Elevated O₃ enhances the attraction of whitefly-infested tomato plants to *Encarsia formosa*

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We experimentally examined the effects of elevated O₃ and whitefly herbivory on tomato volatiles, feeding and oviposition preferences of whiteflies and behavioural responses of *Encarsia formosa* to these emissions on two tomato genotypes, a wild-type (Wt) and a jasmonic acid (JA) defence-enhanced genotype (JA-OE, 35S). The O₃ level and whitefly herbivory significantly increased the total amount of volatile organic compounds (VOCs), monoterpenes, green leaf volatiles (GLVs), and aldehyde volatiles produced by tomato plants. The 35S plants released higher amount of total VOCs and monoterpene volatiles than Wt plants under O₃+herbivory treatments. The feeding and oviposition bioassays showed that control plants were preferred by adult whiteflies whereas the 35S plants were not preferred by whiteflies. In the Y-tube tests, O₃+herbivory treatment genotypes were preferred by adult *E. Formosa*. The 35S plants were preferred by adult *E. formosa* under O₃, herbivory and O₃+herbivory treatments. Our results demonstrated that elevated O₃ and whitefly herbivory significantly increased tomato volatiles, which attracted *E. formosa* and reduced whitefly feeding. The 35S plants had a higher resistance to *B. tabaci* than Wt plant. Such changes suggest that the direct and indirect defences of resistant genotypes, such as 35S, could strengthen as the atmospheric O₃ concentration increases.

Plants are a source of a large diversity of volatile organic compounds (VOCs), such as monoterpenes, sesquiterpenes and homoterpenes¹. These VOCs can serve as semiochemicals that can be detected by other organisms to reveal the host presence², to signify availability of food and mating sites³,⁴ and also to aid in navigating to food sources⁵,⁶.

Insect feeding influences the nutrient condition⁷; secondary metabolite production, i.e., jasmonic acid (JA is a plant hormone involved in regulating secondary metabolite production among other things)⁸–¹⁰; and the type and amount of herbivore-induced plant volatiles (HIPVs) released by the plant¹¹–¹². HIPVs can function as plant defences by directly repelling herbivores from ovipositing and host-seeking¹³ and by attracting herbivore enemies, such as parasitic wasps, predatory arthropods and possibly even insectivorous birds¹⁴–¹⁶. For example, the monoterpenes volatiles of *Chrysanthemum morifolium* repel ovipositing females of the diamondback moth (*Plutella xylostella*), a lepidopteran that does not normally lay eggs on *C. morifolium*¹⁷. Volatiles, such as the aphid alarm pheromone from transgenic *Arabidopsis thaliana*, repelled the green peach aphid (*Myzus persicae*) from feeding, although wild-type *Arabidopsis* does not normally produce this pheromone¹⁸. Laboratory and field studies have shown that HIPVs attract parasitoids and/or predators to many plant species that reduce the risk of damage from herbivorous insects¹⁹–²¹. Predatory mites preferred the odour of Lima bean plants infested with two-spotted spider mites (*Tetranychus urticae*) to that of uninfested plants¹¹. The pea leafminer, *Liriomyza huidobrensis*, caused an increased emission of volatiles in tomato plants and consequently increased the attraction of the parasitoid *Opius dissitus*²². Enhancement of these interactions between the HIPVs and the natural enemies of herbivores can aid the development and delivery of integrated pest management programs¹²,²².

Recently, the global atmospheric concentration of ozone (O₃) has risen from less than 10 ppb (parts per billion) a century ago to 40 ppb today and is projected to continue to increase at an annual rate of 1–2%²³ to 68 ppb by the year 2050²⁴. Elevated O₃ changes plant biochemistry, including the activation of many plant defence responses²⁶–²⁸. Elevated O₃ is also changing the atmospheric life times of phytogenic VOCs, including the HIPVs²⁹. Due to these alterations, the behavioural and life history parameters of herbivorous insects are also influenced³⁰,³¹. O₃ stress can increase VOC emissions from plants, including terpenoids and green leaf volatiles (GLVs)³²,³³. For
example, Blande et al. reported increased emissions of some monoterpenes (α-pinene and/or β-pinene, (E)-β-ocimene) and higher total monoterpene emissions from hybrid aspens (Populus tremula × tremuloides Michx.) grown under moderately elevated O₃. Furthermore, O₃ fumigation has been reported to promote the emission of herbivore-induced volatiles. Differences in the quality and quantity of the volatile mixtures induced by a high O₃ concentration will affect tritrophic interactions among plants, herbivorous insects and natural enemies. However, little is known regarding HIPVs’ induction by piercing-sucking insects and the effects of herbivores and their natural enemies under elevated levels of O₃.

