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To cite this article: Paolo Salazar-Mendoza, José Maurício S. Bento, Diego B. Silva, Sérgio F. Pascholati, Peng Han & Cesar Rodriguez-Saona (2023) Bottom-up effects of fertilization and jasmonate-induced resistance independently affect the interactions between tomato plants and an insect herbivore, Journal of Plant Interactions, 18:1, 2154864, DOI: [10.1080/17429145.2022.2154864](https://doi.org/10.1080/17429145.2022.2154864)

To link to this article: <https://doi.org/10.1080/17429145.2022.2154864>



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Bottom-up effects of fertilization and jasmonate-induced resistance independently affect the interactions between tomato plants and an insect herbivore

Paolo Salazar-Mendoza ^a, José Maurício S. Bento ^a, Diego B. Silva ^a, Sérgio F. Pascholati ^b, Peng Han ^c and Cesar Rodriguez-Saona ^d

^aDepartment of Entomology and Acarology, 'Luiz de Queiroz' College of Agriculture, University of São Paulo, Piracicaba, Brazil; ^bDepartment of Plant Pathology and Nematology, 'Luiz de Queiroz' College of Agriculture, University of São Paulo, Piracicaba, Brazil; ^cYunnan Key Laboratory of Plant Reproductive Adaptation and Evolutionary Ecology /Institute of Biodiversity, School of Ecology and Environmental Sciences, Yunnan University, Kunming, China; ^dDepartment of Entomology, Rutgers University P.E. Marucci Center, Chatsworth, NJ, USA

ABSTRACT

Whether nutrient availability interacts with induced resistance to alter plant chemistry and, consequently, the preference and performance of herbivores on plants remains unclear. We hypothesized that changing fertilizer inputs modulates responses induced by exogenous application of the defensive phytohormone methyl jasmonate (MeJA) against *Tuta absoluta*, a devastating pest of tomatoes. We found that tomato plants grown at or 2-fold above optimal fertilizer rates had higher nutrient content and were more preferred by *T. absoluta* females for oviposition and were better hosts for their offspring. MeJA increased phenolic content and volatile emissions in plants, which correlated with lower *T. absoluta* oviposition preference and offspring performance. However, we found no significant interactions when fertilizer and MeJA were applied simultaneously, such that induced responses against *T. absoluta* in tomatoes were similar regardless of fertilizer rate. These results provide novel insights into the bottom-up effects of fertilization and induced resistance on plant-insect herbivore interactions.

ARTICLE HISTORY

Received 21 September 2022
Accepted 30 November 2022

KEYWORDS



Tuta absoluta; methyl jasmonate; fertilization; preference-performance; phenolics; plant volatiles


Introduction

Most plants must frequently deal with a variety of biotic stresses, such as the attack by insect herbivores, and in response, they can protect themselves through physical and chemical resistance traits to avoid or reduce herbivore damage (Karban and Myers 1989; War et al. 2012). These resistance traits can be constitutive, i.e. always present, or inducible, i.e. only produced or mobilized in response to damage by herbivores (Karban and Myers 1989). Induced plant resistance occurs upon recognition of an herbivore attack and may often increase the levels of physical and chemical defensive traits that, in turn, reduce the preference (i.e. antixenosis) and performance (i.e. antibiosis) of herbivores on plants (Bezemer and Van Dam 2005; Eyles et al. 2010; Alba et al. 2011; Poelman 2015). The expression of many of these plant resistance-related traits is regulated through hormones (Stella de Freitas et al. 2019). Specifically, the activation of inducible resistance in plants against chewing insects and necrotrophic pathogens is mainly regulated by the jasmonic acid (JA) defensive pathway (Thaler et al. 2001; Howe and Jander 2008; Erb et al. 2012; Acevedo et al. 2015; Tortorici et al. 2022). For instance, exogenous application of jasmonates, i.e. JA or its volatile derivative methyl jasmonate (MeJA), often induces the production of secondary metabolites in plants that deter herbivore feeding, reduce their survival, or inhibit their digestion, i.e. direct resistance traits, in a manner

like those induced by chewing herbivores (Chen et al. 2005; Wei et al. 2021). In addition, exogenous jasmonate application induces volatile emissions in plants that can modify the herbivore's behavior (Rodriguez-Saona et al. 2001; Cao et al. 2014) and attract their natural enemies, i.e. indirect resistance traits (Kessler and Baldwin 2001; Yu et al. 2018). Thus, these jasmonates are often used to mimic herbivory and induce plant resistance (Thaler et al. 2001; Tortorici et al. 2022).

In addition to biotic stresses, abiotic stresses can also affect plant chemistry, leading to changes in trophic cascades through bottom-up forces (Hunter and Price 1992; Power 1992; Amtmann et al. 2008; Chen et al. 2010; Han, Becker, et al. 2019). One important factor that could trigger strong bottom-up effects in plant-insect interactions is plant nutrient availability (Poelman 2015; Han et al. 2022). However, despite its importance, plant nutrient availability has received little attention within the practical context of integrated pest management (IPM) (Han et al. 2022). In agroecosystems, fertilizer application often alters plant quality via changes in the plant's nutritional status, which in turn may affect the survival, growth, and behavior of insect herbivores (Joern et al. 2012; Han et al. 2014; Islam et al. 2017; Li et al. 2021). For instance, nitrogen is an essential nutrient in regulating leaf photosynthesis (Hou et al. 2019) that has been widely studied in terms of its impact on insect herbivores (Sétamou et al. 1993;

CONTACT Paolo Salazar-Mendoza  paolo.salazar@usp.br  Department of Entomology and Acarology, 'Luiz de Queiroz' College of Agriculture University of São Paulo, Piracicaba, SP 13418-900, Brazil

 Supplemental data for this article can be accessed online at <https://doi.org/10.1080/17429145.2022.2154864>

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Han et al. 2022). Low nitrogen levels in plant tissues are known to reduce herbivore survival, performance, and/or fertility (Awmack and Leather 2002; Schoonhoven et al. 2005; Han et al. 2014). In contrast, high nitrogen levels in plants often result in increased performance of herbivores, which may subsequently alter their population dynamics, leading to rapid herbivore outbreaks (Throop and Lerdau 2004; Schoonhoven et al. 2005).

Despite this knowledge, it is still unclear how plants cope with simultaneous biotic and abiotic stressors, such as protection against herbivores under limited nutrient availability. Because the activation of defense pathways can demand considerable resources, induced resistance in plants is assumed to be energy-intensive (Gershenson 1994; Kessler and Baldwin 2002; Hahn and Maron 2016). In this way, plants continuously deal with the dilemma of how to allocate their resources to growth or defense, particularly when these resources are limited (Herms and Mattson 1992). According to the resource availability hypothesis, fast-growing plants that are adapted to resource-rich environments should have high foliar nutrient concentrations, high tissue turnover rates, and low investment in antiherbivore defenses and, consequently, should experience high levels of herbivore damage (Coley 1987). In contrast, plants in resource-poor environments should show slow growth rates and enhanced resistance to herbivores. Thus, according to this hypothesis, we expect trade-offs between nutrient availability and plant resistance to herbivores.

In tomato (*Solanum lycopersicum* L.) plants, exogenous MeJA application increased defensive proteins, including trypsin proteinase inhibitors and polyphenol oxidases, that reduced the performance of insect herbivores such as the corn earworm, *Helicoverpa zea* (Boddie) (Paudel et al. 2014) and the cotton bollworm, *Helicoverpa armigera* Hübner (Tan et al. 2012). Additionally, low nitrogen inputs applied to tomato plants increase concentrations of soluble phenolics, glycoalkaloids, polyphenol oxidases, and volatile compounds (Stout et al. 1998; Larbat et al. 2016; Islam et al. 2017; Becker et al. 2021) and impair the performance (Han et al. 2014; Larbat et al. 2016), longevity (Blazhevski et al. 2018), and fertility (Blazhevski et al. 2018) of the South American tomato pinworm *Tuta absoluta* (Meyrick), as well as the attraction of the whitefly *Bemisia tabaci* (Genadius) (Islam et al. 2017). However, the interactive effects of jasmonate-induced resistance and nutrient availability on the preference-performance relationship of *T. absoluta* in tomato plants have not been studied.

