Tobacco as a Trap Crop for *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) in Cotton[1]

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Abstract A 3-yr study evaluated tobacco as a trap crop for the tobacco budworm, *Heliothis virescens* (F.), in cotton. Small plot experiments were conducted on an experimental farm at Mississippi State University in Starkville, MS, in 1996 and on a commercial farm in Aliceville, AL, in 1997 to determine the ability of small strips of tobacco to trap *H. virescens* in cotton field plots. In the 1996 experiment, tobacco budworms eggs were significantly higher on tobacco than on cotton from 7 June through 19 June and from 10 July through 22 July. In 1997, *H. virescens* eggs were significantly higher on tobacco than on cotton for every sampling date throughout the growing season. The conclusion derived from these small plot experiments was that *H. virescens* females preferred tobacco over cotton as an ovipositional site. Therefore, in 1998, a large-scale field experiment was conducted to determine the effectiveness of tobacco as a trap crop for *H. virescens* in commercial cotton fields in Funston, GA. In this experiment, the number of *H. virescens eggs* was significantly lower in cotton fields with tobacco trap crops compared to control cotton fields without tobacco trap crops on 2 and 9 July. Also, economic threshold for *H. virescens* was not reached in these cotton fields with tobacco trap crops. In contrast, the economic threshold for this pest was met in cotton fields without tobacco trap crops on two dates during the growing season. For each year of the study, percentage total real mortality (r_x) for eggs and larvae of *H. virescens* on tobacco was very high, ranging from 91.4-99.9%. Larval mortality was attributed in part to parasitization by *Toxoneuron nigriceps* (formerly *Cardiochiles nigriceps*) Viereck and *Campoletis sonorensis* Cameron and an infection by an ascovirus of *H. virescens*. Thus, tobacco served as a trap crop and sink for *H. virescens* in cotton in this study.

Key Words tobacco budworm, trap crop, life table, *T. nigriceps*, ascovirus

The tobacco budworm, *Heliothis virescens* (F.), and the corn earworm, *Helicoverpa zea* (Boddie), are two of the most economically important pests of cotton in the United States (Williams 2005). Both of these pest species can attack tobacco, but density of *H. virescens* larvae can be very high on tobacco whereas density of *H. zea* larvae is generally very low on this crop (Neunzig 1969, Manley et al. 1991). Even though *H. virescens* is polyphagous, it appears to have a preference for tobacco. In the southeastern United States, *H. virescens* females oviposit on tobacco whenever this crop is available and infest cotton usually when tobacco is unavailable or when tobacco senesces and becomes unattractive to the pest (Fitt 1989).

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Trap crops are plant stands grown to intercept a pest insect before it attacks the cash crop (Hokkanen 1991). An important quality for an effective trap crop is that it must be more attractive to the pest as either a food source or oviposition site than the main crop (Vandermeer 1989). Considering the likely ovipositional preference of *H. virescens* for tobacco, establishing an attractive tobacco crop at the time when cotton plants are susceptible to *H. virescens,* has excellent potential for intercepting these pests before they infest cotton.

In addition to using a plant species highly attractive to the pest, a trap crop needs to be a sink for the pest species, or the pest has to be eliminated through crop destruction or application of insecticides. The solitary endoparasitoid *Toxoneuron nigriceps* (formerly *Cardiochiles nigriceps*) Viereck is basically host specific for *H. virescens* because parasitization of *Heliothis subflexa* (Guenée) by this parasitoid is relatively low (4.5%) (Lewis et al. 1967), and *Spodoptera exigua* (Hübner) is a rare host (0.02% parasitization) for this wasp (Ruberson et al. 1994). *Toxoneuron nigriceps* females prefer tobacco to cotton (Tillman and Mullinix 2003), and the parasitoid can contribute substantially (50-100% mortality) to the biological control of *H. virescens* on tobacco (Tingle and Mitchell 1982, Johnson and Manley 1983, Jackson et al. 1996). Thus, it was hypothesized that a tobacco trap crop could become a sink for *H. virescens.* Consequently, the primary objective of this 3-yr project was to evaluate tobacco as a trap crop for *H. virescens* in cotton fields. In addition, parasitism by *T. nigriceps* and percent infection by an ascovirus was determined for *H. virescens* larvae in tobacco. This research examined three trap crop experiments, the first comparing the ability of small strips of tobacco and cotton to trap *H. virescens* in the center of small cotton field plots on an experimental farm. In the second season, the ability of small strips of tobacco and cotton planted along the edge of a commercial cotton field to trap *H. virescens* in cotton was investigated. Lastly, a large-scale field experiment was conducted to determine the effectiveness of tobacco, planted in a strip in the center of a commercial cotton field, as a trap crop for *H. virescens* in cotton.

