Effects of Gibberellic Acid on Biological Parameters of the Larval Endoparasitoid *Apanteles galleriae* (Hymenoptera: Braconidae)

FEVZİ UÇKAN,[1,2] AYLİN TÜVEN,[3] AYLİN ER,[3] AND EKREM ERGİN[1]

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ABSTRACT The impact of the plant growth regulator gibberellic acid (GA_3) on parasitoid development and reproduction was examined using the endoparasitoid *Apanteles galleriae* Wilkinson (Hymenoptera: Braconidae). The effects of GA_3 were assessed by rearing *A. galleriae* on hosts fed the growth regulator and then measuring a several life history traits: developmental time from egg to adult, adult longevity, body sizes, fecundity, and sex ratios. GA_3 treatment yielded dose-dependent changes in adult longevity and duration of development. For example, at GA_3 doses >10 ppm, the life span of both male and female adult wasps decreased by 19–23 d in comparison with parasitoids that developed on GA_3-free hosts. Likewise, the length of development from egg to adult emergence significantly increased when *A. galleriae* developed on hosts fed the growth regulator at doses >200 ppm. In contrast, GA_3 did not seem to alter adult body sizes, sex ratios, or fecundity, with the exception that F_2 progeny production decreased by >40% at high concentrations (≥200 ppm). The potential significance of plant growth regulators on natural enemies used in integrated pest management programs is discussed.

KEY WORDS *Apanteles galleriae*, gibberellic acid, toxicity, parasitoid, risk assessment

Plant growth regulators (PGRs) are commonly used in agriculture as chemicals that regulate plant development through the induction of inhibitory and stimulatory pathways. Recently, there has been a great attempt in the use of PGRs as successful chemosterilants against insect pests (McDonald et al. 1988, Silva et al. 2003, Paulson et al. 2005). Despite that PGRs are a valuable tool used in agriculture and pest management systems, some drawbacks can exist, such as their side effects on natural enemies of certain pest insects. Some of these chemicals also are found in plants as endogenous hormones, which are likely included in diets of phytophagous insects (Nakajima and Kawazu 1980, Visscher 1983). Therefore, it is conceivable that natural enemies of pests may be affected by PGRs in their trophic interaction with pests, by direct contact, or both.

Gibberellins are a large family of tetracyclic diterpenoid PGRs that are associated with many plant growth and developmental processes (Sun and Gubler 2004). Gibberellic acid (GA_3), a type of gibberellins, plays important roles in many cellular processes by promoting stem elongation, overcoming dormancy in seed and buds, and involvement in parthenocarpic fruit development, flowering, mobilization of food reserves in grass seed germination, juvenility, and sex expression (Salisbury and Ross 1992). The influence of GA_3 treatment on development, survival, longevity, and reproductive potential of insects has recently been studied in several insect pests (Kaur and Rup 2002, 2003a; Harikesh and Bhattacharya 2003). Although PGRs are used for pest control on a variety of crops, very little information exists on their physiological and biochemical effects toward beneficial insects.

Hymenopteran parasitoids are far more susceptible to environmental pollutants than their lepidopteran hosts (Büyükgüzel 2006, Uçkan et al. 2007). *Apanteles galleriae* Wilkinson (Hymenoptera: Braconidae) is a koinobiont, solitary, larval endoparasitoid of several lepidopterans, including the pyralid wax moths *Galleria mellonella* L., *Achoria grisella* F. (Lepidoptera: Pyralidae), *Achoria innotata* Walker, and *Vitula edmandsae* (Packard) (Shimamori 1987, Watanabe 1987, Whitfield et al. 2001). Larvae of these host species are serious pests in beehives because they feed on combs, wax, and honey. Because some host species of this parasitoid also feed on plants during larval stages, the accumulation of environmental pollutants and transmission of these compounds to their parasitoids is likely to occur (Sak et al. 2006, Ergin et al. 2007). Therefore, *A. galleriae* adults feeding on honey, fruit nectar, and host larvae also may be exposed to GA_3 broadly used in agriculture either by direct contact or as a secondary consumer via their hosts. Here, we assessed GA_3-related changes in egg-to-adult developmental time, longevity, size, number of offspring produced, and sex ratio of *A. galleriae*.

[1] Department of Biology, Faculty of Science-Literature, Kocaeli University, İzmit–Kocaeli, 41300, Turkey.
[2] Corresponding author, e-mail: fevzi.uckan@kou.edu.tr.
[3] Department of Biology, Faculty of Science-Literature, Balıkesir University, Balıkesir, 10145, Turkey.

