

Effects of Jasmonate on insect pests and natural enemies in Bt and non-Bt cotton fields

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ABSTRACT

Worldwide, organic cotton production and processing is largely at an experimental level. Although occupying a niche market, organic cotton production is steadily increasing, which increases the need for biological control research. Foliar jasmonic acid applications are known to change levels of polyphenol oxidase in plants; polyphenol oxidase is an oxidative enzyme implicated in resistance against several insect herbivores. Our experiments were aimed at evaluating the effects of jasmonic acid ("Jasmonate") applications on late stage (9-10 weeks after planting) and early stage (6-7 weeks after planting) cotton as a means of attracting natural enemies, and thus reducing the impact of insect pests on different cotton cultivars, including transgenic cultivars expressing *Bacillus thuringiensis* (Berliner) endotoxins (Bt). In late stage cotton, treatments consisted of: (i) conventional cotton (Stoneville 474), (ii) conventional cotton + Jasmonate, (iii) transgenic cotton (Deltapine NuCOTN 33B), and (iv) transgenic cotton + Jasmonate. Treatments in early stage cotton consisted of: (i) glyphosate-resistant transgenic cotton (DPL 420 R), (ii) glyphosate-resistant transgenic cotton + Jasmonate, (iii) glyphosate-resistant, Bt transgenic cotton (DPL 420 BR), and (iv) glyphosate-resistant, Bt transgenic cotton + Jasmonate. Lower numbers of cotton pests (flea-hopper, boll weevil, bollworm and cotton aphid) were present on Jasmonate treated plants compared to un-treated plants in the late and early stages. In contrast, cotton of both stages treated with Jasmonate recruited greater numbers of fire ants, Orius, spiders, lacewings, syrphids, Scymnus, and coccinellids relative to untreated cotton. Moreover, the effects of Jasmonate increased with time for both predators and cotton fleahoppers: effects were weak one and three days after application, and moderate to strong seven days after application. In general, Bt cultivars (with or without Jasmonate) hosted higher numbers of natural enemies than non-Bt cultivars. The effects of Jasmonate treatment on predation of sentinel beet armyworm eggs were variable, with greater predation rates at three (but not 10) days after application in late stage cotton, and at 10 (but not three) days after application in early stage cotton. Parasitism rates were greater in Jasmonate-treated cotton at three and 10 days after application in both late and early stage cotton. Overall, the results

suggested that Jasmonate applications contributed to indirect pest resistance in both Bt and non-Bt cultivars by recruiting greater numbers of natural enemies with minimal effects on pests. Although greater numbers of cotton fleahopper were recruited, this species acts as both a pest and predator in cotton. Enzyme elicitors such as Jasmonate may be valuable pest management tools, especially when pest densities are high.

Introduction

More insecticide is used on conventional cotton than any other single crop, which epitomizes the worst effects of chemically dependent agriculture (Swezey and Broome, 2000). In contrast, use of toxic and persistent chemical pesticides and fertilizers, as well as genetically modified organisms, is not allowed under organic agriculture (Alfoeldi, 2001). Organic cotton is produced in agricultural systems that produce food and fiber according to clearly established standards, and seeks to build biologically diverse agricultural systems, replenish and maintain soil fertility, and promote a healthy environment (Tostado, 2002).

Jasmonic acid is found in many plant species and is involved in regulating diverse plant functions, including plant resistance and senescence (Creelman and Mullet, 1997). Plants are known to produce jasmonic acid following herbivore damage, which results in increased production of compounds involved in resistance against herbivores (Constable *et al.*, 1995; Thaler *et al.*, 1996; McAuslane *et al.*, 1997). In tomatoes, application of jasmonic acid results in induced production of proteinase inhibitors and polyphenol oxidases and a decrease in the preference, performance, and abundance of many common herbivores in the field, including western flower thrips (*Frankliniella occidentalis* Pergande), beet armyworm (*Spodoptera exigua* Hübner), and cabbage looper (*Trichoplusia ni* Hübner), among others (Thaler *et al.*, 1996, 1999a, b, c). These herbivore species and beet armyworm in particular, can be important pests of tomatoes (Lange and Bronson, 1981).

Interactions between transgenic plants and arthropod natural enemies may be advantageous, disadvantageous, or neutral in an anthropocentric context. Thus, it is important to investigate their potential benefits and side effects. Indeed, an evaluation of side effects is a mandatory part of most environmental risk assessments for transgenic plant cultivars (Schuler *et al.*, 1999). The effects of conventional microbial and synthetic insecticides on beneficial organisms, which provide a means of judging the acceptability of risks posed by transgenic plants, are reviewed elsewhere (Croft, 1990). Current insect-resistant transgenic plants express *Bacillus thuringiensis* (Berliner) endotoxins, which provide high levels of resistance to a range of

lepidopteron and coleopteran insect pests feeding on these plants (Roush, 1996, 1997a, b; Gould, 1998). The potential impact of transgenic plants on natural enemies in general and on parasitoids in particular has so far received little attention.