Materials and Methods

Insect species. Heliothines collected from tobacco and cotton were identified to species and instars (for larvae) using a Nikon SMZ-2T dissecting microscope (Nikon Vision Co., Inc., Tokyo, Japan) and following Neunzig's (1969) description of *H. virescens* and *H. zea* immature stages. In the laboratory, field-collected *H. virescens* larvae were held in diet cups (Perkins et al. 1973) for emergence of parasitoids or appearance of infection by pathogens. If a tobacco budworm larva did not pupate and did not appear to be infected with a pathogen, the larva was dissected to determine the presence of an immature parasitoid. Predators and *T. nigriceps* and *Campoletis sonorensis* Cameron adults were identified by the author. Infection of tobacco budworm larvae by an ascovirus or a nuclear polyhedrosis virus was verified by John J. Hamm. Voucher specimens of all insects and the ascovirus are held in the USDA-ARS, Crop Protection & Management Research Laboratory in Tifton, GA.

1996 experiment. This experiment determined the ability of small strips of tobacco to trap *H. virescens* in the center of small cotton field plots on an experimental farm at Mississippi State University in Starkville, MS, in 1996. For this and subsequent experiments, the NC 71 variety of tobacco and the DP 90 variety of cotton were used. Tobacco was hand-transplanted in bedded rows whereas cotton was planted using conventional planting and tillage practices. Tobacco plants were spaced 1.2 m apart

in the row to ensure that plants remained isolated for life table evaluations. Twenty-five plants were planted per row so that there was a total of 50 plants per tobacco trap crop. Plant density for cotton ranged from 4-5 plants per ft. of row. In 1996, tobacco and cotton were planted on 3 May and 26 April, respectively.

Twelve equally-sized (29.3 m long × 150 rows deep) cotton field plots were established. These plots were divided into six blocks with two plots in each block. Within each block, a tobacco trap crop and a cotton control treatment were each randomly assigned to a plot for each of the six blocks (replications) in a randomized complete block design. Then 2 rows, 29.3 m in length, of either tobacco (tobacco trap crop strip) or cotton (cotton control strip) were planted in the center of each cotton field plot. The four treatments were the tobacco trap crop strip, the cotton control strip, the cotton field plot associated with the strip of tobacco trap crop, and the cotton field plot associated with the strip of the cotton control.

For this and subsequent experiments, whole plant sampling was conducted every 3-7 d to monitor immature heliothines on tobacco and cotton during the growing season. Ten to 20 cotton plants were randomly sampled from each of the cotton treatments for each sampling date. All tobacco plants in the tobacco trap crop strip were sampled for each sampling date from early June to early August. All heliothine eggs and larvae found during whole plant sampling on cotton plants were collected. In tobacco, heliothine eggs were counted, but not collected. Heliothine eggs were collected only from cotton because it was assumed that most, if not all, heliothine eggs on tobacco would be *H. virescens*, but both this pest and *H. zea* were expected to oviposit on cotton. Each egg found on tobacco in the field was examined for the typical black coloring indicative of parasitization by egg parasitoids of this pest. Heliothine larvae were collected from 25% of the tobacco plants each sampling date and returned to the laboratory for identification and observation for biological control.

