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RESEARCH PAPER

Sex pheromone of the tea aphid, *Toxoptera aurantii* (Boyer de Fonscolombe) (Hemiptera: Aphididae)

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Abstract The tea aphid, *Toxoptera aurantii*, also called the "black citrus aphid", is one of the most destructive insect pests in commercial tea plantations and gardens in southern China. In autumn, declining day length triggers production of winged *T. aurantii* sexuparae, which produce both winged males and wingless oviparae. Oviparous females then release sex pheromone that attracts potential mates. GC–MS analysis of volatile headspace extracts of *T. aurantii* oviparae revealed that they emit (4a*S*,7*S*,7a*R*)-nepetalactone (I) and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (II) in a ratio of 4.3–4.9:1. Field-trapping experiments with synthetic I and II singly or as two-component blends of different doses and ratios showed significant attraction of *T. aurantii* males, as well as weak attraction of sexuparae. Identification of the *T. aurantii* sex pheromone provides a new opportunity for developing a pheromone-based monitoring and management strategy for the sexual phase of tea aphids and, possibly, the alate sexparous generation in late summer and fall.

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Introduction

The tea aphid, *Toxoptera aurantii* (Boyer de Fonscolombe), also called the "black citrus aphid", is widely distributed in the tropics and subtropics, including South America, Africa, India, Eastern Asia, Australia, the Mediterranean region, Central America, and the Southern US. This species has also been recorded from more temperate regions, such as England, and Oregon and Maryland in the US (Carver 1978; Agarwala and Bhattacharya 1995). *T. aurantii* is a polyphagous aphid, having been recorded from plants in more than 190 genera from 80 families. Many of its hosts are economically important shrubs and fruit trees, such as citrus, coffee, tea, cacao, avocado, litchi, mango, fig, loquat, *Cinchona* spp., *Annona* spp., *Macadamia* spp., *Piper* spp., and *Artocarpus* spp. (Carver 1978). It has been reported to be a major citrus pest in many parts of its range (Carver 1978); however, in southern China where Chinese tea, *Camellia sinensis* (L.) (Theaceae), is grown *T. aurantii* is an extremely destructive pest (Zhang and Zhong 1983), damaging fresh leaves and tender shoots that constitute the highest quality commercial teas.

Although *T. aurantii* has a diverse range of hosts, this aphid is a non-host-alternating species (i.e., autoecious, monoecious) and reportedly lacks sexuals (i.e. anholocyclic) (Carver 1978; Agarwala and Bhattacharya 1995). However, in the subtropics of China, this species does have an autoecious, holocyclic life cycle with 10–15 or more generations per season that feed solely on tea

plants (Peng 1986). In the fall, as the photophase decreases, winged sexuparae of *T. aurantii* emerge, which produce both wingless pheromone-emitting oviparae and winged males. Males respond to sex pheromone released by oviparae, likely from glands on the hind legs similar to many other species in the Aphidinae (Pickett et al. 1992). Mated oviparae lay eggs on tea leaves where they overwinter, eventually giving rise to the fundatrix population in spring, followed by 10–15 summer parthenogenic generations. In the tropical China, *T. aurantii* has a typical anholocyclic life cycle without sexual communication (Peng 1986).

To date worldwide, sex pheromones have been identified from 20 or so aphid species all belonging to the subfamily Aphidinae (Dawson et al. 1990; Pickett et al. 1992, 2013; Boo et al. 2000; Birkett and Pickett 2003; Goldansaz et al. 2004; Zhu et al. 2006; Stewart-Jones et al. 2007; Symmes et al. 2012). Aphid sex pheromones typically include (4a*S*,7*S*,7a*R*)-nepetalactone (I) and/or (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (II) (Pickett et al. 2013). In contrast, the damson-hop aphid, *Phorodon humuli* (Schrank), uses (1*R*,4a*R*,7*S*,7a*S*)-nepetalactol and (1*S*,4a*R*,7*S*,7a*S*)-nepetalactol as its sex pheromone (Campbell et al. 1990). In addition, (1*S*,2*R*,3*S*)-dolichodial has recently been proposed as a possible third sex pheromone component for some aphidine species, including the rosy apple aphid, *Dysaphis plantaginea* (Passerini) (Dewhirst et al. 2008). Specific ratios of the common aphid sex pheromone components, I and II, are important, particularly among sympatric species, for species isolation (Birkett and Pickett 2003; Stewart-Jones et al. 2007); ratio specificity seems essential for both intraspecific communication and interspecific reproductive isolation (Stewart-Jones et al. 2007). Oviparae-produced sex pheromones also reportedly attract gynoparae and may act as aggregation pheromones in some aphid species (Lilley and Hardie 1996; Boo et al. 2000; Powell and Hardie 2001; Zhu et al. 2006).

