mitigate various biotic and abiotic stresses in plants has gained increasing attention since decades. These new agricultural practices could reduce the necessity of pesticides and water, which are also compatible with the sustainable development goals of United Nations (Desa, U.N. 2025).

To the best of our knowledge, there is no information concerning the priming effect of abiotic stress and the synergistic action of BABA on tomato seedlings against FORL. Therefore, the impact of salt stress on both inoculated and uninoculated plants that were treated with BABA and ASM were examined. BABA doses determined by preliminary phenotypic experiments were also tested in the recent studies conducted with ASM that tested under abiotic stress.

2. Materials and Methods

2.1. Plant material

Five-week-old tomato seedlings (*Lycopersicon esculentum* Mill. cv. Ikram F1, Syngenta) with four fully expanded leaves were used for all experiments. The plants were grown in pots in a soil mix containing sand, perlite, and peat compost in the controlled atmosphere rooms at 25 ± 5°C with 68-80% relative humidity (RH). The soil-mix also contained a slow-release fertilizer (14-12-14, NPK). Natural light was supplemented by a single 1000-watt sodium vapor lamp during a 16 h photoperiod.

2.2. Fungal pathogen and inoculation

The FORL culture was obtained from stock collection of Molecular Microbiology Unit in Department of Molecular Biology and Genetics at Muğla Sıtkı Koçman University. The pathogen was grown on potato dextrose agar (PDA) at 25°C for 4 days and then transferred to autoclaved soil tubes. The fungus was grown

for 5 days in the tubes, and then stored at 4°C. The isolate, recovered as needed from storage, was performed on PDA at 25°C for 4 days prior to inoculation of plants. All experiments were conducted at 25°C.

2.3. Pretreatment with ASM and BABA

ASM (Bion, Syngenta, Frankfurt, as 50% active ingredients in wettable powder formulation obtained by Molecular Microbiology Unit in Department of Molecular Biology and Genetics at Muğla Sıtkı Koçman University) was dissolved in distilled water to obtain a concentration of 0.2 mg mL^{-1} and then sprayed on whole seedlings (ca. 200 ml per seedling) according to Baysal et al. (2003). BABA was made up as aqueous solutions with a final concentration of 125, and 500 μg mL^{-1}. Twenty-four hours prior to inoculation either solution was drenched into pots or uniformly sprayed onto plant leaves that treatments were adjusted to experiment design. Control plants were sprayed with water as well (Baysal et al. 2007).

2.4. Salt stress induction

The plant roots, including the ones sprayed with BABA and ASM at different concentrations as well as controls, which were washed with water properly, and were detached into 100 m*M* NaCl solution were exposed to salinity-induced abiotic stress for 10 min or sprayed onto leaves. The control plants which are (-) control were not exposed to salinity-induced abiotic stress and watered with only tap water as mentioned in Baysal et al. (2007).

2.5. Effect of ASM and the different BABA concentrations with salt stress against FORL

Plants were sprayed with various concentrations of BABA alone or, and the plants were subjected to salt stress either by detaching their roots at their base with 100 m*M* NaCl for 10 min or spraying (ca. 100 μL^{-1} per leaf). The foliage of seedlings was drenched with (ca. 20 ml per plant) 125, 500 μg mL^{-1} BABA alone, or in combination with salt stress (100 m*M*; by detaching of plant roots). Control plants were sprayed with water (ca. 200 μL^{-1} per leaf), and seedlings were covered with plastic bags.

The plants were inoculated with the spore suspension as described in Vakalounakis and Fragkiadakis (1999) by day 1 post treatment. The level of resistance induced in seedlings against FORL was evaluated 4, 7, 10 and 20 days after inoculation (dai) using a 0-3 arbitrary scale according to Vakalounakis and Fragkiadakis (1999). A mean disease severity index (DSI%) was calculated from each treatment by adding the ratings for the 36 plants (two replicates of 4 plants for each treatment) and expressing the value as a percentage using the formulas as follows: DSI = [∑(rating no. x no. of plants in rating) x 100] / (total no. of plants x highest rating)], disease incidence = [∑ (number of plants having the same disease index) x (disease index)} / {(number of all plants tested) x 4}] x 100.

2.6. Experimental design and statistical analyses

Each treatment involved four plants and four replicates were performed for the analysis. Differences between the mean values were assessed through two independent experiments, each with four replicates. An analysis of variance (ANOVA) was performed using randomized design, and Duncan's post hoc test was used to evaluate the differences among the treatments at $p < 0.05$ using SPSS-Software (ver. 30.0) (Table 1 and Table 2).