In this study, we hypothesized that nutrient availability interacts with jasmonate-induced resistance to affect plant chemical defenses and the preference and performance of *T. absoluta* on tomato plants. Specifically, we asked the two following questions: (1) What are the bottom-up effects of fertilization and MeJA on tomato plant growth and resistance traits (direct and indirect) and on the preference and performance of *T. absoluta*? (2) Do fertilization and MeJA interact to affect tomato plant growth and resistance traits and the preference and performance of *T. absoluta*? Our study aims to better understand how nutrient availability may modulate plant resistance traits against a specialist herbivore of tomato and other solanaceous plants, which can have practical implications within an IPM framework.

Materials and methods

Plants and insects

We tested our hypothesis in a system that consisted of tomato plants and the herbivore *T. absoluta* (Lepidoptera: Gelechiidae), a serious insect pest of tomatoes in its native range (South America) that has recently invaded new areas around the world (Desneux et al. 2010; Mansour et al. 2018; Han, Bayram, et al. 2019; Desneux et al. 2022).

Tomato plants, *S. lycopersicum* cv. Santa Clara, were grown from seeds in a greenhouse under natural light and temperature conditions ($24 \pm 5.5^\circ\text{C}$) in Basaplant soil (Base Agro, São Paulo, Brazil) in plastic cells; the cultivar Santa Clara is highly susceptible to *T. absoluta* (Proffitt et al. 2011). Seedlings at 6–7 cm high (15–20 days after sowing) were transferred to 1.9-L round plastic pots ($17 \times 15 \times 12$ cm) containing Basaplant and coconut fiber (1:1). Plants were maintained in the greenhouse, irrigated as needed, and used in experiments (see ‘MeJA treatment’ below) when they had six fully expanded leaves (40–45 days after sowing).

Tuta absoluta was obtained from a laboratory colony initiated in 2018 from larvae and pupae collected from commercial tomato farms located in Paulínia (São Paulo, Brazil). The colony was maintained on tomato plants, cv. Santa Cruz, in the Department of Entomology and Acarology at ESALQ/USP (Piracicaba, São Paulo, Brazil). Larvae and adults were kept in separate cages ($60 \times 60 \times 30$ cm) covered with a fine mesh under controlled conditions ($25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ relative humidity [RH], 12:12 light:dark [L:D]). An aqueous honey solution (10%) was provided on a cotton wool as a food source for adults inside the cage. Adults used in oviposition studies were 2–3 days old, and eggs used in performance studies were 60–72 h old.

Fertilization regimes

After being transplanted to the round plastic pots, 15–20 days after sowing as described above, plants were grown in soil treated with one of the following four different rates of Basacote® Plus 6M nitrogen, phosphorus, and potassium (NPK) 16:8:12(+2) (Compo, Münster, Germany), a slow-release fertilizer: (1) low = 0.05 g/L (0.025 \times), (2) medium = 1 g/L (0.5 \times), (3) optimal = 2 g/L (1 \times), and (4) high = 4 g/L (2 \times). These rates were based on recommendations of the manufacturer (https://www.compo-expert.com/sites/default/files/2020-01/Folder_Basacote_EN_2018.pdf).

Because tomato plants do not grow well without fertilizer, the lowest fertilizer rate used was 0.025 \times the optimal rate; in addition, we tested a rate below and a rate above the optimal rate following methods in de Lange et al. (2019). Fertilizer applications were made once. Different sets of plants were used to study the effects of fertilization on the preference and performance of *T. absoluta* and on plant chemistry (see details below).

MeJA treatment

To determine a MeJA concentration that affects *T. absoluta* performance on tomatoes, we conducted a preliminary study to test the effects of different MeJA concentrations on *T. absoluta*. Plants (40–45 days old) were individually

sprayed 25 days after the fertilizer treatment with suspensions of 15 mL MeJA (Sigma-Aldrich, St. Louis, MO, USA) at 0 (control), 1, 2, or 3 mM dissolved in 0.1% Tween-20. Control treatments were sprayed with 0.1% Tween-20 only. Treatments were applied to plants using an atomizer until run-off. To avoid contamination, MeJA and control sprays were performed in different greenhouses maintained under the same environmental conditions mentioned above, and plants remained in separate greenhouses until the start of the experiments. Three days after the MeJA and control treatments, four *T. absoluta* eggs were individually placed on different leaves within plants; 16 plants (replicates) were used for each treatment. After larval development was completed, pupal weights were recorded.

Based on the results from these preliminary studies (see Supplemental Figure 1), we conducted all the experiments on the effects of MeJA application on the preference and performance of *T. absoluta* and on plant chemistry (see details below) using 15 mL of a 2 mM MeJA solution per plant. This (2 mM) was the lowest MeJA concentration that negatively affected *T. absoluta* pupal weight. All these experiments were conducted three days after the MeJA treatment, as in Tan et al. (2012), and different sets of plants were used for each experiment.

Oviposition preference

Three choice experiments were carried out to determine *T. absoluta* oviposition preference in response to fertilizer rates and induction by MeJA on tomato plants. All experiments were conducted in an empty greenhouse under natural light and temperature conditions ($24 \pm 5.5^\circ\text{C}$). In all experiments, *T. absoluta* adults were removed from the plants after 24 h and the number of eggs laid on each plant was counted. Each choice experiment was replicated 8 times.

Two-choice tests. We conducted two-choice tests to compare the oviposition preference of *T. absoluta* between MeJA-induced plants and non-induced (control) plants, under the same fertilization rate. Plants from each treatment were placed 0.8 m apart on opposite sides of a cage ($100 \times 70 \times 50$ cm), covered with fine netting, in a greenhouse. Cages were at least 2 m from each other and 6 *T. absoluta* adults (3 males and 3 females) were released inside each cage.

Four-choice tests. We conducted four-choice tests to compare the oviposition preference of *T. absoluta* among plants exposed to the four different fertilization rates (low, medium, optimal, and high) under the same induction status (i.e. plants induced by MeJA or non-induced plants). The four plants were arranged randomly in a square pattern at 1 m from each other inside a greenhouse ($4 \times 4 \times 4$ m). Twelve *T. absoluta* adults (6 males and 6 females) were then released inside the greenhouse. Each replicate was run on a separate day.

Multiple-choice test. We conducted multiple-choice tests to compare the oviposition preference of *T. absoluta* among all eight treatment combinations (plants under four different fertilization regimes that were induced and not induced by MeJA). Plants were arranged in a (3.5 m diameter) circle inside a greenhouse ($4 \times 4 \times 4$ m), such that a plant from each treatment combination was placed randomly at about 1 m from each other. Following, 24 *T. absoluta* adults (12 males and 12 females) were released inside the greenhouse. Each replicate was run on a separate day.

Offspring performance

To assess *T. absoluta* offspring performance on plants, four *T. absoluta* eggs were placed with a fine bush on plants inside of cages ($45 \times 30 \times 30$ cm) covered in fine netting and kept in a greenhouse under natural light and temperature conditions ($24 \pm 5.5^\circ\text{C}$). The eggs were individually placed in different leaves within the plants and were inspected daily until they hatched. If an egg failed to hatch, a newly emerged larva was placed on the same leaf. Larval survival, developmental time (days) from egg to pupa, and pupal weights were recorded. Thirteen plants (replicates) were used for each of the 8 treatment combinations, i.e. plants under different fertilization regimes treated or not treated with MeJA.

Plant growth

Aboveground plant dry weight and plant height were used as proxy for plant growth. Plants ($n = 8$) for each of the 8 treatment combinations were cut just above the soil surface from the pots, their lengths were measured, and were then dried in paper bags in a drying oven (Quimis Q317M32, São Paulo, Brazil) at 60°C for 72 h. After drying, samples were weighed to determine differences on dry plant biomass among treatments.

Soil nitrogen levels

To quantify the amounts of nitrogen in the soil, soil samples (~ 100 g, $n = 5$) were taken from pots from each of the 8 treatment combinations. Soil samples were dried at 45°C for 72 h and sieved (~ 2 -mm mesh), and total nitrogen was quantified by the Kjeldahl method (Nelson and Sommers 1980).

Nutrient levels in leaves

Leaf samples (140 g, $n = 5$) were taken for each of the eight treatment combinations and dried in a stove at 60°C for 72 h. Dried samples were ground and then subjected to sulfuric digestion to determine nitrogen concentrations by the Kjeldahl method (Nelson and Sommers 1980) and subjected to nitric-perchloric digestion to determine the concentration of phosphorus, potassium, calcium, magnesium, and sulfur (Zarcinas et al. 1987).

