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Behavioral mechanism of transfer and dispersal of *Propylaea japonica* in cotton adjacent to sorghum fields

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Increasing crop biodiversity, such as by adjacent managed crops, is recognized as an effective biological control measure. However, few studies have focused on the mechanisms involved in how adjacent managed crops increase natural enemy populations, leading to reduced pest numbers. This study investigated the hypothesis that cotton grown adjacent to sorghum would positively influence the feeding and oviposition preferences of the ladybug *Propylaea japonica*, which predates cotton aphids, leading to enhanced pest control. The populations of *Aphis gossypii* were significantly lower and those of *P. japonica* were significantly higher in cotton grown adjacent to sorghum compared with monoculture cotton fields. Regardless of diet on which the larva of *P. japonica* were reared (*Melanaphis sacchari*, *A. gossypii*, and 50% *M. sacchari* + 50% *A. gossypii*), the adults always consumed significantly more *M. sacchari* compared with *A. gossypii. P. japonica* also showed significantly higher feeding and oviposition preferences for host plants bearing aphids to only host plants. *P. japonica* fed *M. sacchari* preferred to lay eggs on cotton, whereas those fed *A. gossypii* preferred to lay eggs on sorghum. These results suggest that the habitat of natural enemies can be expanded by influencing their feeding and oviposition preferences to achieve pest control in adjacent cropping systems. This research, which incorporates field and laboratory studies, suggests an approach for the successful conservation and biological control of cotton aphids using adjacent managed cotton and sorghum crops.

KEYWORDS

adjacent managed, *Propylaea japonica*, feeding preference, oviposition preference, *Aphis gossypii*, *Melanaphis sacchari*

Introduction

Large monoculture farming systems reduce farmland biodiversity and have altered the composition and stability of arthropod populations in agriculture, promoting pest outbreaks as well as decreasing the number and effectiveness of natural enemies, particularly indigenous generalist predators (Thies et al., 2005; Mkenda et al., 2019). The adjacent management of crops has been shown to be an efficient tool to enhance the abundance and diversity of natural enemies and reduce the abundance of pests, decreasing crop damage and providing direct benefits by reducing the need for pesticides (Meehan et al., 2011; Paredes et al., 2013). High crop species richness can suppress pest populations, suggesting that crop species richness also enhances biological control services (Sheng et al., 2017). Greenstone et al. (2014) reported that growing soybean adjacent to cotton as part of a conservation biological control strategy significantly decreased the number of the target pest, *Megacopta cribraria* shield bugs. Natural enemies that moved from adjacent wheat fields to cotton fields were able to maintain the cotton aphid population below the threshold at which significant damage would be caused (Men et al., 2004). Therefore, adjacent crop management has been used to increase natural enemy efficiency to reduce the incidence of crop pests (Scheid et al., 2011; Simpson et al., 2011). There have been many field studies of adjacent crop management on the interactions of pests and their natural enemies. However, little is known about the mechanisms involved.

Host plants on which prey feed affect the nutritional quality of those prey, in turn affecting the feeding preference, development, and mortality of their predators (Banihashemi et al., 2017). The nutritional quality of host plants is an important factor influencing the vigor of predators because not all prey species are equally nutritious (Zhang et al., 2012). Plants respond to herbivore-induced damage by releasing density-related volatiles (Cotes et al., 2015). These volatiles can be used by natural enemies to find their prey on infested plants (Pettersson et al., 2005). For example, the adults of many natural enemies of aphids orient to volatile compounds emitted by host plants in response to aphid feeding (Sasso et al., 2009). Volatiles from aphid-infested cotton have a key role in mediating the orientation behavior of the ladybug *Propylaea japonica* (Thunberg) (Coleoptera: Coccinellidae) (Wang et al., 2015). Such attraction is likely to increase the fitness of *P. japonica* because aphids represent a complete food source for both adults and juveniles (Obrycki et al., 2009).

Both the presence and quality of prey have strong effects on not only the retention of adult predators, but also their reproductive output (Hodek and Honek, 2009). For example, the quantity or quality of a prey directly influence whether a female predator will oviposit on the host plant (Yao et al., 2021). In general, natural selection favors predators that lay eggs in a site that is most appropriate for their offspring (Putra et al., 2009). For example, egg clusters of the ladybug *Hippodamia convergens* are typically found only on aphid-infested sorghum plants in the field but not on uninfested plants (Michaud and Jyoti, 2007). In addition, the abundance and quality of aphids in a habitat affects the survival of larvae (Seagraves, 2009). There is an optimal number of coccinellid eggs that can be laid in an aphid colony to maximize the number of surviving offspring (Rondoni et al., 2014) and aphids constitute a staple food for ladybugs that oviposit in the vicinity of aphid colonies (Oliver et al., 2006). However, how predator feeding and oviposition preferences suppress aphids in adjacent managed host crops is unclear.

Aphids are very serious insect pests in most agroecosystems in the world (Figueroa et al., 2018). The cotton aphid *Aphis gossypii* and sugarcane aphid *Melanaphis sacchari* are the two most dominant species in northern China (Ma et al., 2006; Guo et al., 2011). *A. gossypii* is an important cotton pest, which causes severe damage to crops, leading to economic losses, whereas *M. sacchari* is one of the most important pests on sorghum (Wu and Guo, 2005; Guo et al., 2011). The ladybird *P. japonica* preys upon a variety of crop pests in northern China, predominantly aphids and, thus, serves as an excellent biological control agent (Gao et al., 2010). Aphid availability and quality affect the fecundity and survival of *P. japonica* (Tang et al., 2013). Previous studies showed that sorghum was a source of ladybirds in cotton and, thus, incorporation of sorghum on farms growing cotton has the potential to enhance the biocontrol of cotton aphids on cotton in the field (Tillman and Cottrell, 2012). However, the mechanisms affecting the transfer and dispersal of *P. japonica* between sorghum and cotton remain to be elucidated.