Recently, electrophysiological and behavioral studies have revealed that various predators and parasitoids of *T. aurantii* use aphid related volatiles (Han and Han 2007), as well as certain tea volatiles from healthy or aphid-damaged plants (Han and Chen 2000, 2002a, b, c) as prey/host-finding semiochemical signals. However, the sex pheromone of *T. aurantii* has yet to be identified, and its identification would provide a foundation for developing pheromone-based monitoring and management of this economically important aphid.

Here we report the identification of the sex pheromone of *T. aurantii*, and describe the behavioral responses, including the diel periodicity of response, for males and alate sexuparae to different ratios and doses of synthetic pheromone components/blends in the field.

Materials and methods

Collections of insects and volatiles

Oviparae of *T. aurantii* were collected from tea plants in an organic tea garden (32° 00′N; 119° 40′E) in Danyang, Jiangsu Province, China, on 20 November 2012. Several freshly cut tea shoots and young leaves with 20 *T. aurantii* oviparae were placed in a 2-l glass aeration system with a water-saturated cotton ball. The sample was aerated with activated carbon-filtered air at 300 ml/min for 24 h; volatiles were adsorbed onto 50 mg of Porapak Q (50/80 mesh; Supelco, Bellefonte, PA, USA) held in a glass tubing between two glass wool plugs, which were extracted with 1 ml of hexane into a 2-ml glass vial. Un-infested tea shoots and leaves were also sampled and aerated in the same fashion. The aeration extracts were kept in freezer (−20° C) before GC–MS analyses.

Chemical analysis

The aphid aeration extract was concentrated to 50 µl under N_2 and analyzed by coupled gas chromatography–mass spectrometry (GC–MS) using an HP 6890 GC coupled to an HP 5973 mass selective detector using a polar GC column (HP-INNOWAX; 30 m × 0.53 mm × 1.0 µm film thickness; Agilent Technologies, Wilmington, DE, USA), and a non-polar Agilent GC column (HP-5MS, 30 m × 0.25 mm × 0.25 µm film thickness). Two microliters of the concentrated sample was injected in splitless mode for each column. Helium was used as the carrier gas, and the injector and detector temperatures were 250 and 300 °C, respectively. Column temperature was programmed from 50 °C for 1 min, to 240 °C at 10 °C/min, with a final hold for 10 min. Ionization was electron impact at 70 eV. Compounds of interest were identified by comparison of retention times and mass spectra to those for authentic standards.

Chemical standards and lures

(4a*S*,7*S*,7a*R*)-Nepetalactone (compound I; 98 % chemical purity by GC–MS analyses) was isolated from commercial catnip oil by a pH-sensitive chemical separation technique (Chauhan and Zhang 2008), and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (compound II; ∼90 % chemical purity by GC–MS analyses, ∼6 % were iridodial diastereomes, keto-enol tutomers due to GC conditions) was prepared by $NaBH_4$ reduction of (4a*S*,7*S*,7a*R*)-nepetalactone as previously described (Hooper et al. 2002; Chauhan et al. 2004).

Lures for Experiments 1 and 2 (described below) contained a total of 10 mg of compounds I and/or II. A 100 µl

of 10 % hexane solution of each treatment was applied to a 45 × 15 × 4 mm piece of felt sealed inside a polyethylene bag (50 × 20 mm; 0.3 mm thickness); control lures each contained 100 µl of hexane only. Lures for Experiment 3 were prepared similarly with dosage modifications described below.

Field-trapping experiments

Three field-trapping experiments were carried out in an organic tea garden (31° 95′N; 118° 75′E) in Xuancheng, Anhui Province, China, during fall of 2013.

Experiment 1 tested attraction of *T. aurantii* males and winged sexuparae to synthetic I and II, singly or in combinations. The following ratios of I and II, respectively, were tested: 10/0, 9/1, 7.5/2.5, 5/5, 2.5/7.5, 1/9, and 0/10, plus a control. The lures were placed in the white delta traps with sticky inserts (Pherobio Technology Co., Ltd., Beijing, China), and deployed in the tea garden from 26 October to 1 November 2013. Six sets (blocks) of delta traps were placed in lines along the tea plant rows on wooden sticks ~1.5 m above the ground, just above the tea plant canopy. Baited traps within each set with the differing treatments were 10 m apart with their initial positioning randomized, and trap sets (lines) were at least 20 m apart. Traps were monitored daily, and sticky inserts were refreshed and trap positions were re-randomized once on 29 October.

