

REVIEW ARTICLE

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Interactions between *Bacillus thuringiensis* and entomophagous insects



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Abstract

The interactions between insect pathogens, parasitoids, and predators have been proposed as “intraguild predation (IGP).” It occurs when two species share a host or prey (and therefore may compete) or when they engage in a trophic interaction with each other (parasitism or predation). Laboratory studies revealed that many predacious species attack and consume *Bacillus thuringiensis* (Bt)-infected prey with no detrimental effects on the biological parameters of the predators. However, some studies indicated adverse impact of Bt on development and biology of the predators. As for parasitoids, some studies showed no detrimental effects on the biology of the parasitoids when reared on Bt-infected hosts and others revealed negative effects on their biological aspects. Such negative effects were found to be related to Bt concentration and timing of treatment (parasitism or infection). The biological parameters of the offspring of the adult parasitoids that had emerged from infected parasitized larvae were not affected. Also, ingestion of Bt by adult parasitoids did not affect the longevity or fecundity of such parasitoids. Concerning Bt crops, a recent published report in 2019 stated that over the past 20+ years, extensive experience and insight have been gained through laboratory and field studies of non-target effects of crops producing Cry proteins. Overall, the vast majority of the studies demonstrated that the insecticidal proteins developed today do not cause adverse effects on natural enemies (parasitoids and predators) of target pests.

Keywords: *Bacillus thuringiensis*, Bt crops, Parasitoids, Predators, Intraguild predation

Background

The interactions between insect pathogens, parasitoids, and predators have been proposed as “intraguild predation (IGP)” (Rosenheim et al. 1995). It occurs when two species share a host or prey (and therefore may compete) or when they engage in a trophic interaction with each other (parasitism or predation). This interaction may impact the population dynamics of biological control agents and target pests. Common forms of IGP include pathogens that infect both herbivores and their parasitoids, facultative hyperparasitoids which can parasitize either the herbivore or a primary parasitoid of the herbivore, and predators that feed upon parasitized herbivores and cannibal predators. Thus, IGP can be intense resulting in high levels of mortality for one or both of natural enemies, while the total mortality

imposed on the target pest populations is minimal (Rosenheim et al. 1995). In this respect, Labauda and Griffin (2018) reported that despite such negative interactions occur in the laboratory, it is less often documented in the field. Although laboratory-reared insects are more susceptible to pathogens, the ecological components and behavioral responses of the natural enemies should be taken into consideration to explain the low or scarce incidence of entomopathogens infecting natural enemies (predators and parasitoids) under field conditions (Scorsetti et al. 2017).

Beline (2018) reported that entomopathogens and other biological control agents can be synergistic, additive, or antagonistic depending on the specific biological control agents as well as their rate, timing of application, and the host species. As demonstrated by Ferguson and Stiling (1996), synergistic interactions result in a higher mortality than the combined individual mortalities of the pest population. Additive interactions occur if the natural enemies do not interact, and thus, the total level of mortality is

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equivalent to the combined individual mortalities caused by each agent. The antagonistic interactions occur if the total mortality is less than when either natural enemy acts alone. Roy and Pell (2000) reported that synergistic interactions between pathogens and insect predators or parasitoids can enhance control efficacy, whereas antagonistic interactions reduce total control efficacy. Roy et al. (1998) stated that predators may consume pathogen-infected prey and thus may remove the pathogen from the environment. However, Caceres (2009) mentioned that such predators may defecate viable amount of a pathogen which increases the numbers of infected hosts and, consequently, the distribution of the pathogen in the environment. In addition, Fazal (2004) stated that integration of biological control agents may substantially contribute to sustainable management of damage caused by insects in both greenhouses and fields.

Bacillus thuringiensis

B. thuringiensis (*Bt*) is a Gram-positive, soil-dwelling bacterium commonly used as a biological control insecticide. It was first discovered in 1901 by the Japanese biologist Shigetane Ishiwatari as a cause of sotto disease that was killing silkworms, and named *Bacillus sotto*. In 1911, Ernst Berliner isolated this bacterium from dead Mediterranean flour moth in Thuringia, Germany, and named it *B. thuringiensis*. In 1915, Berliner reported the existence of a parasporal body or crystalline inclusion (called crystal) close to the endospore within *Bt* spore but the activity of the crystal was not then discovered. In 1956, it was found that the main insecticidal activity against insects was due to the parasporal crystal (Abbas 2018).

