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Intraspecific and interspecific attraction of three *Tomicus* beetle species during the shoot-feeding phase

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Abstract

The shoot beetles *Tomicus minor*, *Tomicus yunnanensis*, and *Tomicus brevipilosus* have been decimating *Pinus yunnanensis* trees for more than 30 years in Southwestern China. To understand the chemical ecological relationship between pines and *Tomicus*, and among the three beetle species, we compared the attraction of these beetles to damaged shoots, extracts from damaged shoots, and volatiles from damaged shoots collected by the dynamic headspace sampling method. Experiments were performed using a modified open-arena olfactometer. The male *T. minor* and both sexes of *T. brevipilosus* were more strongly attracted to damaged shoots than to undamaged shoots and they showed attraction to shoots damaged by the same species. Female *T. minor* and both sexes of *T. yunnanensis* were attracted to shoots damaged by female *T. brevipilosus*. The three beetle species were attracted to shoot extracts and dynamic headspace volatiles from shoots damaged by the same species and sex. Female *T. minor* and male *T. yunnanensis* were also attracted to dynamic headspace volatiles from shoots damaged by both sexes of *T. brevipilosus*. The results suggested that specific semiochemicals that are induced or produced by *T. brevipilosus* also attract *T. minor* and *T. yunnanensis*. The semiochemicals in damaged shoots affect the attraction of the three beetle species and play an important chemical communication role in weakening the host trees during the beetles' shoot-feeding phase.

Keywords: attraction, *Tomicus*, *Pinus yunnanensis*, walking bioassay

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Introduction

Pine shoot beetles of genus *Tomicus* (Coleoptera: Curculionidae: Scolytinae) are destructive to forests worldwide (Bakke, 1968; Postner, 1974; Långström, 1983; Långström & Hellqvist, 1990, 1993). In Southwestern China, *Tomicus minor*, *Tomicus yunnanensis*, and *Tomicus brevipilosus* are the most destructive pests of *Pinus yunnanensis* Franch (Ye, 1992; Ye & Lieutier, 1997; Långström *et al*., 2002). They attack the fresh shoots of living trees, which can weaken the host and curtail growth (Stark, 1952; Chararas, 1962; Byers, 1992), sometimes harming 100% of the shoots and causing death directly (Ye & Li, 1994; Ye & Lieutier, 1997; Ye & Ding, 1999; Långström *et al*., 2002; Lieutier *et al*., 2003). In Yunnan province, *Tomicus* has caused extensive mortality of Yunnan pines (*P. yunnanensis*), affecting over 200,000 ha of pine plantations (Lieutier *et al*., 2003), and 93,000 ha of Yunnan pines have withered because of damage (Ji *et al*., 2007).

In Southwestern China, three bark beetle species coexist together with different compositions in different locations. *T. minor* mostly occurs together with *T. yunnanensis* and sometimes with *T. brevipilosus* or both of them. In the southwest part of Yunnan, the main species is *T. brevipilosus*. We also observed that *T. minor* and *T. yunnanensis*, but not *T. brevipilosus*, coexisted in the same shoot when dissecting damaged shoots in the laboratory. However, the tunnels of the three species were not interconnected in the shoots. Lu *et al*. (2014) found that the entrance hole of *T. minor* was the closest to the apical bud, and that of *T. yunnanensis* was furthest away from the apical bud.

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The pioneer bark beetle identifies susceptible trees by kairomonal, visual, and/or gustatory cues (Lindgren & Borden, 1989) or volatiles derived from the host trees (Byers *et al.*, 1985; Lanne *et al.*, 1987; Byers, 1989; Ye & Li, 1994; Ye & Lieutier, 1997; Lieutier *et al.*, 2003; Poland *et al.*, 2003). *Tomicus piniperda* is not considered an aggressive species in Europe (Långström & Hellqvist, 1993) and there is no evidence of an aggregation pheromone (Byers *et al.*, 1985; Löyttyniemi *et al.*, 1988); rather, host-tree monoterpenes (kairomones) were attractive (Byers *et al.*, 1985; Byers, 1995). However, *T. piniperda* was attracted to myrtenol and trans-verbenol (Volz, 1988), which had been isolated and identified from the hindgut extracts of boring females of *T. piniperda* (Lanne *et al.*, 1987). Song *et al.* (2005) trapped *T. piniperda* using semiochemical lures in Changchun City in Northeastern China, and observed that α-pinene was the most attractive terpene and that α-pinene was significantly more attractive to *T. piniperda* when it was mixed with trans-verbenol.