Tomato, Solanum lycopersicum, is an economically important vegetable worldwide and a commonly used model plant for biologists. It is also an O₃-sensitive species. Bemisia tabaci (Hemiptera: Aleyrodidae) is one of the most noxious insect pests worldwide. Encarsia formosa is the main parasitoid of B. tabaci, and the use of E. formosa for whitely management is now accepted as a biological control agent. Previous research indicated that several JA-overexpression mutants exhibit greater resistance against insects than wild-type plants. Wei et al. (2011) showed that there are ecological trade-offs between JA-dependent direct and indirect defenses in genetically modified plants. Our previous research indicated that the JA-overexpression tomato mutant 35S was resistant to B. tabaci under a high O₃ concentration and whitely infestation and there was a reduction in the fitness of conspecific B. tabaci that fed on three previously infested tomato genotypes that differed in the JA pathway. However, the mechanism(s) by which VOCs affect whitely feeding and oviposition and the behavioural responses of E. formosa induced by whitely infestation remain unclear under elevated O₃ conditions.

Here, we hypothesise that elevated O₃ levels and whitely infestation will affect the type and amount of tomato volatiles produced, which will affect the feeding and oviposition preferences of whiteflies and their interaction with E. formosa. To test this hypothesis, the effects of elevated O₃ and whitely infestation on two tomato genotypes, including the wild-type and a JA-defence-enhanced genotype (35S), in association with the phloem feeder B. tabaci Gennadius biotype B and a natural enemy, E. Formosa, were examined in open-top chambers in the field. Our specific objectives were to determine: (1) whether elevated O₃ levels alter the emission of whitely-induced volatiles, (2) the effects of VOCs on the feeding and oviposition preferences of B. tabaci and (3) the effects of VOCs on the behavioural responses of E. formosa.

### Results

#### Volatile emission rate

O₃ level, whitely herbivory, tomato genotypes and the interactions between the whitely herbivory and tomato genotypes significantly affected the total amount of VOCs, monoterpene volatile emissions, GLVs and aldehyde production. The interactions between O₃ and whitely herbivory significantly affected the total amount of VOCs, monoterpene volatile emissions and aldehyde volatiles (Table 1).

The monoterpene volatile emissions included terpinolene, (+)-α-pinene, (+)-3-carene, D-limonene, α-phellandrene, ocimene and β-phellandrene in the two tomato genotypes. The GLVs were Z-3-hexanol and E-2-hexanol. The aldehyde volatiles referred to nonanal and octanal (Fig. 1A, B, C, D).

Elevated O₃ levels increased the VOC emissions 4.85-fold in the Wt genotype (F₃, 12 = 382.234, P = 0.000) and 7.48-fold in the 35S genotype (F₃, 12 = 195.509, P = 0.000) (Table 1, Fig. 1A). Elevated O₃ levels enhanced the monoterpene emissions 5.12-fold in the Wt genotype (F₃, 12 = 372.234, P = 0.000) and 7.80-fold in the 35S genotype (F₃, 12 = 198.668, P = 0.000) (Table 1, Fig. 1B).

Whitely herbivory increased the total amount of VOC emissions 5.12-fold in the Wt genotype (F₃, 12 = 382.234, P = 0.000) and 3.41-fold in the 35S genotype (F₃, 12 = 195.509, P = 0.000) (Table 1, Fig. 1A). Whitely herbivory increased the monoterpene emissions 5.56-fold in the Wt genotype (F₃, 12 = 372.234, P = 0.000) and 3.38-fold in the 35S genotype (F₃, 12 = 198.668, P = 0.000) (Table 1, Fig. 1B).

For the two plant genotypes, the total amount of VOCs is highest under O₃ + herbivory treatment. The sum of the peak areas show the total amount of VOCs from the 35S plants was 656.75 ± 22.85, whereas that from Wt plants was 554.53 ± 56.65. The 35S plants released higher levels of monoterpene volatiles than the Wt plants under control, O₃ and O₃ + herbivory treatments (Fig. 1A, B).

### Feeding and Oviposition Preferences of B. tabaci.

O₃ level, whitely herbivory and tomato genotypes significantly affected the feeding and oviposition preferences of B. tabaci.