During sporulation process, *Bt* produces crystalline proteinaceous inclusion (parasporal inclusion body) adjacent to the endospore, which have has been found to be toxic for invertebrates, mainly insects from the orders Lepidoptera, Coleoptera, and Diptera) (Andrews et al. 1987). These parasporal inclusions (or α -endotoxins) are formed by different insecticidal crystal proteins and are encoded by Cry (from crystal) and Cyt (from cytoletic) genes (Hofte and Whitely 1989). *Bt* subspecies can synthesize more than one inclusion which may contain different Cry toxins (Hofte and Whitely 1989).

Mode of action of *Bacillus thuringiensis*

Bt spores have to be ingested by the susceptible insect to cause infection. The parasporal body (or crystal, or crystalline inclusion, known as Cry toxin) in *Bt* spore becomes active by proteolytic enzymes in the alkaline gut juice of the host (pH 8–10). Most Cry toxins are actually pro-toxins of about 130 to 140 kDa, and after activation, they become 60–70 kDa (Bravo et al. 2007). The activated toxin passes through the peritrophic membrane and binds to specific receptors on apical microvillar brush border membrane of the epithelial cells

of the midgut making pores through which the toxin penetrates to such cells. The cells then become swollen, and the swelling continues until the cells lyse, separate from the basement membrane, and fall in the lumen of the midgut. The alkaline gut juices then leak into the hemocoel causing increase of hemolymph pH which leads to paralysis and death of the insect (Soberon et al. 2010). However, Broderick et al. (2006) mentioned that the naturally occurring bacteria in the host-gut (*Escherichia coli* and *Enterobacter*) penetrate to the hemocoel through the disrupted epithelium, caused by *Bt* toxins, and multiply causing sepsis of the hemolymph and death of the insect. In moderately susceptible insects to *Bt*, such as *Spodoptera* spp., the endospore has a considerable role in killing the insect by producing toxins during its vegetative growth in the hemolymph (Crickmore et al. 2014). However, Gill et al. (1992) reported that the insects or any living organisms that do not have the receptors in gut epithelial cells are not killed by *Bt*.

***Bacillus thuringiensis* crops (*Bt* crops)**

Bt crops are plants genetically engineered (modified) to contain the toxins (Cry toxins) from the crystalline parasporal body to be resistant to certain insect pests. “Plant Genetic Systems,” in Belgium, was the first company to produce a *Bt* crop (tobacco) in laboratory in 1985, but the crop was not commercially successful. However, in 1995, the Environmental Protection Agency (EPA) in the USA approved the commercial production and distribution of the *Bt* crops (corn, cotton, potato, and tobacco). Recently, *Bt* crops are currently planted in almost 100 million ha worldwide. Adoption of *Bt* crops has greatly reduced the abundance of targeted pests in such crops and, in addition, has enabled the application of IPM programs and the increase of natural enemy populations (Abbas 2018). *Bt* toxins can be found in the whole plant including roots, stems, leaves, pollen, and fruits. However, concentrations can vary considerably in different plant tissues across different developmental stages of the plant and among different *Bt* toxins (Eisenring et al. 2017).

Interactions between *B. thuringiensis* and predators

Laboratory studies

Mahmoud (1992) found that both the 4th larval instar and adults of the coccinellid predator, *Coccinella undecimpunctata* (L.) (Coleoptera), attacked and consumed *Bt*-infected larvae of *Spodoptera littoralis* Bois. (Lep.: Noctuidae). No statistical differences in prey consumption were found between healthy and infected prey. In addition, no detrimental effects on the predator larvae were observed when fed on infected prey and they completed their development to adults which were capable of mating and ovipositing. The larvae and adults that fed

on infected prey were found to excrete viable spores in their feces.

