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Survival and development of *Campoletis chlorideae* on various insect and crop hosts: implications for *Bt*-transgenic crops

M. K. Dhillon and H. C. Sharma
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India

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Abstract: The parasitic wasp, *Campoletis chlorideae* is an important larval parasitoid of *Helicoverpa armigera* a serious pest of cotton, grain legumes and cereals. Large-scale deployment of *Bt*-transgenic crops with resistance to *H. armigera* may have potential consequences for the development and survival of *C. chlorideae*. Therefore, we studied the tritrophic interactions of *C. chlorideae* involving eight insect host species and six host crops under laboratory conditions. The recovery of *H. armigera* larvae following release was greater on pigeonpea and chickpea when compared with cotton, groundnut and pearl millet. The parasitism by *C. chlorideae* females was least with reduction in cocoon formation and adult emergence on *H. armigera* larvae released on chickpea. Host insects also had significant effect on the development and survival of *C. chlorideae*. The larval period of *C. chlorideae* was prolonged by 2–3 days on *Spodoptera exigua*, *Mythimna separata* and *Achaea janata* when compared with *H. armigera*, *Helicoverpa assulta* and *Spodoptera litura*. Maximum cocoon formation and adult emergence were recorded on *H. armigera* (82.4% and 70.5%, respectively) than on other insect hosts. These studies have important implications on development and survival of *C. chlorideae* on alternate insect hosts on non-transgenic crop plants, when there is paucity of *H. armigera* larvae on transgenic crops expressing *Bt*-toxins.

Key words: *Achaea janata*, *Helicoverpa armigera*, *Mythimna separata*, *Spodoptera litura*, alternative hosts, biocontrol, transgenics, tritrophic interactions

1 Introduction

The larval endoparasitoid, *Campoletis chlorideae* Uchida (Hym., Ichneumonidae), parasitizes diverse insect species of Lepidoptera (Yan and Wang 2006), however, information on its parasitism potential, development and survival on different insect and crop hosts is scanty. Under natural conditions, *Helicoverpa armigera* (Hübner) is the most preferred host of *C. chlorideae* on a number of crops, such as cotton, groundnut, chickpea, pigeonpea, sorghum and pearl millet (Patel and Patel 1972; Bhatnagar et al. 1982; Kumar et al. 1994). However, introductions of transgenic crops have raised the concerns regarding their impact on natural enemies (Sharma and Ortiz 2000).

The eggs of *C. chlorideae* hatch in 1.0–1.5 days, total egg + larval development period takes about 7–8 days, and the larval feeding is completed on the *H. armigera* larva (Sharma and Dhillon 2005). On completion of larval development, the *C. chlorideae* larva emerges from the host larva. It weaves a cocoon around itself and the pupal period extends for about 6 days. Post-embryonic development of *C. chlorideae* is completed in about 13–14 days.

Considerable progress has been made over the past two decades in handling and introduction of novel genes into crop plants to impart resistance to biotic stresses, tolerance to abiotic stresses, improve nutrition and increase crop yields. Genes from bacteria, such as *Bacillus thuringiensis* (*Bt*), have been deployed successfully for pest control through transgenic crops on a commercial scale (Hilder and Boulter 1999; Sharma et al. 2001). Transgenic cotton cultivars with resistance to *H. armigera* have been released for cultivation in several countries (James 2005), while transgenic chickpea (Ramakrishna et al. 2005) and pigeonpea (Sreelatha et al. 2005) with resistance to this pest are currently under development. To ensure a sustainable deployment of transgenic insect-resistant plants, it is important to assess their compatibility with other control tactics including the natural enemies. The *Bt* proteins prolong the larval period, reduce cocoon formation and adult emergence of *C. chlorideae* when reared on *Bt*-intoxicated *H. armigera* larvae (H. C. Sharma, unpublished data; Zhang et al. 2006). Therefore, deployment of *Bt*-transgenic pigeonpea, chickpea and cotton with resistance to *H. armigera* might have a considerable influence on the activity and abundance of *C. chlorideae* in different agro-ecosystems. Thus, there is a need to generate information on influence of insect and crop hosts as alternatives for the development and survival of *C. chlorideae* under the situations of large-scale cultivation of *Bt*-transgenic crops. Therefore, the

present studies were undertaken to investigate the influence of the insect and crop hosts on the development and survival of *C. chlorideae* under laboratory conditions. These studies have potential implications for developing appropriate strategies for area-wide deployment of transgenic crops, and conservation of natural enemies in the ecosystem.

