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Preference and performance of the two-spotted spider mite *Tetranychus urticae* (Acari: Tetranychidae) on strawberry cultivars

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Abstract

The two-spotted spider mite (TSSM), *Tetranychus urticae* Koch (Acari: Tetranychidae), is one of the most serious pests of strawberry worldwide. Understanding the preference of TSSM for particular cultivars of strawberry and performance on them helps identify host-plant resistance to this pest mite. In this study, we tested preference, developmental duration, fecundity and population levels of TSSM on 14 strawberry cultivars. TSSM showed strong preference for the Chinese cultivars of Yanxiang, Baixuegongzhu, and Jingtaoxiang. Development of TSSM on the cultivars varied from 32.32 to 36.82 days; it was longest on the cultivars Hongxiutianxiang and Baixuegongzhu, and shortest on Yanxiang, Jingzangxiang, and Darselect as well as on a wild variety (Wuye). TSSM had high fecundity on the cultivars Yanxiang, Taoxun, Hongxiutianxiang, Jingzangxiang, Albion and Baixuegongzhu as well as on Wuye, whereas egg production was lowest on Sweet Charlie, Portola, Akihime, and Benihoppe. After 28 days of plant infestation with 10 pairs of adults, the cultivars Yanxiang, Taoxun, Jingzangxiang, Jingtaoxiang, and Baixuegongzhu had the highest number of mites (> 1000 per plant), whereas mite numbers on Albion and Camarosa were low. The population size of TSSM was correlated with fecundity, but no correlation was found between other preference/performance measures. Our study suggests that a rapid increase of population size of TSSM on cultivars of strawberry is related to high fecundity, and also that there are substantial differences in preference and performance across cultivars.

Keywords *Tetranychus urticae* · Strawberry · Host · Cultivar · Developmental duration · Fecundity

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Introduction

The two-spotted spider mite (TSSM), *Tetranychus urticae* Koch (Acari: Tetranychidae), is a serious pests on many vegetables, flowers, and fruit trees (Bostanian et al. 2003; Gerson and Weintraub 2012; Park and Lee 2005). It attacks a wide range of host plants including more than 140 families and 1100 species (Bi et al. 2016; Grbic et al. 2011). In the field, the control and management of TSSM predominantly relies on chemicals (Van Leeuwen et al. 2013; Vassiliou and Kitsis 2013). The frequent usage of acaricides and the high reproduction of TSSM has resulted in a high level of resistance and cross-resistance to various pesticides (Bi et al. 2016; Grbic et al. 2011; Khajehali et al. 2011; Kwon et al. 2015; Van Leeuwen et al. 2008; Van Nieuwenhuyse et al. 2009).

In order to delay the development of resistance, practices that do not rely on acaricides have been developed, such as biological control using predatory mites (such as *Phytoseiulus persimilis*) and microorganisms (Castilho et al. 2015; Gigon et al. 2016; Howell and Daugovish 2013; Wu et al. 2016), combinations of natural enemies and compatible acaricides (Abraham et al. 2013; Rhodes and Liburd 2006), intercropping garlic plant with strawberry (Hata et al. 2016), ultraviolet-B light (Koveos et al. 2017; Tanaka et al. 2016), regulation of humidity (Suzuki et al. 2012), and atmospheric control (Gong et al. 2018; Oyamada and Murai 2013). Resistant cultivars of crops provide another possibility for non-chemical pest management (Costa et al. 2017; Gonzalez-Dominguez et al. 2015), and variation in the preference of TSSM for—and in their fitness on—certain cultivars of the same crop has been reported. For instance, Jin et al. (2016) and Khanamani et al. (2013) found differences in the development rate and fecundity of TSSM on different cultivars of eggplant in China and Iran. TSSM also differs in development and reproduction on varieties of bean and soybean (Najafabadi et al. 2014; Sedaratian et al. 2011).

