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Research

The Combined Effect of Elevated O_3 Levels and TYLCV Infection Increases the Fitness of *Bemisia tabaci* Mediterranean on Tomato Plants

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Abstract

Global change and biotic stress, such as tropospheric contamination and virus infection, can individually modify the quality of host plants, thereby altering the palatability of the plant for herbivorous insects. The bottom-up effects of elevated O_3 and *tomato yellow leaf curl virus* (TYLCV) infection on tomato plants and the associated performance of *Bemisia tabaci* Mediterranean (MED) were determined in open-top chambers. Elevated O_3 decreased eight amino acid levels and increased the salicylic acid (SA) and jasmonic acid (JA) content and the gene expression of pathogenesis-related protein (*PR*1) and proteinase inhibitor (*PI*1) in both wild-type (CM) and JA defense-deficient tomato genotype (*spr2*). TYLCV infection and the combination of elevated O_3 and TYLCV infection increased eight amino acids levels, SA content and *PR*1 expression, and decreased JA content and *PI*1 expression in both tomato genotypes. In uninfected tomato, elevated O_3 increased developmental time and decreased fecundity by 6.1 and 18.8% in the CM, respectively, and by 6.8 and 18.9% in the *spr2*, respectively. In TYLCV-infected tomato, elevated O_3 decreased developmental time and increased fecundity by 4.6 and 14.2%, respectively, in the CM and by 4.3 and 16.8%, respectively, in the *spr2*. These results showed that the interactive effects of elevated O_3 and TYLCV infection partially increased the amino acid content and weakened the JA-dependent defense, resulting in increased population fitness of MED on tomato plants. This study suggests that whiteflies would be more successful at TYLCV-infected plants than at uninfected plants in elevated O_3 levels.

Key words: *Bemisia tabaci* Mediterranean, elevated O_3, *tomato yellow leaf curl virus*, jasmonic acid, tomato

The growth-limiting resources such as physical and chemical qualities of plant tissues could be reallocated by the changes of environmental stress (Agrell et al. 2005, Cui et al. 2012). Generally, the phloem-feeding insects (e.g., whitefly) could be affected by plant physiology associated with nutrition and resistance (Zhang et al. 2013). Widespread studies have shown that phytohormones such as jasmonic acid (JA) play an important role in the external stress response and in the maintenance of the balance between defense and growth, which may mediate the cascading effects of biotic and abiotic stress on herbivorous insects and their natural enemies along the food chain (Zhang et al. 2012, Cui et al. 2016). Systemic JA signaling can effectively transmit wounding-associated signals from the site of local attack to potentially vulnerable systemic regions during priming defense (Conrath et al. 2006, Thines et al. 2007). Priming defense is a physiological process in which plants prepare to respond more quickly or more actively to climate change and biotic stress (Frost et al. 2008). This process extensively affects and modifies insect and plant interactions in response to environmental stress, pathogenic infection, and insect occurrence (Sun et al. 2013, 2017).

The global atmospheric concentration of ozone (O_3) has risen by 0.5–2.5% per year from 10 nl/liter in the 1900s to 40 nl/liter today (Blande et al. 2010, Yuan et al. 2016), and is predicted to reach 75 nl/liter by 2050 (Ainsworth et al. 2012, IPCC 2014). O_3 is by far the most phytotoxic air pollutant and is a strong oxidant (Overmyer et al. 2009). After entering the plant stomata, O_3 is broken down in the apoplast to form reactive oxygen species (ROS), which in turn trigger an active oxidative burst within the plant, affecting substances such as carbohydrates and proteins and altering lipid oxidation (Yang et al. 2017, Zhang et al. 2017, Cui et al. 2018). O_3 reacts primarily with the plasma membrane, causing alterations in lipoxygenase activities and increasing the production of linoleic acid, a precursor of JA biosynthesis (Rao et al. 2000, Wasternack and Hause 2013). Elevated O_3 levels trigger JA biosynthesis, resulting in alteration of insect occurrence via priming defense (Bilgin et al. 2008,

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Guo et al. 2017). However, few studies have examined the effects of O_3-induced peroxidation in defense priming, especially on phloem-sucking insects.

In addition to abiotic stress, viral infection can shape whitefly–virus–plant associations. Begomoviruses are the most harmful group of plant viruses in tropical and warm temperate regions of the world, and outbreaks of whiteflies in many regions are often accompanied by *tomato yellow leaf curl virus* (TYLCV), which is one of the most destructive monopartite begomoviruses and has spread worldwide (Bilgin et al. 2008, Guo et al. 2017). TYLCV reportedly increases the fitness of the vector Mediterranean (MED) whitefly via suppression of the JA defense pathway (Sun et al. 2017). Furthermore, the pathogenicity factor ßC1 promotes the repressive role of ASYMMETRIC LEAVES1 (AS1) in the regulation of JA signaling, which benefits vector whitefly performance and geminivirus spread (Yang et al. 2008). Viral infection reduced the expression of the basic helix–loop–helix zipper transcription factor MYC2 (downstream gene of JA pathway) via priming defense and suppressed the synthesis and release of terpenoid such as β-myrcene, which is favorable for whitefly preference and feeding (Dombrecht et al. 2007, Li et al. 2014). However, the interactive effects of viral infection and elevated O_3 levels on plant-whitefly interactions are largely unknown.