Natural enemies of herbivorous insects are known to utilize volatile infochemicals emitted by plants under herbivore attack during host location (Turlings *et al.*, 1990, 1991; Dicke, 1994; Mattiacci *et al.*, 1994; Du *et al.*, 1996; Paré and Tumlinson, 1997; Turlings and Benrey, 1998). Moreover, herbivore feeding may attract natural enemies and deter additional herbivore oviposition on plants (DeMoraes *et al.*, 2001). Studies of the mechanisms of induction of plant synomones used by natural enemies have provided information on elicitors (e.g. volicitin), mediators of responses within plant tissues (e.g. jasmonic acid), induced volatiles, and specificity of plant responses (Turlings *et al.*, 1993; Boland *et al.*, 1995; Mattiacci *et al.*, 1995; Alborn *et al.*, 1997; Karban and Baldwin, 1997; De Moraes *et al.*, 1998; Du *et al.*, 1998; Paré and Tumlinson, 1998; Paré *et al.*, 1998). Moreover, herbivore oviposition, in addition to herbivore feeding, can induce volatile emissions in plants that are attractive to egg parasitoids. Meiners and Hilker (1997) showed that oviposition of the elm leaf beetle, *Xanthogaleruca luteola* Muller, induces leaves of the field elm (*Ulmus minor* Miller) to emit volatiles that are attractive to the egg parasitoid *Oomyzus gallerucae* (Fonscolombe). Herbivore infested plants release volatiles that attract natural enemies and repel herbivores (De Moraes *et al.*, 1998, 2001). Moreover, it has been suggested that the Jasmonate pathway may regulate production of volatile compounds that attract foraging parasitoid wasps (Boland *et al.*, 1995; Alborn *et al.*, 1997; Ozawa *et al.*, 2000). Several studies show that Jasmonate treatment of plants fortifies their indirect defenses by attracting greater numbers of natural enemies under both field and laboratory conditions (Thaler *et al.*, 1999a; Gols *et al.*, 1999).

The present study was designed to test whether treatment with Jasmonate affects recruitment of natural enemies and herbivores by cotton plants at early and late growth stages in the field. Specifically, the objectives of this study were to assess the effects of Jasmonate on: (i) Recruitment of cotton fleahopper (*Pseudatomoscelis seriatus* Reuter), boll weevil (*Anthonomus grandis* Boheman), bollworm *Helicoverpa* sp. and cotton aphid (*Aphis gossypii* Glover) and their associated natural enemies; *Orius* nymphs and adults, larvae of Syrphidae, spiders (Genera; *Phidippus* and *Salticus*), *Scymnus* adults, *Chrysoperla carnea* (Stephens) larvae, *Coccinella* larvae and adults, and fire ants *Solenopsis invicta* (Buren) at early and late growth stages of experimental plants, and; (ii) Recruitment of parasitoids and predators of beet armyworm using sentinel individuals.

Experimental procedure

Cotton plots

Three experimental dry-land cotton fields were planted on the Texas A&M University experimental farm near College Station, Texas. The first two fields were used to evaluate effects in late stage cotton, and were planted 13 April 2001, as part of yearly cotton cultivar tests conducted at Texas A&M University. Both fields were 40 rows (102 cm wide) by 45.6 m long, and were separated from each other by ca. 60 m. Plots within each field were outlined by dividing each row into three 15.2 m segments and selecting two adjacent row segments that served as subplots. Three plots in each field were randomly selected and planted with a transgenic cotton cultivar expressing *B. thuringiensis* (hereafter "Bt") endotoxins (*B. thuringiensis* subsp. *kurstaki* Cry1A(c) d-endotoxin, Deltapine NuCOTN 33B) and three with a cultivar not expressing *B. thuringiensis* endotoxins (hereafter "non-Bt") (Stoneville 474). Thus, each cultivar was replicated six times in the late stage cotton field. Both fields were subjected to conventional management practices. The third field, used to evaluate early stage cotton, was planted at 15 May 2001 also on the Texas A&M University experimental farm, and was located ca. 2 km from the first two fields. This field was 400 rows (102 cm) wide by 70 m long, and was divided into six plots of 40 rows separated by 11 unplanted rows. Three alternate plots were planted with a commercial cultivar expressing Bt endotoxins and resistance to glyphosate herbicide (DPL 422 BR) and the remaining three with a cultivar expressing glyphosate resistance (hereafter "non-Bt") (DPL 420 R). Two subplots within each of six plots (three Bt and three non-Bt plots) were outlined by selecting 12 m row segments. Thus, each cultivar was replicated three times in the late-planted field. The field was subjected to conventional management practices.

Treatments

Half of the plots/subplots in the early- and late-planted cotton fields were treated with Jasmonate (Jasmonic acid, Aldrich Chemical Company, Milwaukee, WI, 53233, USA) to assess its influence on herbivore and natural enemy recruitment by plants. Thus, four treatments were evaluated in both the early- and late-planted fields: (i) untreated non-Bt cultivar (hereafter NBT/NJA); (ii) non-Bt cultivar treated with Jasmonate (NBT/JA); (iii) untreated Bt cultivar (BT/NJA), and; (iv) Bt cultivar treated with Jasmonate (BT/JA). Treatments (i) and (iii) were treated with a control solution (see below). Thus, each treatment was replicated six times in late stage cotton and four times in early stage cotton. Jasmonate was prepared for application to cotton plants by mixing 3 ml in 3 ml of acetone and 8 l of water. The control solution consisted of 3 ml of acetone mixed in 8 l of water. The Jasmonate concentration used was chosen on the basis of greenhouse studies and is considered below levels toxic to plants (Thaler *et al.*, 1996). Jasmonate was applied with a

backpack sprayer to flowering cotton plants (40-45 leaves/plant) in the late stage cotton field, and each plant received ca. 11.8 μM of Jasmonate. Plants in the early stage field were treated before flowering (20-25 leaves/plant), and each plant received ca. 8 μM . In each case, neighboring plants were protected from Jasmonate or acetone (control) treatment by covering with plastic during application.

