Effects of Snowdrop Lectin on Mexican Rice Borer (Lepidoptera: Pyralidae) Life History Parameters

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ABSTRACT The effects of the snowdrop lectin, Galanthus nivalis agglutinin (GNA), delivered through an artificial diet, on growth, development, and life history parameters of the Mexican rice borer, *Eoreuma loftini* (Dyar), were evaluated in the laboratory. Incorporation of GNA at three treatment levels, 0.5, 1.0, and 2.0% of total dietary protein, in the larval diet significantly decreased larval survivorship and percentage of adults emerging relative to a control diet lacking GNA, whereas differences were not observed among the three treatment levels. Both larvae and pupae in the control were 8–25% larger than those in the GNA treatments, but differences were not observed between larvae in the GNA treatments. Furthermore, presence of GNA did not affect larval and pupal developmental periods, longevities, and fecundities compared with the control. Mexican rice borer life history parameters, such as net reproductive rate and intrinsic rate of increase, were substantially reduced by the presence of GNA in the diet, but differences were not evident among the three GNA treatment levels.

KEY WORDS host plant resistance, *Eoreuma loftini*, *Galanthus nivalis* agglutinin, life table parameters, *Galanthus nivalis* L.

SUGARCANE IS AN IMPORTANT cash crop in the lower Rio Grande Valley of Texas, where it contributes >10% of agricultural receipts (NASS 2002). In the 2001–2002 growing season, about18,200 ha of commercial sugarcane was harvested in the lower Rio Grande Valley, which yielded a total production of ≈765,100 tons of cane, making it the fourth largest source of domestic sugar in the United States. However, a number of constraints significantly compromise sugarcane production in the lower Rio Grande Valley, particularly water shortages and various pests and diseases. The Mexican rice borer, *Eoreuma loftini* Dyar (Lepidoptera: Pyralidae), has become the most significant sugarcane pest in the region (Legaspi et al. 1997) after its accidental introduction from Mexico in 1980 (Johnson 1984). The pest status of *E. loftini* has dramatically increased over the years, and currently its populations represent >95% of stalkborers recovered from sugarcane fields and cause boring damage to 20–30% of internodes. Meagher et al. (1994) estimated that yearly economic losses caused by this pest exceed $575 per ha, and Legaspi et al. (1997) reported that $10–$20 million are lost annually because of stalkborer damage in the lower Rio Grande Valley.

The Mexican rice borer remains the key sugarcane pest in the lower Rio Grande Valley despite a number of attempts to develop effective control measures (Browning and Melton 1987, Pfannenstiel and Meagher 1991, Meagher et al. 1994, Meagher et al. 1996, Legaspi et al. 1997, Sétamou et al. 2002). Accordingly, emphasis was recently placed on developing insect resistant transgenic sugarcane lines from elite varieties. Transgenic sugarcane expressing the snowdrop lectin, Galanthus nivalis agglutinin (GNA), was developed at the Texas Agricultural Experiment Station, Weslaco, by transferring a GNA-producing gene from the snowdrop lily (*Galanthus nivalis* L., Amaryllidaceae) to sugarcane line CP65–357 (Irvine and Mirkov 1997). GNA is a lectin that specifically binds α-D-mannose and is variably toxic to a number of insect species among Homoptera, Coleoptera, and Lepidoptera (Van Damme et al. 1998, Sétamou et al. 2002), while exhibiting low to nil mammalian toxicity (Van Damme et al. 1998). Sétamou et al. (2002) reported that incorporation of GNA transgenic sugarcane tissue in artificial diet at ≈0.5% of total dietary protein negatively affected a number of Mexican rice borer life history parameters and hypothesized that GNA at the level present in transgenic sugarcane tissue, 0.9%, would result in stronger effects. Thus, the current study was conducted to assess the dose–response of various Mexican rice borer life history

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parameters to GNA incorporated into an artificial diet. Evaluating the effects of different levels of GNA on Mexican rice borer life history parameters will improve our understanding of the mechanisms by which GNA-expressing sugarcane may contribute to managing populations of this key pest.