Thus, the current study investigated: (1) the effects of adjacent managed cotton–sorghum ecosystems on *P. japonica* and its aphid prey; (2) the effects of aphid species on the consumption by, and behavioral responses of, *P. japonica* fed *M. sacchari*, *A. gossypii*, and 50% *M. sacchari* + 50% *A. gossypii*; and (3) the effects of host plant type (sorghum; cotton; sorghum inhabited by *M. sacchari*; and cotton inhabited by *A. gossypii*) on the feeding and oviposition preferences of adult *P. japonica*.

Materials and methods

Field experimental design

The field experiment was performed in 2021 at the Experimental Base of Shandong Agricultural Academy of Science, Jinan, Shandong, China (116.99°E, 36.97°N). Experimental units were 10 m × 100 m sorghum plots (variety Lunuo 8) planted adjacent to 40 × 100 m cotton plots (variety Lumianyan 28). A mono cotton field was used as a control. In the cotton and sorghum fields, each plot was sampled by using a 5-point random sampling method, and the number of *A. gossypii*, *M. sacchari*, and *P. japonica* on three cotton and three sorghum plants per point was recorded on 16 August 2021.

P. japonica breeding

Individuals *P. japonica* were collected from the Experimental Base of Shandong Agricultural Academy of Science in the field. The offspring of these *P. japonica* were reared in an artificial chamber (PRX-500D-30, Haishu Safe Apparatus, Ningbo, China), which was maintained at 28°C and 75% relative humidity (RH) under a photoperiod of 14 h:10 h light:dark. Newly hatched *P. japonica* were fed on three different diets (*M. sacchari*, *A. gossypii*, or 50% *M. sacchari* + 50% *A. gossypii*).

Host plants

Plants of two crops, cotton (variety LuMianYan 28) and sorghum (variety Lunuo 8), were selected for this study. Plants were grown in a potting mixture of peat moss, vermiculite, organic fertilizer, and perlite (10:10:10:1 by volume) in a greenhouse under natural light at 28 ± 2°C. Plants were randomly placed in the artificial chamber and re-randomized once a week to avoid positioning effects. No fertilizer or pesticides were used throughout the experiment.

Feeding and oviposition preference of *P. japonica*

The feeding preference of *P. japonica* was evaluated on sorghum, cotton, sorghum inhabited by *M. sacchari*, and cotton inhabited by *A. gossypii*. *P. japonica* individuals were collected directly from fields located in the Experimental Base, Shandong Agricultural Academy of Science. The experiment was conducted in a covered square cage (2.0 × 2.0 × 2.0 m). Twelve plants (three sorghum plants, three cotton plants, three sorghum plants inhabited by *M. sacchari*, and three cotton plants inhabited by *A. gossypii*) were placed in a random order at an equal distance from the center point to form a circle. Twenty adults *P. japonica* were placed on the center point within a replicate. The positions of the adult beetle were checked and recorded daily at 2-h intervals from 05:00 h to 21:00 h for 3 days.

The oviposition preference of *P. japonica* was assessed following the same method as described above for the feeding preference. *P. japonica* fed on *M. sacchari*, *A. gossypii*, and 50% *M. sacchari* + 50% *A. gossypii,* respectively. Five mated and ovipositing adult females (10 days old) were released in the center of square cover cage. The number of eggs laid on each plant was counted after 3 days to determine the oviposition preference.

Prey biomass consumption

The prey biomass consumed by *P. japonica* was determined using no-choice and free choice tests. A 24-h-starved adult female *P. japonica* (10 days old) that had previously been fed one of three different diets (*M. sacchari*, *A. gossypii*, or 50% *M. sacchari* + 50% *A. gossypii*) was provided with third-instar larvae of *M. sacchari* and *A. gossypii*. In the no-choice test, *P. japonica* was provided with 100 *M. sacchari* or *A. gossypii* larvae. In the free choice test, *P. japonica* was provided with 50 *M. sacchari* and 50 *A. gossypii* larvae. After 24 h, the number of unconsumed aphids was counted. The biomass consumption of *P. japonica* was then calculated based on the weight of 100 aphids and feeding ratio.

Y-tube experiments

A Y-tube olfactometer was used to investigate the behavioral responses of *P. japonica* adults that had fed on one of five diets (*M. sacchari*, *A. gossypii*, or 50% *M. sacchari* + 50% *A. gossypii*, fed on *M. sacchari* then fed on *A. gossypii* for 1 day and fed on *A. gossypii* then fed on *M. sacchari* for 1 day) to: (1) intact sorghum vs. intact cotton; (2) sorghum bearing *M. sacchari* vs. cotton bearing *A. gossypii*; and (3) *M. sacchari* vs. *A. gossypii*. For the treatments of different plants, plant was placed in a glass enclosure which connected to the ends of arms with five centimeters rubber tube. For the treatment of *M. sacchari* vs. *A. gossypii*, aphids were placed on the end of the arms.

The behavioral responses of *P. japonica* were determined in a 40 mm-diameter × 36 cm-long glass Y-tube olfactometer with a 60° inside angle. The flow rate was 4.8 L/min (equal to 3.8 m/min inside the tube) in each Y-tube arm. A single *P. japonica* was placed in the olfactometer for 10 min. A "no choice" outcome was recorded when the adults remained inactive during the test period. A "first choice" outcome was recorded when the adults moved >25 cm into either arm (visually assessed by a line marked on each arm). Each experimental pair was repeated with at least adult 80 *P. japonica*.

Statistical analysis

Two-way factorial ANOVA (SPSS 13.0, SPSS Inc., Chicago, IL, USA) was used to analyze the feeding preference and prey biomass consumption of adult *P. japonica*. One-way ANOVA was used to analyze the effect of adjacent crop management on the population numbers of *M. sacchari*, *A. gossypii*, and *P. japonica* in the field. Differences among means were determined using Tukey's test at $P < 0.05$. X^2 tests were used to analyze the adult *P. japonica* feeding and oviposition preferences and to examine the significance of differences in the choosing behaviors of *P. japonica* in the olfactometer test.

