Systemic Induced Resistance to the Root-Knot Nematode in Tomato by Chemical Inducers

H. Charehgani1*, A. Karegar1, M. Djavaheri1, and A. Niazi2

ABSTRACT

Systemic Acquired Resistance (SAR) as a management strategy for plant parasitic nematode is a state of resistance increased after a previous infection of plant to a biotic pathogen. Induction of SAR is accompanied by local and systemic enhancement of Salicylic Acid (SA). SA increase in plant is concomitant with PR1 expression. We examined the effect of three chemicals including SA, Abscisic Acid (ABA), and DL-β-Amino-n-Butyric Acid (BABA) on the root-knot nematode *Meloidogyne incognita* on tomato plants. The expression of *PR1* genes and 9-Cis-Epoxycarotenoid Dioxygenase (*NCED*) as markers for SAR and ABA-related activity genes was investigated in growth chamber conditions. Results showed that all elicitors reduced the population of nematode as compared to the control. Shoot length, shoot fresh and dry weight of nematode infected tomatoes pre-treated with BABA increased by 20, 25, and 8 % and number of eggs, galls, egg masses and reproduction factor decreased by 33, 18, 18, and 20%, respectively. All elicitors increased the expression of *PR1* and *NCED* genes in nematode infected tomato. These data suggest that SA, BABA and ABA activate similar defenses in tomato plants, which is partly SA- and ABA-related. SA, BABA, and ABA pretreated tomatoes infected with *M. incognita* trigger a SAR-response and lead to the control of the nematode under controlled conditions.

Keywords: Abscisic acid, DL-β-amino-n-butyric acid, Gene expression, *Meloidogyne incognita*, Salicylic acid.

INTRODUCTION

Various types of plant resistance such as non-host resistance, *R*-gene mediated resistance and basal resistance have been mentioned for plant resistance against plant pathogens. Basal resistance is dependent on some plant hormones such as Ethylene (ET), Jasmonic Acid (JA) and Salicylic Acid (SA) (Verhagen et al., 2006). Induced Resistance (IR) is part of basal resistance, which is not available in healthy plant. IR can be induced by limited pathogen infection, avirulent pathogens, beneficial non-pathogenic bacteria and fungi, and certain chemicals (Walters and Fountaine, 2009). One of the well-studied examples of IR is Systemic Acquired Resistance (SAR), which occurs following a localized infection in plants. Other types of IR are Induced Systemic Resistance (ISR) and β-Aminobutyricacid-IR (BABA-IR), which involves JA/ET. Following localized infection, SAR expands systemically and occurs away from the infection sites (Buonaurio et al., 2009). Synthetic chemicals such as SA, JA, Acibenzolar-S-Methyl (ASM), 2,6-dichloroisonicotinic Acid (INA), Ethylene (ET), BABA or many other chemicals at levels that are not toxic can lead to the induction of local and systemic resistance

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BABA is a synthetic amino acid, which induces resistance in plants (BABA-IR). Natural defenses and internal mechanisms of plant are used by this type of resistance (Buonaurio et al., 2009). In this process, Abscisic Acid (ABA) and SA-dependent signaling pathways play an important role. ABA augmented formation of callose against pathogenic fungi and oomycetes (Ton et al., 2005). Moreover, ABA leads to stomatal closure and improves plant tolerance to drought and salinity stress. 9-Cis-Epoxycarotenoid Dioxygenase (NCED) gene involved in ABA biosynthesis. BABA-IR is effective against broad-spectrum of biotrophic, necrotic or hemibiotrophic pathogens, and even abiotic stress such as drought and salinity stress (Buonaurio et al., 2009).

Root-knot nematodes (Meloidogyne spp.) have been known as the most important plant pathogenic nematodes all over the world. They are one of the main obstacles to provide enough food in many developing countries. Based on different reports, root-knot nematodes cause reduction in tomato (Lycopersicon esculentum Mill.) yield over 50% (Natarajan et al., 2006).