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Materials and Methods

Insects. Laboratory colonies of the host *A. grisella* and the parasitoid *A. galleriae* were established from adults that were collected from several beehives located in the vicinity of Rize, Turkey. Larvae and adults of *A. grisella* were reared on honeycomb at 25 ± 1°C, 60 ± 5% RH, and a photoperiod of 12:12 (L:D) h. Early instars of the host were exposed to *A. galleriae* adults for parasitoid rearing. Adults of *A. galleriae* were fed a 30% (wt:vol) honey solution and kept at the same rearing conditions with the host species. The methods used to establish and maintain successive cultures of both host and parasitoid species were described by Uçkan and Gülel (2000) and Uçkan and Ergin (2003).

Chemical Application. Various doses (2, 5, 10, 50, 100, 200, 500, and 1,000 ppm) of GA_3 (Agro-Gibb 20 g/liter, Agrosan, Bursa, Turkey)-treated distilled water were incorporated into the synthetic diet of host larvae, which includes crumbled honeycomb, bran, honey, glycerin, and distilled water as described by Bronskill (1961) and modified by Sak et al. (2006).

Bioassays. An individual mating pair of the host, *A. grisella* (1- to 2-d-old at 25°C) was placed in 250-ml jars containing 1 g of honeycomb to provide a mating and oviposition substrate. The adults were removed from the jars on the fifth day. Early instars (1–2 d old at 25°C) of the host species (25–57 larvae) were exposed to 5 g of host diet treated with the selected doses of GA_3 in each jar. Host larvae were then exposed to an individual mating pair of adult parasitoids (1–2 d old at 25°C) in jars 2 d later. Parasitoid adults were fed a 30% (wt:vol) honey solution soaked in cotton balls and removed from the jars after 5 d. Parasitized host larvae were maintained at 25 ± 1°C, 60 ± 5% RH, and a photoperiod of 12:12 (L:D) h. Hosts that were parasitized as described above but reared on a diet that included distilled water without GA_3 served as the control.

All jars were observed daily until the emergence of adult parasitoids. The time required for completion of parasitoid development from egg deposition to adult eclosion was recorded, as was the total number of progeny per female and sex ratio of each parasitoid's clutch. To determine the impact of GA_3 on the F_2 generation, randomly selected newly emerged adult parasitoids from the treated hosts were paired and allowed to parasitize hosts that were fed a diet free of gibberellic acid. Parasitized hosts were then maintained as described above. Each experiment was replicated five times with specimens chosen randomly from different populations at different times.

Longevity of newly emerged adult female and male wasps from each treatment was assessed by placing an individual mating pair ($n = 15$ pairs) into an 80-ml cup containing a cotton ball saturated in a 30% (wt:vol) honey solution. Cups were covered with a mesh cloth, and they were held under the environmental conditions mentioned above for the stock cultures. Food was replenished at 2-d intervals. Parasitoids were observed at 24-h intervals until all parasitoids had died. Adult body sizes (length) of GA_3-treated wasps and controls were determined by randomly selecting 15 females and 15 males from each treatment and then measuring length from head to the tip of the abdomen by using an Olympus S2X 12 stereodissecting microscope equipped with a calibrated eyepiece micrometer.

Statistics. GA_3-induced variations in egg-to-adult developmental time, longevity, size, number of viable offspring developing to adulthood, sex ratio, and number of F_2 progeny were inferred using one-way analysis of variance (ANOVA). Subsequently, means were separated using Tukey's honestly significant difference (HSD) test (SPSS Inc. 1999). An arcsine square-root transformation was performed on percentage values before analysis (Sokal and Rohlf 1995). Results were considered statistically significant when $P < 0.05$.

Table 1. GA_3-related changes in egg-to-adult developmental time of *A. galleriae*

GA_3 (ppm)	Egg-to-adult developmental time (d)	
	Range	Mean[a] ± SE[b]
Control	31–37	34.6 ± 1.47a
2	30–42	36.0 ± 2.59a
5	37–41	39.2 ± 0.66a
10	39–40	39.2 ± 0.20a
50	28–39	30.6 ± 2.11a
100	28–36	33.6 ± 1.44a
200	28–40	33.6 ± 2.40a
500	45–48	47.4 ± 0.60b
1,000	45–49	47.0 ± 0.84b

[a] Average of five replicates at each treatment.
[b] Values followed by the same letter are not significantly different from each other (Tukey's HSD test; $P > 0.05$).