Total phenolics

We measured levels of total phenolics as proxy of a direct resistance trait. Total phenolic content was determined by a modification of the Folin-Ciocalteu method (Ainsworth and Gillespie 2007). In short, leaf samples (0.3 g) were frozen in liquid nitrogen and placed into 15-mL glass tubes with 4 mL methanol (50%). The extract was incubated in a water bath (Marconi MA156, São Paulo, Brazil) for 1.5 h at 80°C and centrifuged (Sorvall instruments RC5C centrifuge, Dupont, DE, USA) at 20,000 g for 15 min at room temperature, and then the supernatant was collected in a new tube (Kofalvi and Nassuth 1995). A total of 150 μL of this extract was mixed with 150 μL Folin reagent (Sigma Aldrich, Merck, Germany), previously diluted with water (1:1), and allowed to stand for 5 min. Then, 3 mL of Na_2CO_3 (2%) was added. After 5 min, the mixture was measured at 750 nm on a spectrophotometer (Hitachi U-1900, Tokyo, Japan). A

standard curve was prepared with chlorogenic acid at concentrations of 0, 10, 20, 30, 40, 50, 100, 150, and 250 $\mu\text{g}/\text{mL}$ (Bray and Thorpe 1954). Five samples (replicates) of each of the 8 treatment combinations were analyzed.

Collection and analysis of volatile emissions

We measured volatile emissions as a proxy of an indirect resistance trait. Headspace volatile samples were taken from tomato plants exposed to one of the four fertilizer regimes and one of the two induction treatments for 4 h during daytime under laboratory conditions ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH). Pots containing the plants were wrapped with aluminum foil to avoid trapping volatiles from plastic and soil. After that, plant shoots were individually enclosed in a 15-L glass chamber and connected to a volatile collection system (Analytical Research Systems Inc., Gainesville, FL, USA). Clean humidified air was pushed at 0.8 L/min into the glass chamber connected to a column containing an adsorbent polymer (30 mg; Hayesep-Q, Alltech Associates, Deerfield, IL, USA) that trapped the volatiles, which was connected to a vacuum pump pulling air at the same flow rate. Following, the polymer column was eluted with 150 μL of distilled hexane, and the samples were stored in glass vials at -30°C until analysis. Dry weight of the plant shoots was determined. Five replicates for each of the 8 treatment combinations were sampled.

Volatile quantification was performed by gas chromatography coupled to a flame ionization detector (GC-FID; GC2010 Shimadzu, Kyoto, Japan) operated at 280°C . Nonyl acetate (Sigma Aldrich, St. Louis, MO, USA) was added (10 μL of a 10-ng/ μL solution) in each sample as an internal standard. A 2- μL aliquot of each sample was injected in the column with helium as the carrier gas (24 cm/s). The relative amount of the compounds in each sample was determined based on a comparison of their peak area with that of the internal standard and standardized per unit of fresh shoot biomass (g) for each of the replicates. For volatile identification, the most representative sample of each treatment was further analyzed by gas chromatography coupled to a mass spectrometer (GC-MS; Agilent 6890 Series GC system G1530A), following the same set-up of the GC-FID analysis. Volatile compounds were tentatively identified by comparing the mass spectra obtained in the GC-MS run with the NIST11 library database and by comparison with published Kovats retention indices. Authentic standards were used to confirm the identities of α -pinene, β -myrcene, α -phellandrene, limonene, γ -terpinene, and β -caryophyllene (Sigma-Aldrich, Merck KGA, St. Louis, Missouri, USA).

Data analyses

The experimental design was 4×2 factorial, with four fertilizer regimes and two induction treatments for a total of eight treatment combinations. Prior to the analyses, all data were checked for normality using the Shapiro-Wilk test and homogeneity of variances using the Levene's test. All data analyses were performed in Minitab version 17 (Minitab 2013) and R software version 2022.02.3 (R Core Team 2022) using the packages 'hnp,' 'means,' and 'multcomp.'

Two-choice tests to determine *T. absoluta* oviposition preference were analyzed using Student's *t* tests. Four-choice

and multiple-choice tests were analyzed using two-way analysis of variance (ANOVA), testing for the effects of fertilizer rates, MeJA-induced resistance, and the interaction between them (fixed factors); replicate was included in the model as a random factor.

Larval survival, egg-larva developmental times, pupal weights, plant growth, nitrogen in the soil, and total phenolics in leaves were analyzed using two-way ANOVA with fertilizer rates, MeJA-induced resistance, and the interaction between them as independent factors. Prior to the analysis, data on offspring performance were averaged for each plant (replicate), and data on percent larval survival were arcsine-square-root transformed. Replicate was included in the model as a random factor.

Since the components of the nutrient and volatile profiles are not independent, we used two-way multivariate analysis of variance (MANOVA) to analyze the effects of fertilizer rates, MeJA-induced resistance, and their interaction on the levels of leaf nutrients and volatile emissions. A significant MANOVA effect was then followed by generalized linear model (GLM) with a gamma distribution (log link) to assess which individual component within the nutrient and volatile profiles was affected by treatment.

If needed, data were transformed prior to ANOVA and MANOVA analysis by using $\ln(x + 1)$ to meet assumptions of normality. Significant ANOVA effects were subjected to pairwise comparison by Tukey post-hoc tests ($P < 0.05$).

Results

Oviposition preference

Two-choice tests. Induced resistance by MeJA had a significant effect on *T. absoluta* oviposition preference under the low ($t = 2.50$; $\text{df} = 1, 17$; $P = 0.041$) and optimal ($t = 2.63$; $\text{df} = 1, 17$; $P = 0.034$) fertilizer rates; females laid 53% and 46% more eggs, respectively, on non-induced (control) plants than on MeJA-induced plants (Figure 1(a)). Although the trend in oviposition preference between MeJA-induced and control plants was similar at the medium and high fertilizer rates, the difference was not significant (Medium: $t = 1.10$; $\text{df} = 1, 17$; $P = 0.308$; High: $t = 2.15$; $\text{df} = 1, 17$; $P = 0.068$) (Figure 1(a)).

Four-choice tests. Fertilizer regime significantly affected *T. absoluta* oviposition preference on non-induced (control) plants ($F = 9.33$; $\text{df} = 3, 31$; $P < 0.001$) and on plants induced by MeJA ($F = 4.81$; $\text{df} = 3, 31$; $P = 0.011$). On non-induced plants, *T. absoluta* laid 51%, 74%, and 72% more eggs under medium, optimal, and high fertilizer rates, respectively, than at the low rate (Figure 1(b)). Similarly, on MeJA-induced plants, the numbers of eggs laid were 64%, 72%, and 64% higher under medium, optimal, and high fertilizer rates, respectively, than at the low rate (Figure 1(b)).

Multiple-choice tests. The amount of fertilizer significantly affected *T. absoluta* oviposition preference ($F = 10.76$; $\text{df} = 3, 63$; $P < 0.001$). Females laid 40%, 50%, and 54% more eggs on plants under the medium, optimal, and high fertilizer rates, respectively, than at the lower rate (Figure 1(c)). In contrast, MeJA application had no effect on adult oviposition preference ($F = 2.88$; $\text{df} = 1, 63$; $P = 0.096$), and there was no interaction effect between fertilizer rates and induced resistance by MeJA ($F = 0.54$; $\text{df} = 3, 63$; $P = 0.657$).

Offspring performance

Survival. Fertilizer rates affected larval survival of *T. absoluta* significantly ($F = 2.85$; $df = 3, 103$; $P = 0.041$). Larval survival was 13%, 21%, and 16% greater on plants under the medium, optimal, and high fertilizer rates, respectively, than at the lower rate (Figure 2(a)). However, MeJA application had no effect on larval survival ($F = 1.92$; $df = 1, 103$; $P = 0.169$), and there was no interaction effect between fertilizer rates and induced resistance by MeJA ($F = 0.40$; $df = 3, 103$; $P = 0.755$).