The whitefly, *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae), is an invasive agricultural pest worldwide, damaging plants by directly ingesting phloem sap and more seriously by transmitting plant viruses (Stansley and Naranjo 2010). *Bemisia tabaci* MED has recently invaded and spread in China and has caused enormous agricultural loss due to feeding and as a vector of TYLCV (Chu et al. 2010, Rao et al. 2011). Previous studies have shown that TYLCV infection tends to repress the JA-related resistance of tomato plants, whereas O_3 could activate the JA signaling pathway via the lipoxygenase biosynthetic pathway (Wasternack and Hause 2013, Sun et al. 2017). However, the mechanism by which the interaction of viral infection and elevated O_3 levels affect JA signaling and the subsequent influence of *B. tabaci* MED remains unclear. Moreover, once the JA pathway is impaired, it is unclear whether the effect of priming defense can be transmitted and what the response of the MED whitefly is. We proposed a hypothesis that the antagonistic effect of elevated O_3 on virus infection will increase the fitness of whitefly MED via induced nutritional substance and defense pathways of CM and *spr2* tomato plants. Our specific aims were to determine the effects of elevated O_3 levels and TYLCV infection in combination on 1) the nitrogenous nutritional quality of plant in terms of amino acid content of plant leaves, induced defense pathways and related gene expression in two tomato genotypes that differed with respect to the JA-dependent defense pathway and on 2) the performance of *B. tabaci* MED fed on the two tomato genotypes.

Materials and Methods

Experimental Procedures

A split–split plot design was used with O_3 and block (a pair of ambient and elevated open-top chambers [OTCs]) as the main effects, TYLCV as the subplot effect, and tomato genotypes as the sub-subplot effect. The model was as follows:

$$X_{ijklm} = \mu + \mathrm{O}_i + B(\mathrm{O})_{j(i)} + \mathrm{V}_k + \mathrm{OV}_{ik} + \mathrm{VB}(\mathrm{O})_{kj(i)} + \mathrm{T}_l + \mathrm{OT}_{il} + \mathrm{TB}(\mathrm{O})_{lj(i)} + \mathrm{VTB}(\mathrm{O})_{klj(i)} + \mathrm{e}_{m(ijkl)}$$

where O is the O_3 treatment (i = 2), B is the block (j = 3), V is the TYLCV treatment (k = 2), and T is the tomato genotype (l = 2). X_{ijklm} represents the error because of the small-scale differences between samples and variability within blocks (ANOVA, SAS Institute). Totally, there were eight treatments in the present experiment. The whitefly MED developmental time, fecundity, and tomato physiology (amino acids, jasmonic acid [JA], salicylic acid [SA], and their related gene expressions) were determined to examine the differences among treatments.

Open-Top Chambers

The experiment was conducted in six hexagonal OTCs, each 2.2 m in height and 2 m in diameter, at the Observation Station for Global Change Biology, Institute of Zoology of the Chinese Academy of Science, in Xiaotangshan County, Beijing, China (40°11′N, 116°24′E). In the elevated O_3 treatment, O_3 was generated from ambient air by an O_3 generator (3S-A15, Tonglin Technology, Beijing, China). A detailed description of the O_3 generation system and transfer process was provided by Cui et al. (2014). The actual daily O_3 concentration (within 10 h from 8:00 a.m. to 6:00 p.m.) averaged 37.3 nl/liter in the ambient chambers and 72.2 nl/liter in the elevated chambers. The ozone concentration range was 35–39 nl/liter in the ambient chambers and 69–75 nl/liter in the elevated chambers. O_3 concentrations were monitored within OTCs (AQL-200, Aeroqual) hourly. The O_3 treatment was applied for 4 wk. We measured the air temperature and humidity throughout the experiment in the ambient chambers (27.8 ± 1.8°C, 59.8 ± 11.3% RH) and in the elevated chambers (28.3 ± 2.5°C, 59.3 ± 13.1% RH).

Whitefly and Host Plants

The *B. tabaci* MED population was reared on cotton in climate-controlled rooms (27 ± 1°C, 70 ± 10% RH, and 14:10 [L:D] light cycle). The biotype was determined by assessing amplified fragment-length polymorphism markers (Zhang et al. 2005).

Seeds of the following two tomato (*Solanum lycopersicum*) cultivars were used: *Lycopersicon esculentum* cv. Castlemart (CM) and *suppressor of prosystemin-mediated responses 2* (*spr2*; jasmonate-deficient mutant tomato plant). The *spr2* mutant tomato decreases chloroplast *w*3 fatty acid desaturase content, which impairs the synthesis of JA (Li et al. 2003). Two-week-old seedlings were transferred to plastic pots (14 cm diameter, 12 cm height) containing sterilized loamy soil.