Strawberries represent one of the main crops damaged by TSSM (Hata et al. 2016; Monteiro et al. 2014; Osakabe 2002; Sato et al. 2007), and the vegetative propagation of strawberries has facilitated the spread of TSSM. There are more than 3000 cultivars of strawberry, mainly originating from three geographic populations (Asia, Europe and the Americas), which may differ in susceptibility to TSSM. Surface structure of crop leaf as well as nutrition and chemicals can vary among cultivars and may affect the mites suitability (Seki 2016). Giménez-Ferrer et al. (1994) found variation in the population density of TSSM on seven strawberry cultivars, whereas Costa et al. (2017) noted differences in infestation of TSSM on 13 strawberry cultivars, with Camarosa having a lower pest incidence and Dover a higher incidence. In vitro screening of 76 strawberry cultivars for oviposition responses and plant damage led to cultivars being classified into six categories according to their resistance to TSSM (Ferrer et al. 1993). Since the 1980 s, strawberry cultivars from Japan, Europe and USA have been introduced into China, whereas new cultivars have also been developed locally. No Chinese cultivar has been tested in previous studies due to regional restrictions on cultivar use (Costa et al. 2017). Comparisons of cultivars have so far also not considered the effects of plant preference and host plant suitability on TSSM infestation levels.

In the current study, TSSM preference and suitability were investigated for 14 cultivars of strawberry from China, Japan, Europe, and USA, as well as for a wild cultivar. The findings are interpreted within the context of breeding resistant cultivars and field management of TSSM.

Materials and methods

TSSM population and strawberry cultivars

TSSMs were collected from greenhouse strawberry plants in Junmingcheng Agricultural Science and Technology Park at Daxing district, Beijing, China. The TSSMs were reared on seedlings of bean (*Phaseolus vulgaris*) for two generations prior to experiments at 25 ± 1 °C, 50 ± 10% RH, and 16L:8D photoperiod.

Fourteen strawberry cultivars were selected for testing; six were from China, two from Japan, four from USA, one from France, and one was a wild variety (Table 1). Seedlings in the three-leaf (euphylla) stage were transplanted individually to a single pot (10 cm diameter). All cultivars were grown in a greenhouse with 120-mesh insect-proof net.

Preference test

Experiments were conducted in a greenhouse, in a 100-mesh insect-proof net room of 3 × 3 m and 5 m height. All windows of the greenhouse were closed during the experiment to avoid air movement. Different strawberry cultivars were placed in a circle (diameter of inner circle was 90 cm) with seedlings 10 cm apart and no leaves overlapping. In each circle, one seedling was used from each of the 14 cultivars. Bean leaves infested with about 20,000 TSSMs (all mobile stages) were placed in the center of the circle. The bean leaves were organized into a circle shape (20 cm diameter) at the centre of the 14 strawberry cultivars. The soil surface that TSSMs had to cross to arrive at the plants was cleared and smoothed. No contact was allowed between soil surface and seedling leaf. The experiment was repeated 4 × (n = 4). All replicates were conducted at the same time. For each replicate, the position of different cultivars was changed randomly to account for any uncontrolled cues in the surroundings, e.g., light sources or the earth magnetic field. The TSSMs were allowed to make a choice of strawberry cultivars for 4 h. After 4 h, the larvae, nymphs and adult TSSMs on each seedling were counted.

Table 1 Fourteen cultivars of strawberry used in this study

Origin	Code	Cultivar
China	JZ	Jingzangxiang
	HX	Hongxiutianxiang
	JT	Jingtaoxiang
	YX	Yanxiang
	TX	Taoxun
	BX	Baixuegongzhu
Japan	BE	Benihoppe
	AK	Akihime
USA	SC	Sweet Charlie
	AL	Albion
	PO	Portola
	CA	Camarosa
France	DA	Darselect
Wild	WY	Wuye

Population assessment

To assess population build-up of TSSM on cultivars, 50 pairs of male and female adults were placed on a seedling of a cultivar for 12 h before adults were removed using a brush. Eggs from the adults were reared to the adult stage in an incubator (LP-80CCFL-6CTAR, NK System, Japan) at 25 ± 1 °C, 40–60% RH and 16L:8D photoperiod. Ten pairs of male and female newly emerged adults per cultivar were used to inoculate a new seedling of the same cultivar. The larvae, nymphs and adults on this seedling were counted after 14 and 28 days, allowing the TSSMs to complete around two generations. Eight seedlings were tested per strawberry cultivar.

