Effect of Cotton Cultivar on Development and Reproduction of *Aphis gossypii* (Homoptera: Aphididae) and Its Predator *Propylaea japonica* (Coleoptera: Coccinellidae)

LI DU, FENG GE, SANRONG ZHU, and MEGHA N. PARAJULEE[1]

State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, China

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ABSTRACT The effects of three cotton cultivars with low ('ZMZ13'), medium ('HZ401'), and high ('M9101') gossypol contents on the development, reproduction, and survival of *Aphis gossypii* Glover and its predator *Propylaea japonica* (Thunberg) were investigated. Developmental duration and immature survivorship did not vary between aphids on the three cultivars, whereas *A. gossypii* feeding on M9101 (high gossypol cultivar) displayed significantly shorter adult longevity and lower fecundity than aphids fed on 'ZMS13' and 'HZ401'. Free fatty acid content in cotton aphids reared on 'M9101' was greater than in those reared on 'HZ401' and 'ZMS13'. No significant differences in survival and lifetime fecundity of *P. japonica* were observed between *P. japonica* fed cotton aphids reared on the three different cultivars. *P. japonica* fed aphids from 'M9101' showed a significantly shorter developmental period and greater adult weight than those fed aphids from the other two cultivars. The decreased larval developmental duration and increased adult weight of *P. japonica* fed cotton aphids reared on the high gossypol-containing cultivar might have been caused by the high fatty acid content of the prey aphids. Our results indicate that high gossypol in host cotton had an antibiotic effect on *A. gossypii* and showed a positive effect on growth and development of *P. japonica* at the third trophic level. This suggests compatibility between one form of host plant resistance and biological control by predators. The allelochemical contents should be taken into account in integrated pest management for their effects on both herbivores and entomophagous insects.

KEY WORDS *Aphis gossypii*, *Propylaea japonica*, allelochemicals, gossypol, tritrophic interactions

Plant resistance and biological control are two of the core strategies of integrated pest management (IPM) (Wilson and Huffaker 1976). Plant resistance may enhance, reduce, or have no effect on biological control by natural enemies (Hodek 1956, Isenhour et al. 1989, Wang 1991, Malcolm 1992, Giles et al. 2002). Understanding the tritrophic interactions among plant resistance, arthropod pests, and natural enemies is an important step toward harmonizing the pest suppression effect of plant resistance and the effect of natural enemies in effective pest management.

Secondary plant substances or allelochemicals play a major role in plant resistance to pests. Previous research has indicated that allelochemicals could affect population dynamics and nutritional suitability of the herbivores, with potential influence on development, survivorship, and body weight of predators at the third trophic level of the food chain (Hodek 1956, Rice and Wilde 1989, Malcolm 1992, Hauge et al. 1998, Francis et al. 2000). Gossypol, a phenolic sesquiterpenoid aldehyde, is an important allelochemical occurring in glanded cotton varieties. This allelochemical exhibits antibiosis to many pests, including the cotton aphid, *Aphis gossypii* Glover, and contributes to the host plant resistance of glanded cotton varieties (Zhou 1991). Several researchers have investigated the relationship between gossypol level and aphid population abundance (Bottger et al. 1964, Meng and Li 1999). However, the impact of gossypol on the life history characteristics of cotton aphids is not clearly understood.

The effect of gossypol on arthropods at the third trophic level has been evaluated for several parasitoids. In some studies it was suggested that parasitoids could be adversely affected when attacking herbivores fed on plants with a high level of gossypol (Gunasena et al. 1989), whereas other studies showed mixed influences of gossypol on parasitoids (Wang 1991). We are unaware of any research on the effect of gossypol on arthropod predators, particularly in relation to cotton aphids feeding at the second trophic level.

The cotton aphid is an important pest of cotton in China. The lady beetle *Propylaea japonica* (Thunberg) is an effective predator of cotton aphids in

[1] Corresponding author. Texas Agricultural Experiment Station, Rt. 3, Box 219, Lubbock, TX 79403.