Fyfanon ULV (malathion, 1.36 kg [AI]/ha Cheminova, Lemnig, Denmark) was applied by the Boll Weevil Eradication Program for control of the boll weevil, *Anthonomus grandis grandis* Boheman, to tobacco and cotton on 11, 19, and 26 June. On 21 June, Pydrin EC (fenvalerate, 0.22 kg [AI]/ha; DuPont Agricultural Products, Wilmington, DE) was applied to cotton for control of *H. zea* and *H. virescens* larvae.

1997 experiment. This experiment determined the ability of small strips of tobacco planted along the edge of cotton field plots to trap *H. virescens* on a commercial farm in Aliceville, AL, in 1997. Tobacco was transplanted on 24 April, and cotton was planted on 9 May. Unlike the previous season, tobacco was planted before cotton to ensure that large tobacco plants were present when cotton began producing flower buds. Tobacco plants were spaced 1.2 m apart in the row, and 26 plants were planted per row for a total of 52 plants per tobacco trap crop. Malathion was applied by the Boll Weevil Eradication Program to tobacco and cotton on 9 July.

Eight equally-sized (30.5 m long × 70 rows deep) cotton field plots were established along the edge of a large cotton field. These plots were divided into four blocks with two plots in each block. Within each block, a tobacco trap crop and a cotton control treatment were each randomly assigned to a plot for each of the four blocks in a randomized complete block design. Then 2 rows, 30.5 m in length, of either tobacco (tobacco trap crop strip) or cotton (cotton control strip) were planted along the outside edge of each cotton field plot. The four treatments were the tobacco trap crop strip, the cotton control strip, the cotton field plot associated with the tobacco trap crop strip, and the cotton field plot associated with the cotton control strip. Twenty-five to 50 cotton plants were randomly sampled from each of the cotton treatments for each

sampling date. All tobacco plants were sampled for each sampling date. Tobacco and cotton plants were sampled from midJune to midAugust.

1998 experiment. A large-scale field experiment was conducted to determine the effectiveness of tobacco, planted in a strip in the center of a commercial cotton field, as a trap crop for *H. virescens* in cotton in 1998. Six cotton fields, each approximately 1.5 ha in size, were located on a farm in Funston, GA. Two treatments included a cotton field with a tobacco trap crop and a cotton field without a tobacco trap crop. Each treatment was assigned randomly to three cotton fields in a completely randomized design. Tobacco was transplanted on 20 April, and cotton was planted on 11 May. In cotton fields with tobacco trap crops, 2 rows of tobacco, 181.2 m in length, were planted in the center of each cotton field. Tobacco plants were placed 1.8 m apart in the row, and 100 plants were planted per row for a total of 200 plants per tobacco trap crop. For cotton, 50-200 plants were randomly sampled from each of the cotton treatments for each sampling date. For tobacco, 50 plants were randomly sampled for each sampling date. Tobacco and cotton plants were sampled from late May to early September.

Life table analysis. Numbers of eggs and larvae obtained for tobacco and plant population densities were used to calculate abundances of each life stage converted to per hectare basis. Partial life tables for *H. virescens* occurring on tobacco for each of the two generations for the 3 yrs of the study were constructed using the graphical method (Southwood 1978). Real (r_x) and apparent (q_x) mortality were calculated for each life stage (x) based on numbers of individuals entering each life stage (l_x). Larval mortality was classified as parasitized, diseased, and unknown fate. An estimated development time of 3 d was used for healthy eggs (Butler et al. 1979). An estimated development time of 2.4, 1.8, 1.3, 2.0, and 5.8 d at 30°C was used for healthy 1st, 2nd, 3rd, 4th and 5th instars, respectively (Fye and McAda 1972). It was assumed that development time for 6th instars was similar to 5th instars, so 5.8 d was used for development time of 6th instars. An estimated development time of 4 d was used for larvae infected with an ascovirus of *H. virescens* because maximum level of infectivity of the ascovirus is reached in 4 d in the hemolymph of this pest (P. G. T., unpubl. data). Development times of parasitized *H. virescens* larvae were obtained from the literature and are as follows: 15 d for *C. sonorensis* (Isenhour 1986) and 20 d for *T. nigriceps* (Lewis and Brazzel 1966).