T. destruens was attracted slightly to the host volatile α-pinene, but a strong synergistic effect was found in the attraction towards monoterpenes when ethanol was added to the bait (Gallego *et al.*, 2008). There is still limited information on the chemical stimuli that govern host selection by *T. destruens* adults, although they are known to be attracted by Mediterranean pine shoots and their extracts (Faccoli *et al.*, 2008).

Lanne *et al.* (1987) identified trans-verbenol from hindgut extracts of both sexes of *T. minor* collected on Scots pine (*Pinus sylvestris* L.) and suggested that the female may produce aggregation pheromones. However, *T. minor* was observed to damage Scots pine in the upper part of trees in Southern Sweden (Långström, 1983; Lanne *et al.*, 1987), and it was observed to damage *P. yunnanensis* in the lower part of trees in Southwestern China (Lu *et al.*, 2012).

T. yunnanensis attacks *P. yunnanensis* by aggregating on shoots and boring into them during shoot feeding to predispose pines to subsequent trunk attacks in Yunnan province (Ye, 1993, 1997; Ye & Li, 1994; Ye & Lieutier, 1997; Långström *et al.*, 2002; Lieutier *et al.*, 2003). Laboratory tests also showed that *T. yunnanensis* had a positive response to extracts of shoots of *P. yunnanensis* during shoot feeding (Yan *et al.*, 2011). Host-seeking behaviour and pheromones of *T. brevipilosus* have not been reported. However, *T. yunnanensis* and *T. brevipilosus* were identified incorrectly as *T. piniperda* in Southwestern China until 2008 (Kirkendall *et al.*, 2008); therefore, the prevailing understanding of the behaviour of these three beetle species must be reexamined.

Thus far, *Tomicus* beetles are mainly controlled by removing damaged wood, using chemical control (Lu *et al.*, 2000; Gitau *et al.*, 2013), and using trap trees (Braquehais, 1973). Investigation of many possible management tactics using semiochemical strategies (kairomones) has led to operational management programmes, such as the utilisation of semiochemical-baited traps to suppress bark beetle populations and the use of inhibitors to protect vulnerable host trees from attack (Gitau *et al.*, 2013). For example, traps can reduce population densities to levels below the critical threshold (El-Sayed *et al.*, 2006; Hansen *et al.*, 2006; Schiebe *et al.*, 2011).

Control of *Tomicus* is difficult because they have two different dispersion phases: towards the canopy of healthy trees and towards the trunk of dying trees. Their small size, elusiveness, and largely cryptic feeding habit have also made their control difficult. Researches have mainly focused on the trunk-breeding stage. To control damage to trees in Southwestern China, it is imperative to focus on the maturation feeding stage and not only on the breeding stage (Lieutier *et al.*, 2003). The concentration of shoot attacks is the main reason for the extensive tree damage observed in China (Lieutier *et al.*, 2003). Successful shoot feeding weakens the host tree, generating conditions conducive for subsequent trunk breeding. In addition, some *T. minor* individuals may mate in the shoots during the shoot-feeding stage (Ye *et al.*, 2004). Shoot feeding lasts for 7–9 months, thereby severely injuring pine trees. Volatiles released by bark beetles or those released from the host in response to bark beetle infestation may collect more beetles to damage shoots. Therefore, it is important to study the shoot-feeding stage.

The main purposes of this study were to determine: (1) the intraspecific attraction of the three beetle species; (2) the interspecific relationships of the three beetle species; and (3) the existence of semiochemicals that can affect the attraction of the three species during shoot feeding. This study provides an in-depth understanding of the relationship between beetles and pines and among beetle species, in addition to evidence for further identification of the semiochemicals during the shoot-feeding period.