TYLCV Cloning and Inoculation

We infected 64 tomato plants with TYLCV via *Agrobacterium tumefaciens*-mediated inoculation at the second–third true-leaf stage. The infectious clone (pBINPLUS-SH2-1.4A) of TYLCV-Israel [CN: SH2] was constructed into the *A. tumefaciens* strain EHA105 as described previously (Zhou et al. 2009). The TYLCV clone was cultured in LB culture medium with kanamycin (50 μg/ml) and rifampicin (50 μg/ml) at 28°C (250 rpm) for 24 h (OD_{600} = 1.5), after which, 0.5 ml of the culture was injected three times into the phloem (approximately 1 mm in depth) of the tomato stem for inoculation (Huang et al. 2012, Su et al. 2016). Viral infection of the test plants was confirmed by characteristic leaf curl symptoms and by PCR as previously described (Ghanim et al. 2007). Inoculated plants were subjected to further experimental treatments at the sixth–seventh true-leaf stage (approximately 30 d after agroinoculation of the virus) and moved to ventilated cages (1.0 m long, 1.0 m wide, 1.8 m high, 80 mesh) in the OTCs. Two ventilated cages were placed in each of the six OTCs. Infected plants in each cage were inoculated with TYLCV, whereas control plants were mock-inoculated using LB culture medium. The TYLCV infection treatment was applied for 58 d.

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Amino Acid Analysis

Free amino acids were extracted and quantified from the harvested leaves according to Guo et al. (2016). The amino acids in each sample were analyzed by reverse-phase high-performance liquid chromatography (HPLC) with precolumn derivatization using *o*-phthaldialdehyde and 9-fluorenylmethyloxycarbonyl. Amino acids were quantified using the AA-S-17 (Agilent) reference amino acid mixture supplemented with asparagine, glutamine, and tryptophan (Sigma–Aldrich Co., St. Louis, MO). Standard solutions were prepared from a stock solution by dilution with 0.1 M HCl. Analyses were performed using an Agilent 1100 HPLC (Agilent Technologies, Palo Alto, CA); a reverse-phase Agilent Zorbax Eclipse AAA C18 column (5 µm, 250 mm × 4.6 mm) and fluorescence detector were used for chromatographic separation. Amino acid concentrations were quantified by comparison of sample peak areas to standard curves of 20 reference amino acids.

SA and JA Measurements and Quantitative PCR Analysis

Approximately 0.2-g fresh leaf tissue was extracted for quantification of SA and JA levels as described previously (Guo et al. 2016).

Following procedures described by Cui et al. (2017), a sample of fresh leaves from each plant was removed and stored at −78°C for real-time PCR. Each treatment combination was repeated for three biological replicates, and each biological replicate contained three technical replicates. Total RNA was extracted with the RNeasy Plus Mini Kit (Qiagen) following the manufacturer's protocol and was quantified using a NanoDrop (Thermo Scientific). After RNA extraction, 1 µg of RNA was used to synthesize first-strand cDNA using the PrimeScript RT Reagent Kit (TaKaRa) with gDNA Eraser according to the manufacturer's protocol. The quantitative PCR (qPCR) was used to analyze differences in expression. Gene-specific primers for the two genes (pathogenesis-related protein [*PR*1] and proteinase inhibitor gene [*PI*1]) were designed and used for PCR. The 25-µl reactions contained 10.5 µl of ddH_2O, 12.5 µl of SYBR Green PCR Master Mix (Tiangen, Beijing, China), 1 µl of cDNA template, and 0.5 µl of each primer. Specific primers for the target genes were designed based on the tomato EST sequences using PRIMER5 software (Supp Table 1 [online only]). The qPCR program included an initial denaturation step for 15 min at 95°C, followed by 40 cycles of denaturation for 15 s at 95°C, annealing for 30 s at 60°C, and extension for 32 s at 72°C. For melting curve analysis, an automatic dissociation step cycle was added. Reactions were performed in an ABI 7500 real-time PCR system (Applied Biosystems) with data collection at stage 2, step 3 in each cycle of the PCR. The melting curves were used to determine the specificity of the PCR products. A standard curve was derived from serial dilutions to quantify the copy numbers of target mRNAs. The relative level of the target gene was standardized by comparing the copy numbers of the target mRNA with copy numbers of β-*actin* (a housekeeping gene), which remained constant under different treatment conditions. The β-*actin* mRNAs of the control were examined in every PCR plate to eliminate any systematic error. Relative quantification was performed using the $2^{-\Delta\Delta Ct}$ method.

Developmental Time and Fecundity of *B. tabaci*

To assess the impact of O_3, TYLCV, and tomato genotype on *B. tabaci* MED developmental time, four tomato plants of uniform size were randomly selected within each OTC. And three pairs of whitefly adults were placed in a clip cage (3.5 cm diameter, 1.5 cm height) attached to the tomato leaf per tomato plant. The adults were removed after 24 h of infestation, and total 45 eggs were left. The developmental status of the offspring *B. tabaci* was recorded using a microscope daily until adult eclosion every day. The bioassay of developmental time was conducted from the egg stage until adult eclosion (about 25 d).

To assess the impact of O_3, TYLCV, and tomato genotype on *B. tabaci* MED fecundity, tomato plants of uniform size were randomly selected within each OTC. Twenty pairs of newly emerged *B. tabaci* MED adults were transferred to clip cage (3.5 cm diameter, 1.5 cm height) attached to the tomato leaves, respectively. If a male died, another healthy male was immediately added. The fecundity of each individual whitefly was recorded daily. The bioassay of whitefly fecundity was persistently conducted until female died (about 40 d).