2 Materials and Methods

2.1 Insect cultures

The larvae of *H. armigera* and *Helicoverpa assulta* (Guenee) were collected from farmers' fields, and reared on chickpea-based semi-synthetic artificial diet (Armes et al. 1992) individually in 6-cell well (3 cm diameter and 2.5 cm deep) plates till pupation under laboratory conditions. Moths were released in wooden cages (30 × 30 × 30 cm) and fed on 10% sucrose solution. Nappy liners (soft cotton cloth pieces) were placed inside the cage for oviposition. The cages were kept at 27 ± 2°C and 65–85% RH in the laboratory. Larvae of *H. armigera* were used to maintain the culture of *C. chlorideae* under laboratory conditions.

The *Spodoptera litura* (Fab.) and *S. exigua* (Hübner) egg masses collected from the research farm were brought to the laboratory. After egg hatch, the larvae were reared on sorghum leaf powder based semi-synthetic artificial diet used for rearing *Chilo partellus* (Swinhoe) (Taneja and Leuschner 1985). Adults were released in an oviposition cage made up of an open-ended cylinder (25 cm high and 25 cm diameter) made of galvanized iron wire net with 36 mm mesh size (Sharma et al. 1992). A fine georgette cloth with 6 mm holes at regular intervals was fitted around the outer side of the cylinder. A sheet of white glycine paper (25 × 80 cm) was wrapped outside of the cylindrical cage to serve as an oviposition substratum. Two plastic saucers covered with mosquito net were placed at both the ends of the cylinder. The adult moths were fed on 10% sucrose solution. The cages were kept at 27 ± 2°C and 65–85% RH in the laboratory. The eggs were laid in batches on the glycine paper through the holes from the wire-cage. The glycine paper was changed daily. After egg hatch, the neonates were released on castor leaves, and kept at 10°C in an incubator to have a regular supply of the late second-instars for the experiments.

Larvae of oriental armyworm, *Mythimna separata* (Walker) were collected from sorghum fields at the research farm, and kept in the greenhouse (28 ± 2°C and 70–80% RH). The larvae were reared in plastic jars of 1 l capacity on sorghum leaves. Food was changed as needed. The pupae were kept in plastic jars on moist vermiculite to avoid desiccation. The moths (males and females) were released in a large wooden cage (60 × 65 × 45 cm) in the greenhouse, and provided with dry sorghum leaves as an oviposition substrate. The dry sorghum leaves containing eggs were removed daily and kept in plastic cups for hatching. The late second or early third-instars (3 days old) of *M. separata* were used for parasitization by *C. chlorideae* females.

The late-instars of *Achaea janata* (Linn.) were collected from the castor fields at the research farm, and released inside a large wooden cage (60 × 65 × 45 cm) on castor leaves placed in 250 ml conical flasks containing water. The castor leaves were changed as needed. The pupae were kept in 1 l plastic jars on moist vermiculite. The moths (males and females) were released in a wooden cage in the greenhouse, and provided with castor leaves as oviposition substrate. The conical flasks having castor leaves with eggs were removed daily and kept in wooden cages (30 × 30 × 30 cm) for egg hatching. The late second or early third-instars (3 days old) of the *A. janata* were used for parasitism by *C. chlorideae*.