Results

Effect of adjacent crop management on the numbers of *M. sacchari*, *A. gossypii,* and *P. japonica* in the field

The number of *M. sacchari* on sorghum was significantly higher than the number of *A. gossypii* on adjacent cotton (89.68%; $F = 21.32$, $P < 0.001$; Figure 1A). The same was found for *A. gossypii* populations on mono cotton compared with the number on adjacent cotton (67.05%; $F = 35.90$, $P < 0.001$; Figure 1B). Similarly, the number of *P. japonica* per 100 sorghum plants was significantly higher than on adjacent cotton (84.73%; $F = 209.05$, $P < 0.001$; Figure 1C), as was the number of *P. japonica* per 100 adjacent cotton plants compared with mono cotton ($F = 18.48$, $P < 0.001$; Figure 1D).

Feeding preference

Host plant type significantly influenced the feeding preference of adult *P. japonica*, whereas time of day and host plant type × time of day did not (Table 1). *P. japonica* preferred sorghum to cotton, and with a significantly higher feeding preference for both types of host plant bearing aphids compared with host plants without aphids (Figure 2).

Y-tube experiments

P. japonica fed *M. sacchari* showed a significant preference for the odor of sorghum compared with cotton ($P < 0.01$; Figure 3A). However, there was no difference in preference for host plant odor between the other four treatment groups (i.e., *P. japonica* fed 50% *M. sacchari* + 50% *A. gossypii*, *A. gossypii* + *M. sacchari* for 1 day, or *A. gossypii*, *M. sacchari* + *A. gossypii* for 1 day) (Figure 3A).

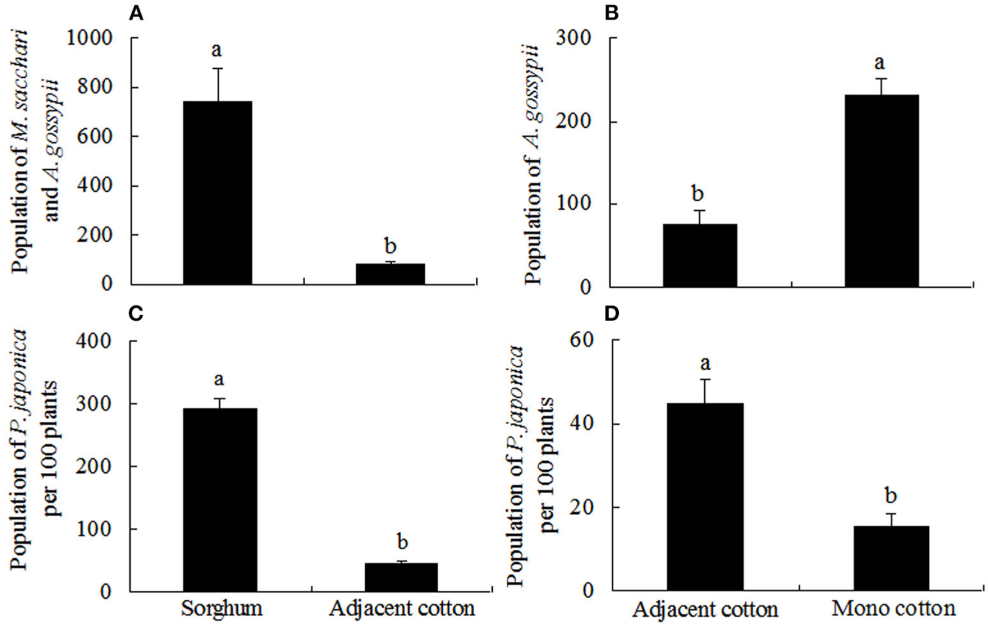

FIGURE 1
Effect of adjacent crop management on the numbers of *M. Sacchari*, *A. Gossypii* and *P. Japonica* in the field. **(A)** Population of *Melanaphis sacchari* on sorghum and *Aphis gossypii* on adjacent cotton. **(B)** Population of *A. gossypii* on adjacent cotton and mono cotton. **(C)** Population of *P. japonica* per 100 plants of sorghum and adjacent cotton. **(D)** Population of *P. japonica* per 100 plants on adjacent cotton and mono cotton. Different lowercase letters indicate significant differences among different crops (Tukey's test: $P < 0.05$).

TABLE 1 ANOVA of the effects of host plant type and time of day on the feeding preference of *Propylaea japonica*.

Source	df	*F*	*P*
Host plant type	3	269.223	<0.001
Time of day	5	0.026	1
Host plant type × time of day	15	0.974	0.488

P. japonica fed *M. sacchari* showed a significant preference for the odor of sorghum bearing *M. sacchari* compared with cotton bearing *A. gossypii* ($P < 0.05$; Figure 3B). However, there was no difference in preference for sorghum bearing *M. sacchari* vs. cotton bearing *A. gossypii* between the other four treatment groups (see above) (Figure 3B).

P. japonica fed *M. sacchari* significantly preferred *M. sacchari* to *A. gossypii* ($P < 0.001$; Figure 3C). However, there was no difference in preference for *M. sacchari* vs. *A. gossypii* in any of the other four treatment groups (see above) (Figure 3C).

Prey biomass consumption

Aphid species significantly influenced the biomass consumed by *P. japonica* in the no-choice and free choice tests (Table 2).

In the no-choice test, *P. japonica* adults fed *M. sacchari* ($F = 5.12$, $P < 0.05$), *A. gossypii* ($F = 4.72$, $P < 0.05$), and 50% *M. sacchari* + 50% *A. gossypii* ($F = 6.50$, $P < 0.05$) consumed significantly more *M. sacchari* compared with *A. gossypii* (by 25.74, 21.02, and 24.07%, respectively) (Figure 4A). However, there was no significant difference in the biomass of *M. sacchari* or *A. gossypii* consumed by *P. japonica* adults fed on above three treatments (Figure 4A).