Statistical Analyses

A split–split plot design and statistical model were used in the experiment. The main effects of O_3, TYLCV, and tomato genotype on plant and MED performance (amino acids content, SA and related gene, JA and related gene, developmental time and fecundity of *B. tabaci*) were tested. Differences among means were determined using Tukey's test at $P < 0.05$. Pearson's correlations were calculated to analyze the relationships between the *B. tabaci* performance and biochemical indices of tomato plants. All raw data sets meet the assumptions of Gaussian distribution and homoscedasticity with no transformation.

Results

The Effect of Elevated O_3 Levels on Tomato Biochemical Properties, MED Developmental Time, and Fecundity

To determine amino acids content in tomato plants, three replicates of tomato sampling were analyzed. Elevated O_3 levels decreased the concentrations of Ala, Arg, Cys, Gly, Ile, Leu, Lys, Phe, and Trp (Supp Table 2 [online only], Supp Fig. 1 [online only]). Elevated O_3 concentrations significantly decreased the levels of Asn, Asp, Gln, Glu, Met, Pro, Ser, and Val from a range of 44.4–81.4% in the CM plant and from a range of 25.7–74.4% in the *spr2* plant (Table 1, Fig. 1A–H).

To determine SA content and related gene *PR*1 in tomato plants, three replicates of tomato sampling were analyzed. Elevated O_3 levels increased SA content and the relative expression of *PR*1 mRNA by 1.7- and 28.4-fold, respectively, in the CM genotype and by 1.3- and 12.3-fold, respectively, in the *spr2* genotype (Table 2, Fig. 2A and B).

To determine JA content and related gene *PI*1 in tomato plants, three replicates of tomato sampling were analyzed. Elevated O_3 concentration increased JA content and the relative expression of *PI*1 mRNA by 70.5% and 1.1-fold, respectively, in the CM plant and by 1.4- and 1.5-fold, respectively, in the *spr2* plant (Table 2, Fig. 3A and B).

To determine the developmental time of whitefly MED, 45 replicates of eggs were observed. Elevated O_3 concentration significantly increased the developmental time by 6.1% in the CM genotype and by 6.8% in the *spr2* plant (Table 2, Fig. 4A). Twenty pairs of emerged whiteflies MED were observed to analyze the fecundity. Elevated O_3 concentration significantly decreased the fecundity by 18.8% in the CM genotype and by 18.9% in the *spr2* plant (Table 2, Fig. 4B).

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Table 1. Effects of O_3 level, TYLCV infection, and plant genotype on tomato amino acid content

Factor	Asn	Asp	Gln	Glu	Met	Pro	Ser	Val
O_3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
TYLCV	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Tomato genotype	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
O_3 × TYLCV	0.118	0.543	0.400	0.105	0.031	0.001	0.057	0.714
O_3× Genotype	0.650	0.834	0.469	0.001	0.443	0.264	0.046	0.817
TYLCV × Genotype	<0.001	0.001	0.001	<0.001	0.129	0.102	0.001	0.012
O_3× TYLCV × Genotype	0.158	0.480	0.001	0.068	0.035	0.065	0.002	0.011

P values from ANOVA are shown. Asn (asparagine); Asp (aspartic acid); Gln (glutamine); Glu (glutamic acid); Met (methionine); Pro (proline); Ser (serine); Val (valine).