In Experiment 2, the diurnal rhythm of male tea aphid flight was evaluated using the six delta traps that were baited with the 1:1 ratio pheromone lures from Experiment 1 upon completion of that test. These traps were equipped with new sticky inserts and deployed as above from 1 to 4 November at the same location. The traps were monitored every 2 h during the photophase, and the numbers of aphids captured were recorded for three consecutive days. Due to the low population density, data from all the six traps were pooled to calculate mean catches of *T. aurantii* males/6-trap/2-h periods for each of the three trapping days.

Experiment 3 evaluated the behavioral responses of *T. aurantii* males and alate sexuparae to the 1:1 pheromone blends of I and II at different dosages (0, 0.1, 0.33, 1, 3.3, 10, and 33 mg per lure) using three sets of seven white delta traps each with a sticky insert during 1–4 November 2013. These traps were deployed as in the first experiments, about 50 m away in the same tea garden. Traps within each set were baited with the various dosages of pheromone, plus blank controls, placed 10 m apart with their initial positions randomized, and trap sets (lines) were at least 20 m apart. These traps were monitored and re-randomized daily.

Statistical analysis

Trap-catch data were $\log(x + 1)$ transformed to fit the assumption of homogeneity of variance for ANOVA. Means were compared by ANOVA followed by the Ryan-Einot-Gabriel-Welsh (REGW) multiple Q test (SPSS 16.0 for Windows) at $\alpha = 0.05$.

Results

Chemical analysis

Analyzing aliquots of the Porapak Q extract by GC–MS on the polar (Fig. 1) and non-polar (Fig. 2) GC columns revealed the presence of (4a*S*,7*S*,7a*R*)-nepetalactone (I) (Fig. 3a) and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (II) (Fig. 3b) in the head-space of the fresh tea shoots (with leaves) infested with *T. aurantii* oviparae. Due to the co-elution of compound II with a sesquiterpene compound (on polar column) or methylnaphthalene (on non-polar column), the ratio of compounds I and II in the aphid aeration sample was determined by the relative abundances of two characteristic selected ions (SI) for each compound: ions at *m/z* 166 and 123 for I, and ions at *m/z* 168 and 135 for II (Fig. 3). Thus, the natural ratio of I:II was estimated to be 4.3–4.9:1 (Figs. 1, 2). These two iridoids were not detected from any aeration samples of un-infested tea shoots and leaves (also see Han and Chen 2002b, c, 2004), nor was (1*S*,2*R*,3*S*)-dolichodial detected from the aeration sample of *T. aurantii* oviparae.

Field-trapping experiments

In Experiment 1, delta traps baited with 7.5/2.5 (3:1) and 5/5 (1:1) loading ratios of synthetic I and II, respectively, caught the most *T. aurantii* males and winged sexuparae, each of which were significantly higher than those of either component individually, all other combination ratios, and blank control traps (Fig. 4). Either I or II alone, or their binary blend at 9:1 ratio was weakly attractive to *T. aurantii* males (Fig. 4).

Experiment 2 showed that the diurnal rhythm of male tea aphid flight started between 7:00 and 9:00 in the morning, and peaked from 15:00 to 17:00 in the afternoon. Male flight ceased before 21:00, with no trap catches observed during the scotophase (Fig. 5).

In Experiment 3, trap catches of *T. aurantii* males increased with dosages of the 1:1 binary sex pheromone blend to a maximum at the highest dose tested (33 mg/lure) (Fig. 6). The lowest attractive dose for *T. aurantii* males occurred at 0.33 mg/lure. No significant dose–responses