In different studies, foliar spray and soil-drenching with chemical inducers such as SA, INA, MeJA, Gamma-Aminobutyric Acid (GABA), BABA, ASM and Methyl Salicylate (MeSA) have been done in plants infected with root-knot nematodes. Molinari et al. (2014) showed PRI gene was up-regulated in roots and shoots of SA-treated tomato plants and infected with M. incognita. Foliar spray of SA on cowpea infected with M. incognita significantly reduced the reproduction factor of nematode and induced expression and accumulation of PRI1 protein in the leaves (Nandi et al., 2002). Meller et al. (2018) showed PRI gene was up-regulated in leaves of potato plants pre-treated with BABA. Foliar spray of BABA inhibited development of M. javanica on oat (Oka et al., 1997). In many cases, they reduced nematode population (Fatemy et al., 2012), increased induced resistance (Mohamed, 2010; Sanz-Alferez et al., 2008) and increased the activity of Reactive Oxygen Species (ROS) scavenging enzymes (Sahebani and Hadavi, 2009; Sahebani et al., 2011). Brueske (1980) showed an increase in Phenylalanine Ammonia-Lyase (PAL) and polyphenol oxidase activities in tomato plants infected with M. incognita. PAL plays a key role in regulation of phenylpropanoid production in plants. Increases in the H2O2 accumulation, induction of defense enzymes involved in the phenylpropanoid pathway (Nandi et al., 2003), and scavenging reactive oxygen species i.e., guaiacol peroxidase, polyphenol oxidase, catalase (Sahebani and Hadavi, 2009), and accumulation of phenolics and PR proteins would have contributed to the control of root knot nematodes (Anita et al., 2004). PAL has been considered as a part of defense mechanism in plants against biotic and abiotic stress (Peiser et al., 1998).

The objective of the present study was to investigate the effect of SA, ABA and BABA on the root-knot nematode M. incognita on tomato plants, and expression of PRI and NCED genes as markers for SAR and ABA-related activity genes.

MATERIALS AND METHODS

Plant and Nematode Materials

To obtain M. incognita second stage juveniles (J2s), the nematode population originally from Khorasan Province, Iran (identified by Katooli et al. (2020) based on the study of perineal pattern and Inc-14 primer), was maintained in a greenhouse in Shiraz (Iran) on susceptible tomato (cv.
Early-Urbana) at 27±5°C. To do this, the infected roots were washed with water, cut into small pieces (2-3 cm) and mixed with 0.5% NaOCl in a blender to cover the roots. Roots were chopped in a blender for 30 sec at low speed, followed by passing through a series of sieves including 80, 200 and 500 mesh inch⁻¹. Eggs on the 500 mesh sieve were gently washed by cold tap water to free them from NaOCl and collected into a Petri dish (Hussey and Barker, 1973). The eggs were stored in incubator at 28°C for four days to hatch (Baghaee Ravari and Mahdikhani Moghaddam, 2015).

**Inducer Treatment and Pathogen Inoculation**

Seeds of tomato (cv. Moneymaker) were sown in a mixture of one part sand and one part peat moss in 1 kg plastic pots. Plants were grown at 30/25°C the day/night temperatures with 16 hours light in a growth chamber. Tomato seedlings at four-leaf stage were sprayed (≈1 mL per plant) with 0.5 mM BABA or SA, 0.1 mM ABA or water as a control. These concentrations were selected according to biological effect on *M. incognita*, based on Charehgani et al. (2014) studies. After 24 hours, the seedlings were inoculated with ≈1,300 J2s in 1 mL of water. The experiments were carried out in completely randomized designs with five replications. Five replicates of each treatment were harvested 60 days after inoculation, nematode indices including eggs/root system as described by Hussey and Barker (1973), galls and egg masses/root system as described by Taylor and Sasser (1978), and reproduction factor and host growth indices including fresh shoot and root weight, dry shoot weight and shoot height were determined. The reproduction factor was calculated by dividing the final population density of the nematode by the initial nematode population density. Twenty-four, 48, and 72 hours after induction (0, 24 and 48 hours after nematode inoculation (hai)), leaf samples were collected. For this purpose, five samples of each plant, treated by SA, BABA, ABA, SA+Nematode, BABA+Nematode, ABA+Nematode and water (as control), at each time point were collected, frozen immediately in liquid nitrogen, and stored at −80°C. Total RNA was obtained with the total RNA isolation kit (DENAzist Asia. Co., Mashhad, Iran), following the manufacturer’s instructions, after tissue extraction. Total RNA was isolated from each sample and random primers (Table 1) were used in the cDNA synthesis using the cDNA synthesis Kit (Fermentas Inc., Vilnius, Lithuania). The cDNA was used as the template for the qRT_PCR reaction to determine the expression of the PR1 and NCED genes. For qRT_PCR reaction, SYBR Green qRT_PCR kit (BioEasy) was used. The quantification was accomplished using the Elongation factor1-alpha (ef-1) as an endogenous control. For qRT_PCR data, the relative expression of target gene was calculated based on the Threshold Cycle (CT) method. The CT for each sample was calculated using the Line-gene K software and the method by Larionov et al. (2005). When replicate PCRs are run on the same sample, it is more appropriate to average CT data before performing the $2^{ΔΔCT}$ calculation. All qRT_PCR reactions were done in triplicate, on cDNA from two independent