Carvalho et al. (2012) studied the effect of *Bt*-infected larvae of *Plutella xylostella* (L.) as prey, on the nymphs and adults of the pentatomid predator, *Podisus nigrispinus* (Pallas) (Hemiptera), and found that *Bt* did not affect their biological parameters compared to the control. Similarly, Megalhaes et al. (2015) investigated the influence of *Bt* var. *kurstaki* and the commercial product "Agree" (a combination of *Bt* var. *kurstaki* and *Bt* var. *aizawai*) on the biological aspects of *P. nigrispinus* when fed on infected larvae of *P. xylostella*. They found that the infected larvae were consumed more than the healthy ones throughout the nymphal development with no effect on nymphal survival or the population growth parameters. However, de Carvalho et al. (2018) reported that rearing *P. nigrispinus* nymphs on *Bt*-treated larvae of *Tenebrio molitor* (L.) (Coleoptera: Tenebrionidae) affected the oviposition periods and the total egg numbers deposited by the predator's female.

Field studies

Dutton et al. (2003) assessed the effects of spraying Dipel (a *Bt* commercial product) against *Spodoptera litoralis* larvae infesting maize, on *Chrysoperla carnea* Steph. larvae in a greenhouse. The results showed negative impact on the predator's larvae including a significant increase in mortality, a prolonged developmental period, and a slight decrease in adult's weight.

Interactions between *B. thuringiensis* and parasitoids

Laboratory studies

Survival of parasitoid progeny in *Bt*-infected hosts

Mahmoud (1992) reported that *Bt*-infected *Spodoptera litoralis* larvae had no significant effect on percentages of parasitism by the braconid larval parasitoid, *Microplitis rufiventris* Kok. When the *Bt*-treated larvae were exposed to the parasitoid 1, 2, 3, 4, and 5 days post-infection, percentages of successful parasitism averaged 65, 35, 45, 60, and 60%, respectively, which did not differ significantly from those in healthy larvae. Blumberg et al. (1997) stated that development of the immatures of *Microplitis croceipes* (Cresson) in *Helicoverpa armigera* (H.) host larvae *Bt*-infected 3 days before exposure to the parasitoid was detrimental to the parasitoid because of premature host mortality. However, feeding parasitoid adults on *Bt* preparation mixed with honey was not harmful to the wasps.

Atwood et al. (1997) evaluated the impact of *Bt* var. *kurstaki* on *Cotesia marginiventris* (Cresson) survival in parasitized *Heliothis virescens* (Fab.) larvae. The infected larvae were exposed to the parasitoid females immediately, 24 or 48 h after parasitism. The results showed that combination of *Bt* and *Cotesia* increased mortality

of host larvae than that of either alone. Emergence of *C. marginiventris* larvae from parasitized host larvae was inversely related to *Bt* concentration and the timing of *Bt* treatment after parasitism. In all instances, greater adult parasitoid emergence was noted when host exposure to *Bt* was delayed for 48 h post-parasitism. Similar results were obtained by Atwood et al. (1999) with *Bt*, the braconid *Microplitis croceipes*, and the host *H. virescens* and at the same concentrations of *Bt*.

Ebrahimi et al. (2012) evaluated the effects of *Bt* var. *kurstaki* on immature stages of the ichneumonid parasitoid, *Diadegma insulare* (Cresson), within larvae of its host *Plutella xylostella* and on the adult stage as a *Bt*-honey solution. They found that percent formation of the parasitoid pupae from host larvae treated with LC₁₀, LC₃₀, and LC₅₀ of *Bt* and then exposed to the parasitoid females after 48 h were 5, 3, and 2%, respectively, which were much lower than that of the parasitoid alone (41%). They also found that the survival of adult parasitoid fed on *Bt*-honey solution at the field rate of *Bt* product (1000 ppm) did not differ significantly (95%) from that of the control (97%).