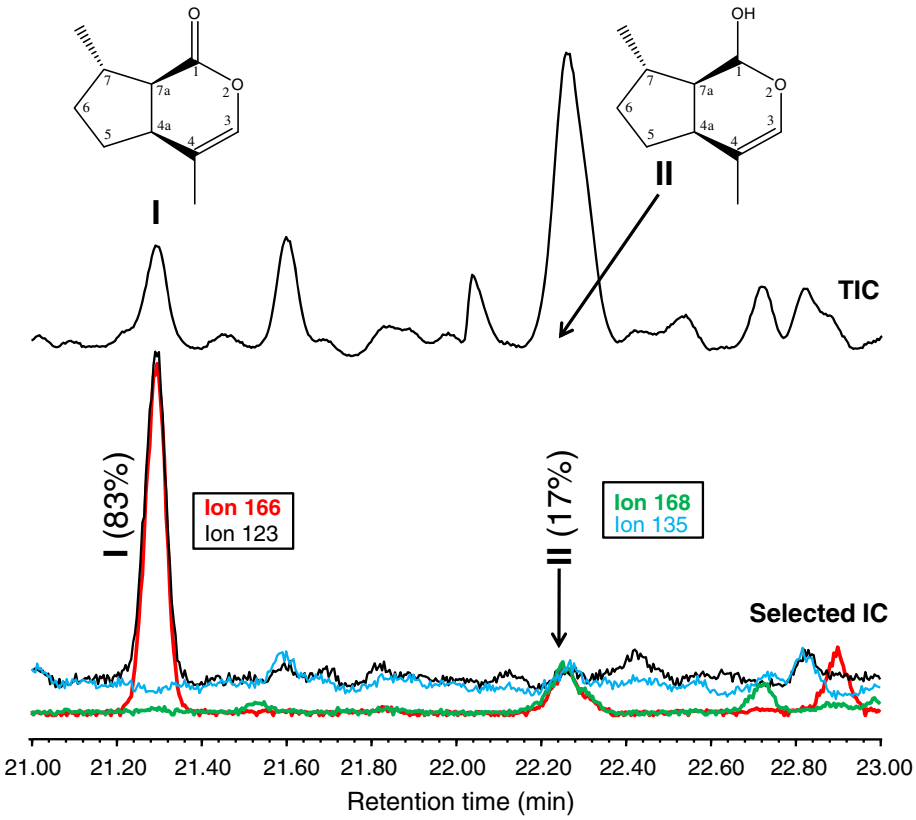

Fig. 1 Reprehensive gas chromatography–mass spectrometry (GC–MS) traces of the aeration extract of *T. aurantii* oviparae on a polar column. *Upper trace*: total ion current (*TIC*) chromatogram; *lower traces*: select ion current (*SIC*) chromatograms. **I**: (4a*S*,7*S*,7a*R*)-nepetalactone; **II**: (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol

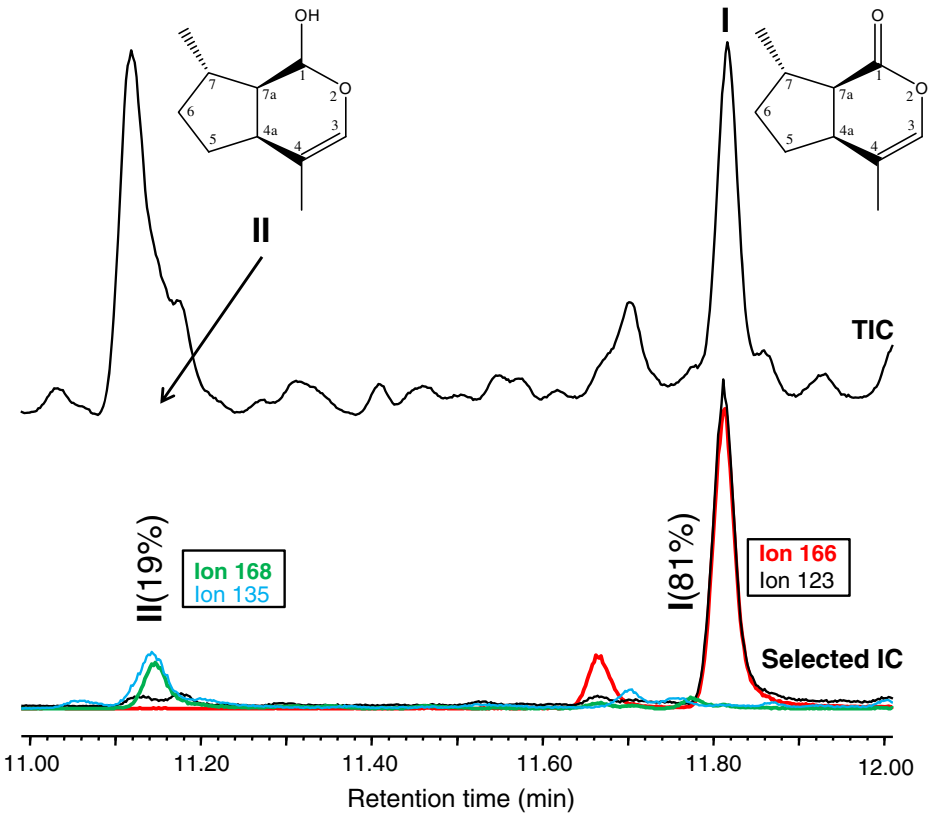

Fig. 2 GC–MS traces of the aeration extract of *T. aurantii* oviparae on a non-polar column. *Upper trace*: total ion current (*TIC*) chromatogram; *lower traces*: select ion current (*SIC*) chromatograms. **I**: (4a*S*,7*S*,7a*R*)-nepetalactone; **II**: (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol