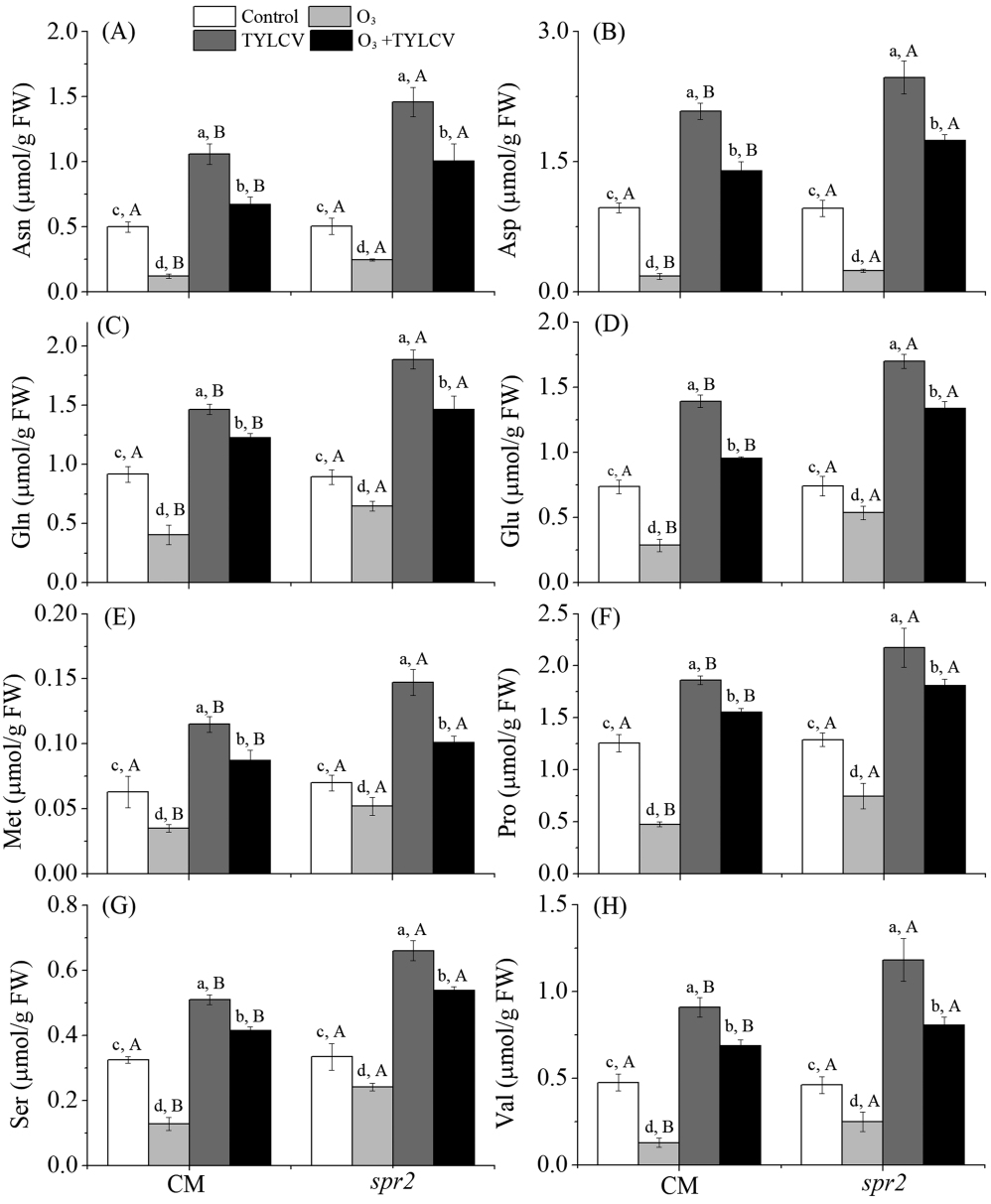

Fig. 1. Concentrations of (A) asparagine (Asn), (B) aspartic acid (Asp), (C) glutamine (Gln), (D) glutamic acid (Glu), (E) methionine (Met), (F) proline (Pro), (G) serine (Ser), and (H) valine (Val) in the two tomato genotypes (CM, *spr2*) grown under ambient and elevated O_3 levels with and without TYLCV infection after 4 wk. Different lowercase letters indicate significant differences among the four treatments in the same tomato plant, and different uppercase letters indicate significant differences between the two tomato genotypes within the same treatment (Tukey's test: $P < 0.05$).

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Table 2. Effects of O_3 level, TYLCV infection, and plant genotype on *Bemisia tabaci* MED developmental time and fecundity and biochemical properties of tomato

Factor	SA	JA	*PR*1	*PI*1	Developmental time	Fecundity
O_3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
TYLCV	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Tomato genotype	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
O_3 × TYLCV	<0.001	<0.001	0.272	<0.001	0.406	<0.001
O_3 × genotype	<0.001	0.875	<0.001	<0.001	0.663	0.816
TYLCV × genotype	0.003	0.001	<0.001	0.001	0.406	0.098
O_3 × TYLCV × genotype	0.058	0.209	0.015	0.030	0.452	0.245

P values from ANOVA are shown. SA (salicylic acid), JA (jasmonic acid); *PR*1 (pathogenesis-related protein); *PI*1 (proteinase inhibitor).

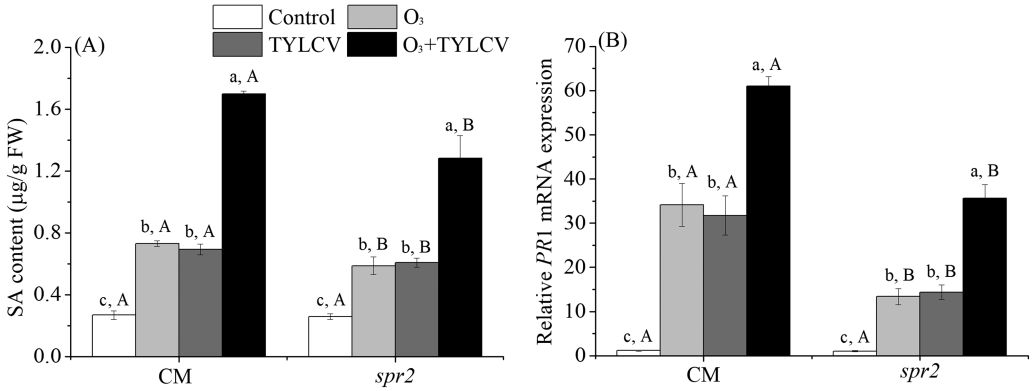

Fig. 2. Concentrations of (A) salicylic acid (SA) and relative expression of gene encoding (B) pathogenesis-related protein (*PR*1) in the two tomato genotypes (CM, *spr2*) grown under ambient and elevated O_3 levels with and without TYLCV infection after 4 wk. Different lowercase letters indicate significant differences among the four treatments in the same tomato plant, and different uppercase letters indicate significant differences between the two tomato genotypes within the same treatment (Tukey's test: $P < 0.05$).