Discrimination between *Bt*-infected and healthy larvae

Pre-feeding of *H. armigera* on an artificial diet treated with Dipel at lethal concentrations of 0.08 and 0.16 mg/g of the diet did not prevent *Microplitis croceipes* from oviposition in the infected host larvae (Blumberg et al. 1997). Mohan et al. (2008) found that the female parasitoid, *Campoletis chloridae* Uchida, did not discriminate between healthy and *Bt*-infected larvae of *Helicoverpa armigera* for oviposition. Schoenmaker et al. (2011) found that the females of the ichneumonid parasitoid, *Tranosema rostrale rostrale* (Brishke), were able to detect and avoid *Bt*-infected host larvae (the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lep.: Tortricidae)) that exhibited a lethal response to the pathogen and, to a lesser extent, larvae that could survive *Bt* infection.

Effect of *Bt* on biological parameters of the parasitoids

Wallner et al. (1983) noticed an indirect effect on the braconid parasitoid, *Rogas lymantriae* Watanabe, parasitizing the gypsy moth, *Lymantria dispar* (L.), larvae that fed on artificial diet mixed with *Bt*. The sex ratio among the parasitoid offspring was found to lean towards males as the female parasitoid deposited more fertilized eggs in larger untreated host larvae. Dequech et al. (2005) investigated the effect of *Bt* var. *aizawai* on larvae of *Spodoptera frugiperda* (Smith) and its parasitoid, *Campoletis flavicincta* (Ashmead). They found that the average mortality percentage of both (parasitized and infected) larvae was higher (96.0%) than the only parasitized (78.4%) and the only infected ones (44.3%). The biological parameters of the offspring of the parasitoids' adults that had emerged from infected parasitized larvae were not affected.

Mohan et al. (2008) reported that the growth and survival of the parasitoid, *Campoletis chlorideae*, in its host larvae, *Helicoverpa armigera*, were normal when the host larvae were fed with sub-lethal doses or subjected to short time exposure to lethal doses of *Btk*. However, the parasitoid offspring developed slowly, and the pupal and adult durations as well as adult emergence rate were significantly reduced if the parasitoid was developing inside a severely *Bt*-infected host larvae. Oluwafemi et al. (2009) found that *Bt* or *Habrobracon hebetor* Say alone caused 41.7 and 35.4% mortality, respectively, in *Plutia interpunctella* (H.) larvae whereas the combined treatment with *Bt* and the parasitoid increased host mortality to 86%.

Famil et al. (2012) investigated the longevity, host preference, lengths of life stages, and numbers of offspring of the ecto-larval parasitoid, *H. hebetor*, on its host, *Ephestia kuehniella* Zeller, larvae treated with lethal and sub-lethal doses of *Bt*. They found that the average daily number of eggs deposited/parasitoid female decreased from 3.9 in the control to 1.4 and 2.7 in lethal and sub-lethal doses, respectively. The respective average of longevity of adult parasitoid decreased from 15.6 to 12.3 and 13.7 days. At the lethal dose of *Bt* treatment, duration of the egg and larval stages of the parasitoid showed significant prolongation compared to the control but the pupal stage duration decreased.

Similarly, Sedaratian et al. (2014) investigated the effects of *Bt* on biological parameters of *H. hebetor* parasitizing *H. armigera*. The neonate larvae were treated with sub-lethal doses of *Bt* (LC₂₅), and the surviving larvae that reached the 4th instar were then exposed to the parasitoid for 24 h. The results showed that the successful development of immature stages (from egg to adult) was 89% in the control compared to 61% in *Bt*-treated larvae. The total developmental period of the parasitoid (from egg to adult) averaged 14.1 and 12.3 days, respectively. The respective total deposited eggs/female were 140.8 and 41.2.

Salles et al. (2015) reported that *Btk* infection of *Spodoptera exigua* (H.) larvae previously parasitized with *Campoletis flavicincta* did not affect, significantly, the developmental periods of the parasitoid or its longevity. de Carvalho et al. (2018) investigated the possible impact of *Bt* on the pupal parasitoid *Palmistichus elaeisis* Delvare and LaSalle (Hym.: Eulophidae) of *Tenebrio molitor* when the larvae were fed on wheat bran treated with 6 different concentrations of *Bt* ("Agree"; commercial product) (0–4 gm/kg). When the formed pupae were exposed to *Palmistichus* females. The biological characters of emerged adult parasitoids were not affected.