Results

Adult emergence time of *A. galleriae* reared on *A. grisella* larvae exposed to different doses of GA_3 was only significantly longer than those parasitoids that developed on untreated hosts at the 500 and 1000 ppm (Table 1; $F = 13.949$; df = 8, 36; $P = 0.000$). Wasp development from egg to adult at 25°C normally requires 31–37 d. However, parasitoids reared on hosts exposed to GA_3 concentrations >200 ppm required

Table 2. GA_3-related changes in adult longevity of *A. galleriae*

GA_3 (ppm)	Adult longevity (d)			
	Male		Female	
	Range	Mean[a] ± SE[b]	Range	Mean[a] ± SE[b]
Control	45–55	49.14 ± 1.95a	42–53	48.17 ± 1.88a
2	39–60	48.15 ± 4.27a	36–49	40.39 ± 2.35a
5	42–58	48.07 ± 3.06a	36–49	42.09 ± 2.60a
10	56–62	59.36 ± 1.27a	42–47	43.72 ± 0.92a
50	29–35	31.58 ± 1.35b	24–33	25.62 ± 1.75b
100	24–36	31.09 ± 2.17b	15–29	23.20 ± 2.63b
200	21–37	29.80 ± 2.71b	19–31	26.52 ± 2.75b
500	29–35	31.80 ± 1.32b	25–26	25.80 ± 0.20b
1,000	22–34	26.80 ± 1.96b	24–26	24.60 ± 0.40b

[a] Average of 15 individuals at each treatment.
[b] Values followed by the same letter are not significantly different from each other (Tukey's HSD test; $P > 0.05$).

Table 3. GA_3-related changes in adult size of *A. galleriae*

GA_3 (ppm)	Adult size (mm)			
	Male		Female	
	Range	Mean[a] ± SE[b]	Range	Mean[a] ± SE[b]
Control	2.40–2.90	2.63 ± 0.15a	2.75–3.00	2.85 ± 0.08a
2	2.30–2.90	2.65 ± 0.18a	2.60–2.95	2.80 ± 0.10a
5	2.20–2.90	2.60 ± 0.21a	2.64–2.95	2.81 ± 0.09a
10	2.30–2.80	2.50 ± 0.15a	2.85–3.00	2.93 ± 0.04a
50	2.40–3.20	2.70 ± 0.25a	2.80–3.20	3.03 ± 0.12a
100	2.30–2.80	2.53 ± 0.15a	2.50–3.20	2.83 ± 0.20a
200	2.40–2.75	2.55 ± 0.10a	2.60–3.10	2.80 ± 0.15a
500	2.60–2.90	2.73 ± 0.09a	2.60–3.10	2.83 ± 0.15a
1000	2.40–2.95	2.73 ± 0.17a	2.50–2.75	2.61 ± 0.07a

[a] Average of 15 individuals at each treatment.
[b] Values followed by the same letter are not significantly different from each other (Tukey's HSD test; $P > 0.05$).

14–18 d longer than controls to complete development (Table 1).

The mean longevity of GA_3-treated adults decreased significantly at doses between 50–1000 ppm compared with lower concentrations tested and wasps reared on untreated hosts (Table 2; for males: $F = 23.230$; df = 8, 126; $P = 0.000$ and for females: $F = 26.042$; df = 8, 126; $P = 0.000$). The longevity of males and females treated with GA_3 decreased by >30% at doses >10 ppm compared with controls (Table 2). Adult body sizes of male and female wasps did not differ significantly from those parasitoids reared on untreated hosts (Table 3; for males: $F = 0.268$; df = 8, 126; $P = 0.968$ and for females: $F = 0.849$; df = 8, 126; $P = 0.574$).

The total number of progeny produced by a single parasitoid female throughout its adult life was, on average, 89.0 ± 7.76 when hosts were fed on a GA_3-free diet. GA_3 treatment did not considerably affect the number of offspring produced by *A. galleriae*, regardless of the dose tested (Table 4; $F = 1.52$; df = 8, 36; $P = 0.184$). The sex ratio of parasitoid progeny was male-biased and fluctuated among treatments. The ratio of females decreased considerably at 50, 100, and 200 ppm with respect to 5 ppm (Table 4; $F = 3.84$; df = 8, 36; $P = 0.002$). However, there were no significant differences in the sex ratio of progeny produced by wasps reared on GA_3-treated hosts with respect to the controls. By contrast, GA_3 treatment reduced the total number of wasp offspring produced in the F_2 for wasps reared on hosts exposed to the growth regulator at any concentrations >5 ppm (Table 5; $F = 7.118$; df = 8, 36; $P = 0.000$).