Chinese cotton agroecosystems (Ge and Ding 1996). Cotton cultivars with a high gossypol level are anecdotally considered resistant to cotton aphids and have been adopted by cotton growers solely for the purpose of cotton aphid management. However, no research information is available on the tritrophic interaction between high-gossypol, aphid-resistant cotton cultivars, *A. gossypii,* and the aphid predator *P. japonica.*

Because there is a lack of information on how gossypol affects the population dynamics of cotton aphids and their predators, we designed a study to 1) quantify the effects of gossypol level in cotton plants on development, reproduction, and survivorship of *A. gossypii* and its predator *P. japonica;* and 2) develop a functional relationship between this form of host plant resistance and predator effectiveness. Tritrophic interactions involving cotton, cotton aphids, and lady beetles are discussed.

Materials and Methods

Plant and Insect Cultures. Three commercial cotton cultivars, 'ZMS13', 'HZ401', and 'M9101', with gossypol content of 0.0601, 0.4403, and 1.116%, respectively, were grown in 10-cm-diameter plastic pots in separate environmental chambers maintained at 26 ± 1°C, ≈70% RH, and a photoperiod of 14:10 (L:D) h. The cotton cultivars and the percentage of gossypol content of the cultivars were supplied by the Institute of Cotton, Chinese Academy of Sciences, China. Experimental plants were grown individually in each pot, with equal amount of fertilizer solution applied to each plant at a 3-d interval.

Both *A. gossypii* and its predator *P. japonica* were collected from cotton fields and reared in the laboratory for at least two generations on the cotton 'SM3' (gossypol content of 0.1176%) to develop insect colonies for the experiment. *A. gossypii* and *P. japonica* from the experimental colonies were transferred separately to three cotton cultivars ('ZMS13', 'HZ401', and 'M9101') for culture in three separate environmental chambers. Aphids were kept at least 2 wk on host plants before being used to feed *P. japonica.* All experiments were conducted in environmental chambers maintained at 26 ± 4°C and 60–80% RH under a photoperiod of 14:10 (L:D) h. Uniformity in the size of *A. gossypii* and *P. japonica* individuals used in the study was maintained by visually inspecting each test insect before deployment.

Aphid Life History Parameters. For each cotton cultivar, 60 newly born aphid nymphs (<4 h old) were confined singly in glass tubes (3 cm in diameter by 7 cm in depth) with fresh cotton leaves (2–4-leaf developmental stage) and reared through their entire life cycle. Individual aphids were monitored, and molting and mortality data were recorded at an 8-h interval. When reproduction began, the number of nymphs produced per aphid was recorded. Nymphs were removed every 8 h until the adult aphid died. Cotton leaves were replaced daily throughout the study. Several cohorts of aphids from each cultivar were collected and frozen for chemical analysis. Free fatty acid content was measured for each aphid cohorts by using a one-step extraction colorimetric assay (Wei 1979).

Lady Beetle Life History Parameters. Fifty newly eclosed larvae of *P. japonica* were individually reared on each cultivar in glass tubes (4 cm in diameter by 8 cm in depth) and supplied with an excess of aphids of mixed third and fourth instars. Molting and mortality were monitored every 12 h. Aphids were added and cotton leaves were replaced daily. Upon adult emergence, adult beetles were sexed and each newly eclosed individual adult male and female were weighed using a Cahn 20 automatic electrobalance (Cahn, St. Louis, MO). One male and one female lady beetle reared using aphids from the same cultivar treatment were put together in a glass arena (6 cm in diameter by 8 cm in depth) to allow mating and egg production. Numbers of eggs laid per arena were recorded, and eggs were removed every 12 h until the female died. In addition, ≈20 newly eclosed larvae were reared to adulthood on each cultivar and frozen for chemical analyses. Free fatty acid was measured for each cohort of lady beetles by using the one-step extraction colorimetric assay used for cotton aphids (Wei 1979).

Data Analysis. Data on life history parameters (e.g., stage-specific developmental duration, mortality, and reproduction) of both *A. gossypii* and *P. japonica* were subjected to a one-way analysis of variance (ANOVA), with cultivar as a source of variability. When a significant treatment effect was observed ($P < 0.05$), means were separated using the least significant difference (LSD) method (SPSS for Windows, version 10.0; SPSS Inc., Chicago, IL).

Results

Biological Parameters of *A. gossypii.* Stage-specific developmental durations of *A. gossypii* ($F = 0.112$; df = 2, 95; $P = 0.894$) (Table 1) and rates of immature survivorship (Table 2) did not vary between aphids reared on the three cultivars. However, gossypol content had a significant effect on adult aphid longevity ($F = 11.647$; df = 2, 96; $P < 0.0001$). The cotton cultivar with the highest level of gossypol ('M9101') resulted in significantly lower aphid adult longevity compared with the cultivars containing medium ('HZ401') or low ('ZMS13') levels of gossypol (Table 1).