Developmental duration

A leaf-disc method was used for studying development. Detached strawberry leaves were washed with water, then with 70% ethanol, and finally air dried. Leaves were cut to fit a Petri dish (6 cm diameter). A 0.2-cm agar layer was poured into the bottom of the Petri dish to keep leaves fresh. One strawberry leaf disk was placed on to the agar layer. The edge of the leaf was sealed with agar to reduce wilting. To generate eggs for inoculating the leaves, 15 pairs of male and female adult TSSMs were added to a strawberry seedling for each cultivar and left for 12 h for oviposition. Five eggs were moved to each leaf disc with a brush, and leaf disks were then held at 25 ± 1 °C, 50 ± 10% RH and 16L:8D photoperiod. Ecdysis and growth status of TSSMs were recorded twice a day at 08:00 and 20:00 until the adults died. The developmental duration of each growth stage of TSSM and adult life span were recorded. Thirty replications were set up for each strawberry cultivar.

Fecundity of TSSM

To obtain TSSM adults at a consistent developmental stage, 15 pairs of adult males and females were added to a strawberry plant and left for 12 h for oviposition. Eggs were reared in an incubator at 25 ± 1 °C, 50 ± 10% RH and 16L:8D photoperiod. A pair of male and female exuvial adults was placed on a leaf-disc prepared as described above. The number of eggs laid by adults was recorded until the adults died. Thirty replicates were set up per cultivar.

Surface structure of strawberry leaf

Five leaves were examined per cultivar from seedlings at the three-leaf stage. TSSM are most found on the underside of leaves until their numbers get quite high. Thus, the leaf setae on the underside of strawberry leaves were counted in four circular leaf areas (3.5 mm diameter) with a Nikon SMZ 1500 stereomicroscope at 5 × magnification. Each leaf region was counted 4 × and 20 leaves were examined per cultivar.

Statistical analysis

The Shapiro–Wilk Normality Test implemented in R function *shapiro.test* was used for testing normality of the data. We used a linear mixed-effects model implemented in the R package *nlme* to test the preference of mites for strawberry cultivars. In the model, the cultivar of strawberry was treated as a fixed factor whereas repeat tests were treated as a random factor. Tukey's honestly significant difference (HSD) test for linear mixed-effects model was undertaken for multiple comparisons of mite numbers in preference data among strawberry cultivars, using the general linear hypotheses analysis implemented *glht* function in the *multcomp* R package. For analysis of fecundity, developmental duration, and population assessment of mites on different cultivars, one-way ANOVA was used for multiple comparisons after normalization implemented in *Anova* function in the R package *car*, whereas for the density of leaf setae, generalized linear models (GLM) with ln-distributed errors was used implemented in the R function *glm*. Multiple comparisons for ANOVA and GLM models were evaluated by Tukey's HSD tests implemented in the *HSD.test* function in the R package *agricolae*.

Pairwise correlations between traits on different cultivars (preference, fecundity, developmental duration, population assessment and density of setae) were analyzed by using the *corr.test* function in the R package *psych* (method = pearson). Correlations were visualized with the R package *corrplot*.

Generalized linear models (GLM) with ln-distributed errors was used to test the correlation between the number of TSSM on different cultivars and multiple factors measured in our study (preference, fecundity, developmental duration and density of setae) using the R function *glm*. We used a stepwise algorithm implemented in stepAIC function in R to choose the best fitting model using forward selection with the Akaike information criteria (AIC).

Results

Preference test

TSSM showed a significant difference in preference for the strawberry cultivars ($F_{42.13} = 94.556$, $P < 0.0001$). After 4 h, the numbers of TSSM on Yanxiang, Baixuegongzhu and Jingtaoxiang were the highest at 120.25, 119.5 and 112 per seedling, respectively (Fig. 1a). The three most attractive strawberry cultivars did not differ significantly from each other for the number of mites attracted. TSSM had a low preference for Portola, Darselect, Hongxiutianxiang and Benihoppe. The number of TSSM on Jingzangxiang was particularly low and differed significantly from the other cultivars (Fig. 1a).