In the free choice test, *P. japonica* adults fed *A. gossypii* ($F = 5.61$, $P < 0.05$) and 50% *M. sacchari* + 50% *A. gossypii* ($F = 26.27$, $P < 0.001$) consumed significantly more *M. sacchari* compared with *A. gossypii* (30.83 and 45.68%, respectively) (Figure 4B). However, there was no significant difference in the biomass of *M. sacchari* or *A. gossypii* consumed by *P. japonica* adults fed on above three treatments (Figure 4B).

Oviposition preference

P. japonica fed *M. sacchari* significantly preferred to lay their eggs on cotton compared with sorghum, and on sorghum bearing *M. sacchari* rather than sorghum alone ($X^2 = 7.630$, $P < 0.05$; Figure 5). *P. japonica* fed *A. gossypii* significantly preferred to lay their eggs on sorghum bearing *M. sacchari* compared with cotton bearing *A. gossypii*, and on sorghum bearing *M. sacchari* compared with sorghum alone ($X^2 = 5.678$, $P < 0.05$; Figure 5). *P. japonica* fed 50% *M. sacchari* + 50% *A. gossypii* significantly preferred to lay their eggs on host plants infested with aphids regardless of the aphid species compared with host plants only (cotton and sorghum) ($X^2 = 10.020$, $P < 0.05$; Figure 5).

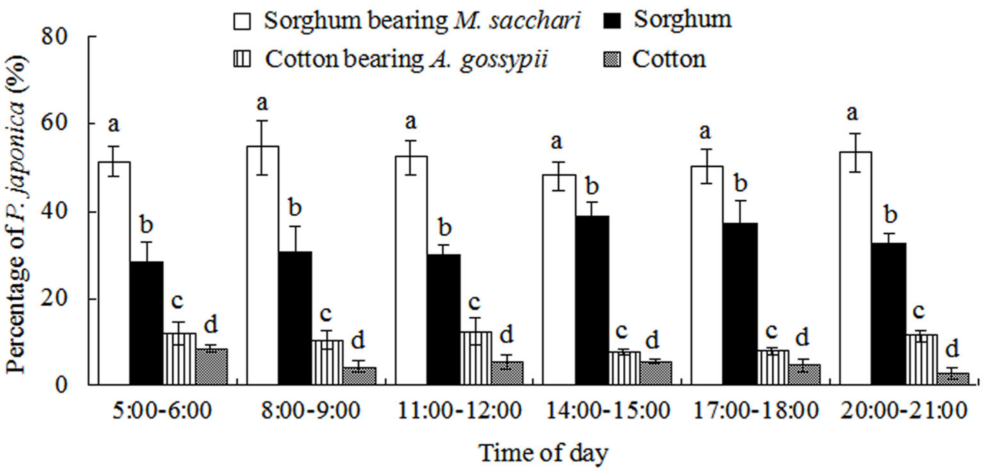

FIGURE 2
Effects of host plant type on the feeding preference of adult *Propylaea japonica*. Different lowercase letters indicate significant differences between host plant type treatments at a set time (X^2 test, $P < 0.05$).