Materials and Methods

Mexican rice borer larvae used in the experiments originated from laboratory colonies maintained on artificial diet (Martinez et al. 1988). Feral individuals were regularly incorporated in these colonies to maintain colony vigor. Eggs laid on paper strips were incubated in glass jars at 25 ± 2°C under a 12:12 h (L:D) photoperiod regimen for 8–10 d until larval emergence.

Three diet treatment levels and a control diet were evaluated in this study. Diet treatments consisted of an artificial diet (Martinez et al. 1988) supplemented with different levels of highly purified (99%) GNA (Sigma, St. Louis, MO). The treatment levels used were 0.5, 1, and 2% GNA of total dietary protein and are hereafter referred to as low, medium, and high, respectively. The control diet consisted of the artificial diet regularly used for rearing Mexican rice borer in the laboratory (Martinez et al. 1988) without addition of GNA. Preliminary analyses following the method described by Bradford (1976) showed that total extractable protein averaged 0.30 μg/μl in the artificial diet. The amounts of GNA incorporated in the diet treatments were according to this average value. To account for extra protein in the form of GNA, the control and low and medium GNA treatments were adjusted by adding toasted, defatted soy flour (Nutrisoy flour; Midland, Decatur, IL), so that all treatments and the control had comparable levels of total dietary protein. Moreover, because of its heat sensitivity (Kaku and Goldstein 1989), GNA was added to the artificial diet only when the diet temperature fell below 40°C. The different diet treatments and control diet were dispensed in small plastic cups at a rate of ≈5 g per cup and allowed to cool to room temperature before use in experiments.

Two days after diet preparation, Western blot and immunostaining procedures were used to confirm that GNA had not denatured during preparation of the diet and was available for insect uptake. Diet treatments were homogenized in 1× SDS (sodium dodecyl sulphate) extraction buffer containing 63 mM Tris-HCl (pH 6.8), 2% SDS, 10% glycerol, and 5% β-mercaptoethanol. Proteins were separated using SDS-polyacrylamide gels comprising a 15% resolving gel and a 4.5% stacking gel. Fifty microliters of each sample extract was loaded within the gel lanes, and electrophoresis was run at 100 V for 2 h. The protein bands were transferred to a nitrocellulose membrane, which was blocked overnight to saturate nonspecific protein binding sites. The membrane was thereafter transferred in a primary and secondary antibody binding solution containing goat anti-rabbit immunoglobulin (IgG). The protein bands on the membrane were stained, air-dried at room temperature, and visualized.

Using a fine camel hair brush, we placed newly emerged Mexican rice borer larvae (0- to 24-h-old) individually in the small cups containing diet and covered them with waxed-paper lids. Sixty cups were assigned to each treatment. The cups were placed in trays, one tray per treatment, and kept in an incubator in which conditions were maintained at 30 ± 1°C, 70 ± 2% RH, and a 12:12 h photoperiod regimen, unless specified otherwise.

Larval survivorship, expressed as proportion living larvae relative to initial cohort size (60 larvae per treatment), was recorded weekly for 3 wk by examining each cup under a microscope. The weights of individual 3-wk-old larvae were recorded to the nearest 0.1 mg. Pupae were collected from cups daily after 3 wk, immediately weighed, and their gender was determined. Pupae were transferred individually to sterile plastic cups covered with a lid and incubated until adult emergence. The periods between eclosion from eggs and pupation and between pupation and adult emergence were scored in days as larval and pupal periods, respectively. Larval and pupal stage survivorship rates were calculated from the numbers of pupae formed relative to the initial numbers of larvae per treatment and the numbers of adults emerged relative to numbers of pupae formed per treatment, respectively. Adult emergence rates were computed from the numbers of emerging adults relative to initial cohort size. On emergence of adults, individual pairs (1♂ + 1♀) from each treatment were placed in clear plastic vials (9.5 cm high × 4.5 cm diameter) for mating and oviposition. The vials were maintained under conditions conducive to maximum fecundity and egg viability, 22 ± 2°C and 60 ± 5% RH (Rodríguez-del-Bosque et al. 1989), and adults were provided a food source in the form of cotton saturated with 50% honey solution (vol:vol). Three paper strips, each 1 cm wide and 5 cm long, were stapled together and placed in the vials as oviposition substrates. Adult longevity (days) and female fecundity (number of eggs laid) were recorded. Egg viability was estimated by placing five groups of 100 eggs per treatment in the incubator and scoring the number of eclosing larvae. Developmental times in days for each life stage (L) were computed as $L = n_i x_i / n_i$, where n_i is the number of individuals and x_i the time required to complete the developmental stage. Life table parameters, net reproductive rate (R_0), generation time (G), and intrinsic rate of increase (r_m), were computed for each of the treatment levels and the control using a jacknife program (Hulting et al. 1990). The "growth index," computed as the ratio between the mean percentage of adults emerged and the mean duration of the immature period (Sétamou et al. 1999) was determined for each of the treatment levels and the control.