Direct effect of *Bt* on adult parasitoids

Mohan et al. (2008) reported that there were no differences in longevity of the parasitoids of, *Campoletis chlorideae* adults fed on bee honey solution containing different

concentrations of *Bt* compared to those fed only on honey solution. Marchetti et al. (2012) studied the effect of feeding adults of *Exorista larvarum* (L.) (Dipt.: Tachinidae), a parasitoid of *Galleria mellonella* (L.) larvae, on sugar soaked with the commercial *Bt* var. *kurstaki* (Foray 48B) at 3 times the dose which is highly virulent to lepidopteran insects. The study showed that the longevity of males and females of the parasitoid, the number of eggs laid by the female, and the percentage of larvae that developed to pupae were not significantly affected compared to feeding on distilled water.

Field studies

Nealis and van Frankenhuyzen (1990) investigated the interactions between *Bt* and the braconid parasitoid, *Apanteles fumiferanae* (Viereck), of the spruce budworm, *Choristoneura fumiferana*, in a semi-field trial. Treatment was carried out by placing parasitized late 3rd instar larvae on foliage before spraying *Bt* at the recommended application rate. The results showed that *Bt* reduced the parasitoid populations by 50–60 % by killing the host before parasitoid emergence. This negative impact of *Bt* was decreased when spraying the parasitized larvae with *Bt* after reaching late 4th instar.

Schoenmaker et al. (2011), in a semi-field experiment, stated that when *Bt*-treated and untreated larvae of the spruce budworm, *C. fumiferana*, were exposed (in caged pots) for 1 week to a complex of indigenous parasitoids, there were no differences between treatments in the rates of parasitism by either the echeumonid, *Tranosema rostrale rostrale*, or the tachinid, *Actia interrupta* Curran, parasitoids. Percentages of parasitism averaged 91 and 92% for untreated and treated larvae, respectively. Also, Singh and Mathew (2015), investigating the effects of *Bt* sprays on natural enemies of the spruce budworm, *C. fumiferana*, found a range of effects from synergism, repellency, and toxicity to no effect.

Effect of *Bt* crops on predators

Laboratory studies

By feeding on *Bt* toxins

Hilbeck et al. (1998) fed the larvae of *Chrysoperla carnea* on artificial diet mixed with Cry1Ab toxin and found that the total mortality in larvae was significantly higher (57%) than in the untreated control (30%). Also, significantly more larvae died (29%) when received Cry1Ab later during their development compared to the control ones (17%). However, no differences in developmental period were observed between treated and untreated larvae. In another study, Hilbeck et al. (1999) obtained almost similar results when *C. carnea* larvae were fed on *Spodoptera littoralis* larvae fed on diet mixed with Cry1Ab and Cry2A toxins at different concentrations.

By feeding on pollen

Mendelsohn et al. (2003) found that pollen from *Bt* corn, containing Cry toxins, which was at relatively very high doses, was not toxic to coccinellids or *Chrysoperla* spp. Adults of the predator, *Chrysoperla carnea*, were found to feed exclusively on pollen and nectar (Li et al. 2010), and its larvae can supplement their diet with pollen (Meissle et al. 2014). Liu et al. (2016) reared the larvae of the coccinellid, *Propylea japonica*, on the pollen of *Bt* or non-*Bt* corn from the first instar larvae until pupation. They found that over 70% of larvae of both groups developed to adults and pupation rates (83 and 84%, respectively) and ecdysis rates (75 and 74%, respectively) did not differ significantly. Romeis et al. (2019) reported that insect predators such as chrysopids (Neuroptera), coccinellids (Coleoptera), and anthocorids (Hemiptera) were found to feed on the plant pollen especially in the absence of their prey.

By feeding in on prey fed on *Bt* plants

Romeis et al. (2019) reported that the predators, *Geocoris* spp. (Hem.:Geocoridae) and *Nabis* spp. (Hem.:Nabidae), were noticed to feed directly on the tissues of plant leaves by sucking the sap, whereas the soil predators such as earwigs (Dermaptera: Labiduridae) and *Calosoma* spp. (Col: Carabidae) might feed on plant roots in the soil. Such habits will make these predators come in contact with Cry toxins in *Bt* crops. However, it does not seem that *Bt* toxins occur in phloem tissue sap in the plants or they may be less occurring than in the green tissues. Consequently, the aphids which suck plant sap as well as their predators will not be harmed in *Bt* crops. In addition, the honeydew of aphids, which is an important source of energy to parasitoids and predators, did not contain *Bt* toxins.