Sentinel beet armyworm eggs and larvae

Laboratory-reared sentinel beet armyworm eggs were used in field experiments to assess the influence of Jasmonate applications on egg predation and parasitism. Newly formed beet armyworm pupae were placed in waxed carton containers lined with paper towels. Upon emergence, moths were allowed to mate and to lay eggs on the paper towel lining. Eggs were collected daily and transferred to 1 l jars containing artificial diet where they were incubated ($25 \pm 1^\circ\text{C}$, 50-70% R.H., and 14L: 10 D lighting regime) until hatching. Fourth instar larvae were transferred to Petri dishes containing artificial diet at a rate of 15-20 larvae per dish, and kept in the same conditions until pupation. Newly laid egg masses (0-24 h old) and 1st to 2nd instar larvae were used for field experiments. At three and 10 days after treatment with Jasmonate, five egg masses with known numbers of eggs (~20 eggs each) were attached on the underside of randomly selected leaves in each of the subplots of the late and early stages cotton fields (24 plots for each stage; half of the plots were Bt and the other half non-Bt) using glue (Tragant, Aldrich Chemical Company, Milwaukee, WI, 53233, USA) in both Jasmonate and non-Jasmonate plots. Thus, a total of 120 egg masses were placed in the field. Egg masses were recovered after 24 h and returned to the laboratory where the numbers of missing or consumed (eaten by predators) eggs per egg mass were scored, and the remaining eggs incubated in glass vials (25 ml) plugged with cotton at $25 \pm 1^\circ\text{C}$ and 70-80% RH. Eggs were subsequently checked daily for eclosion of beet armyworm larvae, parasitism, and egg mortality. At three and 10 days after treatment with Jasmonate, one larva of beet armyworm was placed in each open glass vial (40 ml) with diet, fixed onto bamboo stalks (~100 cm length, 5 mm diam.), and larvae distributed were replicated five times in the cotton canopy of 24 subplots in both Jasmonate and control plots. Thus a total of 120 beet armyworm larvae were placed in the field. After 24 h, larvae were recovered, incubated ($25 \pm 1^\circ\text{C}$ and 70-80% RH.) in the laboratory in plastic (20 ml) cups with diet, and checked daily for pupation, parasitism, and larval mortality.

Data recorded

Cotton pests and their associated natural enemies were quantified by sampling 20 plants per plot prior to Jasmonate applications to assess their baseline densities. Samples were taken again at the 1st, 3rd, 7th

and 14th day after Jasmonate applications. Sampling consisted of taking four beat bucket samples. Beat bucket sampling employs a five-gallon plastic bucket held at a 45 degree angle to the ground while the terminal and as much of the plant as possible is bent over into the bucket and beaten against the side of the bucket (Knutson *et al.*, 2000). Aphids colonized young stage cotton only at the end of the experiment, and were monitored by counting them on the third leaf from the bottom. Cotton pests included cotton fleahopper, boll weevil, bollworm and cotton aphid, while natural enemies included *Orius* nymphs and adults, larvae of Syrphidae, spiders (Genera; *Phidippus* and *Salticus*), Scymnus adults, *Chrysoperla carnea* (Stephens) larvae, *Coccinella* larvae and adults, and fire ants *Solenopsis invicta* (Buren).

Statistical analyses

Mean pest and natural enemy treatment densities were compared via repeated measures analysis of variance (ANOVA), and means were separated as warranted using the Tukey's tests using Statistix version 7.0 (Analytical Software, Tallahassee, FL, USA). Parasitism and predation rates of sentinel eggs were arcsine square-root transformed and treatment means were compared via analysis of variance, and means separated as warranted using Tukey's tests.

Results

Effect of Jasmonate on pest and natural enemy densities in late stage cotton

There was a significant difference ($F = 43.9$, $df = 1, 5$, $P < 0.002$) between Bt- and non-Bt-cotton before Jasmonate applications in overall densities of pests (Figure 1). After Jasmonate applications, differences among treatments in cotton fleahopper densities increased gradually over time (Figure 1a) ($F = 63.7$, $df = 3, 5$, $P > 0.001$). In general, Jasmonate applications appeared to have a repellent effect on cotton fleahopper; within cotton cultivars, fleahopper densities were lower in JA treatments relative to NJA treatments. Overall, cotton fleahopper densities were highest in the NBT/NJA treatment, intermediate in the NBT/JA and BT/NJA, and lowest in the BT/JA. Differences were not evident at the beginning of the experiment between NJA and JA treatments within each of the cotton cultivars (NBT, $t = 7.4$, $df = 1$, $P > 0.004$; BT, $t = 7.9$, $df = 1$, $P > 0.001$). Bollworm densities were highest in NBT/NJA (1.60 ± 0.05), followed by NBT/JA (0.98 ± 0.07), the lowest in BT/NJA (0.1 ± 0.04), and were not recorded on BT/JA ($F = 7.9$, $df = 3, 5$, $P > 0.004$). Boll weevil densities were highest in NBT/NJA (0.60 ± 0.05), followed by BT/NJA (0.4 ± 0.08), and lowest in BT/JA and NBT/JA (0.26 ± 0.04 and 0.12 ± 0.03) ($F = 5.7$, $df = 3, 5$, $P > 0.02$). There was a significant difference ($F = 54.7$, $df = 1, 5$, $P < 0.001$) between Bt- and non-Bt-cotton before Jasmonate application. Bt-cotton hosted higher natural enemy numbers than non-Bt –

cotton. Natural enemy numbers differed significantly between sample days ($F = 32, 7, df = 4, 5, P < 0.001$) (Figure 1b-d, Figure 2a-d). In general, Jasmonate applications appeared to attract natural enemies; within cotton cultivars, natural enemy densities were higher in JA versus NJA treatments. Moreover, the effects of Jasmonate increased gradually with days, and on average peaked at 7 d after application.