Discussion

Our results indicated that the overall time to adult eclosion of *A. galleriae* increased by 40% when wasps were reared on host larvae fed extremely high doses of gibberellic acid. Similarly, a prolongation in the immature developmental time after the application of GA_3 has been reported in *Spodoptera litura* F. (Lepidoptera: Noctuidae) and *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) (Harikesh and Bhattacharya 2003, Kaur and Rup 2003a). The authors reported growth- and developmental inhibitory effects on host species with a considerable decline in larval survival of *S. litura* beyond 200 ppm of GA_3 and 100% mortality in *B. cucurbitae* first instars at higher concentrations of 125, 625, and 3,125 μg/ml, respectively. Treatment with GA_3 also reduced the percentage of emergence and increased the percentage of abnormal *A. grisella* larvae, which may cause a decrease in the percentage of subsequent parasitization, as also was reported in other investigations with different host species and PGRs (Harikesh and Bhattacharya 2003, Kaur and Rup 2003a).

General stress responses in arthropods are known to be energetically demanding events and the organisms may redirect energy to repair mechanisms, and pathological effects may deplete energy reserves (Korsloot et al. 2004). It has been observed that larval glycogen content is reduced at higher doses of GA_3 treatment in *Zaprionus paravittiger* (Godbole & Vaidya) (Diptera: Drosophilidae) (Rup et al. 1998) and *B. cucurbitae* (Kaur and Rup 2003a, 2003b), with a corresponding decrease in total lipid and carbohydrate levels in the latter species. Similarly, the decrease in energy reserves of the host resulting from GA_3-induced stress may prolong the growth and development of the host, and subsequently also for feeding *A. galleriae* progeny dependent on the host energy stores. This stress-induced, trophic interaction repre-

Table 4. GA_3-related changes in number of offspring produced and sex ratio of *A. galleriae*

GA_3 (ppm)	No. offspring and sex ratio					
	Male		Female		Total no. of progeny (mean[a] ± SE)[b]	Female sex ratio (%)[b]
	Range	Mean[a] ± SE	Range	Mean[a] ± SE		
Control	52–74	63.20 ± 4.07	11–40	25.80 ± 6.01	89.00 ± 7.76a	27.70ab
2	23–81	51.60 ± 9.58	4–26	16.00 ± 3.72	67.60 ± 12.86a	22.66ab
5	37–75	51.60 ± 6.71	18–52	31.40 ± 5.74	83.00 ± 4.20a	38.02b
10	37–59	43.00 ± 4.10	15–22	16.80 ± 1.32	59.80 ± 5.42a	28.18ab
50	42–67	53.20 ± 5.74	5–18	11.60 ± 2.91	64.80 ± 8.59a	16.73a
100	34–102	57.60 ± 12.27	4–19	11.20 ± 2.52	68.80 ± 12.20a	17.69a
200	32–91	68.40 ± 9.99	10–17	13.40 ± 1.17	81.80 ± 10.95a	17.22a
500	41–56	50.20 ± 2.78	16–22	19.00 ± 1.34	69.20 ± 3.71a	27.46ab
1,000	32–47	41.20 ± 2.78	13–26	20.20 ± 2.99	61.40 ± 2.09a	32.78ab

[a] Average of five replicates at each treatment.
[b] Values followed by the same letter are not significantly different from each other (Tukey's HSD test; $P > 0.05$).