Population assessment

Fourteen days after adult inoculation, numbers of mites on the cultivars differed significantly overall ($F_{98.13} = 12.8$, $P < 0.001$). The average number of TSSM reached more than 100 per seedling on Jingzangxiang, Baixuegongzhu, Benihoppe, Hongxiutianxiang, Camarosa, Jingtaoxiang, Taoxun and Yanxiang (Fig. 2). The average number of TSSM on Albion, Portola, Akihime and Darselect were significantly lower than on the other strawberry cultivars.

After 28 days, there was also a significant difference among the cultivars ($F_{98.13} = 21.51$, $P < 0.001$). The average number of TSSM on Yanxiang reached 1407.5 per seedling, which was the highest number, followed by Taoxun (1144.5), Jingzangxiang (1095.25), Jingtaoxiang (1065.5) and Baixuegongzhu (1008.13). However, on the other strawberry cultivars

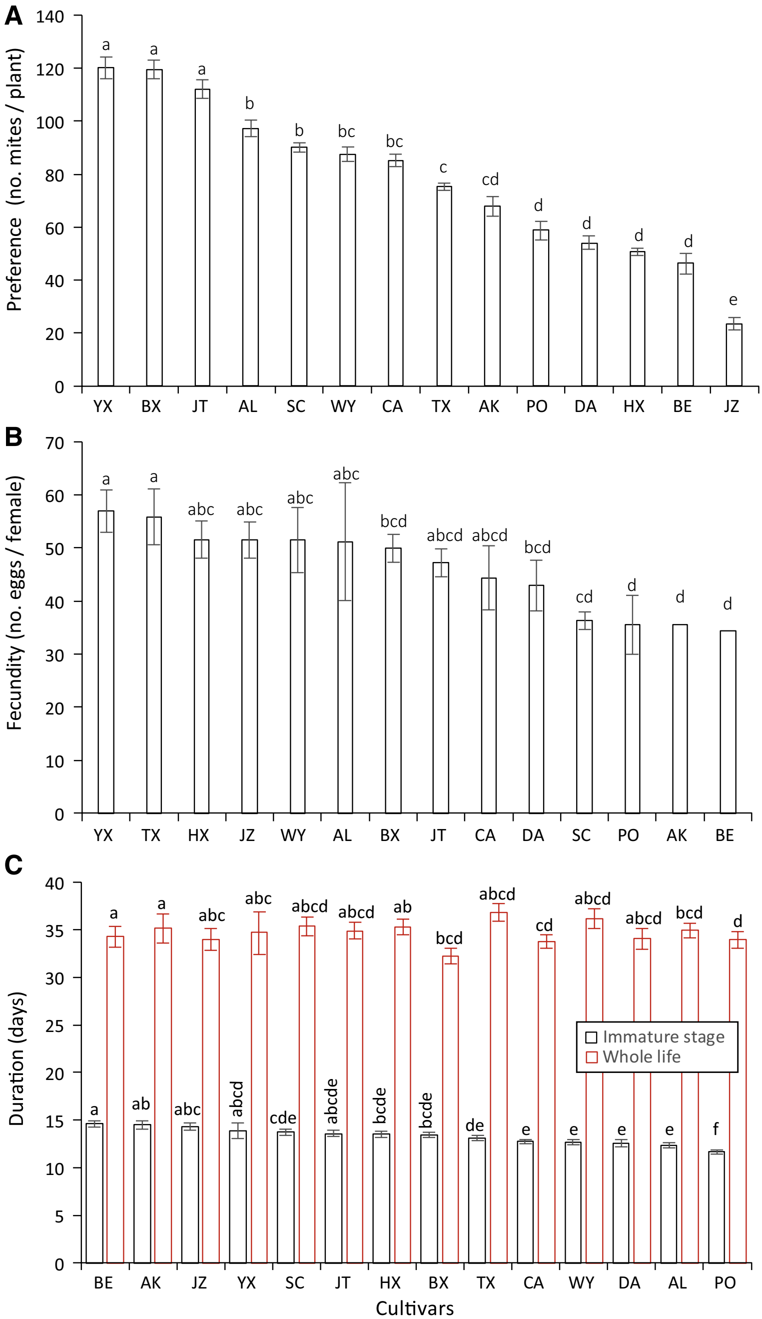

Fig. 1 Mean (± SD) preference (**a**), fecundity (**b**) and developmental duration of the two-spotted spider mite on 14 cultivars of strawberry. Preference is expressed as the number of mites counted after a preference test over 4 h. Fecundity is expressed as the number of eggs laid by one female during her lifetime. Means within a panel capped with different letters are significantly different ($P < 0.05$), based on **a** Tukey's HSD test in linear mixed-effects models and **b**, **c** Tukey's HSD test of multiple comparisons. See Table 1 for an explanation of the cultivar codes

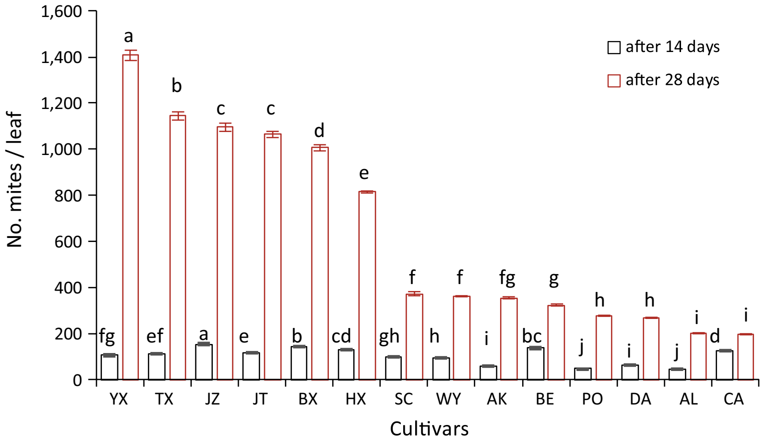

Fig. 2 Mean (± SD) population numbers of two-spotted spider mite produced by 10 pairs of male and female adults on 14 cultivars of strawberry after 14 and 28 days. Means capped with different letters are significantly different (Tukey's HSD test: $P<0.01$). See Table 1 for an explanation of the cultivar codes