Cotton aphid fecundity was significantly influenced by the level of gossypol content ($F = 9.010$, df = 2, 96; $P < 0.0001$). The lifetime fecundity of cotton aphids on 'M9101' was less than one-half that of aphids reared on cultivars with medium or low gossypol contents (Table 1). Analyses of free fatty acids in cotton aphids reared on three cultivars showed that the fatty acid content in aphids increased significantly as gossypol content on host plants increased (Fig. 1).

Biological Parameters of *P. japonica.* Developmental duration of immature stages of *P. japonica* varied when *P. japonica* was fed *A. gossypii* reared on the different cultivars (Table 3). Larval developmental

Table 1. Developmental time and lifetime fecundity (mean ± SE) of *A. gossypii* reared on different cotton cultivars

Cultivar	Nymphal developmental time (h)					Adult life span (h)	Lifetime fecundity
	1st instar	2nd instar	3rd instar	4th instar	Nymphal stage		
ZMS13	32.3a (1.3)	32.5a (1.3)	31.5a (1.5)	32.9a (1.2)	129.2a (2.5)	259.2a (24.0)	25.9a (3.0)
HZ401	29.3a (1.5)	31.3a (1.9)	35.5a (1.7)	34.8a (9.7)	130.8a (3.5)	271.2a (28.8)	24.5a (2.6)
M9101	31.7a (1.4)	30.5a (1.3)	34.1a (9.9)	34.4a (1.8)	130.9a (2.7)	124.8b (14.4)	11.3b (2.2)

Means in a column followed by different letters are significantly different ($P < 0.05$; LSD test for the comparison of means).

Table 2. Percentage (mean ± SE) of survivorship of *A. gossypii* reared on different cotton cultivars

Cultivar	1st instar	2nd instar	3rd instar	4th instar	Nymphal stage
ZMS13	67.7 ± 8.3a	78.4 ± 7.6a	91.1 ± 3.8a	91.6 ± 3.2a	51.1 ± 6.3a
HZ401	77.1 ± 5.3a	65.6 ± 7.5a	85.4 ± 5.8a	86.3 ± 4.6a	50.9 ± 11.9a
M9101	73.1 ± 4.8a	70.0 ± 1.9a	84.2 ± 3.2a	87.5 ± 8.0a	46.0 ± 7.7a

Means in a column followed by different letters are significantly different ($P < 0.05$; LSD test for the comparison of means).

times (total larval duration) of *P. japonica* fed aphids reared on 'M9101' were significantly shorter than those of beetles fed aphids reared on the other two cultivars ($F = 10.463$; df = 2, 94; $P < 0.001$). However, the survivorship of different immature stages of *P. japonica* fed aphids reared on the three cultivars did not vary (larvae: $F = 1.000$, df = 8, $P = 0.422$; pupae: $F = 1.000$, df = 8, $P = 0.422$; larvae + pupae: $F = 0.602$, df = 8, $P = 0.578$) (Table 4). Adult life span of *P. japonica* fed aphids reared on the three cultivars was also not significantly different ($F = 0.232$, df = 2, 23; $P = 0.795$) (Table 4). Lifetime fecundity of *P. japonica* did not vary significantly when fed cotton aphids from different cultivars ($F = 0.791$; df = 2, 23; $P = 0.466$). However, the adult weight of *P. japonica* fed aphids reared on 'M9101' (4.33 ± 0.26 mg) was significantly greater than beetles fed aphids reared on 'HZ401' (3.38 ± 0.28 mg) or 'ZMS13' (3.36 ± 0.13 mg) ($F = 6.81$; df = 2, 29; $P = 0.004$). Significantly more fatty acid was found in *P. japonica* fed cotton aphids reared on 'M9101' compared with those reared on 'HZ401' or 'ZMS13' (Fig. 2).