The rice grain moth, *Corcyra cephalonica* (Stainton) and pink stem borer, *Sesamia inferens* (Walker) were mass reared in the insectary on their natural hosts. Ten- to 16-day-old larvae of *C. cephalonica* (separated from the sorghum grains), and the late second or early third-instars (5 days old) of *S. inferens* were exposed to *C. chlorideae* females for parasitism. After parasitism, the larvae were reared on the respective hosts/artificial diets.

The cocoons of *C. chlorideae* were collected from chickpea fields, and placed individually in glass vials for adult emergence. The wasps were released in 2 l plastic cages for mating, and fed on 10% honey solution. For oviposition, the mated females were transferred to transparent plastic vials (15 ml capacity) kept in an inverted condition in a Petri dish. Single *H. armigera* larva was offered to single female parasitoid for oviposition. In general, the parasitism by *C. chlorideae* took 1–2 min. The parasitized *H. armigera* larvae were removed and placed on chickpea based artificial diet for further development. The culture was maintained at 27 ± 2°C and 65–75% RH.

2.2 Parasitism potential, survival and development of *Campoletis chlorideae* on different insect hosts

Influence of eight host insect larvae (*H. armigera*, *H. assulta*, *S. litura*, *S. exigua*, *M. separata*, *S. inferens*, *A. janata* and *C. cephalonica*) on survival and development of *C. chlorideae* was studied under laboratory conditions. A single host insect larva was offered to single parasitoid female for oviposition at a time. After oviposition, the larvae were removed, and placed on the respective diets for further development. For oviposition, the mated females were transferred to transparent plastic vials (15 ml capacity) kept in an inverted condition on a Petri dish. Three different parasitoid females were used to parasitize fifty larvae of *H. armigera*, *H. assulta*, *S. litura*, *S. exigua*, *M. separata*, *A. janata* and *C. cephalonica* each per replication. The experiments were conducted in a completely randomized design with three replications. Observations were recorded on percentage of host larvae parasitized by *C. chlorideae* (% cocoon formation), egg + larval period (hereafter larval period), pupal period, adult emergence, stabbings per female and sex ratio.

2.3 Influence of host plants on parasitism of *Helicoverpa armigera* larvae by *Campoletis chlorideae*

Studies on the effect of different host plants on parasitism of *H. armigera* larvae by *C. chlorideae* was studied under no-choice and multi-choice conditions at 27 ± 2°C in the laboratory. Six host crops of *H. armigera* (cotton, groundnut, chickpea, pigeonpea, sorghum and pearl millet) were grown in the field under normal package of practices without insecticide application. The seedlings were thinned 1 week after crop emergence. Inflorescences/terminal branches of cotton, groundnut, chickpea and pigeonpea, and the panicles of sorghum and pearl millet at milk stage excised from the plants in the field were immediately placed in conical flasks (150 ml) containing 100 ml of 1% sucrose solution to keep the plants in a turgid condition. The inflorescences/panicles were secured with cotton plugs to keep them in an upright position. The conical flasks with inflorescences/panicles were kept individually (no-choice condition) in the wooden cages (30 × 30 × 30 cm), and 30 laboratory-reared *H. armigera* second instar larvae were released onto inflorescence/panicle

in each cage. Three pairs of *C. chlorideae* were then released inside the cage for parasitism. Under multi-choice conditions, all the host plants were arranged in a circular arena in the wooden cage (60 × 65 × 45 cm), and thirty *H. armigera* larvae were released on each host plant inside the cage. Ten pairs of *C. chlorideae* were released inside the cage, and allowed free access to parasitize the larvae of *H. armigera* for 48 h. The larvae exposed to the parasitoid were removed from the respective hosts inside the cage, kept individually in 15 ml vials, and provided food of the respective host plant or artificial diet. The experiments were conducted in a completely randomized design with three replications. Observations were recorded on number of *H. armigera* larvae recovered and parasitized. Data were also recorded on pupal period, adult emergence and sex ratio of the parasitoid.