and particularly Albion and Camarosa, the number of TSSM was much lower, reaching only 203.13 and 196.5 per seedling, respectively (Fig. 2).

Fecundity

Fecundity differed among the cultivars ($F_{398.13}=4.36$, $P=0.014$). TSSM produced the most eggs on Yanxiang, Taoxun, Hongxiutianxiang, Jingzangxiang, Wuye, Albion, Baixuegongzhu, and Jingtaoxiang, with no significant difference among these cultivars (Fig. 1b). The number of eggs laid on Camarosa, Darselect, Sweet Charlie, Portola, Akihime and Benihoppe was low and differed significantly from the cultivars with high numbers, but not from each other (Fig. 1b).

Developmental duration

Egg duration on the 14 strawberry cultivars differed overall ($F_{406.13}=6.05$, $P=0.038$) and ranged from 4.08 to 5.26 days (Table S1). A significant difference was found between Camarosa (4.08 days) and Taoxun (5.26 days). The average developmental duration for immature stages differed among cultivars ($F_{398.13}=6.87$, $P=0.021$) and ranged from 11.69 (Sweet Charlie) to 14.61 days (Portola) and was longer on Portola, Darselect and Camarosa than on the other cultivars. Across life stages, the longest development durations were on Hongxiutianxiang and Baixuegongzhu, whereas the shortest duration (32.21 days) was on Wuye (Fig. 1c, Table S1).

Leaf structure of strawberry cultivars

Sweet Charlie had the most setae (109.63 seta/cm^2) on the underside of the leaf, which was higher than on Portola (99.75 seta/cm^2). Jingtaoxiang and Wuye had few leaf setae, as did Akihime (7.75 seta/cm^2). Seta density differed among the cultivars ($\chi^2_{98.13}=31.941$,

$P < 0.001$). There was no significant difference among the three cultivars with the lowest densities (Fig. 3).