Adult whiteflies more often preferred the control plants for feeding (Wt: X² = 87.063, P < 0.001; 35S: X² = 62.349, P < 0.001) and oviposition (Wt: X² = 385.914, P < 0.001; 35S: X² = 660.616, P < 0.001) (Fig. 2A, B).

Adult whiteflies preferred Wt plants for feeding under control (X² = 11.645, P = 0.001); O₃ (X² = 25.712, P = 0.000) and herbivory (X² = 3.939, P = 0.047) treatments. Adult whiteflies preferred Wt plants for oviposition under four treatments (control: X² = 177.888, P = 0.000; O₃: X² = 200.166, P = 0.000; herbivory: X² = 50.797, P = 0.000; O₃ + herbivory: X² = 5.69, P = 0.017). Adult whiteflies did not prefer 35S plants for feeding and oviposition under the four treatments (Fig. 3A, B).

The behavioural responses of E. formosa to the odors of two tomato genotypes in various treatments. In a two-choice behavioural assay, O₃ + herbivory treatment plants were preferred...
by adult *E. formosa* for the two tomato genotypes in the Y-tube tests (Fig. 4A). Control treatment plants were not preferred by adult *E. formosa* for the two tomato genotypes in the Y-tube tests (Fig. 4A).

To determine the preference of *E. formosa* for volatiles emitted by different tomato genotypes, behavioural responses were investigated in a dual-choice olfactometer. Behavioural assays in the Y-tube olfactometer showed that the 35S plants were preferred by adult *E. formosa* under O3, herbivory and O3+herbivory treatments (Fig. 4B). Adult parasitoid preferences for the two tomato genotypes were not significantly different under the control treatment (Fig. 4B).

**Discussion**

The herbivorous insect/plant interaction has proven to be a complex process that extends beyond compromising plant fitness to include directly inducing defensive responses by the plant to the herbivore and indirect effects involving VOC emissions by the plant that affect natural enemies35,47. Elevated O3 levels can alter nutritional quality, secondary metabolites and the resistance of plants as well as result in significantly increased VOC emissions45,48. Elevated O3 concentrations (100 ppb up to 250 ppb) resulted in increased monoterpene emissions of 3-year-old *Quercus ilex* L. plants49. Either the acute ozone-exposure or spider mite-infestation could induce the volatile emission of the Lima bean, but under elevated ozone condition, spider mite-damaged plants could release significantly higher amount of volatile emission11. Our previous research showed that elevated O3 levels altered the nutritional content and secondary metabolites in tomato plants45. In this study, we report that elevated O3 concentrations and whitefly infestation significantly increased the total amount of VOCs, monoterpene emissions, GLVs and aldehyde volatile productions of the tomato plants. The monoterpene volatile emissions remain the dominant product among the VOCs. Moreover, the tomato VOC emissions in the O3+herbivory treatment are the highest among the four treatments. The results indicated that the O3 factor and the whitefly infestation factor are related, suggesting that elevated O3 levels significantly abet the emission of whitefly-induced volatiles.

Figure 1 | Emission rate1 of volatile organic compounds (VOCs) from tomato genotypes grown under ambient and elevated O3 with and without *Bemisia tabaci* of herbivore preconditining after three weeks. Different lowercase letters within a row indicate significant differences among the four treatments in a specific tomato cultivar (LSD test: *P* < 0.05); Different uppercase letters indicate significant differences among tomato genotypes within the same O3 and whitefly treatment (LSD test: *P* < 0.05).1 Emission rate = ng of compound released per g (fresh weight) of leaves per hour. Each value represents the average (±SE) of 4 replicates.

Figure 2 | Effects of elevated O3 concentration and whitefly infestation on the feeding and oviposition preferences of whiteflies after three weeks on the two tomato genotypes. Each value represents the average (±SE) of 15 replicates. Different lowercase letters indicate significant differences between the four treatments for a specific tomato cultivar (*X*2 test: *P* < 0.05).
VOC release following elevated O3 levels; herbivore and mechanical damage can repel herbivores. For example, volatiles from the infested transgenic A. thaliana repelled the green peach aphid (Myzus persicae) in comparison to volatiles from control transgenic plants. Cannon (1990) found that O3-induced VOCs from red spruce needles repel spruce budworm larvae. Some studies showed that monoterpenes are biogenic volatile organic compounds that play an important role in repelling herbivore oviposition and feeding. Our results found that adult whiteflies preferred feeding and oviposition on control plants to three other O3 and herbivory treatments, suggesting that the increasing VOCs (especially monoterpenes) following elevated O3 levels and herbivore exposure will repel the whitefly.