Effect of Jasmonate on pest and natural enemy densities in early stage cotton

There was a significant difference between Bt- and non-Bt-cotton in cotton pests before Jasmonate applications ($F = 78, 4, df = 1, 5, P < 0.0009$). Fleahopper numbers decreased in Jasmonate-treated plots compared to un-treated plots (Figure 3a). Similarly to late stage cotton, the effects of Jasmonate on cotton pests (flea-hoppers) increased with days, with the greatest difference between JA and NJA treatments occurring 7 d after application. Differences were not evident at the beginning of the experiment between NJA and JA treatments within each of the cotton cultivars (NBT, $t = 7.3, df = 1, P > 0.005$; BT, $t = 8.4, df = 1, P > 0.002$). Bollworm densities were highest in NBT/NJA (1.90 ± 0.06), followed by NBT/JA (1.2 ± 0.09), the lowest in BT/NJA (0.2 ± 0.03), and were not recorded on BT/JA ($F = 10.3, df = 3, 5, P > 0.005$). Cotton aphid densities were highest in NBT/NJA (32.5 ± 2.66), followed by BT/NJA (17.4 ± 5.5), and lowest in BT/JA and NBT/JA (4.6 ± 1.04 and 6.7 ± 1.3) ($F = 35.7, df = 3, 5, P > 0.002$). There was a significant difference ($F = 96.8, df = 1, 5, P < 0.0005$) between Bt- and non-Bt-cotton before Jasmonate application. Bt-cotton plants hosted higher natural enemy densities than non-Bt cotton plants (Figures 3 and 4). Natural enemy numbers differed significantly ($F = 4.7, df = 4, 5, P < 0.0003$) between sample days. Jasmonate effects increased gradually with days and peaked at 7 d post-application (Figures 3b-d and 4a-d).

Effect of Jasmonate on parasitism and predation of beet armyworm in late stage cotton

Egg predation rates 3 d post application were highest in Jasmonate-treated cotton plants, regardless of cotton cultivar ($F = 5.1, df = 3, 5, P > 0.02$) (Figure 5a). In contrast, egg predation rates 10 d post-application were highest in the BT/JA treatment, lowest in the NBT/NJA treatment, and intermediate in the BT/NJA and NBT/JA treatments ($F = 6.9, df = 3, 5, P > 0.03$) (Fig. 5a). Egg parasitism rates 3 d ($F = 11.5, df = 3, 5, P > 0.0005$) and 10 d ($F = 13.9, df = 3, 5, P > 0.006$) post application were higher in Jasmonate treated versus untreated cotton plants. Specifically, parasitism rates were highest in the BT/JA treatment, lowest in the NBT/NJA treatment, and intermediate in the NBT/JA and BT/NJA treatments (Figure 5b). All eggs were parasitized by *Trichogramma pretiosum*

(Riley).

Effect of Jasmonate on parasitism and predation of beet armyworm in early stage cotton

Egg predation rates 3 d ($F = 3.8, df = 3, 5, P > 0.04$) and 10 d ($F = 5.7, df = 3, 5, P > 0.03$) post-application were highest in the BT/JA treatment, lowest in the NBT/NJA treatment, and intermediate in the BT/NJA and NBT/JA treatments (Figure 5c). Similarly, egg parasitism rates were highest in the BT/JA treatment, lowest in the NBT/NJA treatment, and intermediate in the BT/NJA and NBT/JA treatments (Figure 5d). All eggs were parasitized by *T. pretiosum*. Parasitoids were not recovered from sentinel beet armyworm larvae in any of the plots. Moreover, ~20% of sentinel larvae was not recovered from all plots combined.

Discussion

Our results show that application of Jasmonate to cotton enhanced natural enemy recruitment, while apparently repelling cotton pests, and that these effects were enhanced when JA was applied to Bt plants. This was evident in the higher densities of fire ants, *Orius*, spiders, lacewing larvae, syrphid larvae, *Scymnus*, and various coccinellids, and lower densities of cotton pests present in plots treated with Jasmonate, in both early- and late-stage cotton. In addition, the effect of Jasmonate applications appeared to be greatest in Bt cotton cultivars. The effect of Jasmonate applications varied over time, and peaked at 3 or 7 d post application. The results indicated that there was a significant difference in overall densities of pests between Bt- and non-Bt-cotton before Jasmonate applications. After applications, these differences increased gradually with days. Cotton plants hosted the lowest pest numbers 7 d after Jasmonate treatment. These results are consistent with those of other studies in various crops, including cotton, tomato and potato (Bleichert *et al.*, 1995; Karban and Baldwin, 1997; Thaler, 1999c), in which Jasmonate applications decreased herbivore numbers and increased natural enemy numbers. These results may have significant implications for biological control in cotton crops.

Treatment with Jasmonate increased the attractiveness of cotton plants to natural enemies. This result is consistent with those of other authors (Constable *et al.*, 1995, Duffey and Stout, 1996, Karban and Baldwin, 1997) who found that cotton plants could be induced by Jasmonate and that induction had positive effects on natural enemies and negative effects on the abundance of cotton insects. Understanding the chemical mechanisms of induction will allow predicting which herbivores will be affected by induced responses. Predictability is important if we want to use induced resistance in agriculture especially in organic cotton farms.

Bt- and non-Bt-cotton plants differed significantly

in hosting natural enemies before applying the Jasmonate. Bt-cotton plants hosted higher natural enemy numbers than non-Bt-cotton plants. Jasmonate effects increased gradually over time and natural enemy numbers were highest 7 d after treatment, and in some cases 3 d post-treatment. Natural enemy numbers were higher in Jasmonate treated versus untreated plots. These results are consistent with Thaler (1999b) who reported that the positive effects of Jasmonate increased attraction of natural enemies to induced plants compared to control plants.