Trait associations across cultivars

A positive association was found between fecundity and population numbers ($r = 0.681$, $P = 0.007$) (Fig. 4). However, there was no correlation between other pairs of traits. A multiple regression analysis indicated that the effect of fecundity is significant on population numbers ($t = 2.978$, $P = 0.0155$) but not on preference ($t = -0.079$, $P = 0.94$), developmental duration ($t = 1.518$, $P = 0.16$), or density of leaf setae ($t = -1.268$, $P = 0.24$). Fecundity therefore had an overriding effect on population numbers.

Discussion

Understanding the preference and performance of phytophagous invertebrates on host plants will contribute to the identification of plant resistance. Host selection is the first step that determines infestation level of host plant by pests, and represents a complex process influenced by many factors, such as nutrition, chemical compounds and morphology of host plants and the learning/sensory system of herbivores (Bernays and Chapman 2007; Mworia et al. 2017; West and Cunningham 2002). Our study demonstrated preference of TSSM for particular strawberry cultivars. Identification of mechanisms that mediate preference by TSSM may help in breeding resistant cultivars. However, we did not find a correlation between host plant preference and any performance trait, suggesting that cultivars that are not attractive to TSSM might still be damaged by them. Host plant preference by insects is often divided into host plant finding and host plant acceptance. In fields, TSSM are usually passively dispersed by human activities and wind currents (Brandenburg and

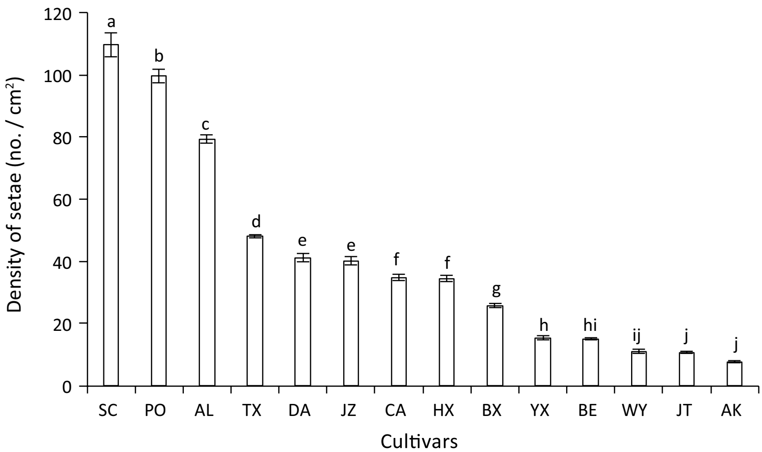

Fig. 3 Mean (± SD) density of leaf setae of 14 strawberry cultivars. Means capped with different letters are significantly different (Tukey's HSD test: $P < 0.01$). See Table 1 for an explanation of the cultivar codes