VOC release following elevated O3 levels, herbivore and mechanical damage can also attract herbivore enemies. The predatory mite Phytoseiulus persimilis prefers volatiles from the Lima bean leaves of plants injured by spider mites to volatiles from uninfested Lima bean leaves. The aphid Myzus persicae caused an increased emission of volatiles triggered by spider mites in pepper plants and consequently increased the attraction of predators. Pinto et al. (2007) found that VOCs, such as terpenes and GLVs of Brassica oleracea, induced by elevated O3 levels are crucial for the orientation of the wasps Cotesia plutellae. Previous studies showed that monoterpenes and GLVs are important cues for natural enemies in host finding. Our results showed that O3 herbivory treatment plants were preferred by adult E. formosa compared to control treatment plants in the two tomato genotypes in the Y-tube tests. The enrichment of VOCs in the O3 herbivory tomato plant treatment significantly attracted E. formosa.

JA-overexpression tomato genotype 35S has higher resistance to sucking insects than Wt plant and thus is considered one of the best plant genotype for insect resistance. Cui et al. (2012a and 2012b) showed that the 35S has the highest resistance to B. tabaci under elevated O3 and whitely infestation. We report here that the 35S tomato genotypes released higher VOC emissions (including the total amount of VOCs, monoterpane volatile emissions, GLVs and aldehyde volatiles) than the Wt tomato plants. The 35S plants were not preferred by adult whiteflies for feeding or oviposition under four treatments, while the 35S plants were preferred by adult E. formosa under O3, herbivory and O3+herbivory treatments. Moreover, the differences between the two tomato genotypes were accentuated under elevated O3. These results showed that JA-overexpression tomato genotype 35S has a significantly higher resistance to the whitefly under elevated O3.

To our knowledge, this is the first systematic study of the responses to elevated O3 levels on tritrophic interactions among plants, herbivorous insects and natural enemies. Our results indicate that elevated O3 and whitely infestation significantly increased the VOC emissions, especially the monoterpane emissions. The tomato VOC emissions in the O3+herbivory treatment were the highest among the four treatments. 35S tomato genotypes released higher VOC emissions, especially monoterpane volatile emissions, than did the Wt tomato plants. The 35S plants had a higher repellent effect on the whitefly and a higher attraction of E. formosa. Such changes suggest that the direct and indirect defence of resistant genotypes, such as 35S, would be further strengthened as the atmospheric concentration of O3 continues to increase.
Methods
Open-top chambers and O3 Treatment. Experiments were conducted using eight octagonal open-top chambers (OTCs), each 2.2 m in height and 2 m in diameter, at the Observation Station for Global Change Biology at the Institute of Zoology of the Chinese Academy of Science, in Xiantangshan County, Beijing, China (40° 11’N, 116° 24’E). Four OTCs were used for each O3 concentration treatment. In the elevated O3 treatment, O3 was generated from ambient air by an O3 generator (35-A15, Tongling Technology, Technology Co., Ltd., China) and then transported to the enclosed OTCs using a fan (HB-429, 4.1 m³ min⁻¹, Ruyong Mechanical and Electrical Equipment Company). Mixed air (O2 and ambient air) was vented into each OTC through columniform polyvinyl chloride pipes (inner diameter 11 cm, outer diameter 16 cm). O3 concentrations were monitored at both the fan output (Shenzhen Yuanshan Electronic Co., Ltd.) and within the OTCs (AQL-200, Aeroqual). From July 28th to August 21th, 2010, except for 2 rainy days, the OTCs were ventilated with air daily from 9:00 a.m. to 5:00 p.m. through a hemispherical stainless steel spray hood (diameter = 30 cm) situated 0.5 m above the canopy at a rate of approximately 4.1 m³ min⁻¹, resulting in approximately 0.59 air changes per minute in each OTC. O3 concentrations were measured once every hour in each chamber receiving O3 treatment.

The two O3 concentration treatments employed were as follows: (1) current ambient atmospheric O3 levels (average value from 9:00 a.m. to 5:00 p.m. on all air treated days of 37.3 nmol mol⁻¹) and (2) twice the current ambient O3 levels (average value from 9:00 a.m. to 5:00 p.m. on all air-treated days of 72.6 nmol mol⁻¹).