Materials and methods

Collection of beetles

The three species of beetles were obtained from naturally infested shoots that were cut from pine trees. The damaged shoots were 30–40 cm long, had many yellow needles, and they were collected in two plantations of pure pine trees in Yunnan province, Southwestern China. The first site was located on a small mountain near Jianshui County (N23°42′37.8″, E102°45′55.0″, 1620 m elevation), where *T. minor* and *T. yunnanensis* were collected on *P. yunnanensis*. The second site was located near Puer City (N22°54′09.20″, E101°15′27.87″, 1400 m elevation), where *T. brevipilosus* was collected on *Pinus kesiya*. Samples were collected from May to September 2013. The trees were 10–30 years old and ranged from 3 to 15 m in height, with a diameter at breast height of approximately 8–20 cm. The shoots were brought back to the laboratory and stored at 4°C. Beetles were dissected from the shoots and separated by species and sex. They were distinguished under a stereoscope by the presence of erect hairs, granules, and punctures on the elytral declivity, as described by Kirkendall *et al.* (2008). Adults were then maintained at 4°C in the dark on moistened absorbent cotton in Petri dishes, at 80% relative humidity, until their use in experiments.

Odour source

Three substances were used as the odour source in an experimental trial. Shoots were separated according to beetle species and sex. First, we used a beetle-damaged shoot as the odour source. The shoot was placed in a glass container with an inner diameter of 12 cm and a length of 50 cm. The container was connected to a constant supply of clean air, produced by a generator, by a Teflon tube that had a 3-mm inner diameter. In the second round of tests, shoot extracts were used. Shoots damaged by different beetle species and sexes were sheared into pieces measuring 2 mm × 2 mm, and 5-g fragments were weighed and soaked in a sample vial containing 10 ml of *n*-hexane for 12 h. The extracts were preserved in 4°C. The third round of tests used the dynamic headspace

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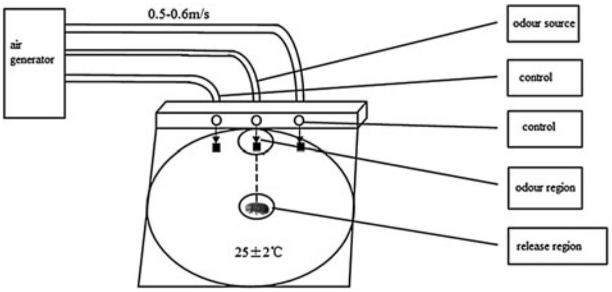

Fig. 1. Laboratory bioassay of walking beetles (black squares represent filter paper; arrows represent airflow direction).

sampling method. Ten damaged shoots for which the damaging species and sexes were known were placed in sealed odourless PE fresh-keeping film (Toppits, Canada) to collect the volatiles. The volatiles were trapped in a glass tube (15 ×- 0.3 cm, Chrompack) containing Porapak Q (adsorbent, 150 mg, Amberlite XAD-2). The glass tube was connected with a Teflon tube, one end of which was connected to the air inlet of the air generator, and the other end of which was connected to the PE fresh-keeping film. The ends of the other Teflon tube were connected to the air outlet of the air generator and the PE fresh-keeping film, respectively. (In other words, both tubes were covered by the odourless PE fresh-keeping film at one end, while the other ends were connected to the air inlet and air outlet of the air generator, respectively.) The airflow rate was 0.5 l min^{-1}. The collecting process was operated in a closed circulation system and lasted for 8 h. Volatiles trapped in Porapak Q were rinsed with 4 ml of *n*-hexane before being concentrated to 2 ml. The eluate was preserved at 4°C.

Laboratory bioassay of walking beetles

The responses of beetles to the three odour sources were tested using a modified open-arena olfactometer. The open-arena bioassay was performed as described by Byers & Wood (1981), Lanne *et al.* (1987), and Byers (2012). The test of taxis was conducted in a flat glass plate in which four circles were drawn, one with a radius of 19 cm and three with a radius of 2 cm. Small circles were drawn in the odour region, and one of them was tangent to the larger circle. The other two small circles were drawn 10 cm away on either side of the small circle that was tangent to the larger circle. The device consisted of an air generator that drew air out of the room through two Teflon tubes (3-mm inner diameter) placed at the 'downwind' side. At the 'upwind' end of the olfactometer system, the air containing the odour was forced through an air generator by a Teflon tube. The other two tubes were placed 10 cm apart, horizontally, on either side of the middle one. The air generator maintained an approximately laminar airflow with a speed of 0.5–0.6 m s^{-1} at the semiochemical source, 15 cm from the centre of the bigger circle. The beetles were released in the centre of the larger circles. The air containing volatiles from three tubes was treated with powdered activated carbon and then blown towards the other end of the larger circle (fig. 1).