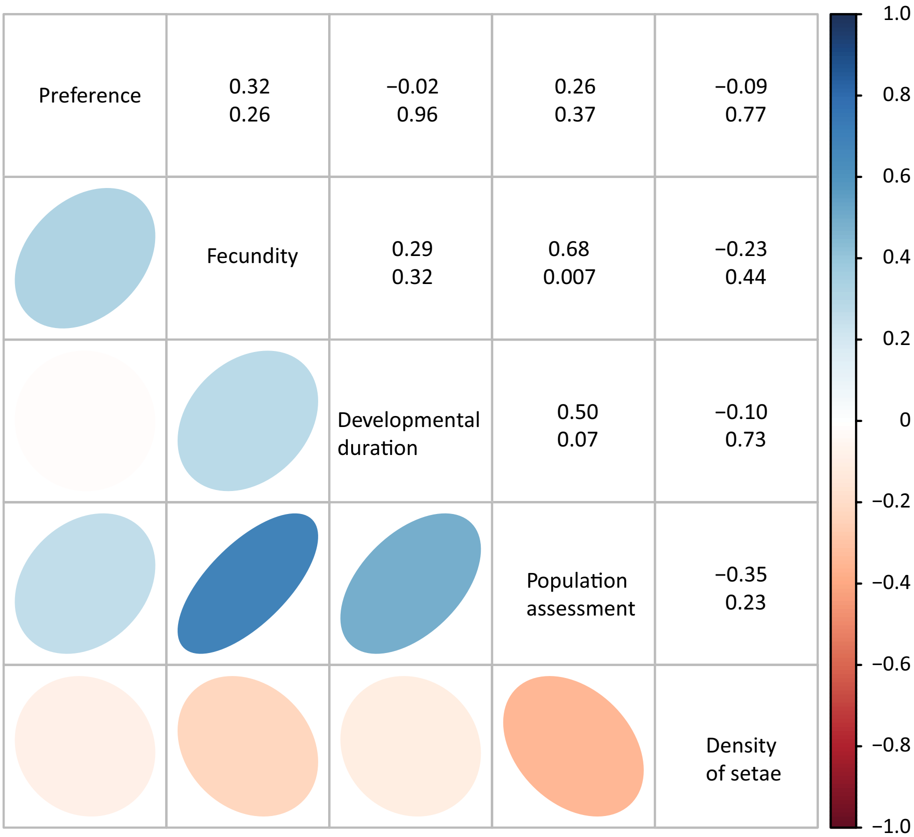

Fig. 4 Correlation among preference, fecundity, developmental duration (immature stages), population assessment (28 days) and density of setae on various strawberry cultivars. The upper triangular of the correlation matrix displays the correlation coefficient value (upper) and *P* value (lower) for each pair, whereas the lower triangular of the correlation matrix displays correlation ellipses. The color of an ellipse indicates the value of the correlation coefficient as shown in the bar to the right of the figure. (Color figure online)

Kennedy 1982) and distributed in aggregates (Dittmann and Schausberger 2017; Krainacker and Carey 1990), suggesting that long-distance finding behaviors are not likely to be important.

We used fecundity and developmental duration, two major parameters commonly studied in previous studies (Ferrer et al. 1993; Jin et al. 2016; Monteiro et al. 2014; Najafabadi et al. 2014), to assess the performance of the mites. Additionally, we measured population levels to assess total performance of TSSM on cultivars. The variable performance of TSSM we detected across cultivars matches previous results on cultivars of bean and strawberry (Ferrer et al. 1993; Giménez-Ferrer et al. 1994; Najafabadi et al. 2014). Fecundity was the most frequently reported TSSM trait influenced by cultivar (Gonzalez-Dominguez et al. 2015; Jin et al. 2016) unlike developmental time that was not markedly affected. This matches previous results on three Mexican strawberry cultivars (Gonzalez-Dominguez et al. 2015) and eggplant (Jin et al. 2016). Our study showed a significant correlation between population numbers and fecundity of TSSM, highlighting the overall importance of fecundity to TSSM fitness.

Performance of phytophagous invertebrates on host plants is affected by nutrition provided by the plants as well as chemical toxins and morphology. The density of leaf setae have previously been reported as affecting the performance of mites (Jin et al. 2016). The thickness of the abaxial palisade tissue of a carnation leaf can affect the ability of mites to feed on spongy tissue during an early life stage (Seki 2016). However, we did not find any correlation between density of setae and preference or performance of TSSM.

Adults tend to feed and lay eggs on leaves with sufficient nutrient content. This not only satisfies the nutritional needs of the adults themselves, but also contributes to the growth of offspring. In this study with various cultivars of strawberry, TSSM showed the highest fecundity (56.95 eggs/female) on cultivar Yanxiang and the lowest (34.29 eggs/female) on Benihoppe. Differences in nutrient contents among strawberry cultivars may be involved but requires further study.

Conclusion

This study analyzed the preference and performance of TSSM on 14 cultivars of strawberry. The study found that TSSM had the strongest preference for Yanxiang, Albion, and Baixuegongzhu, and had the weakest preference for Jingzangxiang and Benihoppe. Although there was no correlation between preference and performance, the rapid buildup of TSSM on some strawberry cultivars related to fecundity points to cultivars that should be avoided where outbreaks of this pest are expected.

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