The LIFETEST procedure of SAS (SAS Institute 1996) was used to test for homogeneity of the larval survivorship curves corresponding to the diet treatment levels and the control. In addition, one-way analysis of variance (ANOVA) was conducted to eval-

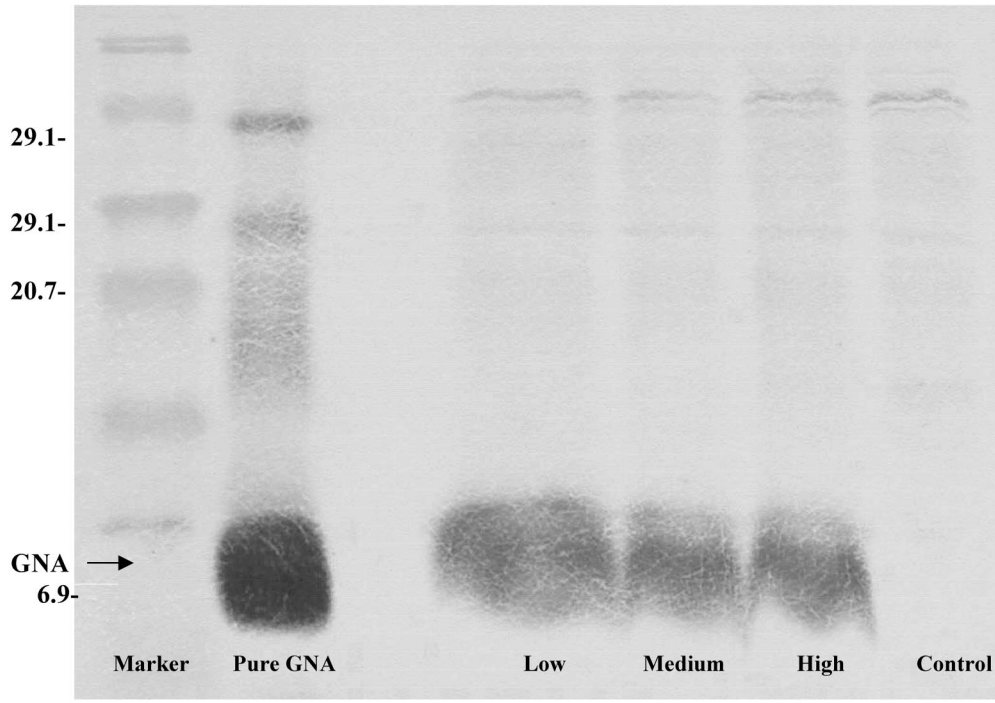

Fig. 1. Western blot analysis of artificial (control) diet and diets containing low, medium, or high levels of GNA offered to *E. loftini* (Dyar). C = control diet (without GNA); Low = 0.5% GNA of total dietary protein; Medium = 1.0% GNA; High = 2.0% GNA.

uate treatment effects on larval and pupal weights, percent pupation and adult emergence, larval and pupal periods, female fecundity, and egg viability using PROC GLM of SAS (SAS Institute 1996). Where significant differences were detected ($P < 0.05$), the Dunnett test was used to compare control versus diet treatment levels, and Student Newman-Keuls test was used to compare among diet treatment levels (Zar 1999). All percentages and proportions were arcsine$\sqrt{x}$-transformed before analysis. Mexican rice borer life table statistics from the various treatments were discriminated by comparing their confidence intervals. Sex ratios (=% ♂♂) were tested for conformity with a 0.5 sex ratio using the Wilcoxon χ^2 test of conformity, and the log-likelihood ratio test was used to test for homogeneity of sex ratios among diet treatment levels and the control (Zar 1999).