Jasmonate-treated Bt-cotton plants hosted the highest number of natural enemies, while the quality of their hosts may have suffered due to induced plant defenses. Thus, natural enemies that have difficulty finding hosts may benefit from the increased attractiveness of induced plants, though hosts may be of lower quality. For natural enemies not limited by host finding, the positive effects of increased host finding will be outweighed by the negative effects of feeding on poor quality hosts from induced plants. For example, Coccinellids were found in a high abundance on induced plants, but syrphid fly larvae were less affected by induced plots. These results correspond with (Thaler 1999a) who found that the wasp *Hyposoteria exiguae* (Viereck) was found in higher abundance on induced plants, but aphelinid parasitoids and syrphid fly larvae (both aphid feeders) were not affected by induced resistance. This could be because coccinellids feed on low density prey (eggs and caterpillars) whereas the syrphid fly larvae feed on high density prey (aphids). The high attractiveness of natural enemies in induced- Bt- plots could pose a problem in finding food for those natural enemies. Therefore, we recommend using Jasmonate only in conventional cotton cultivars to increase their resistance to cotton pests and attract more natural enemies.

Jasmonate-treated plots attracted parasitoids and predators of sentinel beet armyworm eggs more than control plots. These results are consistent with those of Paré and Tumlinson (1998) who found that induction by Jasmonate attracts both parasitic and predatory insects. The results also corresponded with Alborn *et al.* (1997) who reported that volicitin induces plants to emit volatile compounds that attract parasitic wasps and other natural enemies of the insect eggs. Jasmonic acid renders intact cotton leaves attractive to parasitoids. The finding that induction with Jasmonate leads to the formation of attractants for predators and parasitoids agrees with other studies (Gols *et al.*, 1999; Thaler 1999c).

Jasmonic acid is a natural plant hormone, which may reduce herbivory and attract natural enemies in intact cotton leaves. The results discussed here indicate that Jasmonate applications could be used as part of biological control programs to maintain organic cotton production. The results lead to potential practical application that 250-300 ml Jasmonate (spray

using back sprayer) are needed to treat one hectare of cotton. However, the economics of applying Jasmonate in commercial fields must be assessed before any recommendations can be made.

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References

- Alborn, H.T., Turlings, T.C. J., Jones, T.H., Stenhagen, G., Loughrin, J.H. and Tumlinson, J.H. (1997). An elicitor of plant volatiles from beet armyworm oral secretion. *Science*, **76**: 945–949.
- Alfoeldi, T. (2001). Agronomic and ecological performance of organic and conventional farming systems, pp 92-95. Proceedings Sino-Swiss Seminar on Plant Production with sustainable Agriculture - Research and Applications, 28 May to 1 June, 2001, Zhuhai China.
- Blechert, S., Brodschelm, W., Holder, S., Kammerer, L., Kutchan, T.M., Mueller, M.J., Xia, X. and Zenk, M.H. (1995). The octadecanoid pathway: signal molecules for the regulation of secondary pathways. *Proceedings of National Academy of Sciences USA*, **92**: 4099-4105.
- Boland, W.J., Hopke, J., Donath, J., Nuske, J. and Bublitz, F. (1995). Jasmonic acid and coronatine induce odor production in plants. *Angewandte Chemie International Edition*, **34**: 1600–1602.
- Constabel, C.P., Bergey, D.R. and Ryan, C.A. (1995). Systemin activates synthesis of wound-inducible tomato leaf polyphenol oxidase via the octadecanoid defense signaling pathway. *Proceedings of National Academy of Sciences USA*, **92**: 407-411.
- Creelman, R.A. and Mullet, J.E. (1997). Biosynthesis and action of jasmonates in plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**: 355-381.
- Croft, B.A. (1990). *Arthropod Biological Control Agents and Pesticides*. John Wiley and Sons, New York 723 pp.
- De Moraes, C.M., Mescher, M.C. and Tumlinson, J.H. (2001). Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature*, **410**: 577– 580.
- De Moraes, C.M., Lewis W.J., Paré, P.W., Alborn, H.T. and Tumlinson, J.H. (1998). Herbivore-infested plants selectively attract parasitoids. *Nature*, **393**: 570–573.
- Dicke, M. (1994). Local and systemic production of volatile herbivore-induced Terpenoids: Their role in plant–carnivore mutualism. *Journal of Plant Physi-*