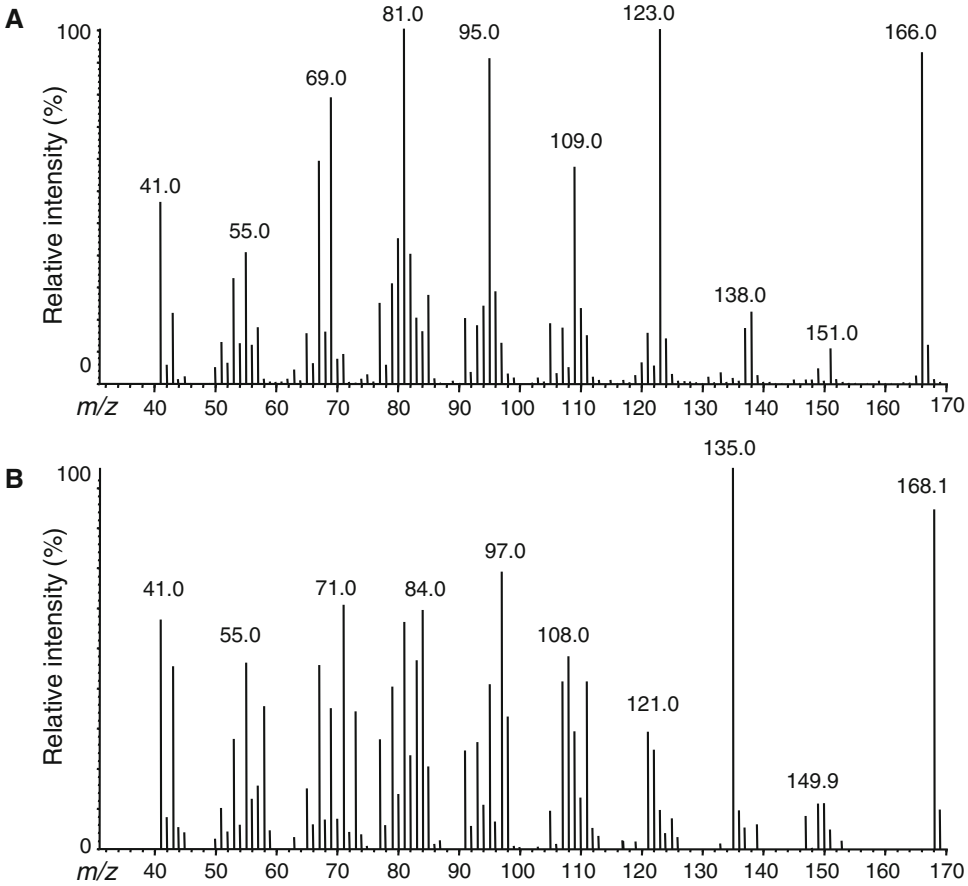

Fig. 3 Electron impact mass spectra (70 eV) of the two aphid sex pheromone components; **a** (4a*S*,7*S*,7a*R*)-nepetalactone (**I**), **b** (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (**II**), respectively, in the aeration extract of *T. aurantii* oviparae