Results

Western blot analysis showed that GNA added to artificial diet was not denatured and was readily available for ingestion and uptake by Mexican rice borer larvae feeding on the diet (Fig. 1). Survivorship of Mexican rice borer larvae was significantly higher in the control compared with any of the treatment levels, but significant differences were not evident among the three treatment levels (Fig. 2). Similarly, larval survivorship was highest in the control, but was similar among the GNA treatment levels (Table 1). Likewise, adult emergence rates were highest in the control, but differences were not evident among the three treatment levels (Table 1). In contrast, pupal survivorship rates did not differ among treatment levels and control (Table 1).

Larvae in the control weighed consistently more (8–25% for males, 13–17% for females) than those in the GNA treatments (Table 2). Similarly, both male and female pupae in the control weighed significantly

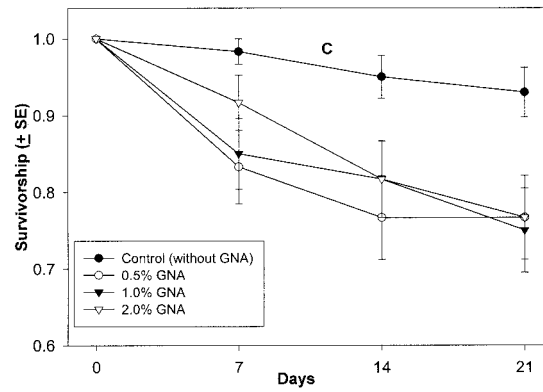

Fig. 2. Survivorship to 21 d of *E. loftini* (Dyar) larvae (±SE) reared on artificial (control) diet or diet containing low, medium, or high levels of GNA. Differences are significant between the control and each of the GNA treatment levels (Wilcoxon $\chi^2 = 8.40$, df = 3, $P = 0.033$), whereas they are not significant among the treatment levels (Wilcoxon $\chi^2 = 0.07$, df = 2, $P = 0.96$).

Table 1. Larval and pupal stage survivorship and adult emergence of *E. loftini* (Dyar) (all ± SE) on artificial (control) diet or diet containing low (0.5%), medium (1.0%), or high (2.0%) levels of GNA

Treatment	Larval survivorship	Pupal survivorship	Adult emergence
Control	91.7 ± 6.0A[a]	89.6 ± 6.1A	81.7 ± 4.4A
Low	75.0 ± 0.0Ba	75.6 ± 8.0Aa	56.7 ± 6.0Ba
Medium	68.3 ± 4.4Ba	82.3 ± 5.6Aa	56.7 ± 7.3Ba
High	71.7 ± 3.3Ba	78.6 ± 7.4Aa	56.7 ± 7.3Ba
F	5.24	0.97	4.30
P	0.03	0.45	0.04

[a] Means followed by the same capital (Dunnett test) or lowercase (Student-Newman-Keuls test, including control) letters within columns are not significantly different ($P > 0.05$).

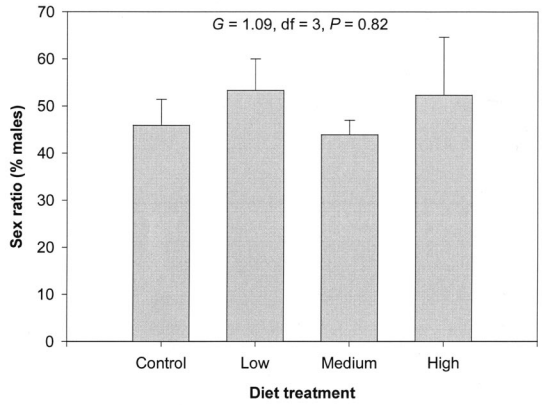

Fig. 3. Sex ratio of *E. loftini* (Dyar) pupae obtained from larvae reared on artificial (control) diet or diet containing low, medium, or high levels of GNA. Control = control diet (without GNA); Low = 0.5% GNA of total dietary protein; Medium = 1.0% GNA; High = 2.0% GNA.