Statistical analysis. For the first two experiments, treatment data were analyzed using PROC MIXED (SAS Institute 1999). Fixed effects were date, treatment, and date × treatment. Random effects were block within date, block × treatment within date, and residual error. For the third experiment, treatment data were analyzed using PROC MIXED (SAS Institute 1999). Fixed effects were date, treatment, and date × treatment. Random effects were replicate within date, replicate × treatment within date, and residual error. Least squares means were separated by least significant difference (LSD) (SAS Institute 1999) where appropriate. Means (± SE) for number of *H. virescens* eggs per plant in the tobacco trap crop in 1998, percent parasitism by *T. nigriceps*, percent *Ascovirus* infection, and percent attacked by both natural enemies in tobacco were determined using PROC MEANS (SAS Institute 1999).

Results and Discussion

1996 experiment. Because all heliothine larvae on tobacco were *H. virescens*, all heliothine eggs observed on plants in the tobacco trap crop strips were assumed to

be tobacco budworm eggs. *Heliothis virescens* females continued to oviposit on both tobacco and cotton after malathion was applied to these plant species on June 11. Thus, it was assumed that this control measure for boll weevils did not have an adverse impact on *H. virescens* oviposition. There were two *H. virescens* generations during the growing season. The first occurred in June on vegetative tobacco and cotton, and the second occurred in July on reproductive tobacco and cotton (Fig. 1A). There was a significant date × treatment interaction for the abundance of *H. virescens* eggs per plant ($F = 11.26$; df = 39, 210; $P = 0.0001$). Tobacco budworms eggs were significantly higher on tobacco in tobacco trap crop strips than on cotton in control cotton strips and field cotton plots from 7 June through 19 June and from 10 July through 22 July (Fig. 1A). For tobacco, *H. virescens* females oviposited eggs on small leaves in the terminal of the plant and on the large lower leaves on the plant. Therefore, it is unlikely that differences in leaf size accounted for the observed differences in number of eggs between tobacco and cotton. For each sampling date, the number of *H. virescens* eggs per plant was not significantly different among the cotton control strip, the cotton field plot associated with a tobacco trap crop strip, and the cotton field plot associated with a cotton control strip (Fig. 1A).

Applying malathion for control of boll weevils, resulted in 100% mortality of all natural enemies in tobacco and cotton. This insecticide has previously been reported to be highly toxic to four natural enemies, *T. nigriceps, Geocoris punctipes* (Say), *Cotesia marginiventris* (Cresson), and *Bracon mellitor* Say, generally found in cotton (Tillman and Mulrooney 2001). Even though tobacco was highly attractive to *H. virescens*, females never laid 100% of their eggs on tobacco in the trap crop strips, so it was very important to conserve natural enemies in tobacco and cotton to help maintain populations of this pest below the economic threshold (5% infestation of 1st instars on plants) in cotton. On 21 June, cotton had to be treated with fenvalerate for control of *H. zea* and *H. virescens* larvae because the natural enemies had been destroyed and thus could no longer maintain these heliothines below economic threshold.

1997 experiment. Again, all heliothine larvae on tobacco were *H. virescens*, and thus all heliothine eggs observed on plants in the tobacco trap crop strip were assumed to be tobacco budworm eggs. There were two *H. virescens* generations during the growing season, the first occurring in June on vegetative tobacco and cotton and the second occurring in July on reproductive tobacco and cotton (Fig. 2A). There was a significant date × treatment interaction for the abundance of *H. virescens* eggs per plant ($F = 4.7$; df = 66, 203; $P = 0.0001$). Tobacco budworms eggs were significantly higher on tobacco in the tobacco trap crop strip than on cotton in the control cotton strip, the cotton field plot associated with the tobacco trap crop strip, and the cotton field plot associated with the cotton control strip for all sampling dates throughout the growing season (Fig. 2A). The number of *H. virescens* eggs per plant was not significantly different among the cotton control strip, the cotton field plot associated with a tobacco trap crop strip, and the cotton field plot associated with a cotton control strip (Fig. 2A). Economic threshold for *H. virescens* was not reached in any of the cotton treatments for any sampling date. Application of malathion on 9 July killed all the natural enemies in tobacco and cotton. However, this disruption of the natural enemies did not result in increased damage in cotton because heliothine larvae were not present on cotton plants when the insecticide was applied.