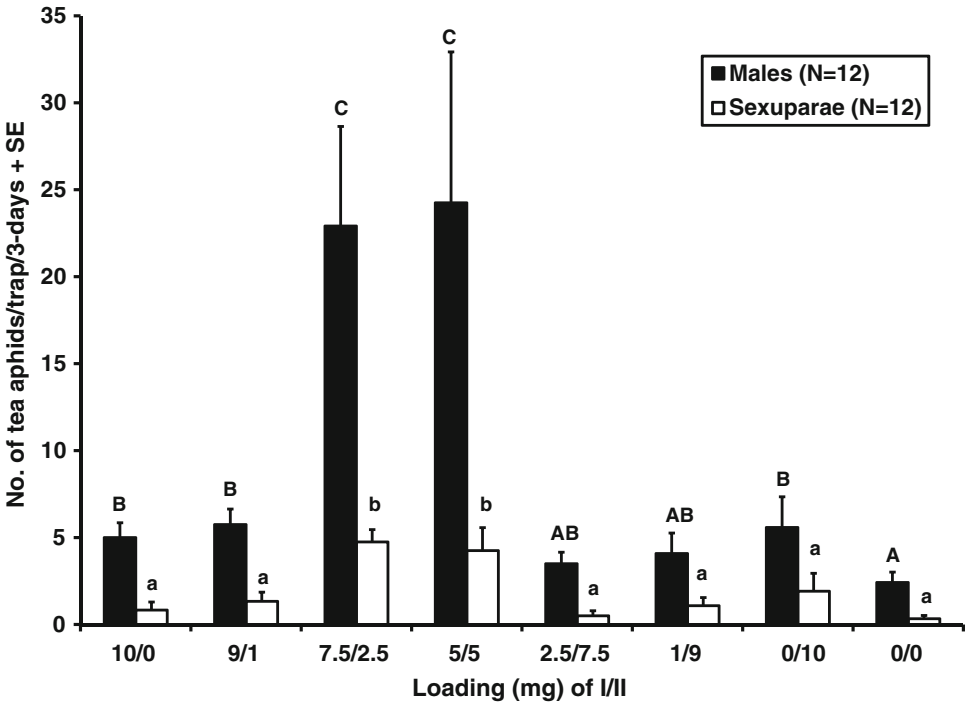

Fig. 4 Mean numbers (±SE) of *T. aurantii* males and alate sexuparae captured in delta traps baited with different loading ratios of its two sex pheromone components, **I**: (4a*S*,7*S*,7a*R*)-nepetalactone and **II**: (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol, in a tea garden at Xuancheng, Anhui, P. R. China, 26 October to 1 November 2013. Bars with the same letter within each sex were not statistically different ($P > 0.05$) by the Ryan-Einot-Gabriel-Welsh (REGW) multiple Q test after ANOVA on $\log(x + 1)$ transformed data

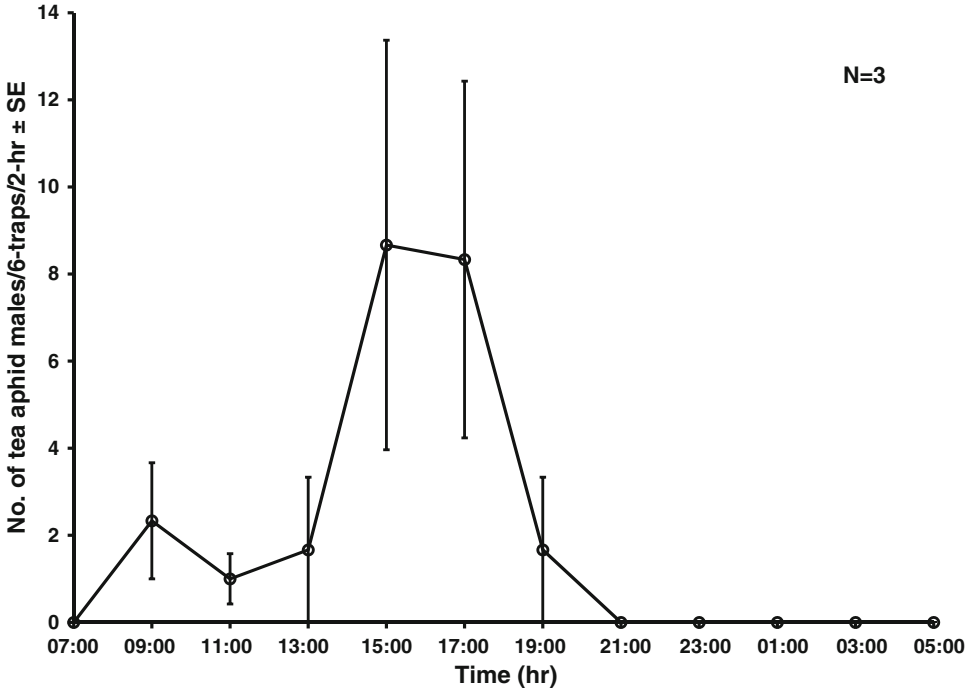

Fig. 5 Diurnal flight activity of *T. aurantii* males to delta traps baited a binary sex pheromone blend of **I** and **II** at 1:1 loading ratio (I/II: 5/5 mg) from 2–4 November 2013 in a tea garden at Xuancheng, Anhui, China. Each point is the mean catch (±SE) of males per six-traps per 2 h intervals for three consecutive days ($N = 3$)