Ponsard et al. (2002) investigated the effect of *Bt* cotton on adult longevity of 4 hemipteran predators of cotton pests. The adults were fed on *Spodoptera exigua* larvae reared on *Bt* cotton leaves. They found that the longevity of *Orius tristicolor* (White) (Fam. Anthocoridae) and *Geocoris punctipes* (Say) (Fam. Geocoridae) decreased by 28 and 27%, respectively, compared to control adults. No effects were found for *Nabis* sp. (Fam. Nabidae) and *Zelus* sp. (Fam. Reduviidae). However, Head et al. (2005) found a non-significant negative impact of *Bt* cotton on *Geocoris* spp., *Orius* spp., ladybeetles, and spiders in comparison with non-*Bt* cotton. Also, Torres and Ruberson (2006) found no detrimental effects on development and reproduction of *G. punctipes* fed on prey reared on leaves of *Bt* cotton.

Similarly, Bai et al. (2006) investigated the effects of *Bt* rice, containing Cry1Ab toxin, on the coccinellid, *Propylea japonica* (Thunberg), by feeding its larvae on the nymphs of the plant hopper, *Nilaparvata lugens* (Stal) (Hem.: Delphacidae), reared on leaves of *Bt* rice. The

results showed that the developmental period, pupation rate, adult ecdysis, and weight of pupae and adults of the predator did not differ significantly than from those of the control. Zhao et al. (2013) evaluated the effect of *Bt* toxins on *P. japonica* when fed on *Aphis gossypii* Glover infesting *Bt* cotton expressing Cry1Ac toxin. The results indicated that there were no distinct differences in the larval development, emerged female weight, or fecundity between predators reared on aphids infesting *Bt* cotton or conventional cotton.

Romeis et al. (2012) reported that the red spider mite, *Tetranychus urtica* Koch, a natural prey for the larvae of the coccinellid, *Adalia bipunctata* (L.), was fed on *Bt* corn before exposure to the predator larvae. The mortality rate among the treated *Adalia* larvae did not differ significantly from that of the control group which was fed on mites reared on conventional corn.

Field studies**In *Bt* crops in general**

Men et al. (2003) and Pilcher et al. (2005) reported decreased populations of predators and parasitoids in transgenic crops compared to conventional ones.

Mendelsohn et al. (2003) stated that beneficial arthropods were noticed to be substantially more abundant in *Bt* crops than in crops treated with chemical pesticides. Naranjo (2009) reported that until 2008, over 63 field studies had been conducted to assess the potential impacts of *Bt* crops on non-target arthropods (in 6 classes, 21 orders, and 185 species) with vast majority of these being natural enemies. All these studies beside tens of studies, as reported (Dang et al. 2017 and Pelligrino et al. 2018), concluded that *Bt* crops have minimal or negligible effects on non-target arthropods, mainly predators and parasitoids.

Similarly, Romeis et al. (2019) reported that over the past 20+ years, extensive experience and insight have been gained through laboratory and field studies of non-target effects of crops producing Cry proteins. Overall, the vast majority of the studies demonstrated that the insecticidal proteins developed today do not cause adverse effects on natural enemies of target pests. Furthermore, when *Bt* crops replace synthetic chemical insecticides for pest control, this creates an environmental support of the conservation of natural enemies.

In *Bt* cotton

A 3-year field study carried out by Moar et al. (2002) revealed that there were no adverse effects on non-target arthropods (parasitoids and predators) in *Bt* cotton fields compared to conventionally grown cotton. In a 6-year field study, Naranjo (2005) assessed the long-term impact of *Bt* cotton producing Cry1Ac toxin on 22 species and strains of foliar-dwelling natural enemies in Arizona.