The Effect of TYLCV Infection on Tomato Biochemical Properties, MED Developmental Time, and Fecundity

TYLCV infection decreased the concentrations of Ala, Arg, Cys, Gly, Ile, Leu, Lys, Phe, and Trp (Supp Table 2 [online only], Supp Fig. 1 [online only]). When the plants were infected with TYLCV, elevated O_3 levels increased the levels of Asn, Asp, Gln, Glu, Met, Pro, Ser, and Val from a range of 23.9–44.6%, in the CM plant and from a range of 40.4–99.2%, in the *spr2* plant (Fig. 1A–H). Regardless of O_3 concentration, TYLCV infection significantly increased the levels of Asn, Asp, Gln, Glu, Met, Pro, Ser, and Val in both genotypes (Fig. 1A–H).

When the plants were infected with TYLCV, elevated O_3 levels increased the SA content and the relative expression of *PR*1 mRNA by 5.3- and 51.7-fold, respectively, in the CM genotype and by 3.9- and 34.4-fold, respectively, in the *spr2* genotype, respectively (Fig. 2A and B). The SA content and gene expression of *PR*1 were highest with the O_3 + TYLCV infection treatment for both genotypes (Fig. 2A and B).

When the plants were infected with TYLCV, elevated O_3 concentration decreased the JA content and the relative expression of *PI*1 mRNA by 36.7 and 53.2%, respectively, in the CM genotype and by 28.2 and 45.3%, respectively, in the *spr2* genotype (Fig. 3A and B). Regardless of O_3 concentration, TYLCV infection significantly decreased the JA content and the relative expression of *PI*1 mRNA in both genotypes (Fig. 3A and B).

When the plants were infected with TYLCV, elevated O_3 levels decreased the developmental time by 4.6% in the CM genotype and by 4.3%, respectively, in the *spr2* plant (Fig. 4A). When the plants were infected with TYLCV, elevated O_3 concentration increased the fecundity by 14.2% in the CM genotype and by 16.8% in the *spr2* plant (Fig. 4B). Regardless of O_3 concentration, TYLCV infection significantly decreased the *B. tabaci* developmental time and increased fecundity in both genotypes (Fig. 4A and B).

The Effect of Tomato Genotypes on Tomato Biochemical Properties, MED Developmental Time, and Fecundity

The levels of Asn, Asp, Gln, Glu, Met, Pro, Ser, and Val were lower in the CM plants than in the *spr2* plants under elevated O_3 concentration, TYLCV infection, and the combined treatment (Fig. 1A–H). CM plants exhibited higher SA content and relative expression of *PR*1 mRNA than *spr2* plants under elevated O_3 concentrations, TYLCV infection, and the combined treatment (Fig. 2A and B). The JA content and the relative expression of *PI*1 mRNA were higher in the CM plants than in the *spr2* plants under the four treatments (Fig. 3A and B). The *B. tabaci* developmental time was longer, and the fecundity was lower in the CM plants than in the *spr2* plants under the four treatments (Fig. 4A and B).

Correlations Between the Performance of *B. tabaci* and Biochemical Indices of Tomato

The rate of development and the fecundity of MED were positively correlated with amino acid content, including the levels of Asn, Asp, Gln, Glu, Met, Pro, Ser, and Val, and negatively correlated with JA content and relative *PI*1 mRNA expression (Table 3). There was no significant correlation between whitefly developmental time and fecundity and SA content, relative *PR*1 mRNA expression, and partial amino acid levels (including Ala, Arg, Cys, Gly, His, Ile, Leu, Lys, Phe, Thr, Try, Tyr; Supp Table 3 [online only]).

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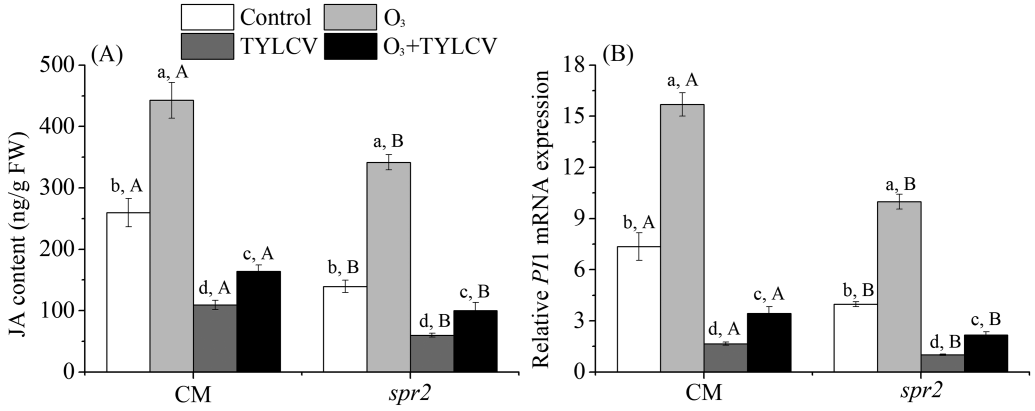

Fig. 3. Concentrations of (A) jasmonic acid (JA) and relative expression of gene encoding (B) proteinase inhibitor (*PI*1) in the two tomato genotypes (CM, *spr2*) grown under ambient and elevated O_3 levels with and without TYLCV infection after 4 wk. Different lowercase letters indicate significant differences among the four treatments in the same tomato plant, and different uppercase letters indicate significant differences between the two tomato genotypes within the same treatment (Tukey's test: $P < 0.05$).