- ology, **143**: 465–472.
- Du, Y., Poppy G.M., Powell, W., Picket, J.A., Wadhams, L.J. and Woodcock, C.M. (1998). Identification of semiochemicals released during aphid feeding that attracts parasitoid *Aphidius ervi*. *Journal of Chemical Ecology*, **24**: 1355–1368.
 - Du, Y., Poppy, G.M., and Powell, W. (1996). Relative importance of semiochemicals from first and second trophic levels in host foraging behaviour of *Aphidius ervi*. *Journal of Chemical Ecology*, **22**: 1591–1605.
 - Duffey, S.S. and Stout, M.J. (1996). Antinutritive and toxic components of plant defense against insects. *Archive of Insect Biochemistry and Physiology*, **32**: 3-37.
 - Gols, R., Posthumus, M.A., and Dicke, M. (1999). Jasmonic acid induces the production of gerbera volatiles that attract the biological control agent *Phytoseiulus persimilis*. *Entomologia Experimentalis et Applicata*, **93**: 77–86.
 - Gould, F. (1998). Sustainability of transgenic insecticidal cultivars: integrating pest genetics and ecology. *Annual Review of Entomology*, **43**: 701-726.
 - Karban, R. and Baldwin, I. (1997). Induced responses to herbivory. The University of Chicago Press, Chicago, Illinois, 319 pp.
 - Knutson, A.E., Naranjo, S.E., Wilson L.T. and Muegge, M.A. (2000). Sampling Predatory Insects and Spiders with the Beat Bucket Method in Texas and Arizona. Proceedings of Beltwide Cotton Production Conference, San Antonio, TX.
 - Lange, W.H. and Bronson, L. (1981). Insect pests of tomatoes. *Annual Review of Entomology*, **26**: 345-371.
 - Mattiacci, L., Dicke, M. and Posthumus, M.A. (1995). b-Glucosidase: An elicitor of herbivore induced plant odor that attracts host-searching parasitic wasps. *Proceedings of the National Academy of Sciences USA*, **92**: 2036–2040.
 - Mattiacci, L., Dicke, M. and Posthumus, M.A. (1994). Induction of parasitoid attracting synomone in Brussels sprouts plants by feeding of *Pieris brassicae* larvae: Role of mechanical damage and herbivore elicitor. *Journal of Chemical Ecology*, **20**: 2229–2247.
 - McAuslane, H.J., Alborn, H.T. and Toth, J.P. (1997). Systemic induction of terpenoid aldehydes in cotton pigment glands by feeding of larval *Spodoptera exigua*. *Journal of Chemical Ecology*, **23**: 2861-2879.
 - Meiners, T. and Hilker M. (1997). Host location in *Oomyzus gallerucae* (Hymenoptera: Eulophidae), an egg parasitoid of the elm leaf beetle *Xanthogaleruca luteola* (Coleoptera: Chrysomelidae). *Oecologia*, **112**: 87–93.
 - Ozawa R., Arimura, G., Takabayashi, J., Shimoda, T. and Nishioka, T. (2000). Involvement of Jasmonate- and salicylate-related signaling pathways for the production of specific herbivore-induced volatiles in plants. *Plant Cell Physiology*, **41**: 391-398.
 - Paré, P.W. and Tumlinson, J.H. (1998). Cotton volatiles synthesized and released distal to the site of insect damage. *Phytochemistry*, **47**: 521–526.
 - Paré, P.W. and Tumlinson, J.H. (1997). De Novo Biosynthesis of Volatiles Induced by Insect Herbivory on Cotton Plants. *Plant Physiology*, **114**: 1161-1167.
 - Paré, P.W., Alborn, H.T. and Tumlinson, J.H. (1998). Concerted biosynthesis of an insect elicitor of plant volatiles. *Proceedings of the National Academy of Sciences USA*, **95**: 13971-13975.
 - Roush, R.T. (1997a). Bt-transgenic crops: just another pretty insecticide or a chance for a new start in resistance management? *Pesticide Science*, **51**: 328-334.
 - Roush, R.T. (1997b). Managing resistance to transgenic crops, pp 49-61. In Carozzi, N., and M. Koziel (eds.), *Advances in insect control: the role of transgenic plants*. Taylor, and Francis, London.
 - Roush, R.T. (1996). Can we slow adaptation by pest to insect transgenic crops? pp 242-263. In G. Persley (ed.), *Biotechnology and integrated pest management*. CABI, London.
 - Schuler T.H., Poppy, G.M., Kerry, B.R. and Denholm, I. (1999). Potential side effects of insect-resistant transgenic plants on arthropod natural enemies. *Trends in Biotechnology*, **17**: 210-216.
 - Stokstad, E. (2002). Organic farms reap many benefits. *Science*, **296**: 1589.
 - Swezey, S.L. and Broome, J.C. (2000). Growth Predicted in Biologically Integrated and Organic Farming Systems. *California Agriculture*, **54**: 26-35.
 - Thaler, J.S. (1999a). Induced resistance in agricultural crops: Effects of jasmonic acid on herbivory and yield in tomato plants. *Environmental Entomology*, **28**: 30-37.
 - Thaler, J.S. (1999b). Jasmonate-inducible plant defenses cause increased parasitism of herbivores. *Nature*, **399**: 686-688.
 - Thaler, J.S. (1999c). Jasmonic acid mediated interactions between plants, Herbivores, parasitoids, and pathogens: A review of field experiments in tomato, pp 319-334. In Agrawal, A., S. Tuzun, and E. Bent (eds.) *Induced plant defenses against pathogens and herbivores: Biochemistry, Ecology, and Agriculture*. APS Press, St. Paul, MN.
 - Thaler, J.S., Stout, M.J., Karban, R. and Duffey, S.S. (1996). Exogenous jasmonates simulate insect wounding in tomato plants (*Lycopersicon esculentum*) in the laboratory and field. *Journal of Chemical Ecology*, **22**: 1767-1781.
 - Turlings, T.C.J. and Benrey, B. (1998). Effects of plant metabolites on the behaviour and development of parasitic wasps. *Ecoscience*, **5**: 321–333.
 - Turlings, T.C.J., McCall, P. J., Alborn, H.T. and Tumlinson, J.H. (1993). An elicitor in caterpillar oral secretions that induces corn seedlings to emit chemical signals attractive to parasitic wasps. *Journal of Chemical Ecology*, **19**: 412–425.
 - Turlings, T.C.J., Tumlinson, J.H., Eller, F.J. and Lewis,

W.J. (1991). Larval-damaged plants: source of volatile synomones that guide the parasitoid *Cotesia marginiventris* to the microhabitat of its host. *Entomologia Experimentalis et Applicata*, **58**: 72–85.

- Turlings, T.C.J., Tumlinson, J.H. and Lewis, W.J. (1990). Exploitation of herbivore-induced plant odors by host seeking parasitic wasps. *Science*, **250**: 1251–1253.

Figure 1. Mean of cotton insects (sample/plant) in late cotton field in Bt, non-Bt and in JA and non-JA cotton plots: (A) Fleahoppers, (B) Ants, (C) Orius and (D) Predatory spiders.