Larval developmental time. The amount of fertilizer ($F = 18.83$; $df = 3, 103$; $P < 0.001$) and induced resistance by MeJA ($F = 6.47$; $df = 1, 103$; $P < 0.01$) had a significant effect on *T. absoluta* developmental time. Larval developmental time was 5–6.5% longer when plants received low

fertilizer rates than under the medium, optimal, and high rates (Figure 2(b)). Induced resistance by MeJA also significantly extended larval developmental times by 1.7% compared to control plants. There was no interaction effect between fertilizer rates and induction ($F = 0.11$; $df = 3, 103$; $P = 0.952$).

Pupal weight. Both fertilizer rates ($F = 20.73$; $df = 3, 103$; $P < 0.001$) and induced resistance by MeJA ($F = 6.62$; $df = 1, 103$; $P = 0.012$), but not their interaction ($F = 0.44$; $df = 3, 103$; $P = 0.723$), had a significant effect on *T. absoluta* pupal weight. Pupal weights were 20%, 24%, and 24% higher in plants under the medium, optimal, and high fertilizer rates, respectively, than at the lower rate (Figure 2(c)). In contrast, pupal weights were 7% lower in plants induced by MeJA than in non-induced plants (Figure 2(c)).

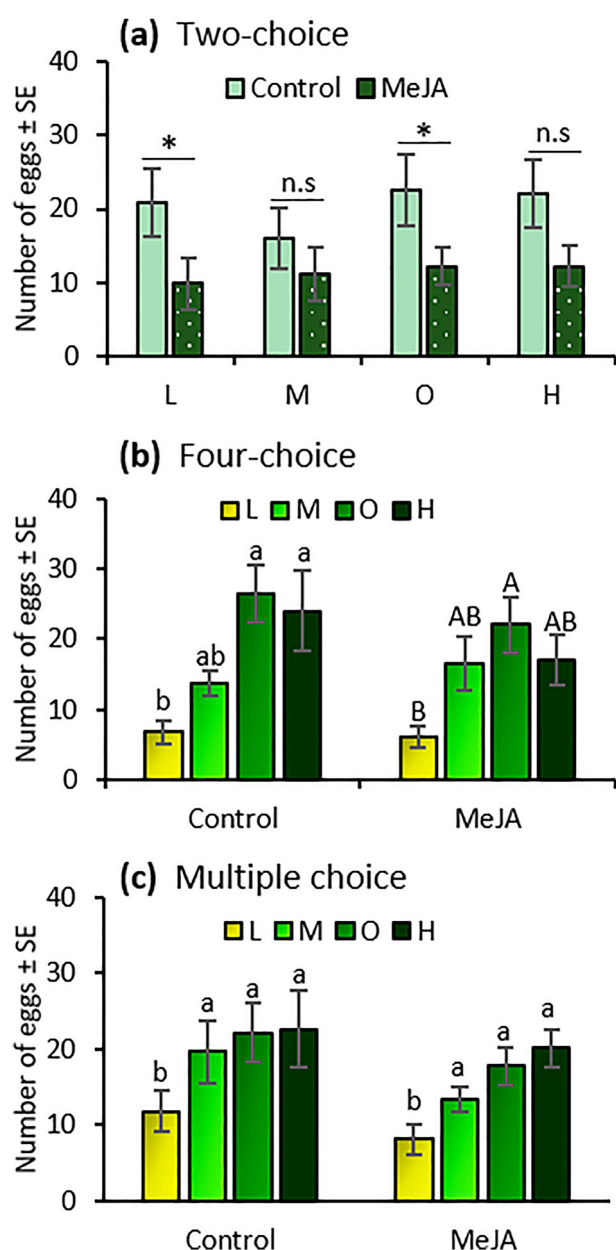


Figure 1. Number of eggs laid by *Tuta absoluta* females (mean ± SE) on tomato plants exposed to four fertilizer regimes (L = low, M = medium, O = optimal, and H = high) with and without induction by methyl jasmonate (MeJA) in two-choice (a), four-choice (b), and multiple-choice tests (c). An asterisk (*) indicates significant differences between treatments. Different letters indicate significant differences among treatments (two-way analysis of variance, $P < 0.05$). $n = 8$; n.s., not significant.

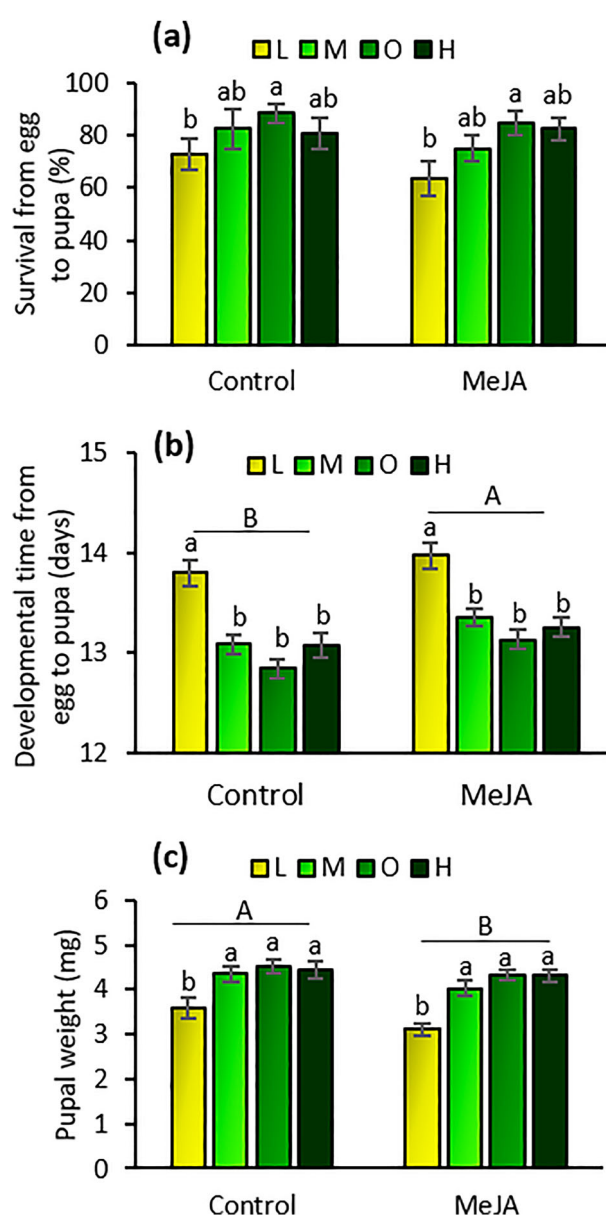


Figure 2. Larval survival (percent ± SE) (a), developmental time from egg to pupa (mean days ± SE) (b), and pupal weights (mean mg ± SE) (c) of *Tuta absoluta* feeding on tomato plants exposed to different fertilizer regimes (L = low, M = medium, O = optimal, and H = high) with and without induction by methyl jasmonate (MeJA). Uppercase letters indicate significant differences between induced and non-induced plants, while lowercase letters indicate significant difference among fertilizer regimes (two-way analysis of variance, $P < 0.05$). $n = 13$.

Plant growth

Plant dry weight was significantly affected by fertilizer rates ($F = 16.34$; $df = 3, 63$; $P < 0.001$). Plant dry weight under the optimal fertilizer input was 53%, 20%, and 23% higher than at the low, medium, and high rates (Figure 3(a)). Plants under the low fertilizer rate had the lowest weight of all the treatments. There were no effects of induced resistance by MeJA ($F = 0.01$; $df = 1, 63$; $P = 0.919$) or an interaction effect between fertilizer and induction on the dry weight of tomato plants ($F = 0.18$; $df = 3, 63$; $P = 0.906$).

Plant height was also significantly affected by fertilizer rates ($F = 35.0$; $df = 3, 63$; $P < 0.001$). Plant height under the optimal and medium fertilizer inputs was higher than at the low and high rates (Figure 3(b)). There were no effects of MeJA induction ($F = 0.02$; $df = 3, 63$; $P = 0.896$) or an interaction effect between fertilizer and induction on the height of tomato plants ($F = 0.15$; $df = 3, 63$; $P = 0.926$).

Soil nitrogen levels

As expected, higher fertilizer rates led to significantly higher nitrogen levels in the soil ($F = 42.64$; $df = 1, 40$; $P < 0.001$) (Figure 4). Also, as expected, there were no effects of MeJA induction ($F = 0.22$; $df = 1, 40$; $P = 0.805$) or an interaction effect between fertilizer regime and induction on the level of nitrogen in the soil ($F = 0.65$; $df = 3, 40$; $P = 0.937$).