Discussion

Cotton gossypol content has been considered one of the key resistance indices of cotton aphids. The significance of gossypol content on *A. gossypii* biology was not known until Bottger et al. (1964) observed that aphid infestations increased in cotton cultivars lacking the gossypol gland. In a more detailed study, Meng and Li (1999) evaluated 10 cotton cultivars and found that cotton gossypol level and aphid infestation were negatively correlated. In our study, no significant difference on developmental duration or survival of immature *A. gossypii* was observed between aphids reared on the three cotton cultivars; however, *A. gossypii* reared on 'M9101' (high gossypol cultivar) had significantly shorter adult longevity and lower fecundity than those reared on the two cultivars with lower gossypol levels. Our results demonstrate that higher levels of gossypol adversely affect the longevity and reproduction of *A. gossypii.* Moreover, a host cotton cultivar with high gossypol may enhance free fatty acid content of cotton aphids. The free fatty acid

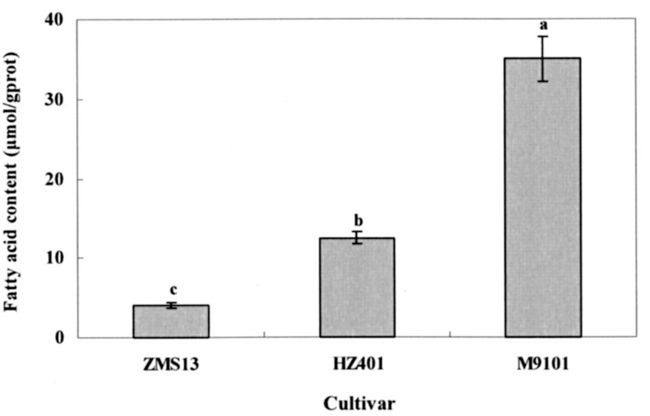

Fig. 1. Fatty acid content (micromoles per gram of protein) of *A. gossypii* reared on different cotton cultivars.

Table 3. Life history parameters (mean ± SE) of lady beetle *P. japonica* fed with *A. gossypii* from different cotton cultivars

Cultivar	Larval developmental duration (h)					Pupal duration (h)	Adult life span (d)	Lifetime fecundity
	1st instar	2nd instar	3rd instar	4th instar	Total			
ZMS13	37.3b (1.3)	22.9a (1.3)	26.5b (1.2)	78.0a (2.7)	164.7a (2.9)	60.0a (1.4)	51.3a (8.9)	259.8a (45.3)
HZ401	39.1ab (1.1)	24.0a (1.0)	36.4a (2.2)	61.8b (3.1)	161.3a (2.1)	59.6a (0.9)	51.8a (6.7)	344.9a (67.6)
M9101	41.4a (1.8)	25.2a (1.4)	26.8b (1.4)	55.2b (2.0)	148.6b (2.7)	59.6a (0.9)	45.4a (5.2)	305.3a (16.1)

Means in a column followed by different letters are significantly different ($P < 0.05$; LSD test for the comparison of means).

Table 4. Percentage (mean ± SE) of survivorship of lady beetle *P. japonica* fed with *A. gossypii* from different cotton cultivars

Cultivar	1st instar	2nd instar	3rd instar	4th instar	Pupal stage	Preimaginal stage
ZMS13	100.0a (0.00)	100.0a (0.00)	100.0a (0.00)	100.0a (0.00)	100.0a (0.00)	100.0a (0.00)
HZ401	100.0a (0.00)	100.0a (0.00)	100.0a (0.00)	100.0a (0.00)	97.0a (3.00)	97.0a (3.00)
M9101	97.0a (3.00)	96.7a (3.30)	100.0a (0.00)	100.0a (0.00)	100.0a (0.00)	93.9a (6.10)

Means in a column followed by same letters are not significantly different ($P > 0.05$; LSD test for the comparison of means.

content in cotton aphids reared on the higher gossypol cotton ('M9101') was 7.6 and 1.8 times higher than that of aphids reared on 'HZ401' and 'ZMS13', respectively. Because aphids store energy in the form of fatty acids, which are in turn used as an energy source by aphidophagous predators (Bashir 1973, Kaplan et al. 1986), the observed differences in fatty acid content among aphids reared on the three cultivar treatments suggest substantial differences in nutritional value of these aphid prey for potential predators.