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**Table 1. Specific primers employed in qRT_PCR reactions.**

<table>
<thead>
<tr>
<th>Primes</th>
<th>Sequences of oligonucleotides</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PR1-1b</strong></td>
<td>Forward: 5′-GCC AGA CTA TAA CTA CGC TAC C-3′</td>
</tr>
<tr>
<td></td>
<td>Reverse: 5′-GAA CCA CCA CCC ATT GTT GC-3′</td>
</tr>
<tr>
<td><strong>NCED</strong></td>
<td>Forward: 5′-GCT TAT TTG GCT ATC GCT GAA C-3′</td>
</tr>
<tr>
<td></td>
<td>Reverse: 5′-CGT CTT CTT CCT TGC TGT TGG-3′</td>
</tr>
<tr>
<td><strong>ef1</strong></td>
<td>Forward: 5′-GGT TAA GAT GAT TCC CAC-3′</td>
</tr>
<tr>
<td></td>
<td>Reverse: 5′-GAC AAC ACC AAC AGC AAC-3′</td>
</tr>
</tbody>
</table>
Table 2. Effect of foliar spray with different inducers on growth indices of non-inoculated and inoculated tomato plants (cv. Moneymaker) with Meloidogyne incognita.

<table>
<thead>
<tr>
<th>Inducers</th>
<th>Tomato plants</th>
<th>Shoot length (cm)</th>
<th>Shoot fresh weight (g)</th>
<th>Shoot dry weight (g)</th>
<th>Root fresh weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Non-inoculated</td>
<td>51.3 ± 2.4b</td>
<td>29 ± 1.2ab</td>
<td>4.2 ± 0.26a</td>
<td>4.12 ± 0.11bc</td>
</tr>
<tr>
<td></td>
<td>Inoculated</td>
<td>49 ± 1.6b</td>
<td>26 ± 0.8b</td>
<td>3.6 ± 0.34b</td>
<td>4.26 ± 0.08abc</td>
</tr>
<tr>
<td>SA (0.5 mM)</td>
<td>Non-inoculated</td>
<td>53.6 ± 2ab</td>
<td>28.5 ± 1.4ab</td>
<td>4.3 ± 0.65a</td>
<td>3.8 ± 0.13c</td>
</tr>
<tr>
<td></td>
<td>Inoculated</td>
<td>52 ± 2.2ab</td>
<td>31.6 ± 2.2ab</td>
<td>4.2 ± 0.14a</td>
<td>4.4 ± 0.05a</td>
</tr>
<tr>
<td>BABA (0.5 mM)</td>
<td>Non-inoculated</td>
<td>49.4 ± 1.8b</td>
<td>28.4 ± 1.6ab</td>
<td>4.1 ± 0.22a</td>
<td>4.1 ± 0.1bc</td>
</tr>
<tr>
<td></td>
<td>Inoculated</td>
<td>61.5 ± 3.5a</td>
<td>34.5 ± 2.5a</td>
<td>3.9 ± 0.38a</td>
<td>4.3 ± 0.09ab</td>
</tr>
<tr>
<td>ABA (0.1 mM)</td>
<td>Non-inoculated</td>
<td>52.4 ± 2.6ab</td>
<td>32 ± 1.1ab</td>
<td>4.3 ± 0.44a</td>
<td>4.32 ± 0.1ab</td>
</tr>
<tr>
<td></td>
<td>Inoculated</td>
<td>55.2 ± 3ab</td>
<td>30 ± 1.8ab</td>
<td>4.1 ± 0.42a</td>
<td>4.29 ± 0.12ab</td>
</tr>
</tbody>
</table>

* Data are presented as the mean±standard deviation of two independent trials with five replicates. Means in a column followed by the same letter(s) are not different according to Duncan's multiple range test (P<0.01).
Table 3. Effect of foliar spray with different inducers on number of eggs, galls and egg masses/root and reproduction factor of inoculated tomato plants (cv. Moneymaker) with *Meloidogyne incognita*.