2.4 Statistical analysis

The data were subjected to analysis of variance (ANOVA) using GENSTAT, (Lawes Agricultural Trust, Rothamstead Experimental Station, UK) 8.0 version in a completely randomized design. The treatment means were compared by least significant differences (LSD) at P = 0.05. The figures presented in tables are the means across replications with F-probability and LSD values.

3 Results

3.1 Influence of host insects on parasitism potential, survival and development of *Campoletis chlorideae*

Host insects had a significant influence on larval and pupal periods, cocoon mortality, sex ratio (table 1), and percent parasitism and adult emergence (fig. 1) of *C. chlorideae*. There was no parasitism by *C. chlorideae* on the larvae of *C. cephalonica* and *S. inferens*. The larval and pupal periods of *C. chlorideae* on different insect hosts varied from 8.1 to 11.7 and 5.2 to 7.4 days respectively (table 1). Larval duration of *C. chlorideae* was prolonged significantly when reared on *M. separata*, *S. exigua* and *A. janata* (10.5–11.7 days) when compared with that on *H. armigera*, *H. assulta* and *S. litura* (8.1–8.5 days). Pupal period was shorter on *H. armigera* and *M. separata*, but significantly prolonged (by 1.5–2.2 days) on *A. janata*. Cocoon formation was maximum on *H. armigera* (81.6%) and minimum on *A. janata* (5.9%) (fig. 1). Mortality of

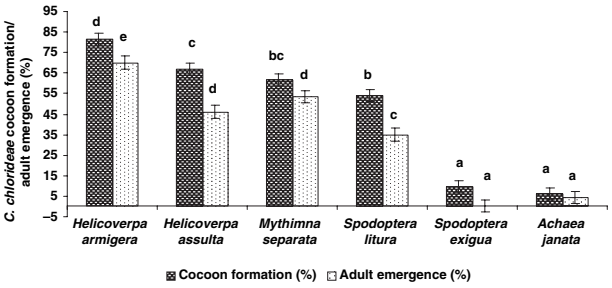

Fig. 1. *Cocoon formation and adult emergence of the parasitic wasp,* Campoletis chlorideae *on different insect hosts. The bars followed by the same letter are statistically nonsignificant at P = 0.05*

C. chlorideae cocoons on different insect hosts varied from 1.5% to 20.8%, being lowest on *A. janata* and highest on *H. assulta* (table 1). Adult emergence was significantly greater on *H. armigera* (70.1%) than on other insect hosts, being lower on *S. exigua* and *A. janata* (< 5%) (fig. 1). Parasitoid stabbings were significantly greater on *H. assulta* (192.0 stabbings per female) than on *H. armigera* and *S. litura* (139.4–170.0 stabbings per female) (table 1). Significantly more females than males (1 : 1.4) were recorded on *H. armigera*, while the reverse was true on *S. litura* (1 : 0.4).

3.2 Influence of host plants on parasitism potential of *Campoletis chlorideae*

Under no-choice and multi-choice conditions, the host plants showed a marked effect on parasitism of *H. armigera* by *C. chlorideae* (table 2 and fig. 2). Under no-choice conditions, significantly greater numbers of *H. armigera* larvae were recovered on cotton (85.6%) and sorghum (82.7%) than on other host plants, and being lowest on pearl millet (50.9%). Under multi-choice conditions, the recovery of *H. armigera* larvae was significantly greater on pigeonpea (91.3%) and chickpea (80.4%) than on other host plants, and least on groundnut (62.4%). Parasitism of *H. armigera* larvae by *C. chlorideae* and adult emergence were significantly greater on cotton and pearl millet than on other host plants, both under no-choice (fig. 2a) and multi-choice (fig. 2b) conditions. On chickpea, the parasitism of *H. armigera* by *C. chlorideae* (13.4% and 21.2%), and adult emergence (9.1% and 17.6%) were low under no-choice (fig. 2a) and multi-choice (fig. 2b) conditions respectively. In