A 10-µl volume of shoot extracts or dynamic headspace volatiles was placed on a piece of filter paper (1.2 cm × 1.2 cm) in the odour region. A volume of 10 µl of *n*-hexane was dropped on the same filter papers placed on either side of the odour region. The *n*-hexane was replaced by filtered air when the attracting substance was replaced by damaged shoots. In the control group, the odour source was replaced by *n*-hexane, and the damaged shoots were replaced by undamaged shoots.

One beetle of each sex was released at the centre of the larger circle for each trial. The number of times that the beetle entered the odour region within 5 min after release was recorded. Each beetle was used only once but the assay was repeated eight times for each beetle. Five beetles were used in each treatment.

Data analysis

The number of times that the beetles entered the odour region was used to evaluate the level of attraction for each substance. Data were subjected to non-parametric tests in SPSS 19.0. Independent samples were evaluated using the Kruskal–Wallis test, which was followed by all possible pairwise multiple comparisons at $\alpha = 0.05$ in all analyses. Figures were drawn in Excel 2010. Values and standard errors in the figures refer to the mean number of times the beetles entered the odour region area for each tested volatile.

Results

Attraction to damaged shoots

The test using damaged shoots indicated that overall, beetles were more attracted to shoots damaged by *T. brevipilosus* (fig. 2). However, male *T. minor* (fig. 2a) showed the strongest attraction to shoots that had been damaged by male *T. minor*. *T. minor* showed no attraction to undamaged shoots or to shoots damaged by either sex of *T. yunnanensis*; similarly, *T. yunnanensis* was not attracted to shoots damaged by *T. minor*.

T. yunnanensis (fig. 2c, d) individuals did not show attraction to shoots that had been damaged by their own species and sex, but males were attracted to shoots damaged by female *T. brevipilosus*.

Male and female *T. brevipilosus* (fig. 2e, f) showed stronger attraction to shoots that had been damaged by their own species than to shoots damaged by others.

Attraction to shoot extracts

Beetles were attracted only to extracts from shoots that had been damaged by beetles of their own species and sex (fig. 3).

Attraction to dynamic headspace volatiles

Beetles were strongly attracted to dynamic headspace volatiles that had been extracted from shoots damaged by their own species and sex; the only exception was female *T. yunnanensis* (fig. 4), which was attracted to dynamic headspace volatiles extracted from shoots damaged by both sexes of its own species.

Discussion

The different behaviours of the three bark beetle species may result from variation in the semiochemicals released from different damaged shoots, as the blend of volatiles released by plants in response to insect attack is specific for each insect–plant system (Engelberth *et al.*, 2004; Arimura *et al.*, 2009). Attraction of the three bark beetles to damaged