<table>
<thead>
<tr>
<th>Inducers</th>
<th>Eggs/Root system</th>
<th>Galls/Root system</th>
<th>Egg masses/Root system</th>
<th>Reproduction factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>9600 ± 240a</td>
<td>245 ± 12a</td>
<td>170 ± 9a</td>
<td>5 ± 0.2a</td>
</tr>
<tr>
<td>SA (0.5 mM)</td>
<td>8650 ± 320bc</td>
<td>210 ± 16b</td>
<td>148 ± 6b</td>
<td>4.2 ± 0.2bc</td>
</tr>
<tr>
<td>BABA (0.5 mM)</td>
<td>7400 ± 160c</td>
<td>200 ± 10b</td>
<td>140 ± 14b</td>
<td>4 ± 0.34c</td>
</tr>
<tr>
<td>ABA (0.1 mM)</td>
<td>9100 ± 360b</td>
<td>230 ± 9ab</td>
<td>153 ± 15b</td>
<td>4.4 ± 0.16b</td>
</tr>
</tbody>
</table>

* Data are presented as the mean ± standard deviation of two independent trials with five replicates. Means in a column followed by the same letter(s) are not different according to Duncan’s multiple range test (*P* < 0.01).

Figure 1. The *PRI* expression in the leaves of non-inoculated as well as inoculated tomato plants with *Meloidogyne incognita*, pretreated with (A) 0.5 mM Salicylic Acid (SA), (B) 0.5 mM DL-β-Amino-α-Butyric Acid (BABA) and (C) 0.1 mM Abscisic Acid (ABA) at 0, 24 and 48 hours after inoculation (hai). Bars represent the mean and standard error of mean of two independent trials with five replicates. Different letters indicate statistically significant differences (Duncan’s multiple range test (*P* < 0.01).

Expression of *PRI* and *NCED* Genes

In the non-treated plants with elicitors, *PRI* and *NCED* expressions were induced on leaves at 24 hours after the nematode inoculation, and significantly decreased at 48 hours (Figure 1). *PRI* expression level increased after foliar spray of SA at the first 24 hours and gradually decreased at the 48 and 72 hours (Figure 1-A). The *PRI*
expression was induced in BABA pre-treated (Figure 1-B) and ABA pre-treated plants (Figure 1-C) at 24 hours and significantly decreased at 48 hours after nematode inoculation. On the contrary, level of *PRI* expression decreased at the first 24 hours and significantly increased at the 48 and 72 hours in non-inoculated plants with ABA-pre-treatment (Figure 1-C). In nematode-inoculated plants treated with SA, BABA and ABA, level of *PRI* expression increased 6.3, 1.8 and 1.7-fold, 2, 11 and 0.9-fold, and 0.1, 1.8 and 0.2-fold at 0, 24, and 48 hours after the nematode inoculation, respectively, as compared to the control plants (Figure 1). According to Figure 2, level of *NCED* expression increased after foliar spray of the elicitor at 48 hours after treatment and decreased at 72 hours after treatment. In nematode inoculated plant treated with SA, BABA and ABA, level of *NCED* expression increased 1.5, 8.5 and 0.4-fold, 0.4, 14.2 and 0.9-fold, and 0.5, 8.2 and 0.3-fold at 0, 24, and 48 hours after the nematode inoculation, respectively, as compared to the control plants (Figure 2).