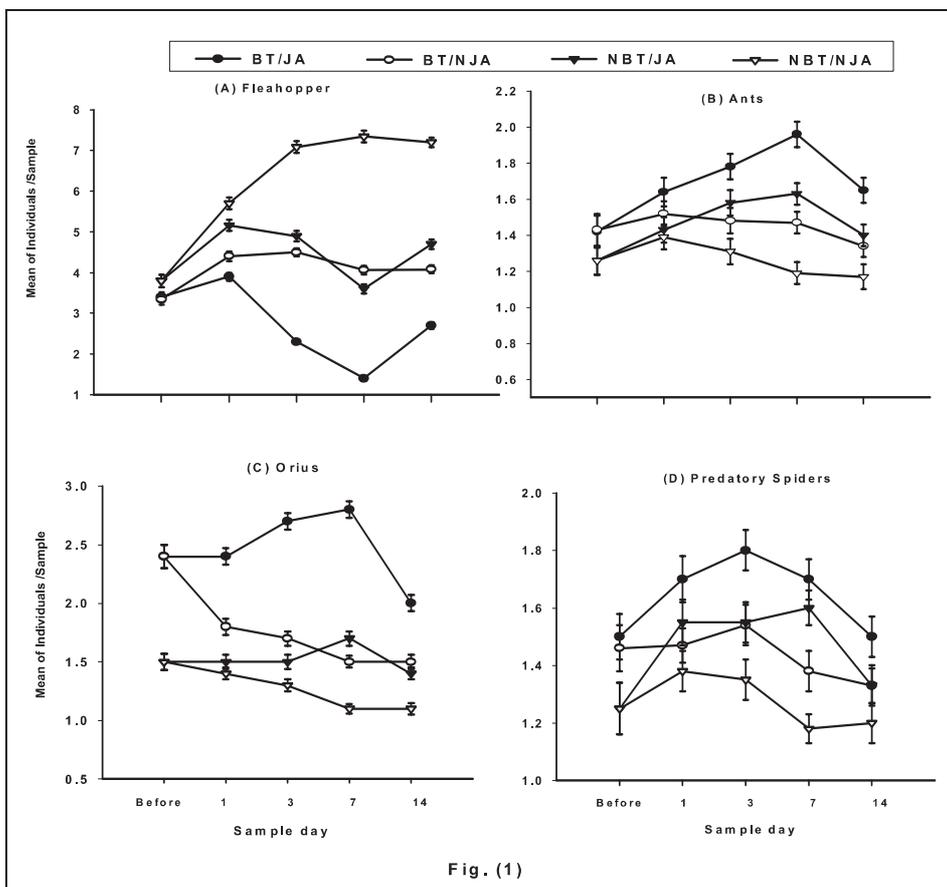


Fig. (1)

Figure 2. Mean of cotton insects-natural enemies (sample/plant) in late cotton field in Bt, non-Bt and in JA and non-JA cotton plots: (A) Lacewing, (B) Syrphid, (C) Sycmnus and (D) Coccinellid. For explanation of symbols, see Figure (1).

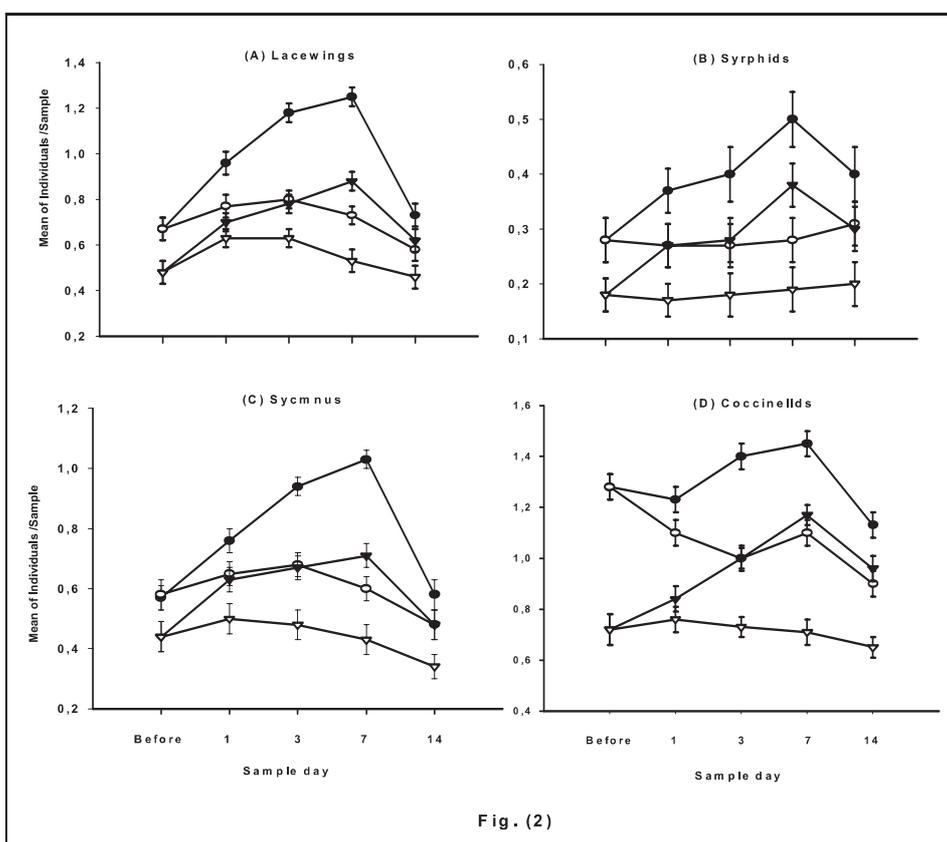


Fig. (2)

Figure 3. Mean of cotton insects (sample/plant) in early cotton field in Bt, non-Bt and in JA and non-JA cotton plots: (A) Fleahoppers, (B) Ants, (C) Orius and (D) Predatory spiders. For explanation of symbols, see Figure (1).