Nutrient levels in leaves

The amount of fertilizer affected the levels of nutrients in tomato leaves (Wilks' Lambda = 0.058; $F = 7.416$; $df = 18, 76$; $P < 0.001$). However, neither MeJA induction (Wilks' Lambda = 0.726; $F = 1.698$; $df = 6, 27$; $P = 0.160$) nor the

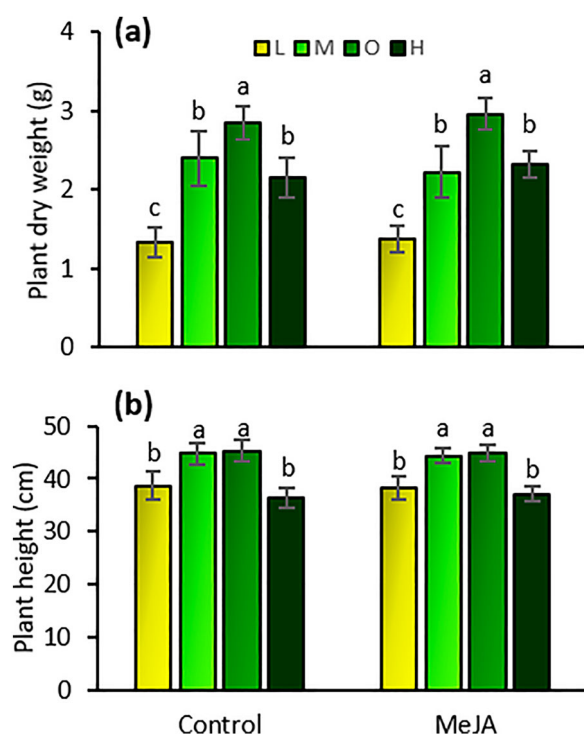


Figure 3. Dry weight (mean $g \pm SE$) (a) and height (mean $cm \pm SE$) (b) of tomato plants exposed to four fertilizer regimens (L = low, M = medium, O = optimal, and H = high) with and without induction by methyl jasmonate (MeJA). Different letters indicate significant differences among treatments (two-way analysis of variance, $P < 0.05$). $n = 8$.

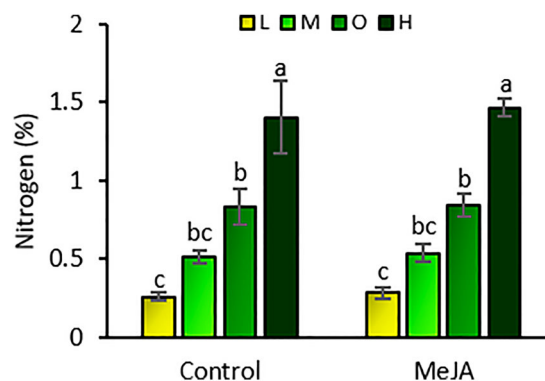


Figure 4. Percentage of nitrogen in the soil (mean percent $\pm SE$) exposed to four fertilizer regimens (L = low, M = medium, O = optimal, and H = high) with and without induction by methyl jasmonate (MeJA). Different letters indicate significant differences between treatments (two-way analysis of variance, $P < 0.05$). $n = 5$.

interaction between fertilizer and induction (Wilks' Lambda = 0.844; $F = 0.263$; $df = 18, 76$; $P = 0.999$) affected nutrient levels. Levels of nitrogen, phosphorus, potassium, calcium, and magnesium in leaf tissue were significantly altered by fertilizer rates (Table 1). Plants under high fertilizer rates had 34%, 15%, and 12% higher levels of nitrogen than under low, medium, and optimal rates, respectively (Figure 5(a)). In the same way, phosphorus levels in high fertilizer plants were 47%, 34%, and 25% higher than at the low, medium, and optimal rates, respectively (Figure 5(b)). Plants under the optimal fertilizer rate had 20%, 10%, and 10% higher concentration of potassium than the low, medium, and high rates, respectively (Figure 5(c)). Plants under the low fertilizer rate had the lowest levels of nitrogen, phosphorus, and potassium of all fertilizer treatments (Figure 5(c)). Conversely, plants under the low fertilizer rate had the highest concentration of calcium and magnesium in leaf tissue of all fertilizer treatments (Figure 5(d,e)). In both cases, plants under the high fertilizer rate had the lowest concentration of calcium and magnesium. The amount of fertilizer did not affect sulfur concentration in leaves (Table 1, Figure 5(f)).

Total phenolics

Total phenolic levels in leaf tissue were not affected by fertilizer rates ($F = 1.79$; $df = 3, 39$; $P = 0.169$). However, MeJA increased total phenolic levels by 14% compared to non-induced plants ($F = 5.67$; $df = 1, 39$; $P = 0.023$) (Figure 6). There was no interaction effect between fertilizer rates and MeJA induction on the levels of total phenolics in tomato plants ($F = 0.05$; $df = 3, 39$; $P = 0.985$).

Volatile emissions

Volatile analyses identified 14 compounds among all treatments. Volatile emissions were affected by MeJA induction (Wilks' Lambda = 0.371; $F = 2.305$; $df = 14, 19$; $P = 0.046$) but not by fertilizer regime (Wilks' Lambda = 0.15; $F = 1.217$; $df = 42, 57$; $P = 0.243$) or the interaction between fertilizer regime and MeJA induction (Wilks' Lambda = 0.146; $F = 1.244$; $df = 42, 57$; $P = 0.220$). MeJA induction increased total volatile emissions and the emissions of 12 terpene compounds (α -pinene, β -pinene, β -myrcene, 2-carene, α -phellandrene, α -terpinene, o-cymene, β -phellandrene,