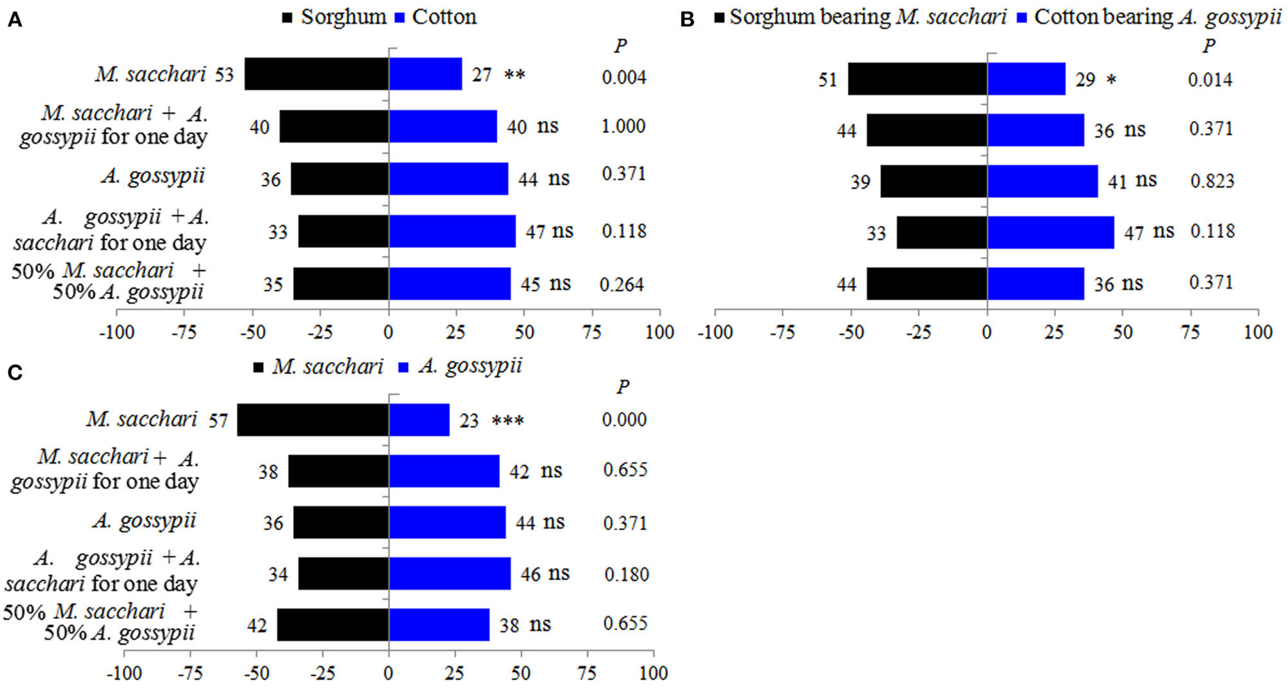

FIGURE 3
Effect of aphid species on the behavioral responses of *Propylaea japonica*, originally fed different diets (*M. sacchari*, *A. gossypii*, 50% *M. sacchari* + 50% *A. gossypii*, fed on *M. sacchari* then fed on *A. gossypii* for 1 day, or fed on *A. gossypii* then fed on *M. sacchari* for 1 day), to sorghum and cotton **(A)**, sorghum with *M. sacchari* and cotton with *A. gossypii* **(B)**, and *M. sacchari* and *A. gossypii* **(C)**. The X^2 test was used to analyze differences between the numbers of *P. japonica* in each arm of the Y-tube (**P* < 0.05; ***P* < 0.01; ****P* < 0.001; ns, non-significant).

Discussion

Researchers have evaluated the role of crop diversity in improving the impact of biological control, which enhances natural enemies and reduces pests (Rusch et al., 2016). High crop species richness suppresses pest populations by increasing the number of natural enemies (Sheng et al., 2017). There is a growing body of evidence suggesting that adjacent habitats positively affect pest regulation by natural enemies compared with monoculture systems (Bianchi et al., 2010). Large numbers of natural enemy taxa that move to adjacent crops provide a biological pest control service (Macfadyen and Muller, 2013). For example, alfalfa grown adjacent to wheat fields significantly increased the abundance of predators, including *Hippodamia variegata* and *Chrysopa sinica*, and decreased the densities of *Macrosiphum avenae* and *Schizaphis graminum*, which are dominant cereal aphid species in wheat fields

(Zhao et al., 2013). In the current study, the number of *M. sacchari* on sorghum was significantly higher than of *A. gossypii* on adjacent cotton, whereas *P. japonica* populations were significantly higher on sorghum than on adjacent cotton, suggesting that the predator population increased with the increasing pest population on the host crop. In addition, *A. gossypii* populations were significantly smaller and *P. japonica* populations were significantly larger in adjacent cotton fields than in monoculture cotton fields. These results were consistent with previous studies of cotton grown adjacent to sorghum (Tillman and Cottrell, 2012). This suggests sorghum is an ideal crop for the conservation of predators that subsequently disperse to adjacent cotton fields and help control the aphid population.

The effects of a host plant on the palatability and suitability of the prey for a predator are well-known (Ugine et al., 2021). Prey preference and prey suitability are important for determining predator behavior, such as feeding and habitat selection (Weber et al., 2006). Published data indicate that induced volatiles attract natural enemies to an infested plant (Tan and Liu, 2014). For example, *Harmonia axyridis* females showed a significant preference for aphid-infested marigolds because of the plant volatiles induced by aphid feeding (Zhang et al., 2022). In the current study, *P. japonica* showed a significantly higher feeding preference for host plants bearing aphids compared with host plants alone. This might be because aphid-infested host plants, such as sorghum and cotton, release significantly higher amounts of volatiles compared with host plants without aphids, thus attracting higher numbers of natural enemies. Our results also showed that *P. japonica* preferred sorghum to cotton, which might be because sorghum is a C4 plant, whereas cotton is a C3 plant. Thus, crops grown adjacent to C3 (cotton) or C4 (sorghum) plants provide ideal systems for studying the transfer and dispersal of natural enemies.

TABLE 2 ANOVA of the effects of *P. japonica* treatment (fed on different diets) and aphid species on the aphid biomass consumed by *Propylaea japonica*.

Different treatment	Factor	*F*	*P*
No choice test	*P. japonica* treatment	1.774	0.178
	Aphid species	16.045	<0.001
	P. japonica treatment × aphid species	0.037	0.963
Free choice test	*P. japonica* treatment	1.126	0.332
	Aphid species	28.361	<0.001
	P. japonica treatment × aphid species	1.74	0.185

Differential biomass consumption is indicative of aphid palatability to ladybugs (Mishra, 2005). Previous studies showed *M. sacchari* is an optimal food source for *P. japonica* among five species of aphids (Liu et al., 2013). The current results showed that *P. japonica* adults consumed significantly more *M. sacchari* compared with *A. gossypii*. This suggests that *P. japonica* prefers to consume *M. sacchari*, which could explain the increased *P. japonica* populations found in sorghum crops grown adjacent to cotton in the field. In our study, *P. japonica* fed *M. sacchari* also showed a significant preference for the odor of sorghum, sorghum bearing *M. sacchari*, and *M. sacchari* alone. After being fed *A. gossypii* for 1 day, these preferences disappeared. This suggests that, as *M. sacchari* populations decrease in the field, *P. japonica* would move to feed on *A. gossypii*, which could lead to a change in preference of *P. japonica* for *M. sacchari*, resulting in the transfer and dispersal of *P. japonica* in adjacent managed cotton–sorghum ecosystems.