Table 1. *Influence of insect hosts on survival, development and progeny production of the parasitic wasp,* Campoletis chlorideae *(ICRISAT, Patancheru, India)*

Insect host	Egg + larval period (days)	Pupal period (days)	Cocoon mortality (%)	Stabbings per female (no.)	Sex ratio (male : female)
Helicoverpa armigera	8.1 a	5.9 ab	11.5 bc	170.0 b	1 : 1.4 c
Helicoverpa assulta	8.5 a	6.2 b	20.8 d	192.0 c	1 : 0.9 b
Spodoptera litura	8.5 a	6.4 b	18.9 cd	139.4 a	1 : 0.4 a
Spodoptera exigua	11.0 bc	6.6 b	9.8 b	*	*
Mythimna separata	11.7 c	5.2 a	8.4 ab	*	*
Achaea janata	10.5 b	7.4 c	1.5 a	*	*
F-probability	< 0.001	< 0.001	0.002	< 0.001	< 0.001
Least significant difference (P = 0.05)	0.95	0.68	8.13	16.24	0.16

*Not observed.
The values followed by the same letter in a column are statistically nonsignificant at P = 0.05.

Table 2. *Recovery of* Helicoverpa armigera *larvae, and development and progeny production of* Campoletis chlorideae *on six host plants under no-choice and multi-choice conditions (ICRISAT, Patancheru, India)*

	Larvae recovered (%)		Pupal period (days)		Sex ratio (male : female)	
Host plants	No choice	Multi choice	No choice	Multi choice	No choice	Multi choice
Chickpea	71.3 b	80.4 bc	6.3 c	5.9 a	1 : 1	1 : 1.23
Cotton	85.6 d	72.0 ab	5.8 ab	5.7 a	1 : 1	1 : 1.08
Groundnut	73.6 bc	62.4 a	5.7 a	5.6 a	1 : 1.2	1 : 0.65
Pearl millet	50.9 a	77.6 b	6.0 b	5.6 a	1 : 1	1 : 0.29
Pigeonpea	77.1 bcd	91.3 c	5.8 ab	5.7 a	1 : 1.3	1 : 0.81
Sorghum	82.7 cd	76.2 b	5.6 a	5.7 a	1 : 1	1 : 0.25
F-probability	< 0.001	0.001	< 0.001	0.261	–	–
Least significant difference (P = 0.05)	10.23	11.08	0.241	0.19	–	–

The values followed by the same letter in a column are statistically nonsignificant at P = 0.05.

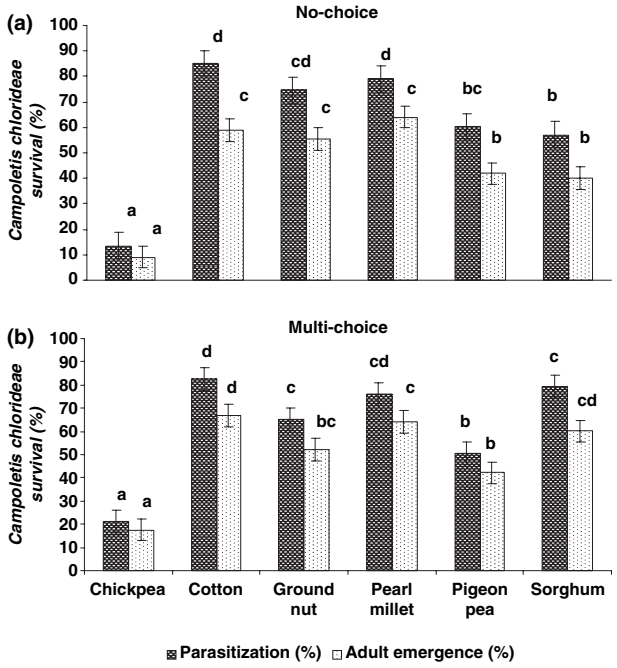

Fig. 2. *Cocoon formation and adult emergence of the parasitic wasp,* Campoletis chlorideae *under no-choice (a) and multi-choice (b) conditions, when* Helicoverpa armigera *larvae were fed on six different host plants. The bars followed by the same letter are statistically nonsignificant at P = 0.05*