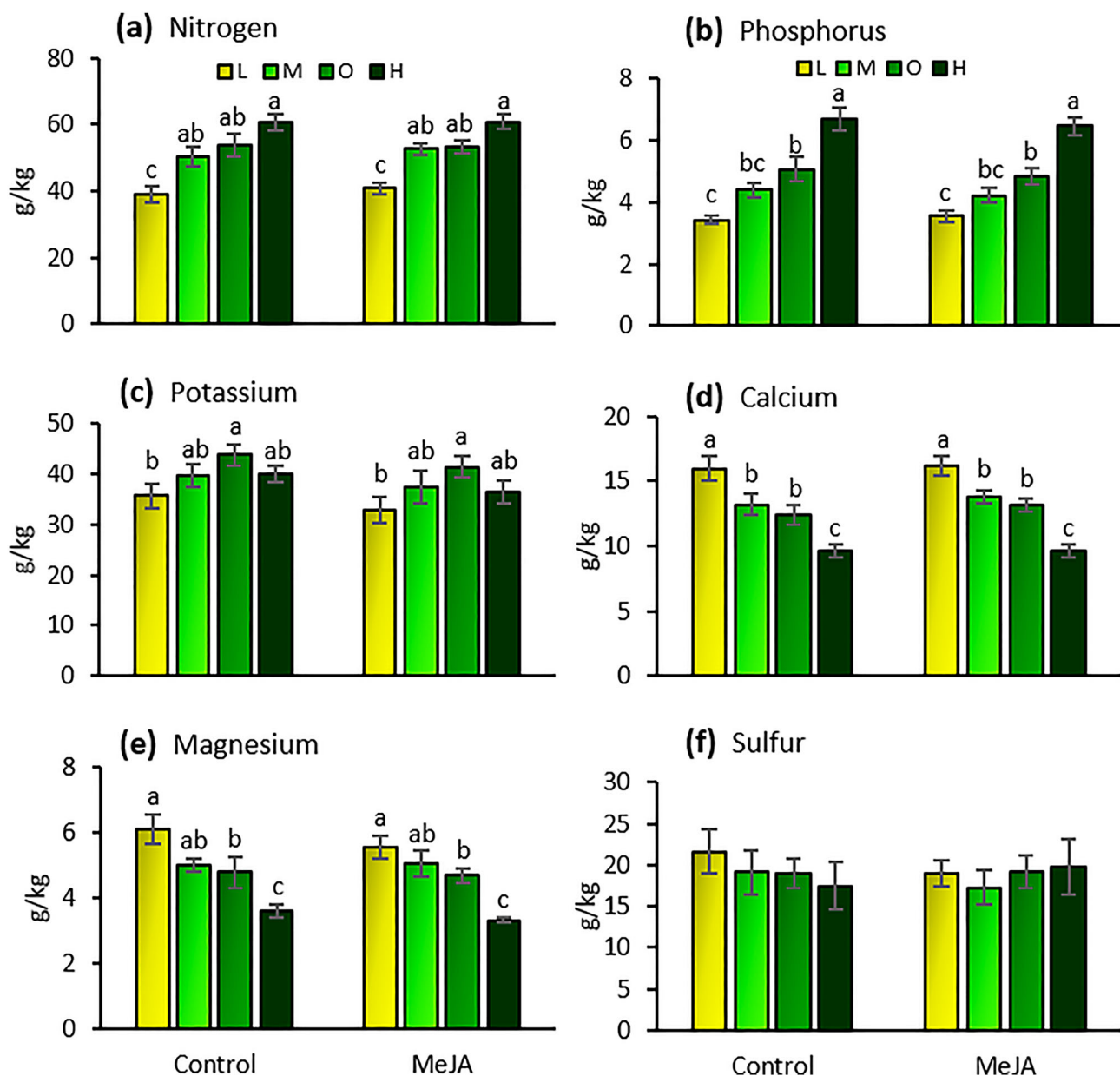


Figure 5. Concentrations of nitrogen (a), phosphorus (b), potassium (c), calcium (d), magnesium (e), and sulfur (f) in the leaves of tomato plants (mean g/kg ± SE) exposed to four fertilizer regimens (L = low, M = medium, O = optimal, and H = high) with and without induction by methyl jasmonate (MeJA). Different letters indicate significant differences among treatments (two-way multivariate analysis of variance, $P < 0.05$). $n = 5$.

limonene, β -ocimene, γ -terpinene, and β -caryophyllene) in tomato plants compared to non-induced plants (Table 2; Figure 7).

Discussion

Although plants often deal with multiple stresses that can affect their growth and defensive traits and subsequently affect their interactions with herbivores (Chapin et al. 1987), most research has focused on understanding these

interactions under a single stress condition. Here, we explored how nutrient availability, a potential abiotic stress, modules induced resistance triggered by the elicitor MeJA against *T. absoluta* in tomato plants. Our study demonstrated that (1) fertilization increased leaf nutrient content of nitrogen, phosphorus, and potassium (NPK), which resulted in greater preference and performance of *T. absoluta*, but had no effect on defensive traits (total phenolic and volatile emissions); (2) MeJA increased levels of defensive traits, which correlated with decreased preference

Table 1. Results of two-way analysis of variance (ANOVA) for the effects of fertilizer rates ('Fertilizer') and induction by methyl jasmonate ('MeJA'), and the interaction between these two factors on the levels of nutrients in tomato leaves.

Source of variation	df ^a	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sulfur	
		F	p ^b	F	p ^b	F	p ^b	F	p ^b	F	p ^b	F	p ^b
Fertilizer	3	26.48	< 0.001	43.92	< 0.001	4.03	0.015	29.81	< 0.001	15.42	< 0.001	0.41	0.744
MeJA	1	0.26	0.62	0.29	0.59	2.87	0.1	0.67	0.42	1.06	0.31	0.05	0.82
Fertilizer × MeJA	3	0.16	0.92	1.93	0.9	0.07	0.98	0.14	0.93	0.27	0.85	0.32	0.81

^aError df = 32.

^bNumbers in bold indicate significant effects at $\alpha = 0.05$.

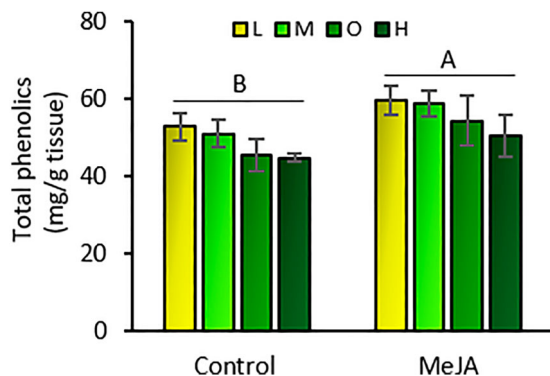


Figure 6. Total phenolic content (mean mg de chlorogenic acid/g fresh tissue \pm SE) in tomato leaves exposed to four fertilizer regimes (L = low, M = medium, O = optimal, and H = high) with and without induction by methyl jasmonate (MeJA). Different letters indicate significant differences between treatments (two-way analysis of variance, $P < 0.05$). $n = 5$.

and performance of *T. absoluta*; and (3) fertilization did not interact with MeJA to affect plant growth and nutrient content, defensive traits, or the preference and performance of *T. absoluta*.

Fertilization triggered bottom-up effects that influenced tomato-*T. absoluta* interactions. In our study, tomato plants under an optimal fertilizer rate had higher growth rates than plants under insufficient (i.e. below optimal) and excessive (i.e. above optimal) fertilizer rates. Nutrient deficiencies can negatively affect plant growth, while an excess of nutrients can be associated with high soluble salt concentrations that can interfere with plant growth (Marschner 1983). These bottom-up effects positively affected *T. absoluta*. In accordance with the preference-performance (or ‘mother knows best’) hypothesis (Jaenike 1978), we observed a strong correlation between *T. absoluta* oviposition preference and larval performance. Females preferred to oviposit and larvae performed better, i.e. had increased survival rates, reduced developmental times, and higher pupal weights, on plants under optimal and high nutrient content. By contrast, plants with low fertilization rates showed low oviposition preference by females and reduced larval performance. These findings were expected since the development success of insect herbivores is often positively correlated with the nitrogen content in their host plants (Sétamou et al. 1993; Awmack and Leather 2002; Shah 2017). In fact, recent studies have also shown that *T. absoluta* females prefer to oviposit on host plants that enhance their offspring performance (Sylla et al. 2019; Silva et al. 2021). *Tuta absoluta* females likely respond behaviorally to visual and chemical changes in host plants due to fertilization, which is an example of antixenosis triggered by bottom-up effects. Interestingly, fertilization rates above optimal reduced plant growth even when nitrogen levels in the soil and leaves were the highest; however, despite this increase in nitrogen levels, *T. absoluta* preference and performance were comparable between optimal and high fertilizer rates, indicating that too much fertilizer did not benefit either the plant or the pest.

The positive effects of fertilization on *T. absoluta* preference and performance can be attributed to changes in plant nutrients and secondary metabolites (Herms and Mattson 1992; Herms 2002). As expected, our study showed that plants under higher fertilizer rates had increased levels of NPK in their leaves. These three elements are essential for the proper growth and development of tomato plants

Table 2. Results of two-way analysis of variance (ANOVA) for the effects of fertilizer rates (‘Fertilizer’) and induction by methyl jasmonate (‘MeJA’), and the interaction between these two factors on the amounts of volatiles emitted from tomato plants.

Compound	Factor	χ^2	P^a	Compound	Factor	χ^2	P^a
(Z)-3-Hexenol	Fertilizer	0.054	0.997	α -Phellandrene	Fertilizer	0.763	0.858
	MeJA	0.067	0.797		MeJA	7.271	0.007
α -Pinene	Fertilizer \times MeJA	0.222	0.974	α -Terpinene	Fertilizer \times MeJA	2.072	0.558
	Fertilizer	1.744	0.627		Fertilizer	1.324	0.723
	MeJA	7.743	0.005		MeJA	5.907	0.015
	Fertilizer \times MeJA	1.575	0.665		Fertilizer \times MeJA	2.004	0.572
β -Pinene	Fertilizer	1.505	0.681	O-cymene	Fertilizer	0.941	0.815
	MeJA	4.688	0.030		MeJA	10.628	0.001
β -Myrcene	Fertilizer \times MeJA	2.811	0.422	β -Phellandrene	Fertilizer \times MeJA	0.644	0.886
	Fertilizer	1.633	0.652		Fertilizer	1.233	0.745
	MeJA	10.18	0.001		MeJA	6.766	0.009
	Fertilizer \times MeJA	2.88	0.41		Fertilizer \times MeJA	1.748	0.626
2-Carene	Fertilizer	1.139	0.768	Limonene	Fertilizer	0.902	0.825
	MeJA	6.998	0.008		MeJA	5.433	0.020
	Fertilizer \times MeJA	1.814	0.612		Fertilizer \times MeJA	1.668	0.644
Total	Fertilizer			β -Ocimene	Fertilizer	2.916	0.405
	MeJA				MeJA	13.678	0.001
	Fertilizer \times MeJA			γ -Terpinene	Fertilizer \times MeJA	2.127	0.546
					Fertilizer	1.786	0.618
				β -Caryophyllene	MeJA	4.501	0.034
					Fertilizer \times MeJA	1.137	0.768
				Humulene	Fertilizer	1.786	0.901
					MeJA	4.045	0.044
Total	Fertilizer \times MeJA			Humulene	Fertilizer \times MeJA	0.491	0.921
					Fertilizer	0.545	0.909
				Total	MeJA	3.579	0.058
					Fertilizer \times MeJA	0.555	0.907
Total	Fertilizer			Total	Fertilizer	1.129	0.770
	MeJA				MeJA	6.77	0.009
Total	Fertilizer \times MeJA			Total	Fertilizer \times MeJA	1.626	0.653

^aNumbers in bold indicate significant effects at $\alpha = 0.05$.