Table 1. The treatments and application method used for pot experiments: various concentrations of BABA, ASM and abiotic stress (salt stress**:** NaCl applied onto leaves or the roots were detached into solution alone showed highly toxic effect on tomato seedlings). **S**: foliage spray. **D**: detaching roots into solution.

BABA (μg mL^{-1})	S	D	ASM (0.2 mg mL^{-1})	S	D	FORL	Abiotic stress (100 m*M* NaCl)	S	D	Pot range numbers
500	-	+	+	+	-	+	-	-	-	1
-	-	-	+	-	-	+	-	-	-	2
125	+	-	-	-	-	+	+	-	+	3
125	+	-	-	-	-	+	+	+	-	4
125	-	+	-	-	-	+	+	+	-	5
-	-	-	-	-	-	+	-	-	-	6
500	-	+	-	-	-	+	-	-	-	7
500	+	-	+	+	-	+	-	-	-	8
-	-	-	-	-	-	-	-	-	-	9

Table 2. The treatments and application method used for pot experiments. Various concentrations of BABA and abiotic stress (salt stress: NaCl treatments applied onto leaves or immersion alone showed highly toxic effect on tomato seedlings). **S**: foliage spray. **D**: detaching roots into solution. BABA was applied at 24 h before inoculation and ASM was applied at 48 h before inoculation.

BABA (μg ml^{-1})	S	D	FORL	Abiotic stress (100 m*M* NaCl)	S	D	Pot numbers
-	-	-	+	-	-	-	1
-	-	-	-	-	-	-	2
125	-	+	+	+	+	-	3
500	+	-	+	-	-	-	4
500	-	+	+	-	-	-	5

3. Results

3.1. Comparison ASM with BABA in Abiotic Stress Condition against FORL

Disease incidence (DI) was calculated on plants showing crown root rot disease or healthy ones as well as with control shown in Figure 1 according to pot range numbers, representing situation by nine different treatments. Low abiotic stress application onto leaves combined with detaching of plant roots into BABA solution had an identical control effect on pathogen growth compared to ASM (0.2 mg mL^{-1}) and BABA (500 μg mL^{-1}) treatments alone. BABA (500 μg mL^{-1}) and ASM spray onto leaves had positive effect on plant growth and control of FORL interestingly, which appeared on plant roots though BABA (by detaching into 500 μg mL^{-1} solution) and ASM (spray) combination did not reduce pathogen growth when it was simultaneously applied (Figure 2). Therefore, further experiments were conducted in order to determine synergistic effect of salt stress combined with low doses BABA treatments in the sight of these previous findings.

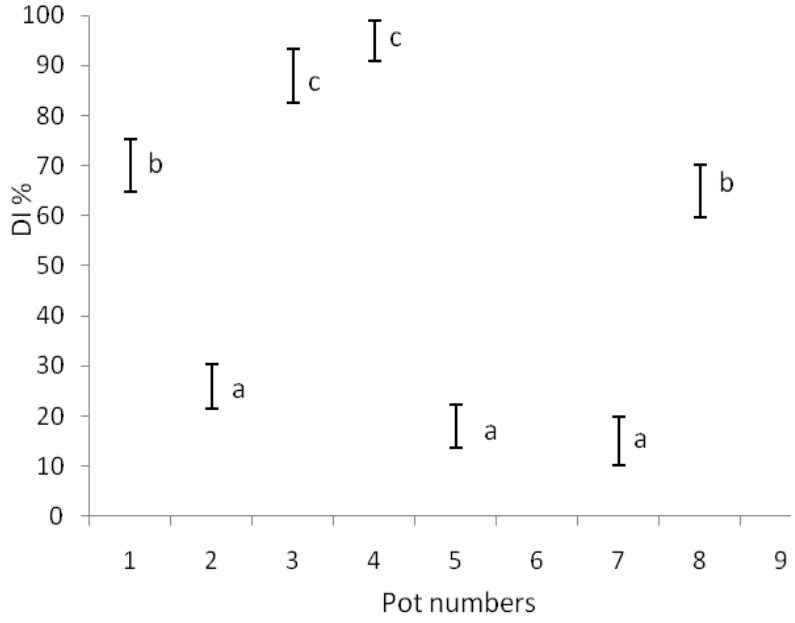

Figure 1. Disease incidences on the tomato seedlings observed in the pots during experiments at 15 days after inoculation. The values (standard deviations of 4 different samples) with the same letters represent values that are not significantly different according to Duncan's multiple range test ($p < 0.05$).

Figure 2. The growth of plants with various treatments indicated in Table 1. Each number was separately given that valid for each pot range according to different treatments tested that shown in Table 1.