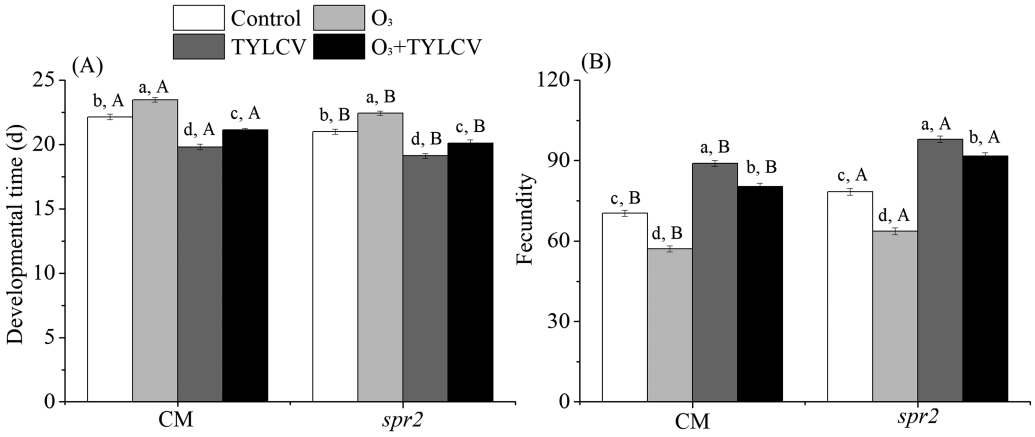

Fig. 4. Developmental time (A) and fecundity (B) of *Bemisia tabaci* MED reared on two tomato genotypes (Wt, *spr2*) grown under ambient and elevated O_3 levels with and without TYLCV infection. Different lowercase letters indicate significant differences among the four treatments in the same tomato plant, and different uppercase letters indicate significant differences between the two tomato genotypes within the same treatment (Tukey's test: $P < 0.05$).

Table 3. Pearson correlations between *Bemisia tabaci* MED developmental time and fecundity and biochemical properties of tomato leaves

Tomato constituents	Developmental time		Fecundity	
	r	*P*	*r*	*P*
JA	0.965	<0.001	−0.966	<0.001
*PI*1	0.948	<0.001	−0.943	<0.001
Asn	−0.961	<0.001	0.968	<0.001
Asp	−0.959	<0.001	0.969	<0.001
Gln	−0.963	<0.001	0.976	<0.001
Glu	−0.971	<0.001	0.975	<0.001
Met	−0.965	<0.001	0.961	<0.001
Pro	−0.971	<0.001	0.984	<0.001
Ser	−0.973	<0.001	0.984	<0.001
Val	−0.960	<0.001	0.967	<0.001

JA (jasmonic acid); *PI*1 (proteinase inhibitor); Asn, (asparagine); Asp (aspartic acid); Gln (glutamine); Glu (glutamic acid); Met (methionine); Pro (proline); Ser (serine); Val (valine).

Discussion

The results of this study revealed that the interactive effects of elevated O_3 levels and viral infection can enhance the population fitness of whitefly fed on tomato plants in terms of developmental time and fecundity. The altered insect performance was due to the O_3-induced responses of tomato plants being differentially influenced by TYLCV infection. Elevated O_3 levels without viral infection decreased the amino acid content, increased the JA content and gene expression levels of *PI*1 in both tomato genotypes, and decreased the performance of MED fed on the two tomato plants. In contrast, viral infection under elevated O_3 levels increased the amino acid content, decreased the JA content and the gene expression levels of *PI*1, and increased the performance of MED fed on the two tomato plants. Furthermore, the performance of MED was in association with *spr2* plants was better than that with CM plants, suggesting that the difference in the JA signaling pathway between the plant genotypes had a significant effect on the performance of the whitefly MED. MED performance was positively correlated with amino acid content and negatively correlated with JA content and relative *PI*1 mRNA expression, suggesting that the interactive effects of elevated O_3 levels and viral infection enhanced the performance of the MED vector insects via bottom-up effects of the host plants.