addition, pupal period of *C. chlorideae* was prolonged on chickpea (6.3 days) and pearl millet (6.0 days) when compared with both groundnut and sorghum, under no-choice conditions (table 2). Although the adults of *C. chlorideae* took longer time to emerge on chickpea, the differences were not significant with other host plants tested. The sex ratio of *C. chlorideae* adults on groundnut and pigeonpea was biased in favour of females under no-choice conditions, while under multi-choice conditions, it was female biased on chickpea, and male biased on groundnut, pearl millet and sorghum.

4 Discussion

The ichneumonid parasitoid, *C. chlorideae*, has been reported to parasitize diverse lepidopteran species, such as *H. armigera*, *H. assulta*, *H. peltigera*, *S. litura*, *S. exigua*, *M. separata*, *Agrotis ypsilon* (Hufn.), *Adisura stigmatica* (Moore), *A. janata*, *Anomis flava* (Fab.), *Pseudaletia separata* (Walker) and *Leucania loreyi* (Duponchel) (Pawar et al. 1989; Sharma and Dhillon 2005; Yan and Wang 2006). About 27 insect species have also been reported as hosts of *C. perdistinctus* (Viereck), including *Heliothis armigera* as a host of this parasitoid during 1970s (Lingren et al. 1970), but subsequently there are no reports on *H. armigera* as a host of *C. perdistinctus*. Such a report evidences the host specificity during the course of speciation among *Campoletis* parasitoids and *Heliothis*/*Helicoverpa* species, as *C. chlorideae* is a potential larval parasitoid of *H. armigera* at present. The parasitism of *H. armigera* larvae by *C. chlorideae* has been reported to be 44.2%, 33.1%, 32.6%, 11.1%, 7.1% and 4.2% in sorghum, chickpea, pearl millet, cotton, groundnut and pigeonpea, respectively (Pawar et al. 1989; Tikar et al. 2001). However, among the alternate host insects, 60% larvae of *S. litura* have been observed to be parasitized by *C. chlorideae* in tobacco (Sathe 1987). Present studies showed significant influence of host insects on the parasitism potential, development and survival of *C. chlorideae*. Differences in development and survival of *C. chlorideae* on different insect hosts may be due to variability in chemical composition of the host insects haemocel. The host plant nutritional quality not only determines the feeding and reproductive potential of the *H. armigera*, but also has indirect effects (through change in biochemical profile of the host larvae) on the suitability, development and survival of the parasitoid *C. chlorideae* (Murugan et al. 2000). The parasitoid wasp, *Campoletis sonorensis* (Cameron) has been reported to have an obligate symbiotic ichnovirus (*CslV*), which is required by the parasitic wasp for successful parasitism of the lepidopteran larval hosts (Kroemer and Webb 2003). The virions are injected along with an egg and ovarian proteins into a permissive host by the wasp during the parasitism, which interacts with the prothoracic glands to reduce ecdysone levels, and thus reduces the growth of parasitized host insect, but enables the survival of wasp progeny (Dover et al. 1988; Gunasena et al. 1989; Kroemer and Webb 2003). These virion-endocrine interactions between endoparasitic insects and their hosts have been reviewed by Beckage (1985). Five of the seven viral genes have been reported to express in *Heliothis*

virescens (Fab.) hosts within 4 h of parasitism (Kroemer and Webb 2003). This may be one of the reasons for variation in development and survival of *C. chlorideae* on different host insects.