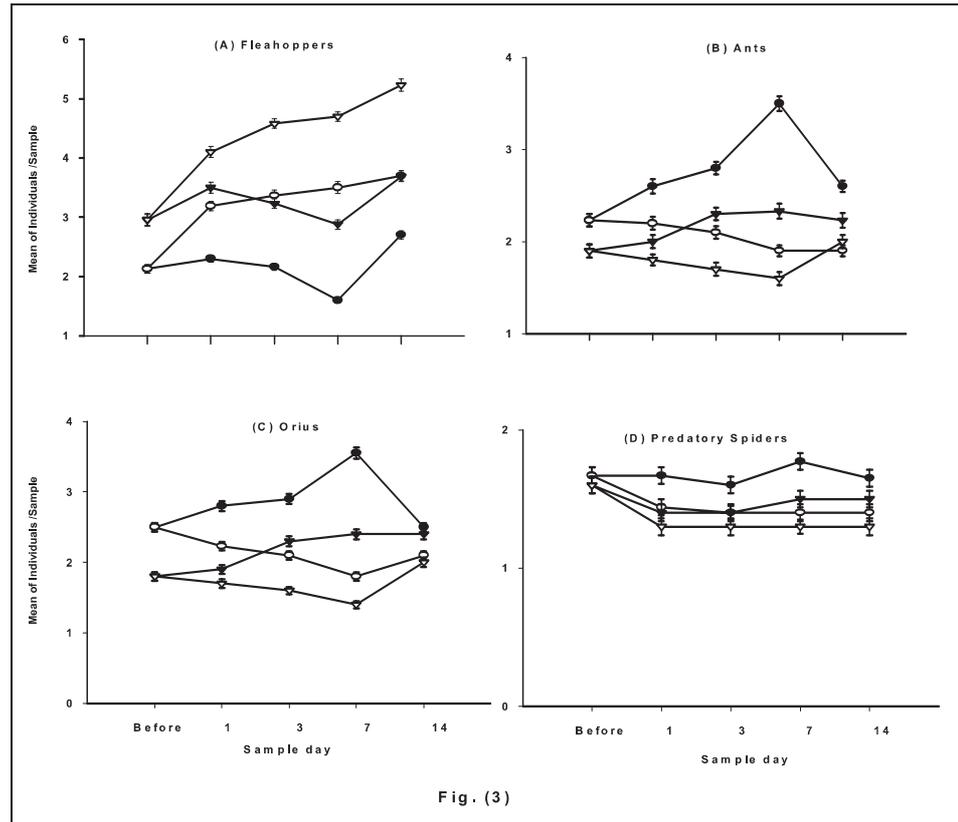


Fig. (3)

Figure 4. Mean of cotton insects-natural enemies (sample/plant) in early cotton field in Bt, non-Bt and in JA and non-JA cotton plots: (A) Lacewing, (B) Syrphid, (C) Sycmnus and (D) Coccinellid. For explanation of symbols, see Figure (1).

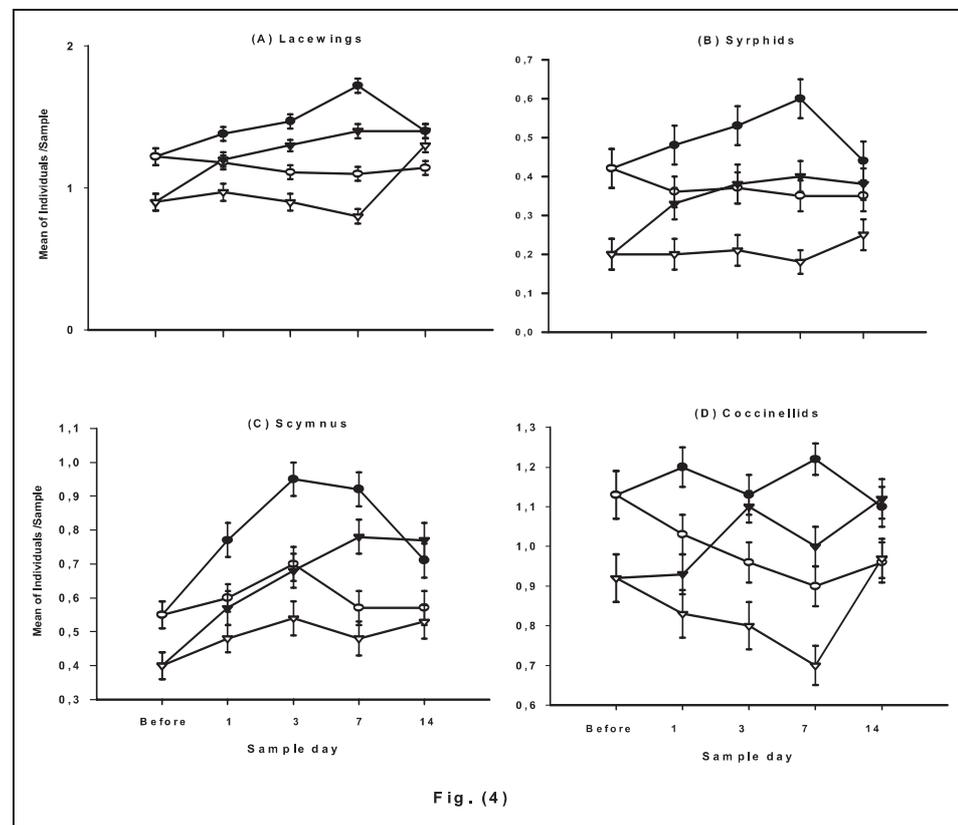


Fig. (4)

Figure 5. Predation and parasitism rates of sentinel Beet Armyworm eggs in late and early cotton in Bt and non-Bt cotton in JA and non-JA plots at 3rd and 10th day after Jasmonate application.