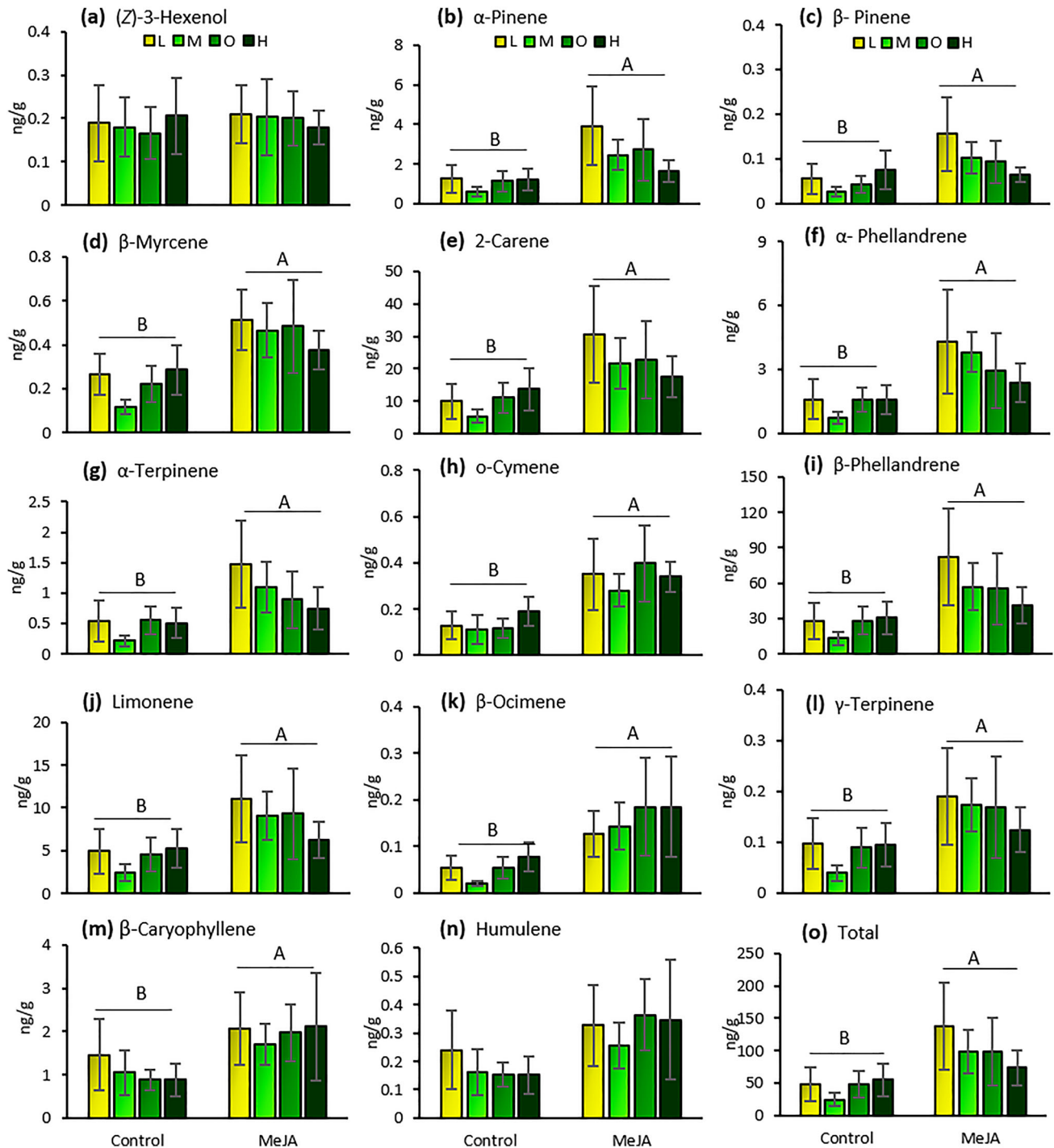


Figure 7. Amounts (mean ng/g fresh tissue \pm SE) of (Z)-3-hexenol (a), α -pinene (b), β -pinene (c), β -myrcene (d), 2-carene (e), α -phellandrene (f), α -terpinene (g), o-cymene (h), β -phellandrene (i), limonene (j), β -ocimene (k), γ -terpinene (l), β -caryophyllene (m), humulene (n), and total volatiles (o) emitted from tomato plants under four fertilizer regimes (L = low, M = medium, O = optimal, and H = high) with and without induction by methyl jasmonate (MeJA). Means followed by different letters indicate significant differences among treatments (GLM, $P < 0.05$). $n = 5$.

(Adams 1986) and of insects (Dale 1988; Schoonhoven et al. 2005; Amtmann et al. 2008; Chan et al. 2021). For instance, nitrogen is positively correlated with amino acid and protein content and its deficiency may limit insect growth (Schoonhoven et al. 2005). Indeed, nitrogen deficiency to tomato plants has been shown to limit *T. absoluta* growth via bottom-up effects (Han et al. 2014). Potassium deficiency may disrupt protein synthesis, which can result in an increase in amino acids and a decrease in sugar content (Dale 1988), and phosphorus can also play an important role in plant resistance against herbivores (Chan et al. 2021). Higher fertilizer rates also decreased levels of calcium and magnesium, and these imbalances in macro-elements could

trigger bottom-up effects that affect the performance of *T. absoluta* on tomato plants (Queiroz et al. 2022); however, compared to NPK, these two elements appear to be less critical to tomato-*T. absoluta* interactions because their levels were not correlated with *T. absoluta* preference and performance. As predicted by the resource availability hypothesis, we expected tomato plants under high fertilizer regimes to have low investment in anti-herbivore defenses (Coley 1987). However, our study did not show changes in levels of total phenolics (direct resistance) or volatile emissions (indirect resistance) in response to fertilization. It is possible that other resistance traits not measured here, such as specific phenolic compounds, glycoalkaloids, and defensive enzymes,

could have increased under low nutrition since nitrogen content may affect the levels of these compounds in tomato plants (Han et al. 2016; Larbat et al. 2016; Becker et al. 2021).

Jasmonates (i.e. JA and MeJA) are elicitors of plant resistance against chewing herbivores such as caterpillars (Chen et al. 2005; Tortorici et al. 2022). Here, we demonstrated that *T. absoluta* females lay fewer eggs on tomato plants treated with MeJA. Previous studies showed that *T. absoluta* females prefer to oviposit on undamaged plants than on plants damaged by conspecific larvae (Anastasaki et al. 2018), which could be mediated by plant volatiles. Indeed, plant volatiles are cues used by females to locate suitable oviposition sites (Webster and Cardé 2017) and to avoid competition by conspecific and heterospecific herbivores (De Moraes et al. 2001; Knolhoff and Heckel 2014). In fact, tomato plants infested by herbivores altered the emission of volatiles, which modified *T. absoluta* oviposition (Anastasaki et al. 2018; Silva et al. 2022). In our study, MeJA-induced plants increased the emission of 12 terpene volatiles and many of them are also increased after *T. absoluta* larval feeding (Anastasaki et al. 2018; Silva et al. 2022). Likewise, tomato seeds treated with JA increased the emission of methyl salicylate and 4,8,12-trimethyltrideca-1,3,7,11-tetraene (Smart et al. 2013). By contrast, a decrease in volatile emission was found when tomato seeds were applied with a low concentration of MeJA (0.8 mM) (Strapasson et al. 2014). Our MeJA treatment increased volatile emissions during the daytime, which could attract the natural enemies of *T. absoluta* and thus increase indirect resistance in tomatoes. For instance, tomato plants damaged by *T. absoluta* emitted higher amounts of α -pinene, α -phellandrene, 3-carene, β -ocimene, and β -phellandrene that increased attraction of the predator *Nesidiocoris tenuis* (Reuter) (Ayelo et al. 2021). Additional studies are needed to determine if MeJA also induces volatile emissions in tomatoes at nighttime.