The study revealed no chronic or long-term effects of *Bt* cotton on such natural enemies. Almost similar results were obtained by Sharma et al. (2007) who recorded higher populations of chrysopids, coccinellids, and spiders in *Bt* cotton than in conventional cotton. Also, Mellet and Scheoman (2007) found that *Bt* cotton had no adverse impact on the abundance of coccinellids.

Yao et al. (2012) studied the potential effects of *Bt* cotton on the seasonal abundance of 5 groups of predators during 3 years (2009–2011) in China. The groups were as follows: (1) the coccinellids, *C. undecimpunctata* (L.), *Adonia variegata* (Goeze), and *Stethorus* sp.; (2) the chrysopids, *Chrysopa formosa* Brauer and *Chrysoperla sinica* (Tjeder); (3) the thripid, *Acolothrips fasciatus* (L.); (4) the anthocorid, *Orius similis* Zhang; and (5) the spider, *Misumenopos tricuspudata* (Fabricius) (Acari: Thumicidae). They found that species composition and seasonal abundance of such predators did not differ significantly between those in *Bt* and non-*Bt* cotton every year.

Lu et al. (2012) reported a remarkable decline in aphid populations in *Bt* cotton fields in 36 locations in 6 districts north of China. They related this decline to the increase of populations of the coccinellids, chrysopids, and spiders. In addition, these increased populations of the predators on *Bt* cotton were found to have a considerable role for insect biological control on cotton, corn, and peanut crops adjacent to *Bt* cotton. Also, Dahi (2013) reported that *Bt* cotton producing Cry1Ac and Cry2Ab did not affect the populations or abundance of common predators-species prevailing in cotton fields in Egypt. These results agree with those reported by Dhillon and Sharma (2013).

Arshad et al. (2015) estimated the populations of insect predators from the 1st week of July to the 2nd week of November in *Bt* cotton and conventional cotton fields. They found that the population densities and abundance of the predators, *C. carnea*, *Coccinella septempunctata*, *Geocoris* spp., and *Minochilus sexmaculatus* (Fab.) (Coccinellidae), did not differ significantly in both fields.

In *Bt* corn

Al-Deeb and Wilde (2003) found that the populations of prevailing predators in a *Bt* corn field did not differ significantly from those on a conventional corn field. These predators were *Hyppodamia convergens* Guer, *Orius insidiosus* (Say), and *Scymnuss* spp. Similarly, Wolfenbarger et al. (2008) detected no significant negative effects for the predators, *Orius* spp., *Coleomegilla* spp., *Hypodamia* spp., or *Chrysoperla* spp., in *Bt* maize.

Effect of *Bt* crops on parasitoids

Laboratory studies

Effect on biological parameters of the parasitoids

Baur and Boethel (2003) stated that the parasitoid, *Cotesia marginiventris*, developed significantly faster in *Pseudaletia*

includens (Walker) larvae fed on the conventional cotton than on *Bt* cotton. However, the parasitoid which developed in host larvae feeding on *Bt* cotton suffered reduced longevity and lower fecundity. Also, *Bt* cotton affected the development of *P. includens* parasitized with the egg-larval parasitoid, *Copidosoma floridanum* (Ashmead), as well as the biological parameters of the parasitoid. Fewer *C. floridanum* adults were found to emerge from hosts fed on *Bt* cotton, but the longevity of such adults was not affected.

Prutz and Dettner (2004) assessed the potential effect of *Bt* corn leaves on *Chilo partellus* (Swinhoe) (Lep.: Crambidae) and its braconid larval parasitoid, *Cotesia flavipes* (Cameron). The percentage of parasitized host larvae which gave rise to adult parasitoids was reduced, and the fresh weight of parasitoid pupae and the dry weight of adults were lower than those from the control. Similarly, Vojtech et al. (2005) stated that *Cotesia marginiventris* (Cresson), the larval parasitoid of *Spodoptera littoralis*, was affected when its host larvae were reared on leaves and stems of *Bt* corn. The survival of parasitoid larvae and their development period inside the host larvae as well as the cocoon weight were significantly negatively affected.