Table 5. GA_3-related changes in number of offspring produced in F_2 generation of *A. galleriae*

GA_3 (ppm)	Total no. of offspring in F_2 progeny	
	Range	Mean[a] ± SE[b]
Control	60–71	64.20 ± 1.88a
2	32–66	49.60 ± 6.33ab
5	21–59	48.00 ± 7.40ab
10	30–58	41.20 ± 5.24b
50	36–43	41.20 ± 1.32b
100	35–58	46.40 ± 5.14ab
200	32–41	37.40 ± 1.83bc
500	27–40	33.20 ± 2.92bc
1,000	18–27	22.80 ± 1.80c

[a] Average of five replicates at each treatment.
[b] Values followed by the same letter are not significantly different from each other (Tukey's HSD test; $P > 0.05$).

sents a potential threat to the survival of parasitoid species because adult eclosion might occur at an inconvenient time and in an unfavorable environmental condition. Consequently, growth regulatory compounds such as GA_3 are bound to play a vital role in the patterns of growth and development of associated phytophagous insects through endocrinal metabolic processes (Kaur and Rup 2002). Parasitoid larvae synchronizing development with its phytophagous host by making use of host hormones may in turn be affected by the changes in the hormonal milieu of the host and display a delay in developmental time.

Comparisons of the longevity of wasps after different GA_3 treatments showed that the disruptive effect was highest at doses between 50 and 1,000 ppm. GA_3 was also found to be highly toxic to both sexes of *A. galleriae.* The influence of GA_3 on longevity also has been observed in *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) and *Z. paravittiger* (Salama and El-Sharaby 1972, Rup and Kalia 1993, Kaur and Rup 2002). That GA_3 reduces the total lipid and carbohydrate levels in insects (Rup et al. 1998, Kaur and Rup 2003b) may be the reason for decreased longevity of wasps. It has been suggested previously that carbohydrates are necessary for a prolonged life span of *A. galleriae* adults (Uçkan and Ergin 2003). The decrease in the longevity of *A. galleriae* also may be attributed to the nonspecific toxicity of diet as amounts of GA_3 increases, resulting in a decline in diet quality and an interference of sufficient food supply from the host by parasitoid (Uçkan and Ergin 2002, Uçkan et al. 2007).

None of the GA_3 doses tested in our study affected the number of parasitoid offspring emerging from treated host larvae. Contrary to the present results, a decrease in the larval survival and adult emergence was reported when larvae of *S. litura* were fed with GA_3 in their diet (Harikesh and Bhattacharya 2003). Our observations may suggest that GA_3 does not have a lethal effect toward developing parasitoid larvae across trophic levels, in this case, via their hosts. Because GA_3 is a terpenoid compound like any of the juvenile hormones (JHs) (Visscher 1980, Kaur and Rup 2002), it is very likely that much of the ingested GA_3 may have been degraded or digested by similar esterases and hydrolases that target JHs and other terpenoids in the midgut of *A. grisella,* and any that was absorbed could have been modified or metabolized by an array of enzymes. The result would be either no effect by the growth regulator or only sublethal effects. It is clear that some GA_3 was absorbed and sequestered by the host as evidenced by the alterations in parasitoid longevity and developmental times. Additionally, the number of females produced declined considerably at doses between 50–200 ppm by comparison with other treatments. Likewise, a considerable decline in the number of wasps produced in the F_2 generation was observed, although the decline did not seem to be dose dependent. Such variability in parasitoid fecundity also was witnessed in the control groups during the F_1 and F_2 generations, and it may be partially linked to a seasonal variation in parasitoid longevity (Uçkan and Gülel 2000).

Studies with plant growth regulators also have shown deleterious effects on reproduction and fecundity in different insect species (Visscher 1980, Kaur and Rup 2002). The influence of GA_3 treatment on the fecundity of several lepidopteran and dipteran species has been hypothesized to be associated with interference in endocrine metabolic processes involved in reproduction because the chemical configuration of GA_3, a terpenoid compound, is similar to juvenile hormone (Visscher 1980, Kaur and Rup 2002). Büyükgüzel (2006) reported that effects on the endocrine system may prevent maturation of germ cells and inhibit deposition of vitellogenin in the eggs, leading to deformed embryos unable to break or digest the eggshell to hatch. The decline in the number of F_2 progeny of wasps in this study may be the result of disruptions in embryonic development in treated females, or malformations during oogenesis or spermatogenesis. Collectively, any of these could lead to a decrease in oviposition period and thus the number of eggs laid by females. However, this study did not address the total egg production of the wasps produced from each treatment; rather, only the number of surviving progeny was recorded. It is very possible that the death rate of the parasitoid eggs may be affected by the concentration of GA_3 in the host diet. It is also likely that the energy required for the production of eggs was channeled into the prolongation of younger stages, i.e., developmental period (Kaur and Rup 2002). Further studies are needed to uncover the influence of PGRs such as GA_3 on the biological parameters of other parasitoids in addition to *A. galleriae.*

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