more (14–17% for males, 6–19% for females) than those in the GNA treatments (Table 2). However, significant differences were not evident among the different GNA treatment levels in both larval and pupal weights of males and females (Table 2). Pupal sex ratios were not affected by GNA treatment level, and did not differ from 1♂:1♀ in each case (control, $G = 0.34$; low GNA, $G = 0.22$; medium, $G = 0.75$; high, $G = 0.11$; df = 1 and $P > 0.05$ in each case; Fig. 3).

Although GNA treatments affected Mexican rice borer immature survivorship and weight, treatments did not affect stage-specific developmental periods or adult longevity. The duration of larval and pupal periods and adult longevity were comparable among the different GNA treatment levels and the control in both males and females (Table 2).

The presence of GNA in the diet did not significantly affect Mexican rice borer fecundity relative to the control (Fig. 4). Moreover, fecundity did not vary significantly among the GNA treatment levels (Fig. 4). Similarly, percentages of eggs hatching varied between 93 and 96% and did not differ among treatment levels and control ($F = 0.42$, df = 3, 16, $P = 0.69$; data not shown). However, reductions in percent ovipositing females (80, 65, 65, and 60% for the control and low, medium, and high GNA treatments, respectively) seemed to be associated with increases in GNA levels, but differences were not significant among the levels ($G = 0.71$, df = 2, $P = 0.35$; data not shown).

The GNA treatment levels negatively influenced Mexican rice borer life table parameters (Table 3). Net reproductive rate, intrinsic rate of increase, total progeny, and growth index were higher in the control relative to the GNA treatments, but were similar among GNA treatment levels. In contrast, finite rates of increase, generation times, and doubling times were similar among the GNA treatments and control.

Discussion

The current study provides novel data concerning the effects of pure GNA delivered through artificial

Table 2. Larval and pupal weights and developmental periods and adult longevity in *E. loftini* (Dyar) males and females reared on artificial (control) diet or diet containing low (0.5%), medium (1.0%), or high (2.0%) levels of GNA

Treatment[a]	Larval weight (g)		Pupal weight (g)		Larval period (d)		Pupal period (d)		Adult longevity (d)	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Control	68.9 ± 2.4	107.8 ± 7.0	48.4 ± 1.5	85.8 ± 3.1	25.1 ± 0.8	27.5 ± 0.7	9.0 ± 0.3	8.5 ± 0.2	7.7 ± 0.3	7.6 ± 0.4
(*n*)	(24) A[b]	(29) A	(25) A	(30) A	(25) A	(30) A	(24) A	(25) A	(24) A	(25) A
Low	63.6 ± 2.9	92.1 ± 6.0	41.2 ± 1.5	72.3 ± 3.7	25.5 ± 0.6	26.9 ± 0.7	8.7 ± 0.3	9.0 ± 0.3	7.8 ± 0.3	6.7 ± 0.3
(*n*)	(22) Aa	(18) Aa	(24) Ba	(21) Ba	(24) Aa	(21) Aa	(21) Aa	(13) Aa	(19) Aa	(12) Aa
Med.	55.7 ± 2.5	94.8 ± 4.7	42.4 ± 2.8	76.1 ± 2.6	26.7 ± 0.9	26.7 ± 0.9	26.7 ± 0.4	8.2 ± 0.2	6.8 ± 0.4	6.6 ± 0.6
(*n*)	(18) Ba	(22) Aa	(18) Ba	(23) Aa	(18) Aa	(23) Aa	(16) Aa	(18) Aa	(16) Aa	(18) Aa
High	55.2 ± 3.4	95.5 ± 9.4	41.8 ± 1.8	81.3 ± 3.9	25.2 ± 0.6	28.1 ± 1.1	8.1 ± 0.4	8.8 ± 0.3	7.5 ± 0.3	6.8 ± 0.6
(*n*)	(21) Ba	(20) Aa	(22) Ba	(21) Aa	(22) Aa	(21) Aa	(18) Aa	(18) Aa	(18) Aa	(18) Aa
F_{sex}	87.66		330.59		10.36		0.08		3.13	
P_{Sex}	<0.0001		<0.0001		<0.002		0.77		0.08	
F_{Tmt}	2.86		5.70		0.27		1.36		2.30	
P_{Tmt}	0.04		0.001		0.84		0.26		0.08	
F_{Int}	0.47		0.91		1.41		1.83		0.80	
P_{Int}	0.70		0.44		0.24		0.14		0.50	