1998 experiment. Throughout the season, a very small proportion (~3%) of heliothine larvae on tobacco was *H. zea*. A lower incidence of *H. zea* on tobacco

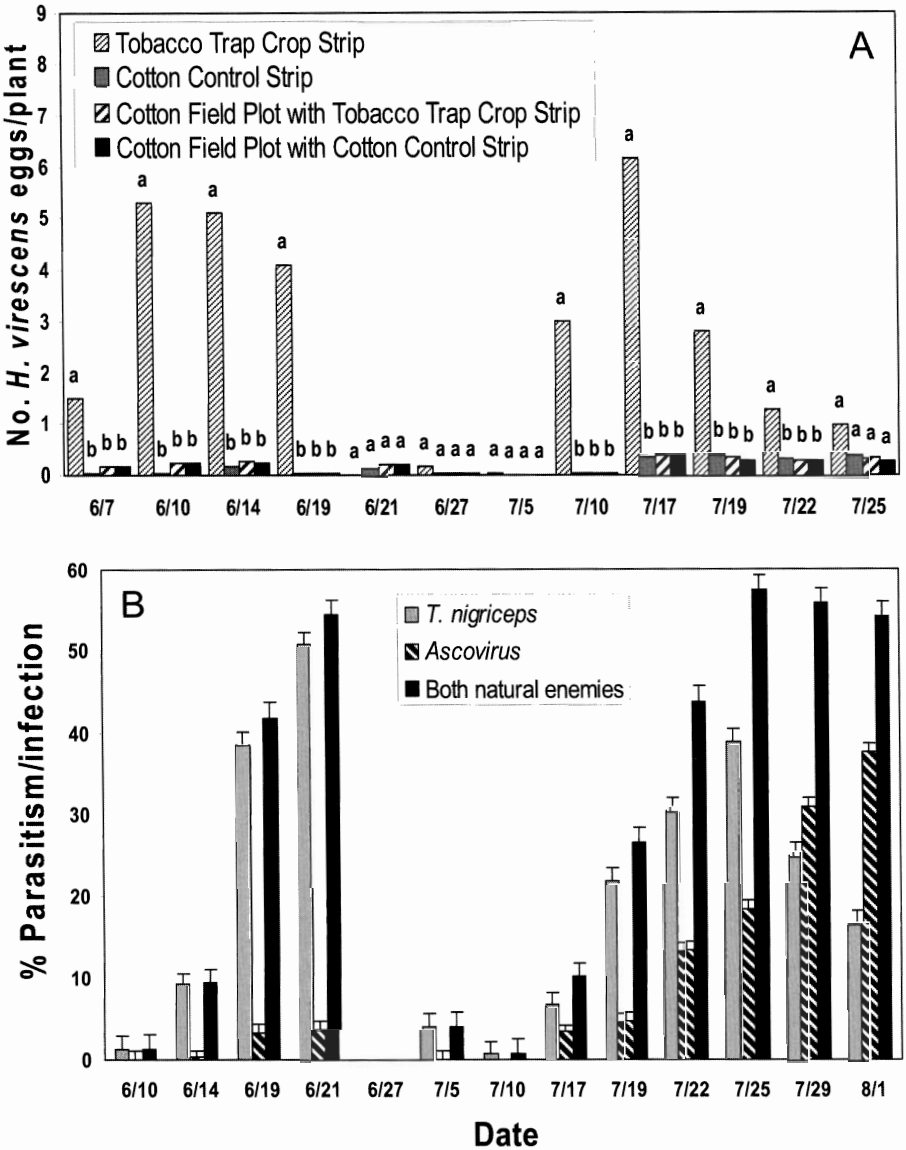

Fig. 1. Trap crop experiment in Starkville, MS in 1996. A. Least squares means for number of *H. virescens* eggs per plant for the four treatments. Means with dates followed by the same letter are not significantly different (PROC MIXED, LSD, $P > 0.05$, $n = 336$, SE = 0.332, df = 210). B. Mean (± SE) percent *H. virescens* larvae parasitized by *T. nigriceps*, infected by *Ascovirus*, and these natural enemies combined in tobacco.