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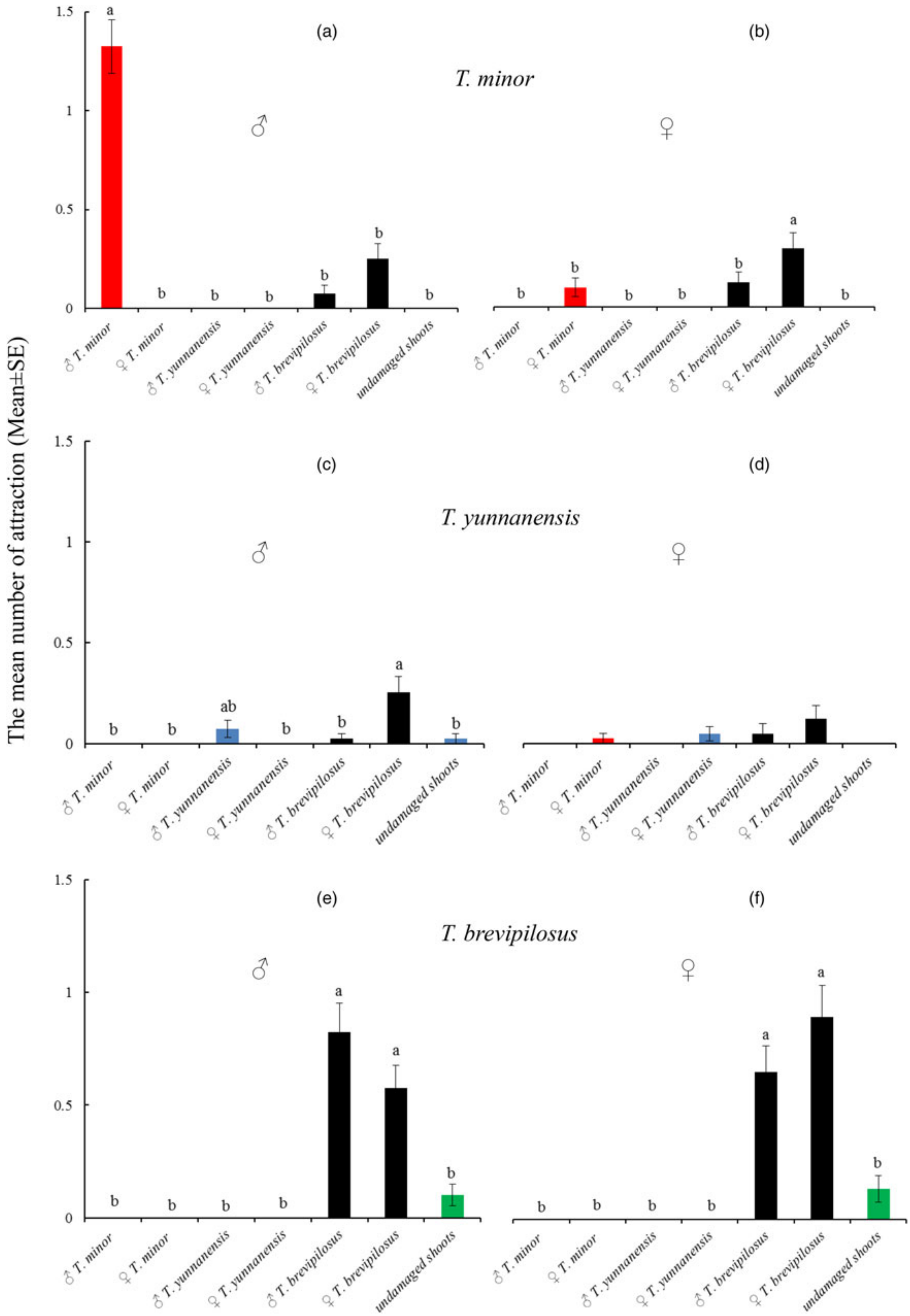

Fig. 2. Attraction of male (a) and female (b) *T. minor*, male (c) and female (d) *T. yunnanensis*, and male (e) and female (f) *T. brevipilosus* to shoots that had been damaged by beetles of different species and sexes. Bars with the same letters are not significantly different. Lowercase letters show significant difference, $P < 0.05$. Kruskal–Wallis test; $n = 40$.