Host plant quality influences the feeding, growth and development of phytophagous insects, and can have profound effects on tritrophic interactions involving plants, herbivores and their natural enemies (Price et al. 1980; Price 1986; Stadler and Mackaeur 1996). Plants release large quantities of volatiles in response to herbivore attack (Dicke et al. 1990; Turlings et al. 1990), which play a significant role in insect host location by the parasitoids (Turlings et al. 1990, 1995; Whitman and Eller 1990; McCall et al. 1993; Steinberg et al. 1993; Agelopoulos and Keller 1994; Mattiacci et al. 1994; Yan and Wang 2006). Changes in biochemical composition of host plants in response to herbivory also affects the growth and survival of herbivores (Gange and Brown 1989; Whitham et al. 1991), which in turn influences the activity and abundance of natural enemies (Bloem and Duffey 1990). In the natural agro-ecosystems, *H. armigera* is the most preferred host of *C. chlorideae* on a number of crop species (Pawar et al. 1989). The recovery of *H. armigera* larvae was greater on pigeonpea and chickpea when compared with cotton, groundnut and pearl millet. However, parasitism by *C. chlorideae* was greater on cotton, pearl millet and sorghum in relation to pigeonpea and chickpea. Glandular exudates from the trichomes of chickpea and pigeonpea play an important role in host plant resistance to *H. armigera* larvae (Yoshida et al. 1995; Green et al. 2002a,b), which in turn greatly influence the activity and abundance of natural enemies on these crops, particularly the hymenopteran parasitoids (Bhatnagar et al. 1982). Adverse effects of glandular trichomes in pigeonpea have also been demonstrated on parasitism levels of *H. armigera* eggs by *Trichogramma* spp. (Romeis and Shanower 1996; Romeis et al. 1998). Sithanantham et al. (1982) observed that parasitism of *H. armigera* larvae in chickpea was lower on the resistant genotypes than on the susceptible ones. Parasitism of *H. armigera* larvae by *C. chlorideae* was lowest on chickpea due to effects of the crop on development and survival of the parasitoid. Natural enemy activity of *H. armigera* on chickpea is generally low possibly because of a dense layer of trichomes as well as the acid exudates secreted on the surface of chickpea leaves and pods (Jalali et al. 1988; Murray and Rynne 1994; Romeis et al. 1999), which possibly reduce the parasitism efficiency of *C. chlorideae* on *H. armigera*.

Sub-lethal effects of *Bt* toxins on the host larvae (sick-host) may reduce the nutritional quality of the insect host, which in turn causes adverse effects on the development and survival of natural enemies (Price 1986; Nordlund et al. 1988; Murugan et al. 2000). The *Cotesia marginiventris* (Cresson) reared on *Bt*-transgenic maize fed *S. littoralis* had significant and negative effects on survival, developmental times and cocoon weights of the parasitoid (Vojtech et al. 2005). Such negative indirect effects through exposure of host Lepidoptera larvae to *Bt*-transgenic cotton under field conditions have earlier been reported on larval parasitoids, *Cotesia marginiventris* and *C. floridanum* (Baur and Boethel 2003) and *C. chlorideae* (Liu et al. 2005; Sharma et al. 2006). Therefore, deployment of *H. armigera* resistant *Bt*-transgenic crops will reduce the abundance of *H. armigera* larvae (the principal host of *C. chlorideae*) in the field. The *H. armigera* host plants, such as cereals, pulses, vegetables and cotton, are grown over an area of about 52 Mha, amongst which only 1.3 Mha area is under *Bt*-transgenic cotton at the moment in India. In such a scenario, the *H. armigera* still have 85% of the non-transgenic cottons to feed on along with the other principle non-transgenic host crops (Fertilizer Association of India (FAI) 2004; James, 2005). Under natural conditions, this parasitoid also has the capacity to survive on alternate insect hosts, such as *S. exigua*, *M. separata*, *H. assulta*, etc. which will help mitigate the adverse effects of transgenic crops (which are much smaller than those of the synthetic pesticides), on the major insect hosts of the parasitoid.

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Author's address: Hari C. Sharma (corresponding author), Principal Scientist – Entomology, ICRISAT, Patancheru 502 324, Andhra Pradesh, India. E-mail: h.sharma@cgiar.org