Cui et al. (2005) reported that the survival and developmental rates of *Microplitis* sp. and *Campoletis chloridae*, the parasitoids of *H. armigera*, decreased when their host was reared on leaves of *Bt* cotton. Sanders et al. (2007) investigated the impact of *Bt* maize expressing Cry1Ab toxin on the development and behavior of the parasitoid *Campoletis sonorensis* (Cameron). The results showed that adult parasitoids which emerged from *Spodoptera frugiperda* larvae fed on *Bt* maize were significantly smaller (by 15–30%) than those emerged from larvae fed on conventional maize. However, the total developmental period of the parasitoid was not affected by *Bt* maize treatment. In choice tests, female parasitoids displayed no preference for host larvae fed on *Bt* maize or conventional maize. No Cry1Ab was detected within adult parasitoids. Salles et al. (2015) investigated the interactions between *Bt* crops, *S. frugiperda*, and its larval parasitoid, *Campoletis flavicincta*. They found that when parasitized and unparasitized larvae were fed on *Bt* maize (expressing Cry1Ab) for 10 days, their mortality did not differ significantly (90 and 87.7%, respectively).

Solmaz et al. (2014) studied the effect of *Bt* cotton on some biological parameters of *Encarsia formosa* Gahan, a parasitoid of *Bemisia tabaci* (Genn.). The results indicated that the total developmental period and the pre-oviposition period of parasitoid females which emerged from the host reared in the *Bt* cotton were significantly longer than those from non-*Bt* cotton. The total numbers of eggs deposited/female were 23.6 and 43.8/female in the *Bt* and non-*Bt* cotton, respectively.

Discrimination between *Bt*-infected and uninfected host

Sanders et al. (2007), in choice tests, found that females of *Campoletis sonorensis* (Cameron) displayed no preference for its host larva (*S. frugiperda*) fed on *Bt* maize or conventional maize.

Direct effect of *Bt* toxins on adult parasitoids

Marchetti et al. (2012) studied the effect of feeding adults of *Exorista larvarum* (Dipt.: Tachinidae), a parasitoid of *Galleria mellonella* (L.) larvae, on sugar soaked with the Cry9Aa from *Bt* var. *galleriae* at 3 times the dose which is highly virulent to lepidopteran insects. The study showed that the longevity of males and females of the parasitoid, the numbers of eggs laid by the female, and the percentage of larvae that gave rise to pupae were not significantly affected compared to feeding on distilled water.

Field studies

Yang et al. (2005) reported that population densities of the parasitoids, *Trichogramma confusum*, *Campoletis chloridae*, and *Meteorus pulchroconis*, were significantly lower in *Bt* cotton fields than in conventional cotton ones. The authors claimed that such lower populations of parasitoids in *Bt* crops could be due to the reduced density of the host insect, *Helicoverpa armigera*. Also, Wu and Guo (2005) recorded lower populations of *Trichogramma* spp., *Microplitis* *Microplitis* sp., and *Campoletis* sp. parasitoids in *Bt* cotton as compared to non-*Bt* cotton.

In contrast, Romeis et al. (2006) reported that field studies confirmed that the abundance and activity of parasitoids were found to be similar in *Bt* and non-*Bt* crops. Also, Fernandes et al. (2007) found no adverse effects of *Bt* maize on the populations of *Trichogramma* parasitoids. Arshad et al. (2015) estimated the populations of insect parasitoids from the 1st week of July to the 2nd week of November in *Bt* cotton and conventional cotton fields. They found that the abundance of the parasitoids, *Trichogramma* spp. and *Apanteles* spp., did not differ significantly in both fields.

Conclusion

Some laboratory studies revealed that *B. thuringiensis* did not cause detrimental effects on the biological parameters of parasitoids and predators whereas others showed significant negative impact on such natural enemies. The negative impact of *Bt*-infected larvae on the development of parasitoids of such larvae is related to *Bt* concentration and timing of infection. Overall, the vast majority of the studies demonstrated that the insecticidal proteins developed today do not cause adverse effects on natural enemies (parasitoids and predators) of target pests.

Abbreviations

Bt: *Bacillus thuringiensis*; Cry: Crystal; Cyt: Cytolethic; IGP: Intraguild predation

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