Previous studies showed that *T. absoluta* larval performance is negatively affected by MeJA application to tomato seeds (Strapasson et al. 2014). In accordance with the preference-performance hypothesis, our study showed that lower oviposition on MeJA-treated tomato plants is correlated with reduced pupal weights and increased larval developmental times. Our MeJA treatment increased total phenolic content in leaves, which could partially explain the reduced *T. absoluta* performance on these plants. Phenolic compounds play an important role in plant resistance against insect herbivores (Summers and Felton 1994; Wallis and Galarneau 2020). Other studies also report increases of defensive enzymes after MeJA treatment in tomato plants (Tan et al. 2012; Paudel et al. 2014). In our study, we used a MeJA concentration that induces a relatively low, but significant, defensive response in tomato plants against *T. absoluta*; however, whether this concentration induces a defensive response similar to that caused by herbivore damage remains unknown. It is also unclear whether stronger bottom-up effects of tomato plants on *T. absoluta* could be induced by higher concentrations of MeJA (> 2 mM), and if these effects could persist over a long period.

We expected potential trade-offs between resistance responses of plants when simultaneously exposed to abiotic and biotic stresses. However, our study showed no interactions between nutrient availability and jasmonate-mediated induced resistance such that each plant stressor acted independently to affect antixenotic and antibiotic resistance against *T. absoluta* in tomato plants, i.e. there

were no fertilizer regime \times MeJA induction interaction effects. This finding suggests that in our bottom-up tomato-*T. absoluta* system, resources allocated for jasmonate-mediated induced resistance did not compete with resources allocated for plant growth. Other studies have also attempted to identify trade-offs between nutrient availability and induced plant resistance and found variable evidence (i.e. negative, neutral, and positive) for these trade-offs (Stout et al. 1998; Cipollini and Bergelson 2001; Schmelz et al. 2003; Lou and Baldwin 2004; Mason et al. 2022; Wang et al. 2022). For example, limited nutrient availability reduced induced resistance in rapeseed plants, but not under high nutrient availability (Cipollini and Bergelson 2001). By contrast, low nutrient availability resulted in increased induction of defense-related plant terpenes and phytohormones in maize (Schmelz et al. 2003) and increased herbivore-induced defenses in cotton (Chen et al. 2008). Recent studies in maize showed that high nitrogen supply improves induced resistance (Wang et al. 2022), while low fertilization reduces induced defenses but only in a resistant genotype (Mason et al. 2022). These studies, together with ours, highlight that predicting the outcomes of bottom-up effects on induced resistance against herbivores can be difficult because these effects depend on many factors, such as the type and strength of the fertilizer treatment (i.e. amount, composition, and rate) and the inducer of plant resistance (i.e. mechanical, herbivory, or elicitor), as well as on the plant's genotype. Future studies using standardized methodologies across multiple crops may help in better predicting the outcomes of these bottom-up effects.

In summary, we demonstrated that, under our testing conditions, the combined bottom-up effects of fertilization and MeJA independently affect the interactions between tomato plants and *T. absoluta*. Managing fertilizer inputs and the level of induced resistance in plants can be strategies to control insect pests in agroecosystems (Han et al. 2022). For instance, we found a lower preference and performance of *T. absoluta* on tomato plants under low fertilizer inputs and on plants treated with MeJA, which was correlated with lower nutrient content and higher levels of induced phenolics and terpene emissions, respectively. These two treatments could, however, negatively affect plant growth and yield. Although low fertilizer regimes are expected to reduce plant growth and yield, the effects of jasmonates on tomato growth and yield are not clear (Thaler 1999; Redman et al. 2001). It is even less clear how simultaneous stressors, such as limited nutrient availability and the activation of induced resistance, affect crop yield. In our study, *T. absoluta* performed well even at half the optimal fertilizer rate, which suggests that lower rates would be needed for its control but to the detriment of plant growth. In contrast, MeJA-induced resistance reduced *T. absoluta* preference and performance without any negative (short term) effects on plant growth, which suggests that manipulating induced resistance in tomatoes could serve as a potential control strategy against this pest. Moreover, it is important to examine how bottom-up effects on induced resistance influence plant interactions with multiple herbivores and their natural enemies (Strapasson et al. 2014; Becker et al. 2021). Our study was conducted in the greenhouse under controlled conditions; therefore, further studies are needed to determine if the bottom-up effects we observed here are consistent under field conditions. Improving our understanding on

methods to manipulate plant nutrient and defense levels can help develop novel IPM strategies against herbivores, such as *T. absoluta*, in agroecosystems.

Acknowledgements

We thank Drs. José R. P. Parra and Flávio C. Montes for assistance with rearing *T. absoluta* in the laboratory. We also thank two anonymous reviewers for helpful comments on an earlier draft of the manuscript.

Funding

We thank the following agencies for financial support: Instituto Nacional de Ciência e Tecnologia de Semioquímicos na Agricultura [Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP and Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq, grant #s 2014/50871-0 and 465511/2014-7]. P.S.-M. was funded by a doctoral scholarship from the Programa de Estudantes-Convênio de Pós-Graduação [PEC-PG/CAPEs, Process: 88881.284335/2018-01], Brazil. C.R.-S. was funded by the United States Department of Agriculture (USDA) Hatch projects NJ08140 and NJ08252. D.B.S. was funded by FAPESP – Process 2016/12771-0.

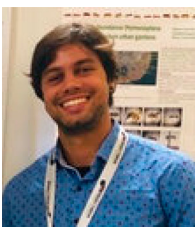
Notes on contributors



Paolo Salazar-Mendoza is a PhD student in the Department of Entomology and Acarology, 'Luiz de Queiroz' College of Agriculture, at the University of São Paulo, Brazil. He is studying the effects of domestication, nutrient availability, and induced resistance on tomato plant defenses against the South American tomato pinworm *Tuta absoluta*.



José Maurício S. Bento is a Full Professor in the Department of Entomology and Acarology, 'Luiz de Queiroz' College of Agriculture, at the University of São Paulo, Brazil. His research comprises chemical communication in insects and plant-insect-natural enemy interactions.



Diego B. Silva is an Associate Scientist at Provivi, Campinas, Brazil. He was a Post-doctoral Researcher in the Department of Entomology at Rutgers University and in the Department of Entomology and Acarology, 'Luiz de Queiroz' College of Agriculture, at University of São Paulo, Brazil. His research

interests include chemical ecology, biological control, and integrated pest management.



Sérgio F. Pascholati is a Senior Professor in the Plant Pathology and Nematology Program, 'Luiz de Queiroz' College of Agriculture, at University of São Paulo, Brazil. His research interests include plant disease physiology and biochemistry, biological control of plant pathogens, and induced plant

resistance to pathogens.



Peng Han is a Full professor in the School of Ecology and Environmental Sciences at Yunnan University, China. His research interests include: (i) revealing the bottom-up effects of environmental variables on plant-insect herbivore-natural enemy tri-trophic interactions, and (ii) monitoring, risk

assessment and integrated management of invasive alien species.



Cesar Rodriguez-Saona is a Full Professor and Extension Specialist in the Department of Entomology at Rutgers University. He obtained his Masters from Oregon State University and his PhD from the University of California, Riverside. His areas of research include chemical ecology, insect-plant interactions, tri-trophic interactions, and host-plant resistance.

ORCID

Paolo Salazar-Mendoza <http://orcid.org/0000-0001-6791-1616>

José Maurício S. Bento <http://orcid.org/0000-0001-8655-5178>

Diego B. Silva <http://orcid.org/0000-0002-6283-3193>

Sérgio F. Pascholati <http://orcid.org/0000-0002-9690-9694>

Peng Han <http://orcid.org/0000-0002-5941-9362>

Cesar Rodriguez-Saona <http://orcid.org/0000-0001-5888-1769>

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