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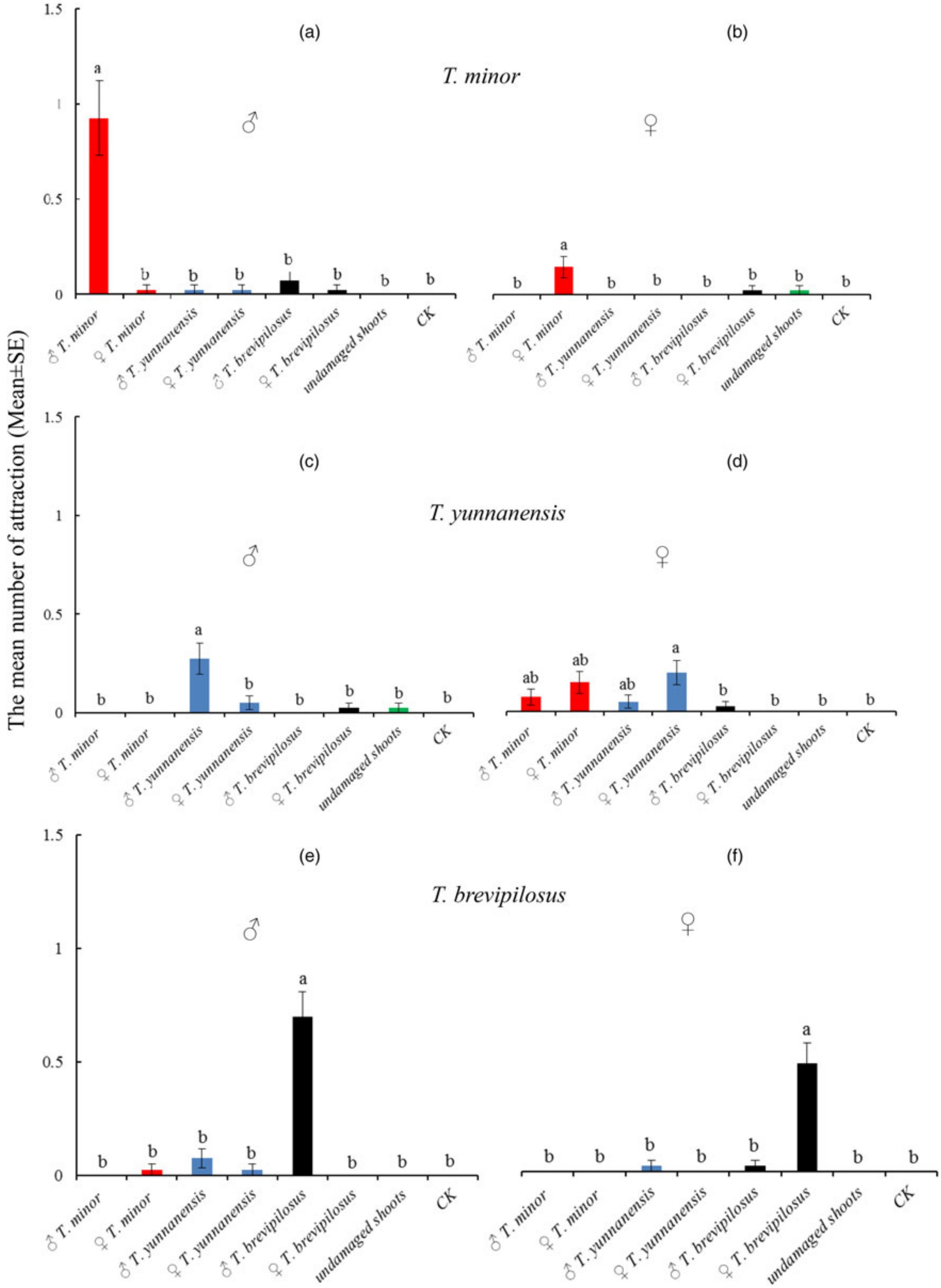

Fig. 3. Attraction of male (a) and female (b) *T. minor*, male (c) and female (d) *T. yunnanensis*, and male (e) and female (f) *T. brevipilosus* to extracts from shoots that had been damaged by beetles of different species and sexes. Bars with the same letters are not significantly different. Lowercase letters show significant difference, $P < 0.05$. Kruskal–Wallis test; $n = 40$.