[a] Subindices "Sex," "Tmt," and "Int" indicate gender, diet treatment, and gender × diet treatment interaction, respectively.
[b] Means followed by the same capital case (Dunnett test) or lowercase (Student-Newman-Keuls test) letters within columns are not significantly different ($P > 0.05$).

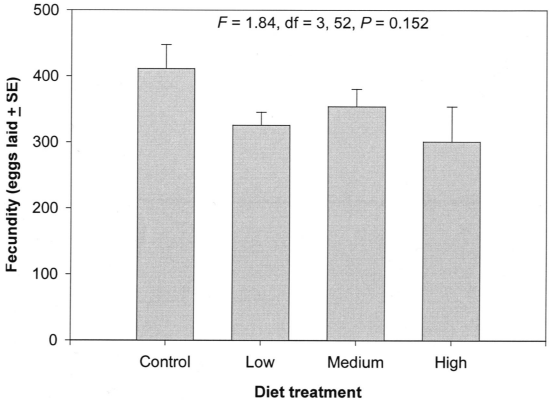

Fig. 4. Fecundity of *E. loftini* (Dyar) females reared on artificial (control) diet or diet containing low, medium, or high levels of GNA. Control = control diet (without GNA); Low = 0.5% GNA of total dietary protein; Medium = 1.0% GNA; High = 2.0% GNA.

diet on Mexican rice borer growth, developmental, and fitness parameters. It expands on a previous study, which showed that artificial diet supplemented with tissue from GNA transgenic sugarcane (GNA content ≈0.9% of total dietary protein), resulting in a ≈0.5% GNA content, affected a number of Mexican rice borer life history parameters (Sétamou et al. 2002). However, that study ignored potential dose–response effects of GNA, i.e., whether higher GNA levels would lead to stronger deleterious effects on Mexican rice borer life history parameters. The results of this study suggest a nil dose–response effect at levels between 0.5 and 2.0% GNA content, and consequently, that development of transgenic sugarcane cultivars producing GNA up to twice the level produced by the currently available one, CP65–357, transgenic line 83, is unlikely to significantly increase resistance against Mexican rice borer.

Specifically, the results of this study showed that the main effects of the GNA treatment levels on Mexican rice borer included significant reductions in larval survivorship, larval and pupal weight, growth index, and several life table parameters. In addition, the percentages of ovipositing females and total fecundity per female also tended to be lower in the GNA treatments, although differences were not significant. In contrast, deleterious effects of the GNA treatments were not recorded on stage-specific developmental times or sex ratio.

The effects of GNA on Mexican rice borer survivorship and growth observed in this study are similar to those attributed to GNA on the tomato moth, *Lacanobia oleracea* L. (Fitches et al. 1997), and legume pod borer, *Maruca vitrata* (F.) (Machuka et al. 1999). Moreover, the effects on larval growth and survivorship observed in this study also were consistent with those observed in the earlier study involving Mexican rice borer and diet based on GNA-transgenic sugarcane (Sétamou et al. 2002), although effects on total fecundity are inconsistent between studies. Specifically, incorporation of GNA transgenic sugarcane tissue into artificial diet resulted in significantly fewer eggs laid by females (Sétamou et al. 2002), whereas incorporation of pure GNA did not lead to a similar effect.