The type of plant can also affect its suitability as a oviposition site for predators, such as ladybugs, and subsequently affect their reproduction (Mirhosseini et al., 2015). Host plants can have a dramatic effect on the survival of coccinellid eggs, with *Coleomegilla maculata* being shown to preferentially lay eggs on aphid-infested plants (Michaud and Jyoti, 2007). Female *Propylea*

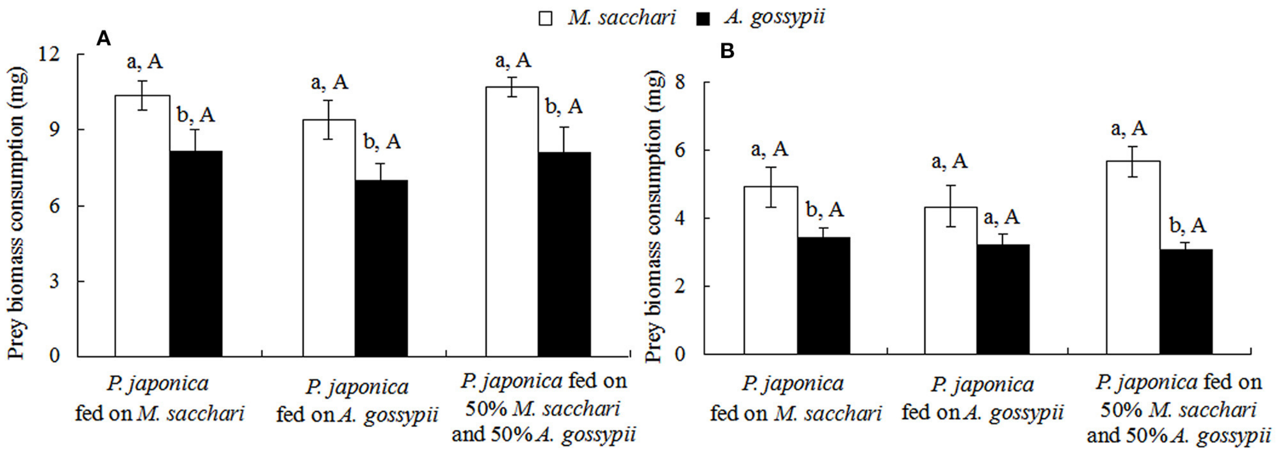

FIGURE 4
Effects of aphid species on the prey biomass consumed by adult *Propylaea japonica* fed different aphid-based diets (*M. sacchari*, *A. gossypii*, and 50% *M. sacchari* + 50% *A. gossypii*) in the no-choice test **(A)** and free-choice test **(B)**. Different lowercase letters indicate significant differences between aphid species within a *P. japonica* treatment, and different uppercase letters indicate significant differences between *P. japonica* treatments involving different aphid species (Tukey's test: $P < 0.05$).

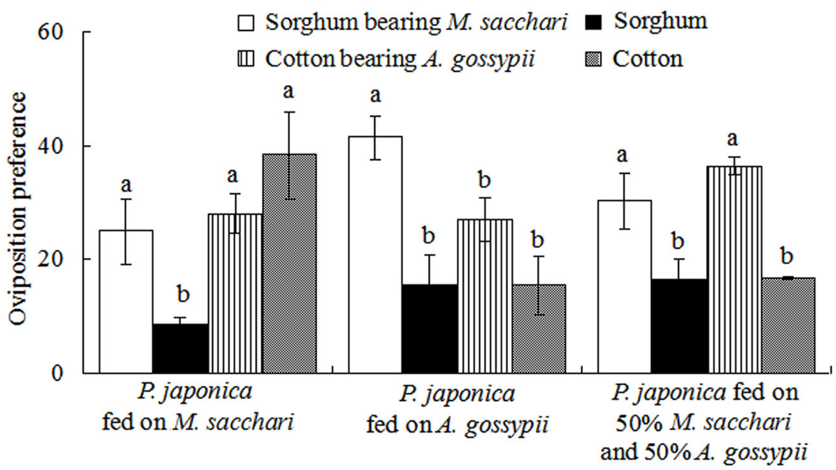

FIGURE 5
Effect of host plant on the oviposition preference of adult *Propylaea japonica* originally fed different aphid-based diets (*M. sacchari*, *A. gossypii*, and 50% *M. sacchari* + 50% *A. gossypii*). Different lowercase letters indicate significant differences between the type of host plant treatment within a *P. japonica* treatment (X^2 test: $P < 0.05$).

dissecta laid numerous eggs on plants with a high aphid density and fewer eggs on plants with a low aphid density (Omkar, 2004). In addition to coccinellids, oviposition preference of hoverflies varies in response to both the presence of aphids as well as their aphid (Amiri-Jami et al., 2016). In the current study, *P. japonica* significantly preferred to lay their eggs on aphid-infested cotton and sorghum, a result consistent with previous studies, presumably because the aphids are a food source for the larvae once they've hatched. It was also found that *P. japonica* fed *M. sacchari* preferred to lay eggs on cotton, whereas those fed *A. gossypii* preferred to lay eggs on sorghum. This suggests that oviposition behavior can be exploited to expand the habitat of ladybugs, an ecological adaptation of predatory natural enemies in the farmland ecosystems.

Conclusions

Our results indicate that an adjacent cropping system of cotton and sorghum can result in significantly higher *P. japonica* populations, leading to decreased aphid abundance compared with monocultures. *P. japonica* preferred to feed and lay eggs on aphid-infested plants over host plants without aphids, and also prefer to oviposit on other host plants. These results suggest that the habitat of natural enemies can be expanded by influencing their feeding and oviposition preferences to achieve pest control in adjacent cropping systems. Thus, increasing crop diversity, which provides favorable conditions for agriculture based on ecological principles, can contribute to the development of sustainable agroecosystems.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

HC and XM conceived, designed, and performed the experiments. LL, YS, WG, SL, and YY contributed reagents, materials, and analysis tools. HC analyzed the data and wrote the paper. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Amiri-Jami, A. R., Sadeghi, H., Gilbert, F., Moravvej, G., and Asoodeh, A. (2016). Oviposition preference of aphidophagous hoverflies toward oviposition site quality: the presence of intra-and interspecific competitor, glucosinolate content, and prey species. *J. Asia-Pac. Entomol.* 19, 275–280. doi: 10.1016/j.aspen.2016.02.002

Banihashemi, A. S., Seraj, A. A., Yarahmadi, F., and Rajabpour, A. (2017). Effect of host plants on predation, prey preference and switching behaviour of *Orius albidipennis* on *Bemisia tabaci* and *Tetranychus turkestani*. *Int. J. Trop. Insect Sc.* 37, 176–182. doi: 10.1017/S1742758416000229