Cotton cultivar with varying gossypol content influenced the biological parameters of predator *P. japonica* at the third trophic level. Significantly shorter larval duration and greater adult weight were observed in *P. japonica* fed aphids reared on the high gossypol 'M9101' than those fed aphids reared on the two cultivars with lower gossypol contents. The decreased larval developmental time and increased adult weight of *P. japonica* fed cotton aphids reared on cotton with high gossypol content indicate a favorable effect of high gossypol on the development and growth of *P. japonica* feeding on aphids infesting the high gossypol cotton plants. This may enhance the biological control potential of the predator. Previous studies indicate that differences in fatty acid content of aphids, as influenced by host plant, may affect survival, growth, and development of aphidophages (Bashir 1973, Kaplan et al. 1986, Giles et al. 2001). Giles et al. (2001) evaluated the nutritional interaction among host plants (alfalfa and faba bean); pea aphid, *Acyrthosiphon pisum* (Harris); and coccinellids *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* Guerin-Meneville. They found that at low prey level, coccinellids supplied with pea aphids reared on alfalfa (which stored more fatty acids than aphids reared on faba bean) had faster developmental rates and larger body sizes than coccinellids supplied with pea aphids reared on faba bean. However, the developmental rates and body sizes were similar at higher prey levels. The convergence of developmental rates and body sizes for coccinellids at high prey level indicates that the differences in prey nutritional value are quantitative. In our experiment, the decreased larval developmental time and increased adult weight for *P. japonica* supplied with cotton aphids from the high gossypol cultivar may have resulted primarily

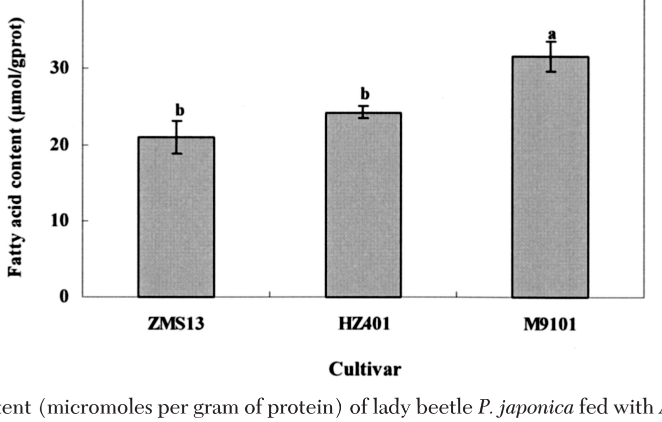

Fig. 2. Fatty acid content (micromoles per gram of protein) of lady beetle *P. japonica* fed with *A. gossypii* from different cotton cultivars.

from the high fatty acid content of the cotton aphids that had been reared on high gossypol cotton. These significant differences in larval developmental time and adult weight for *P. japonica* occurred at excess prey level, indicating qualitative difference in the nutritional value of cotton aphids reared on the different cotton cultivars.

The relationships among resistant host plants, herbivores, and natural enemies have been investigated from several agroecosystems (Hodek 1956, Starks et al. 1972, Rice and Wilde 1989, Malcolm 1992, Hauge et al. 1998, Giles et al. 2001). Host plant resistance may enhance, reduce, or have no effect on biological control by natural enemies (Hodek 1956, Isenhour et al. 1989, Wang 1991, Malcolm 1992, Giles et al. 2002). Van Emden (1995) reported that antibiotic allelochemicals in the host plant could adversely affect growth and development of natural enemies through the passage of plant toxins up the trophic pyramid, causing an incompatibility between host plant resistance and biological control. However, Isenhour et al. (1989) found that fall armyworm, *Spodoptera frugiperda* (J. E. Smith), that fed on fresh foliage of a resistant corn genotype suffered significantly higher rates of predation by adult *Orius insidiosus* Say than did armyworm fed a susceptible corn genotype, indicating that in this case plant resistance enhanced biological control. Our results clearly showed that high gossypol in host plant had antibiosis to *A. gossypii* and had positive effect on growth and development of *P. japonica* feeding on these aphids, suggesting compatibility between plant resistance and biological control. These results provide a valuable advance in the understanding of the biological effect of allelochemicals in an aphid host plant on the development and reproduction of one of its important predators. Furthermore, the tritrophic interactions between cotton, aphids, and lady beetles indicate that differences in the nutritional value of cotton aphids, as influenced by gossypol content in host plant, may affect growth and development of *P. japonica.* Knowledge of the impact of allelochemicals such as gossypol is critical to understanding the interaction among the tritrophic systems of host plants, herbivores, and natural enemies. Future field studies should be undertaken to investigate the potential interactive effect between aphid resistance expressed in high gossypol cotton cultivars and biological control by Coccinellidae on *A. gossypii* and other important cotton pests.

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