3.2. The Effect of Low Dose BABA Combined with Abiotic Stress (Salt Stress) against FORL

Experiments conducted in order to determine the synergism between low dose BABA and abiotic stress showed that nearly 5-fold lower BABA dose combined with abiotic stress resulted in identical effect, which were obtained when the plants were treated with BABA (500 μg mL^{-1}) alone. This case was shown according to disease index values calculated in different period of disease progress (3-20 dpi) in Figure 3 and the growth of plants at 20 dpi in pots were given in Figure 4. The treatments did not demonstrate any difference in the disease index by 4 dpi, but they were significantly lower than the control group. The most suppressive effect on the pathogen was provided with BABA at different concentrations (125-500 μg mL^{-1}) combined with salt

stress by 7 dpi. BABA spray at 500 µg mL^{-1} showed a significant suppressive effect on disease progress of inoculated plants. Detaching roots into BABA solution (125 µg mL^{-1}) with abiotic stress (salt spray) showed remarkable suppressive effect (Figure 3) that also observed on plants treated with BABA (500 µg mL^{-1}) alone either by spraying or detaching. Moreover, detaching of roots into NaCl (100 m*M*) solution led to decrease in plant pathogen resistance though same plants were simultaneously sprayed also with BABA (125 µg mL^{-1}). Disease index values of plants detached into BABA (500 µg mL^{-1}) and the ones treated with BABA (125 µg mL^{-1}) abiotic stress combination showed less than 10 % ratio. The similar suppression effect on pathogen growth was present until 20 days post inoculation (Figure 4).

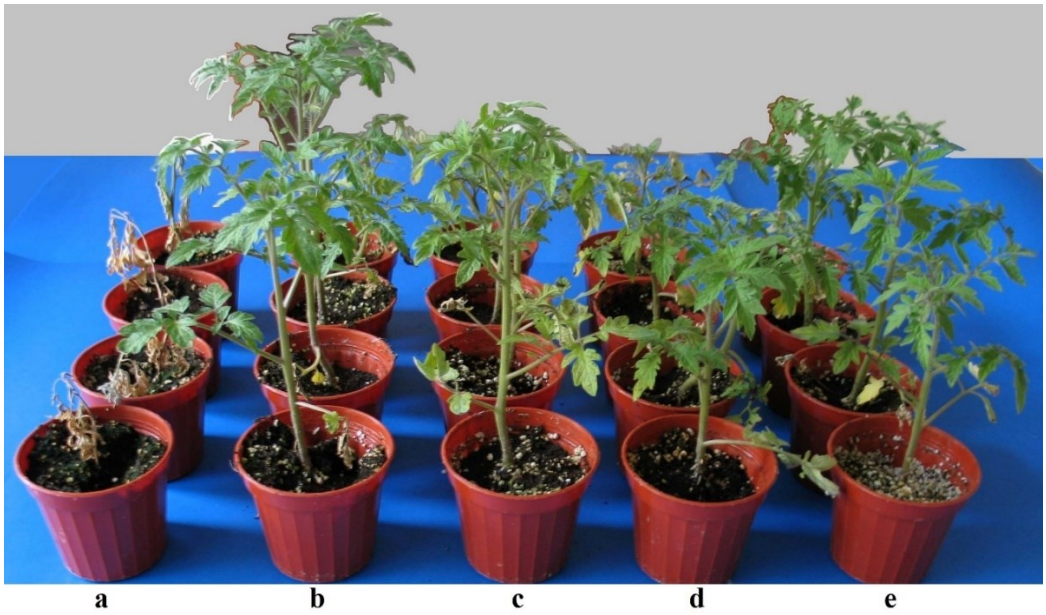

Figure 3. The growth of plants which were exposed to 5 various treatments at 15 days after inoculation: (**a**) FORL inoculated plants (positive control group), (**b**) uninoculated plants (negative control group), (**c**) FORL+BABA immersed (125 µg mL^{-1}) + NaCl (100 m*M*) spray treatment, (**d**) FORL+BABA (500 µg mL^{-1}) immersed treatment, and (**e**) FORL+BABA (500 µg mL^{-1}) spray treatment.