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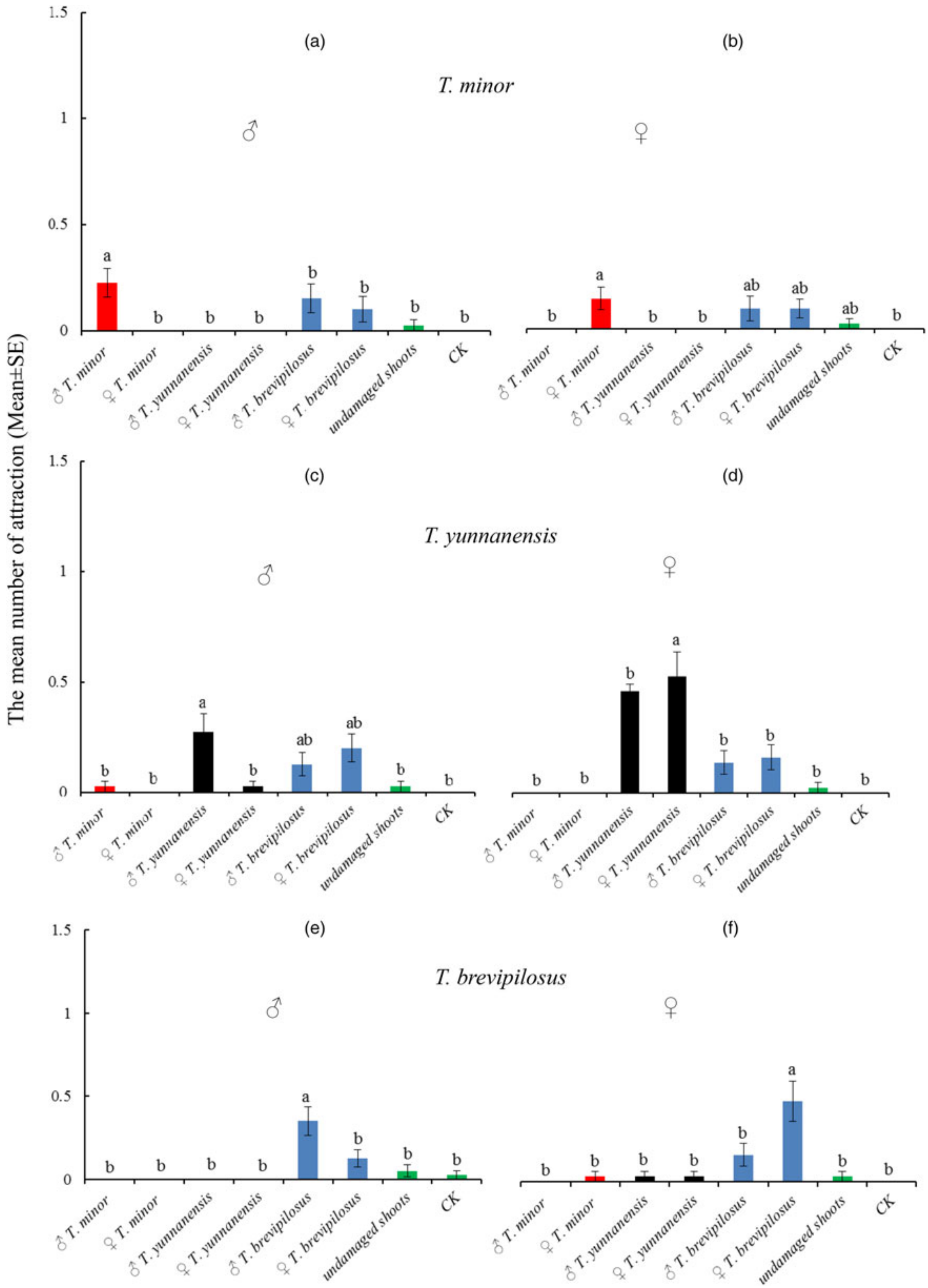

Fig. 4. Attraction of male (a) and female (b) *T. minor*, male (c) and female (d) *T. yunnanensis*, and male (e) and female (f) *T. brevipilosus* to dynamic headspace volatiles extracted from shoots that had been damaged by beetles of different species and sexes. Bars with the same letters are not significantly different. Lowercase letters show significant differences, $P < 0.05$. Kruskal–Wallis test; $n = 40$.

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shoots and dynamic headspace volatiles showed similar trends, which suggests that the volatiles released from shoots damaged by the three bark beetle species affected the behaviour of the beetles. Further studies should investigate the identity of the volatiles and their specific effects.

There was almost no attraction between *T. minor* and *T. yunnanensis* individuals, except that *T. yunnanensis* showed attraction to extracts from shoots damaged by *T. minor*. The lack of attraction may be the result of different phenology and different host preferences and may explain why these two species share little overlap in the wild. It is possible that interspecific communication aids individuals in avoiding interspecific competition (Byers *et al.*, 2013). Similar to the phenomena we observed, in the wild, the same beetle species are mainly discovered on a single shoot or in the same tree.