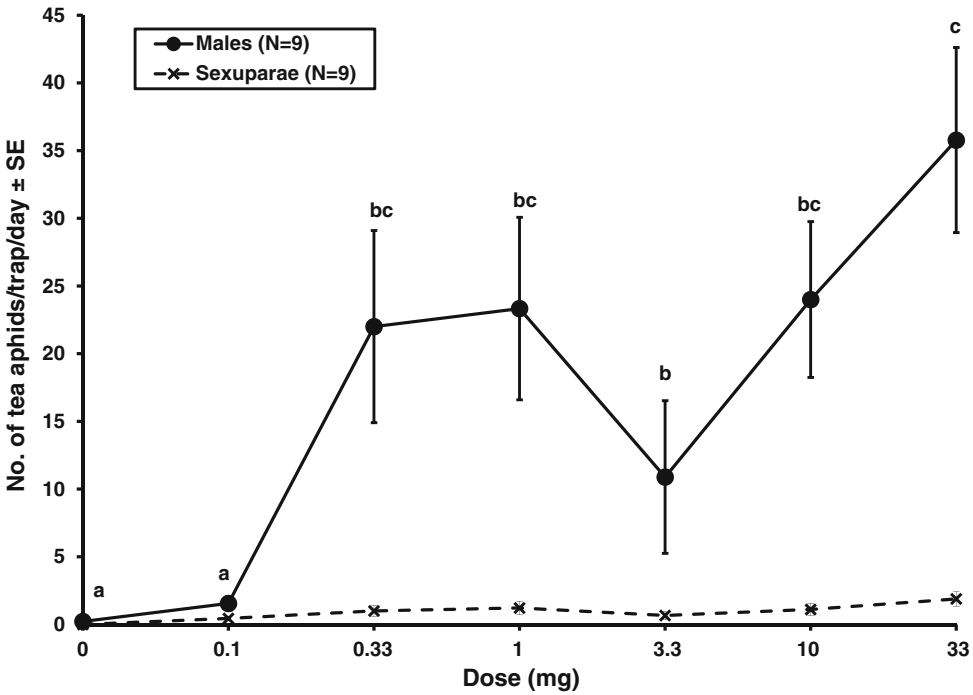

Fig. 6 Mean numbers (±SE) of *T. aurantii* males and alate sexuparae captured in delta traps baited with different doses of the 1:1 ratio of the two identified sex pheromone components (**I** and **II**) in a tea garden in Xuancheng, Anhui, China, from 1–4 November 2013. Means with the same letter within each sex were not statistically different ($P > 0.05$) by the Ryan-Einot-Gabriel-Welsh (REGW) multiple Q test after ANOVA on $\log(x + 1)$ transformed data

were shown for the alate sexuparae, possibly due to its overall low population during the trapping period (Fig. 6).

Discussion

This is the first sex pheromone identification for an autoecious aphid species in the genus *Toxoptera*. The pheromone of *T. aurantii* is similar to many of the mostly heteroecious aphid species whose sex pheromones have been identified (Dawson et al. 1990; Pickett et al. 1992, 2013; Birkett and Pickett 2003; Symmes et al. 2012) in that *T. aurantii* oviparae also produce and release (4a*S*,7*S*,7a*R*)-nepetalactone (I) and (1*R*,4a*S*,7*S*,7a*R*)-nepetalactol (II) in a specific ratio (4.3–4.9:1, for compound I and II, respectively). Our field-trapping bioassays in a tea garden

confirmed that combinations of these two synthetic pheromone compounds at several loading ratios from polyethylene-bag dispensers were significantly attractive to *T. aurantii* males and alate sexuparae, with the loading ratios of 3:1 (I/II: 7.5/2.5 mg) and 1:1 (I/II: 5/5 mg) being the most attractive (Fig. 4). The release ratios of these two synthetic I and II in the binary blends from the dispensers were not measured; however, stronger I-biased release ratios are surely expected in comparison to their corresponding loading ratios since the polar II is expectedly less volatile than I, especially through the relatively non-polar polyethylene membrane. Thus, a synthetic I and II blend with the natural or close to natural release ratios (4.3–4.9:1) should be among the most attractive binary blends for *T. aurantii* males. In fact, males of many aphid species that use I and II as their sex pheromone components respond to a range of ratios of these two compounds; however, they all tend to exhibit a greater response to the ratio emitted by conspecific oviparae (Hardie et al. 1990; Lilley and Hardie 1996; Zhu et al. 2006; Symmes et al. 2012; Pickett et al. 2013). Among the aphid species studied so far, only two of them, the vetch aphid, *Megoura viciae* Buckton (at 6:1 ratio) (Hardie et al. 1990), and the peach aphid, *Tuberocephalus momonis* (Matsumura) (at 4:1 ratio) (Boo et al. 2000) show similar release ratios as does *T. aurantii*; however, neither of the latter species are sympatric with the tea aphid, alleviating interspecific cross-attraction issues. Such disparity in the release ratios supports the hypothesis of species specificity in aphid sex-pheromone systems (Pickett et al. 1992; Guldemond et al. 1993).