Bianchi, F. J. J. A., Schellhorn, N. A., Buckley, Y. M., and Possincham, H. P. (2010). Spatial variability in ecosystem services: simple rules for predator-mediated pest suppression. *Ecol. Appl.* 20, 2332–2333. doi: 10.1890/09-1278.1

Cotes, B., Rännbäck, L. M., Björkman, M., Norli, H. R., Meyling, N. V., Rämert, B., et al. (2015). Habitat selection of a parasitoid mediated by volatiles informing on host and intraguild predator densities. *Oecologia* 179, 151–162. doi: 10.1007/s00442-015-3326-2

Figueroa, C. C., Fuentes-Contreras, E., Molina-Montenegro, M. A., and Ramírez, C. C. (2018). Biological and genetic features of introduced aphid populations in agroecosystems. *Curr. Opin. Insect Sci.* 26, 63–68. doi: 10.1016/j.cois.2018.01.004

Gao, F., Jifon, J., Liu, X. H., and Ge, F. (2010). An energy budget approach for evaluating the biocontrol potential of cotton aphid (*Aphis gossypii*) by the ladybeetle *Propylaea japonica*. *Entomol. Exp. Appl.* 136, 72–79. doi: 10.1111/j.1570-7458.2010.01005.x

Greenstone, M. H., Tillman, P. G., and Hu, J. S. (2014). Predation of the newly invasive pest *Megacopta cribraria* (Hemiptera: Plataspidae) in soybean habitats adjacent to cotton by a complex of predators. *J. Econ. Entomol.* 107, 947–954. doi: 10.1603/EC13356

Guo, C., Cui, W., Feng, X., Zhao, J., and Lu, G. (2011). Sorghum insect problems and management. *J. Integr. Plant Biol.* 53, 178–192. doi: 10.1111/j.1744-7909.2010.01019.x

Hodek, I., and Honek, A. (2009). Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. *Biol. Control* 51, 232–243. doi: 10.1016/j.biocontrol.2009.05.018

Liu, Y., Li, L. H., Men, X. Y., Yu, Y., Zhang, A. S., Li, L. L., et al. (2013). Developmentand fecundity of *Propylea japonica* (Thunberg) fed on different aphids. *Chinese J. Biol. Control* 29, 626–631. doi: 10.16409/j.cnki.2095-039x.2013.04.022

Ma, X. M., Liu, X. X., Zhang, Q. W., Zhao, J. Z., Cai, Q. N., Ma, Y. A., et al. (2006). Assessment of cotton aphids, *Aphis gossypii*, and their natural enemies on aphid-resistant and aphid-susceptible wheat varieties in a wheat–cotton relay intercropping system. *Entomol. Exp. Appl.* 121, 235–241. doi: 10.1111/j.1570-8703.2006.00484.x

Macfadyen, S., and Muller, W. (2013). Edges in agricultural landscapes: species interactions and movement of natural enemies. *PLoS ONE* 8, e59659. doi: 10.1371/journal.pone.0059659

Meehan, T. D., Werling, B. P., Landis, D. A., and Gratton, C. (2011). Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad. Sci. U. S. A.* 108, 11500–11505. doi: 10.1073/pnas.1100751108

Men, X. Y., Ge, F., Yardim, E., and Parajulee, M. (2004). Evaluation of winter wheat as a potential relay crop for enhancing biological control of cotton aphids. *Biocontrol* 49, 701–714. doi: 10.1007/s10526-004-5278-z

Michaud, J. P., and Jyoti, J. L. (2007). Repellency of conspecific and heterospecific larval residues to *Hippodamia convergens* (Coleoptera: Coccinellidae) ovipositing on sorghum plants. *Eur. J. Entomol.* 104, 399–405. doi: 10.14411/eje.2007.059

Mirhosseini, M. A., Hosseini, M. R., and Jalali, M. A. (2015). Effects of diet on development and reproductive fitness of two predatory coccinellids (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 112, 446. doi: 10.14411/eje.2015.051

Mishra, G. (2005). Preference-performance of a generalist predatory ladybird: a laboratory study. *Biol. Control* 34, 187–195. doi: 10.1016/j.biocontrol.2005.05.007

Mkenda, P. A., Ndakidemi, P. A., Stevenson, P. C., Arnold, S. E., Belmain, S. R., Chidege, M., et al. (2019). Field margin vegetation in tropical African bean systems harbours diverse natural enemies for biological pest control in adjacent crops. *Sustainability* 11, 6399. doi: 10.3390/su11226399

Obrycki, J. J., Harwood, J. D., Kring, T. J., and ONeil, R. J. (2009). Aphidophagy by Coccinellidae: application of biological control in agroecosystems. *Biol. Control* 51, 244–254. doi: 10.1016/j.biocontrol.2009.05.009

Oliver, T. H., Timms, J. E. L., Taylor, A., and Leather, S. R. (2006). Oviposition responses to patch quality in the larch ladybird *Aphidecta obliterata* (Coleoptera: Coccinellidae): effects of aphid density, and con-and heterospecific tracks. *B. Entomol. Res.* 96, 25–34. doi: 10.1079/BER2005395

Omkar, and Pervez, A. (2004). Functional and numerical responses of *Propylea dissecta* (Col., Coccinellidae). *J. Appl. Entomol.* 128, 140–146. doi: 10.1111/j.1439-0418.2004.00824.x

Paredes, D., Cayuela, L., and Campos, M. (2013). Synergistic effects of ground cover and adjacent vegetation on natural enemies of olive insect pests. *Agr. Ecosyst. Environ.* 173, 72–80. doi: 10.1016/j.agee.2013.04.016

Pettersson, J., Ninkovic, V. E. L. E. M. I. R., Glinwood, R. O. B. E. R. T., Birkett, M. A., and Pickett, J. A. (2005). Foraging in a complex environment-semiochemicals support searching behaviour of the seven spot ladybird. *Eur. J. Entomol.* 102, 365. doi: 10.14411/eje.2005.053