Herbivory Treatment. Individuals of B. tabaci biotype B were collected on 5 April 2010 from cabbage growing at the Beijing Academy of Agriculture and Forestry. The offspring of these whiteflies were reared on tomatoes. For the infestation treatments, three leaves of each intact plant were encased in a mesh gauze bag and infested with 90 male whiteflies (to avoid the production of offspring) that were replaced every three days, from July 28th to August 21th, 2010.

Host Plants. Two tomato genotypes were selected for the present study: wild-type (WT) tomato plants (Solanum lycopersicum cv. Castlemart) and 35S:systemin, which constitutively activates the defence system in unwounded plants (Turlings et al. 1997). Transgenic tomato plants (cv. Castlemart) and 35S:systemin, transgenic tomato plants (35S). Professor C. Li of the Institute of Genetics and Developmental Biology, Chinese Academy of Science provided these plants. L. esculentum cv. Castlemart was the WT parent for the 35S transgenic plants. The 35S:systemin (35S) JA-biosynthesis mutant transgenic plants overexpress prostyrene synthase, which constitutively activates the defence system in unwounded plants and results in a stronger and more rapidly induced resistance (Xue et al. 2001). After being grown in sterilised soil for two weeks, the tomato seedlings were individually transplanted into small plastic pots (14 cm diameter, 12 cm height) containing sterilised loamy field soil. Plants that were approximately 40 days old with heights of 20–30 cm were moved to the OTCs on 27 July 2010.

Feeding and Oviposition Preferences of B. tabaci. One control plant and one herbivore-preconditioned plant of each tomato genotype were placed into the same cage (dimensions = 60 × 60 × 60 cm) on 7 August 2010 in the open cylinders. They were controlled by preconditioned WT plant and control 35S plant, respectively. The experiment had 15 replicates. For the preconditioning treatment, a cohort of 90 male whiteflies was established and replaced every three days on the lateral 3 leaves to provide a continuous infestation for three weeks in the open cylinders. After three weeks, 50 pairs of adult whiteflies were put into each cage and three days later, the feeding and oviposition preference of each whitefly was recorded.

The second experiment was prepared in the same manner as the above mentioned experiment. The differences were each of 15 cages containing two control plants (one WT and one 35S plant). Each of the other 15 cages contained two preconditioned treatment plants (one preconditioned WT and one preconditioned 35S plant).

Adult parasitoid Encarsia formosa preferences for two tomato genotypes. Y-tube experiments A Y-tube olfactometer was used to investigate the behavioural responses of E. formosa to the volatile blends from different treatments within a tomato cultivar (Turlings et al. 1997). The headspace volatiles were collected from one tomato plant, respectively. The experiment had 15 replicates. For the preconditioning treatment, a cohort of 90 male whiteflies was established and replaced every three days on the lateral 3 leaves to provide a continuous infestation for three weeks in the open cylinders. After three weeks, 50 pairs of adult whiteflies were put into each cage and three days later, the feeding and oviposition preference of each whitefly was recorded.

Collection and quantification of plant volatiles. Volatiles were collected from one randomly selected plant from each combination of O3 concentration, tomato genotype and whitefly herbivory treatment in each chamber (8 individuals from each tomato genotype and herbivore treatment). The headspace volatiles were collected according to Turlings et al. (2001). The shoots and leaves of each plant, except for the stem extending to 4 cm from the soil surface, were sealed in a plastic bag (40 cm wide and 46 cm long). Purified air was pumped (Beijing Institute of Labor Instruments, China) into the bag through a freshly activated charcoal trap (Beijing Chemical Company) and then withdrawn through a glass cartridge (3.0 mm internal diameter and 12.6 cm long) packed with 100 mg of the adsorbent Porapak Q (80–100 mesh, Supelco, Bellefonte, PA, USA); the flow rate was 0.2 L/min. Volatile compounds were rinsed from the Porapak Q with 1000 ml of n-pentane (HPLC grade, Sigma-Aldrich, USA) containing internal standards (200 ng of ethyl heptanoate) for quantification. The
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**Author contributions**

C.H.Y. performed the experiments and wrote the main manuscript text. G.F. designed the experiments. S.J.W., W.J.N. and H.Y.I. helped interpret the data. All of the authors read and approved the final manuscript.

**Additional information**

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