**DISCUSSION**

Several studies have shown that application of high concentrations of chemical resistance inducers on plants lead to phytotoxicity and even plant death. The reason is imposing additional burden to plant by activation of plant resistance
responses. This problem reduces the overall fitness of plant (Molinari and Baser, 2010). As well as in some cases, low concentrations of chemical resistance inducers do not induce resistance in plants (Molinari and Baser 2010; Zhu and Tian, 2012). In this experiment, toxicity was not observed when the inducers were tested. Numerous studies have shown that high concentrations of chemical resistance inducers decrease plant fitness, cause toxicity, and decrease plant growth indices (Molinari and Baser, 2010). The present study revealed that foliar spraying with inducers caused reduction in nematode indices including the number of galls, eggs and egg masses per root system, the number of eggs in egg masses and nematode reproduction factor in comparison with the controls. In most cases, treated plants with BABA showed better effect on reducing nematode populations over the other two inducers. These results were consistent with other studies (Sahebani and Hadavi, 2009; Molinari and Baser, 2010; Mohamed, 2010). Previous studies have shown that protection against some plant pathogens by BABA functions via priming for Salicylic Acid (SA)-inducible defense mechanisms (Zimmerli et al., 2000; Flors et al., 2008). Ji et al. (2015) demonstrated that BABA treatment of rice plants inhibited M. graminicola penetration and led to delayed nematode and giant cell development. Resistance through ABA signaling pathways induced by BABA treatment causes increase of callose formation and ultimately increases resistance against pathogens (Jakab et al., 2005; Ji et al., 2015). Expression patterns of marker genes for the SA and ABA pathways in other pathogens indicate that both pathways always will be active following BABA treatment (Slaughter et al., 2012). Present study revealed that level of PR1 expression increased 9.75-fold at 48 hours after the nematode inoculation as compared to the control plants. This result suggests that salicylic acid accumulated in the early stages of M. incognita infected tomato and then increase in PR1 expression occurred in the leaves tissue. Infection of plants by plant parasitic organisms including fungi, bacteria, viruses, nematodes, parasitic plants, and even insect herbivores nematodes leads to accumulation of SA in different parts of plants (Tripathi et al., 2019). In the present study, it was demonstrated that nematode infection increased expression of PR1 in inoculated plants with different pathogens have been reported in other studies. Mohr and Cahill (2007) showed that SA induced and increased expression of PR1 gene in Pseudomonas syringae pv. syringae-infected Arabidopsis. (Mohr and Cahill, 2007). They showed that SA induced and increased expression of PR1 gene in Pseudomonas syringae pv. syringae-infected Arabidopsis. It has been recently revealed that PR1 protein binds and sequesters host sterols that are required by the pathogens for their growth. The sterol-binding activity of PR1 protein reveals the mode of action of an antimicrobial protein (Gamir et al., 2017). The results of present study showed that PR1 expression level decreased approximately 4.7-fold on the third day after inoculation with nematode over second day after nematode inoculation. It seems that the nematode suppressed the plant defense responses. These results also have been demonstrated in other studies (Putthoff et al., 2003; Jammes et al., 2005; Sanz-Alférez et al., 2008).

Present study revealed that in nematode non-inoculated plants, level of PR1 expression increased significantly in SA-pretreated plants over control plants at 48 and 72 hours after treatment. However, PR1 expression showed down trend at 48, 72 and 96 hours after foliar spraying with SA, such that there were no significant differences among SA-pretreated plants at 96 hours as compared with the control. According to results of Fan et al. (2009), level of PR1 expression increased after SA treatment in Arabidopsis in the first and second days. Then, it gradually decreased in the third and fourth days. Molinari et al. (2014) showed up-regulation of PR1 gene in shoots and
roots of SA-treated tomato one day before *M. incognita* infection.

Level of *PR1* expression increased significantly in inoculated SA-pretreated plants over the control at the first 24 hours after inoculation (48 hours after SA-pretreatment). It seems that increased expression of *PR1* gene, which was induced by SA in the early stages of plant infection by nematode, was not suppressed. In contrast, level of *PR1* expression decreased significantly in the following day, and it reached the same level as the control. The reason can be attributed to suppression of *PR1* expression by effector proteins. These proteins are produced by nematode after deploying root tissue and early stages of giant cells formation (Smant and Jones, 2011; Dehghanian et al., 2020).