Putra, N. S., Yasuda, H., and Sato, S. (2009). Oviposition preference of two hoverfly species in response to risk of intraguild predation. *Appl. Entomol. Zool.* 44, 29–36. doi: 10.1303/aez.2009.29

Rondoni, G., Ielo, F., Ricci, C., and Conti, E. (2014). Intraguild predation responses in two aphidophagous coccinellids identify differences among juvenile stages and aphid densities. *Insects* 5, 974–983. doi: 10.3390/insects5040974

Rusch, A., Chaplin-Kramer, R., Gardiner, M. M., Hawro, V., Holland, J. M., Landis, D. A., et al. (2016). Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agric. Ecosyst. Environ.* 221, 198–204. doi: 10.1016/j.agee.2016.01.039

Sasso, R., Iodice, L., Woodcock, C. M., Pickett, J. A., and Guerrieri, E. (2009). Electrophysiological and behavioural responses of *Aphidius ervi* (Hymenoptera: Braconidae) to tomato plant volatiles. *Chemoecology* 19, 195–201. doi: 10.1007/s00049-009-0023-9

Scheid, B. E., Thies, C., and Tscharntke, T. (2011). Enhancing rape pollen beetle parasitism within sown flower fields along a landscape complexity gradient. *Agric. For. Entomol.* 13, 173–179. doi: 10.1111/j.1461-9563.2010.00516.x

Seagraves, M. P. (2009). Lady beetle oviposition behavior in response to the trophic environment. *Biol. Control* 51, 313–322. doi: 10.1016/j.biocontrol.2009.05.015

Sheng, J., Gao, F., Andile, M., Wang, L., Sandhu, H. S., Ouyang, F., et al. (2017). Crop diversity and land simplification effects on pest damage in Northern China. *Ann. Entomol. Soc. Am.* 110, 91–96. doi: 10.1093/aesa/saw058

Simpson, M., Gurr, G. M., Simmons, A. T., Wratten, S. D., James, D. G., Leeson, G., et al. (2011). Attract and reward: combining chemical ecology and habitat manipulation to enhance biological control in field crops. *J. Appl. Ecol.* 48, 580–590. doi: 10.1111/j.1365-2664.2010.01946.x

Tan, X. L., and Liu, T. X. (2014). Aphid-induced plant volatiles affect the attractiveness of tomato plants to *Bemisia tabaci* and associated natural enemies. *Entomol. Exp. Appl.* 151, 259–269. doi: 10.1111/eea.12190

Tang, L., Wu, J., Ali, S., and Ren, S. (2013). The influence of different aphid prey species on the biology and life table parameters of *Propylaea japonica*. *Biocontrol Sci. Techn.* 23, 624–636. doi: 10.1080/09583157.2013.780580

Thies, C., Roschewitz, I., and Tscharntke, T. (2005). The landscape context of cereal aphid-parasitoid interactions. *Proc. R. Soc. B Biol. Sci.* 272, 203–210. doi: 10.1098/rspb.2004.2902

Tillman, P. G., and Cottrell, T. E. (2012). Incorporating a sorghum habitat for enhancing lady beetles (Coleoptera: Coccinellidae) in cotton. *Psyche* 2012, 1–6. doi: 10.1155/2012/150418

Ugine, T. A., Gill, H. K., Hernandez, N., Grebenok, R. J., Behmer, S. T., and Losey, J. E. (2021). Predator performance and fitness is dictated by herbivore prey type plus indirect effects of their host plant. *J. Chem. Ecol.* 47, 877–888. doi: 10.1007/s10886-021-01251-4

Wang, P. Y., Su, J. W., Ouyang, F., and Ge, F. (2015). Orientation behavior of *Propylaea japonica* toward visual and olfactory cues from its prey-host plant combination. *Entomol. Exp. Appl.* 155, 162–166. doi: 10.1111/eea.12295

Weber, D. C., Rowley, D. L., Greenstone, M. H., and Athanas, M. M. (2006). Prey preference and host suitability of the predatory and parasitoid carabid beetle, *Lebia grandis*, for several species of *Leptinotarsa* beetles. *J. Insect Sci.* 6, 1536–2442. doi: 10.1673/1536-2442(2006)61:PPAHSO2.0.CO;2

Wu, K. M., and Guo, Y. Y. (2005). The evolution of cotton pest management practices in China. *Annu. Rev. Entomol.* 50, 31–52. doi: 10.1146/annurev.ento.50.071803.130349

Yao, F. L., Lin, S., Wang, L. X., Mei, W. J., Monticelli, L. S., Zheng, Y., et al. (2021). Oviposition preference and adult performance of the whitefly predator *Serangium japonicum* (Coleoptera: Coccinellidae): effect of leaf microstructure associated with ladybeetle attachment ability. *Pest Manag. Sci.* 77, 113–125. doi: 10.1002/ps.6042

Zhang, L., Qin, Z., Zhao, X., Huang, X., and Shi, W. (2022). Effects of aphid-induced semiochemicals from cover plants on *Harmonia axyridis* (Coleoptera: Coccinellidae). *Pest Manag. Sci.* 78, 3305–3313. doi: 10.1002/ps.6956

Zhang, S. Z., Li, J. J., Shan, H. W., Zhang, F., and Liu, T. X. (2012). Influence of five aphid species on development and reproduction of *Propylaea japonica* (Coleoptera: Coccinellidae). *Biol. Control* 62, 135–139. doi: 10.1016/j.biocontrol.2012.05.002

Zhao, Z. H., Hui, C., He, D. H., and Ge, F. (2013). Effects of position within wheat field and adjacent habitats on the density and diversity of cereal aphids and their natural enemies. *Biocontrol* 58, 765–776. doi: 10.1007/s10526-013-9536-9