Olfactory receptor neurons for the two common aphid sex pheromone components, I and II, have been reported not only from the male aphid antennae, but also from the antennae of gynoparous (Hardie et al. 1994; Park and Hardie 2002; Campbell et al. 2003; Zhu et al. 2006) and some virginoparous aphids (Hardie et al. 1994; Park and Hardie 2002; Fernández-Grandon et al. 2013). In fact, significant attraction of winged gynoparae to sex pheromones of conspecific oviparae has been shown for several aphid species, including *P. humuli* (Hardie et al. 1996; Lösel et al. 1996a, b), *T. momonis* (Boo et al. 2000), and soybean aphid (*Aphis glycines* Matsumura) (Zhu et al. 2006), leading to the suggestion that aphid sex pheromones may act as aggregation pheromones for the gynoparae (Lilley and Hardie 1996; Powell and Hardie 2001; Zhu et al. 2006). In the current study, the alate sexuparae of *T. aurantii* were also significantly attracted to the sex pheromone binary blends at 3:1 and 1:1 loading ratios of I:II, respectively, even though captures were much less than that for conspecific males; thus, attraction of alate sexuparae may be higher during their peak emergence. It is unknown if the alate virginoparous *T. aurantii* will also be attracted to sex pheromone during spring and summer. Interestingly, however, a recent Y-tube olfactometry study of *Myzus persicae* (Sulzer) virginoparae showed that they were repelled by high concentrations of I (Fernández-Grandon et al. 2013).

Our field trapping bioassay clearly showed that *T. aurantii* males only respond to its sex pheromone during the daytime, with a peak being around 15:00–17:00 in the afternoon (Fig. 5). This diurnal rhythm is consistent with the diel pattern (or circadian cycle) of female calling behavior and sex pheromone release reported for several aphid species such as *D. plantaginea* (Stewart-Jones et al. 2007), *Schizaphis graminum* (Rondani) (Dawson et al. 1990), and *Aphis spiraecola* Patch (Jeon et al. 2003). In a field dose–response test, Zhu et al. (2006) showed that trap catches of *A. glycines* males increased with loading from 0 to 30 mg of synthetic pheromone. Our field bioassay on *T. aurantii* males showed a similar dose–response pattern with the highest dose (33 mg/lure) catching the most males, and 0.33 mg/lure being the lowest attractive dose.

Identification of the tea aphid sex pheromone provides a new opportunity for developing a pheromone-based monitoring and management strategy for the sexual phase of this aphid, and possibly even for the alate sexparous generation in the summer and fall. It is not known if this synthetic pheromone blend will be attractive or repellent to alate virginoparous *T. aurantii* females in spring and summer. Resolution of this contingency awaits future field-testing.

Prior to the current study, chemical ecological studies of *T. aurantii* in tea gardens and plantations focused on the attractiveness of tea plant volatiles (Han and Han 2007), including some green leaf volatiles (GLVs) from the tea shoots and leaves (e.g. 1-hexanol) that were reportedly attractive throughout the growing season to alate *T. aurantii* females (Han et al. 2012). Combining attractive GLVs with the attractive colors (light yellow or green), plus the shape of tender tea shoots may result in oriented flight and landing of winged *T. aurantii* females on the host tea shoots (Han et al. 2012). Additionally, there is some evidence that interactions and/or synergism exist between aphid sex pheromones, host plant volatiles (Powell and Hardie 2001; Pickett et al. 2013), and visual cues (Hardie et al. 1996; Han et al. 2012); therefore, future research is needed to investigate these potential synergisms. The commercial availability of both pheromone components I and II in polyvinyl chloride formulations (Agrisense BCS Limited, Pontypridd, Wales) should facilitate this type of research in the future.

Finally, another intriguing aspect of synthetic aphid sex pheromone is that many natural enemies of aphids, such as predatory green lacewings (Boo et al. 2003; Zhang et al. 2006; Koczor et al. 2010), ladybirds (Leroy et al. 2012) and parasitoids (Powell and Pickett 2003), use aphid sex

pheromones as host/prey-finding kairomones. Therefore, synthetic aphid pheromones alone or in combination with other plant-based attractants are potentially useful for manipulation of the aphid predators and parasitoids for enhanced biological control. Since tea is extremely important in the beverage industry worldwide, any non-toxic approaches including semiochemical-based trapping and beneficial insect manipulation may play a critical role in integrated pest management for tea cultivation, especially for organic tea production.

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