Results of the present study revealed that BABA will increase markedly *PR1* expression and will activate SAR resistance pathways if the plant is attacked by nematodes. It can be inferred that despite pretreatment of plants with BABA, plant defense responses will not increase, while these defense responses will increase following infection by the nematodes. In conclusion, additional burden were not imposed on plant after BABA treatment. These results were consistent with results of Zimmerli et al. (2000). The results of BABA effects on reduction of nematode populations showed positive effect of this synthetic chemical on damage reduction of *M. incognita* on tomato through increased plant defense responses. Increased *PR1* gene expression due to pretreatment of plants with BABA shows that BABA-IR is dependent on SA signaling pathways. The relationship between BABA and SA-dependent signaling pathways to protect plants was proved by Ton et al. (2005). The plant hormones SA and ABA play pivotal roles in biotic and abiotic stresses, respectively. Several studies have shown that they individually or antagonistically act together in plant (Park et al., 2007; Flors et al., 2008; Yasuda et al., 2008). Therefore, an accurate hormonal balance is essential for the survival of plants under stress conditions. Seo and Park (2010) showed positive interactions between ABA and SA signaling pathways. They showed that the *MYB96* transcription factor, which is ABA-dependent signaling pathways, induces plant resistance via an induction of SA biosynthesis and increase in pathogenesis-related proteins. Hence, *MYB96* transcription factor is an intermediate molecule of ABA-SA crosstalk. Another study has shown that external treatment of Arabidopsis with SA and ABA increased some plant metabolites more than treatment with these hormones individually. These results also showed ABA-SA crosstalk (Okamoto et al., 2009). Present study revealed that level of *PR1* expression increased significantly at 48 and 72 hours after ABA-pretreatment of non-inoculated plants compared to 24 hours after ABA-pretreatment. These results were consistent with results of Seo and Park (2010). Pretreatment of plants with ABA has lower effect on induction of *PR1*-dependent defense responses than inoculated untreated plants. Probably, this is due to an antagonistic interaction between ABA and SA. This antagonistic interaction was consistent with results of Park et al. (2007), Flors et al. (2008) and Yasuda et al. (2008) studies. Of course, reduction of nematode populations by pretreatment of plants with ABA showed ABA had increased plant defense via another ways. ABA is activated as a result of response to stress in plants. Some studies also have shown ABA content increases during biotic stresses (Asselbergh et al., 2008; Kyndt et al., 2017). ABA is a key regulator of defense response in plants (Adie et al., 2007). Levels of ABA increased rapidly during pathogen attack. (de Torres-Zabala et al., 2007). On the other hand, it was noted that increase of SA biosynthesis due to increase of ABA and, then, enhancing of pathogenesis-related proteins leads to increased plant resistance (Seo and Park, 2010). Increased plant resistance limits nematode activity. Hence, probably, nematode decreases *NCED* expression 48 h after inoculation by effector proteins, which were secreted into feeding sites to suppress the plant defense responses.
On the other hand, giant cell formation by nematode will cause water stress in plants. Therefore, plant tries to minimize nematode damage by enhancing the ABA level. Infection of plant with nematode increase genes involved in ABA biosynthesis such as NCED.

Results of Sakhabutdinova et al. (2003) showed that pretreatment of plants with SA increased ABA concentration in plants under drought stress and then ABA concentration decreased gradually over time. Since NCED gene is required for ABA biosynthesis, the results of this research is confirmed.

The results showed that pretreatment of plants with BABA led to increase in NCED expression in leaf tissue and, probably, ABA accumulation in plant. Different studies revealed that two Arabidopsis mutants impaired in either ABA biosynthesis (aba1) or ABA signaling (abi4) lost their ability to react to BABA treatment (Jakab et al., 2005). Therefore, various studies and the present study demonstrate that BABA-IR is dependent on both ABA and SA signaling pathways (Ji et al., 2015).

Overexpression of NCED gene increases ABA levels (Thompson et al., 2000; Iuchi et al., 2001). These results showed that ABA increase under stressed conditions, and no elevation of the essential precursor involved in ABA synthesis was observed under unstressed conditions, even in ABA-pretreated plants. These results were consistent with results of Fan et al. (2009).

In conclusion, population of M. incognita decreased following application of the inducers SA, BABA and ABA in nematode-inoculated tomato plants, and the pre-treated plants showed enhanced expression of PR1 and NCED genes. This study confirmed that BABA-IR in the Meloidogyne-infected tomato depends on SA and ABA signaling pathways.

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