Previous studies showed that elevated O_3 levels could decrease nutritional content and increase levels of defensive-related substances in plant tissues (Ye et al. 2012, Cui et al. 2012). Excessive production of ROS can disrupt plant metabolism and thus leading to irreversible injury to plasma membrane and nutrients (Apel

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and Hirt 2004). Furthermore, ROS leads to activation of defense signaling pathways and the accumulation of secondary metabolites in response to elevated O_3 concentration (Simon et al. 2010, Ye et al. 2012). For example, elevated O_3 levels significantly decreased the total amino acid content of tobacco plants (Ye et al. 2012). Elevated O_3 levels induced the accumulation of both JA and SA and upregulated the expression of the associated marker genes (Pazarlar et al. 2017). Similarly, in our study, elevated O_3 levels significantly decreased the amino acid content and increased the JA and SA levels and related defensive gene expression in both CM and *spr*2 tomato plants. Among herbivorous insects, the green peach aphid, *Myzus persicae*, exhibited lower population growth rates when exposed to elevated O_3 levels than when exposed to ambient O_3 (Menendez et al. 2010). Relatively few eggs and larvae of the leaf beetle, *Agelastica coerulea*, were found when these insects were fed O_3-exposed plants (Inoue et al. 2016). It was suggested that increased O_3 levels are disadvantageous to the performance of both phloem-sucking insects and chewing insects. Likewise, the MED whitefly negatively affected by elevated O_3 levels, which is consistent with the increased developmental duration and decreased fecundity. Previous studies also showed that secondary metabolism can negatively affect the performance of piercing-sucking insects (Walling 2000, Yan et al. 2018). For example, total phenolics and condensed tannins decreased whitefly population densities, growth rate, and delayed developmental time (Mansour et al. 1997, Bialczyk et al. 1999). We assumed that whitefly could be more vulnerable to total phenolics and condensed tannins because elevated O_3 could accumulate these secondary metabolites in plant tissue (Cui et al. 2012).

Plant viruses could indirectly alter the behavior and performance of the insect vectors through the host plant mutualistically or antagonistically (Liu et al. 2013). Viral infection can change the primary and secondary compounds as well as resistance-related substances produced by the host plant, which in turn could differentially affect the performance of *B. tabaci* MED and MEAM1 (Shi et al. 2014, Sun et al. 2017). In our study, we also found that TYLCV infection significantly increased MED fecundity and shortened the developmental time. TYLCV can be transmitted by *B. tabaci* in a persistent and circulative manner (Ghanim 2014). Persistent and circulative viruses can increase nutritional assimilation. Viral infection of tobacco with tomato yellow leaf curl China virus (TYLCCNV) improves the amino acid content, and the vector performs better on virus-infected tomato than on uninfected controls (Wang et al. 2012). Our results also showed that TYLCV infection led to an unequal increase in the amino acid content of tomato plants. The interactions between pathogenicity factor ßC1 and MYC2 can suppress terpenoid synthesis and release via repressing the JA signaling pathway (Luan et al. 2013, Bingham et al. 2014). JA-induced defenses in plants were shown to confer resistance to whitefly (Su et al. 2016). In our study, TYLCV infection significantly suppressed the JA content and the expression of related defensive genes. Further research showed that the combination of elevated O_3 levels and TYLCV infection shortened the developmental time of MED and increased the fecundity in the two tomato plants compared with the control plants. The results showed that the increased population growth of MED on TYLCV-infected tomato plants promotes diffusion and spread of the MED vectors, which carry the virus to new place under elevated O_3 levels. This finding suggests that the virus offsets the adverse effects of elevated O_3 levels on vector performance. In other words, the vector or virus may manipulate the host plant for its own benefit under elevated O_3 levels.

The JA defense-enhanced tomato genotype *35S* exhibits a stronger JA signal and greater resistance than the wild-type plant, whereas JA-deficient mutants exhibit reduced resistance against insects (Zarate et al. 2007, Wei et al. 2011). For example, JA-deficient mutants of *Arabidopsis thaliana* accelerate silverleaf whitefly nymphal development compared to wild-type plants (Zarate et al. 2007). The whitefly egg counts improved on JA-deficient tomato plants than on wild-type tomato plants (Sun et al. 2017). In our results, the MED whitefly exhibited lower fecundity and longer developmental time in association with CM plants than with *spr2* plants regardless of O_3 levels and viral infection, indicating that diminished JA-dependent defenses were responsible for improved performance. This study suggests that whiteflies would be more successful at infesting TYLCV-infected plants than at infesting uninfected plants in environments with elevated O_3 levels. It suggests that the environmental carrying capacity with respect to whiteflies will gradually increase with the increasing O_3 concentration and viral infection.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Supplementary Table S1. Sequences of primers used for real-time quantitative PCR.

Supplementary Table S2. Effects of O_3 level, TYLCV infection, and plant genotype on amino acid content in tomato. *P* values from ANOVA are shown.

Supplementary Table S3. Pearson correlations between *B. tabaci* developmental time and fecundity and biochemical properties of tomato leaves.

Supplementary Fig. S1. Concentrations of (A) alanine (Ala), (B) arginine (Arg), (C) cysteine (Cys), (D) glycine (Gly), (E) histidine (His), (F) isoleucine (Ile), (G) leucine (Leu), (H) lysine (Lys), (I) phenylalanine (Phe), (J) threonine (Thr), (K) tryptophan (Trp), and (L) tyrosine (Tyr) in the two tomato genotypes (CM, *spr2*) grown under ambient and elevated O_3 levels with and without TYLCV infection after 4 weeks.

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