T. brevipilosus only showed strong attraction to shoots that had been damaged by the same beetle species. Furthermore, the three odour sources from shoots that had been damaged by *T. brevipilosus* were attractive to *T. minor* and *T. yunnanensis*, but not vice versa. It thus appears that dynamic headspace volatiles from shoots damaged by *T. brevipilosus* contain semiochemicals that attract *T. minor* and *T. yunnanensis*. This phenomenon may be mediated by herbivore-induced plant volatiles that effect the interactions between plants and arthropods (Arimura *et al.*, 2009; Karban, 2011), as beetle species may use the volatiles to control population quantity and maintain the ecological balance.

The shoots damaged by male and female *T. minor* attracted the same sex of *T. minor*. The same situation was observed for *T. yunnanensis*. However, the shoots damaged by *T. brevipilosus* attracted both sexes of *T. brevipilosus*. Liu *et al*. (2010) introduced 10 males or females, or 10 pairs of *T. yunnanensis*, into *P. yunnanensis* bolts, and the infested bolts captured both sexes of *T. yunnanensis*. We used the same method to trap *T. minor* in 2011; regardless of whether the bolts were inoculated with males, females or both sexes of the two beetle species, both sexes of the two beetle species were collected from each bolt (unpublished data). Therefore, conditions are different between the shoot-feeding and trunk-breeding periods.

The damage caused by the three *Tomicus* species in Southwestern China may be related to their aggregation on particular trees during the shoot-feeding period (Ye & Li, 1994; Ye & Lieutier, 1997; Långström *et al.*, 2002; Lieutier *et al.*, 2003). In wild lure experiments, we were not able to trap the three bark beetle species by only using host volatiles (terpinenes), whereas the beetles were lured by terpinenes mixed with terpinene alcohol (volatiles collected from the hindguts of bark beetles) (unpublished data). We speculate that the specific behaviour of three bark beetles in response to different odour sources during the shoot-feeding phase may not only be associated with the host volatiles. In addition, the three odour sources were mainly attractive to the same species and sex of bark beetles, which suggests the existence of special behaviour of the three bark beetle species during the shoot-feeding period.

The shoot extracts were extracted using *n*-hexane, which may include a number of non-volatiles or impurities because an optimal quantity of volatiles compounds is normally released by the plants into the atmosphere, whereas a different blend of volatiles is produced in response to herbivory (Arimura *et al.*, 2009). Therefore, the extraction method may affect the chemical composition of dynamic headspace volatiles of damaged shoots. The dynamic headspace sampling method should be used over the shoot extract method to collect the different volatiles of different shoots in further studies.

In China, the tested *Tomicus* species are oligophagous on pine trees, such as *P. yunnanensis* and *P. kesiya* (Kirkendall *et al*., 2008). *P. yunnanensis* occupies the middle and northern areas of Yunnan where the three beetle species were observed, and *P. kesiya* is distributed in Southwestern Yunnan (Zhang *et al*., 2014), where *T. brevipilosus* specimens were collected. We did not collect the three beetle species from the same sites or the same host trees for this experiment. The behavioural responses of *T. brevipilosus* to damaged shoots of *P. yunnanensis* and *P. kesiya* should be compared, and the chemical components of volatiles released by shoots damaged by *T. brevipilosus* from *P. yunnanensis* and *P. kesiya* should be identified in future work.

The semiochemicals released by the three beetles during this stage have not been elucidated. Further studies should include an analysis of the chemical component of dynamic headspace volatiles from damaged pines and hindguts of the three beetle species during different stages. These volatiles could be used to trap bark beetles in the wild. The relationships of the three beetle species with regard to semiochemical effects and the chemical mechanism of the relationships should be studied. Three possible attraction hypotheses should be tested: (1) pheromones exist that affect the behaviour of the beetles; (2) the behaviour is affected by the induced volatiles of host tree kariomones; and (3) both the pheromone and kariomone have interactive effects during the shoot-feeding stage. Such studies will promote the development of new semiochemical-based management methods to ensure the health of forestry.

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