In the current study, significant differences between the control and GNA treatment levels in some life history parameters can be attributed to the added GNA, because a single base-artificial diet was used for preparing control and GNA treatments. Thus, the reductions in larval survivorship and growth observed in this study could be explained by differences in amount of diet consumed by larvae, nutritive quality of the treatments, and/or toxic effects of GNA on larvae. GNA is a mannose-binding glycoprotein that reduces uptake and absorption of nutrients (Sauvion et al. 1996, Powell et al. 1998). However, significant differences were not observed in this study among the various GNA treatments, indicating that the effects of GNA on Mexican rice borer were not dose-dependent within the range 0.5–2.0% of total dietary protein. The results of previous studies also suggest the absence of a strong dose–response effect to GNA in susceptible insects (Gatehouse et al. 1997). It is unlikely that detoxification of GNA occurs after ingestion, given that GNA is a highly stable molecule able to withstand proteolytic activity in the lepidopteran larval gut (Gatehouse et al. 1997). Thus, greater ingestion of GNA is expected to lead to stronger detrimental effects in susceptible insects. However, the lack of correlation between GNA levels in diet and effects on life history parameters suggests that either Mexican rice borer larvae excrete most ingested GNA, or GNA primarily has an antifeedant rather than toxic effect.

Table 3. Life table parameters and growth index of *E. loftini* (Dyar) reared on artificial (control) diet or (diet containing low (0.5%), medium (1.0%), or high (2.0%) levels of GNA

Treatment	R_0[a]	r_m	λ	T	DT	Total progeny	GI
Control	156.9 ± 14.8a[b]	0.113 ± 0.003a	1.12	44.8	6.1	304.8 ± 29.8a	2.34
Low	73.8 ± 10.0b	0.097 ± 0.004b	1.10	44.5	7.2	158.3 ± 21.4b	1.63
Medium	90.9 ± 14.8b	0.101 ± 0.004b	1.11	44.7	6.9	162.1 ± 26.4b	1.63
High	81.8 ± 13.2b	0.095 ± 0.005b	1.10	46.3	7.3	171.6 ± 27.6b	1.62

[a] $^1R_0$ = net reproductive rate; r_m = intrinsic rate of increase; λ = finite rate of increase; T = generation time in days; DT = doubling time in days; all calculated using jacknife program (Hulting et al. 1990). GI = growth index (ratio between percentage adults emerged and mean duration of immature period for each diet treatment; larval and pupal periods only) (Sétamou et al. 1999).

[b] Means followed by the same lowercase letters within columns are not significantly different as indicated by overlapping 95% confidence intervals; confidence intervals not computed for means in columns lacking lowercase letters.

The fact that the effects of the low GNA treatment were comparable with those of the medium and high GNA treatments suggests that the presence of GNA at a concentration of 0.5% of total dietary protein may have been sufficient to reduce diet consumption by larvae. Although the amounts of diet consumed by larvae were not measured in this study, a previous study showed that stalk damage by Mexican rice borer larvae on GNA-transgenic sugarcane was lower than in conventional sugarcane, which supports a hypothesis in which GNA has an antifeedant effect in Mexican rice borer (Legaspi et al. 1997; M.S. and J.S.B., unpublished data). Gatehouse et al. (1997) and Fitches et al. (1997) also reported similar reductions in leaf feeding damage by *L. oleracea* on GNA transgenic potato.

Overall, the presence of GNA in the artificial diet led to substantial reductions in a number of Mexican rice borer life history parameters, suggesting that GNA can play an important role in reducing population and damage levels of this pest in the field. However, because of the lack of a dose–response effect, it is possible that increasing the GNA content of transgenic sugarcane lines will not lead to greater impacts on survival and growth of the Mexican rice borer and better control in the field, as previously suggested by Sétamou et al. (2002). Emphasis in the current study was placed on the effect of different levels of GNA delivered through an artificial diet on various Mexican rice borer life history parameters, while ongoing studies investigate GNA mode of action and why the effect of the lectin was not dose-dependent.

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