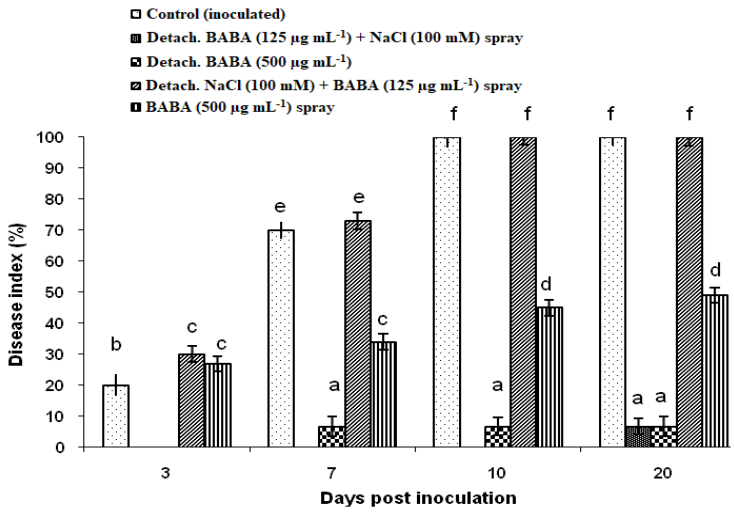

Figure 4. Disease index on plants inoculated with FORL was expressed as the mean of two separate experiments (in each experiment 4 pots were pooled at every time point (3-20) at post inoculation period). The values with the same letters represent data that are not significantly different according to Duncan's multiple range test ($p < 0.05$).

4. Discussion

Priming is considered a component of systemic immunity responses in plants; however, the precise mechanism underlying priming remain incompletely understood (Conrath 2011). Previous studies have established that BABA is capable of inducing a wide array of defense mechanisms, which are contingent upon the specific type of pathogens and plants involved. BABA demonstrates the capacity to generate reactive oxygen species (resulting in hypersensitivity response) and enhances physical barriers through processes such as callose deposition and lignin accumulation in cell walls (Hamiduzzaman et al. 2005; Ton and Mauch-Mani 2004; Ton 2005). Another mechanism facilitated by BABA involves the alteration of biochemical responses to stress. For instance, BABA promotes the biosynthesis of secondary metabolites such as phenols, anthocyanin, and phytoalexins, while concurrently enhancing the activity of enzymes linked to active oxygen species, lignification, and plant secondary metabolism (Andreu et al. 2006; Barilli et al. 2010; Chamsai et al. 2004; Justyna and Ewa 2013; Olivieri et al. 2009; Slaughter et al. 2008; Wu et al. 2010). Moreover, the activation of defense genes and the accumulation of pathogenesis-related (PR) proteins implicated in antimicrobial activity have been observed in numerous BABA-treated plants, including tomato, pepper, potato, and rape (Altamiranda et al. 2008; Cohen 1994; Hwang et al. 1997; Šašek et al. 2012). However, contrasting examples exist, with some studies indicating no accumulation of PR proteins following root application of BABA (Jakab et al. 2001; Siegrist et al. 2000).

Priming is increasingly recognized as a critical process in various forms of systemic plant immunity, including systemic acquired resistance (SAR) and induced systemic resistance (ISR) (Conrath 2011). In the present study, a practical and effective approach was suggested in controlling FORL by synergistic effect between salt stress and BABA on tomato. By resistance priming with synergistic effect of salt stress was higher than BABA alone in pathogen challenge. This study showed to induce substantial levels of plant resistance in tomato plants, 125 μg mL^{-1} of BABA combined with salt stress (100 m*M* NaCl) could result in significantly reduced symptoms and FORL growth. In previous studies, BABA was shown to be resistance inducer on tomato and had been tested against fungal and bacterial pathogens (Baysal et al. 2005a; 2005b; Cohen 2002).

The findings suggest that applying BABA alongside salt stress led to the activation of plant resistance when the plants were exposed to a pathogen. The potential signal released by the pathogen could be significant in initiating the plant's defense mechanisms. In this case salt stress shows a synergistic effect on BABA-treated plants' resistance and leads to an enhancer effect on BABA even though the concentration was lower than the most efficient level (500 μg mL^{-1}). Consequently, the activation of resistance could be linked to the impact of BABA on FORL, which could be connected to its influence on the pathways involved in pathogen defense and responses to abiotic stress.

In conclusion, this study indicates that applying BABA at reduced doses under salt stress conditions can enhance systemic resistance in tomato plants against FORL infection more effectively than BABA alone, even at just about a quarter of the optimal effective concentrations. Salt stress has a synergistic effect on increasing BABA's effect. Accordingly, it may be proposed that when a pathogen targets the root system, the induction of stress responses through foliar application could enhance the synergistic interaction between BABA and abiotic stress factors; conversely, when the pathogen infects aerial tissues, stress induction at the root level may confer a comparable synergistic effect (Baysal et al. 2007). Moreover, the observed reduction in pathogen damage following the combined application of ASM and BABA—despite their distinct modes of induction—may, to some extent, be attributed to overlapping or convergent mechanisms of action within the plant system. These findings could be correlated well with the chemical structure difference of two stimulants, which one is an analog of gamma aminobutyric acid (GABA) and the other is an analog of salicylic acid. Furthermore, the lab studies carried out showed positive results of this combination in inducing resistance of tomato plants to root knot nematodes, *Meloidogyne incognita* (Devran and Baysal 2018).

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