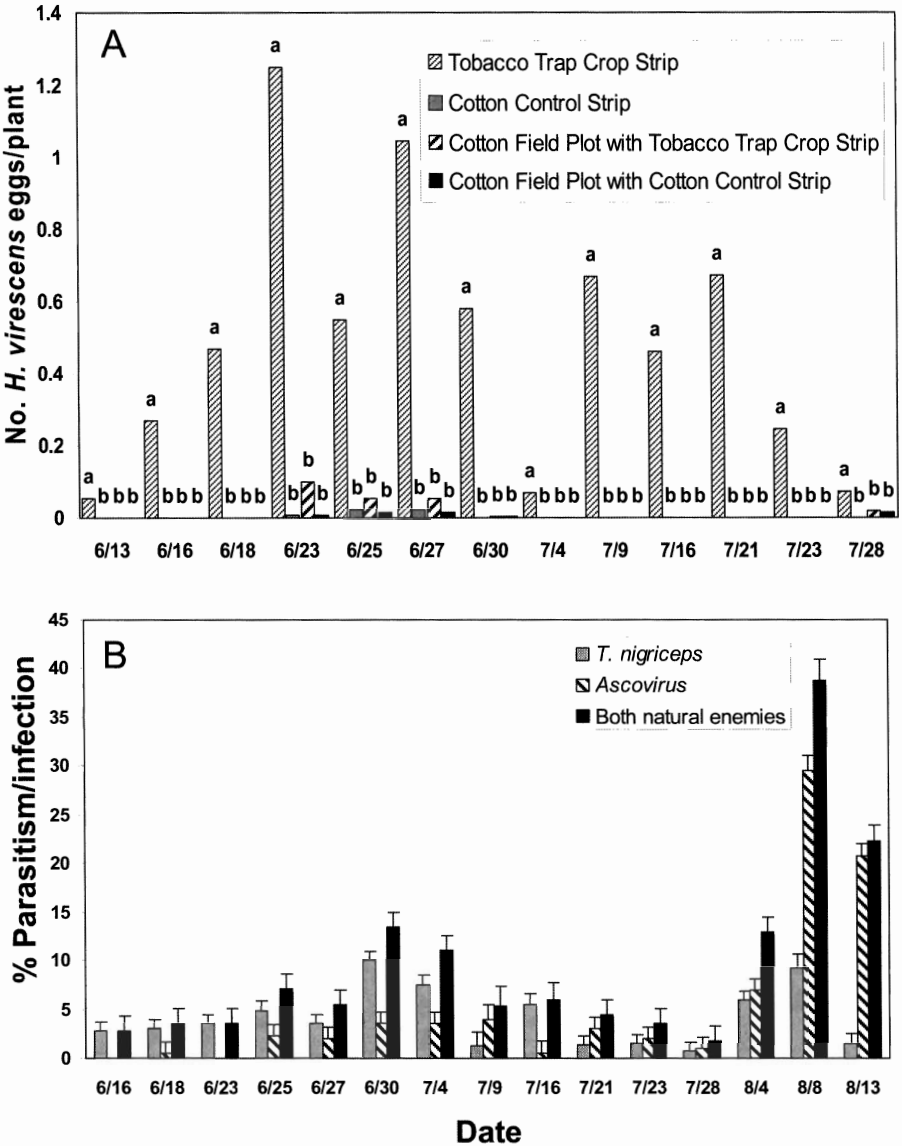

Fig. 2. Trap crop experiment in Aliceville, AL 1997. A. Least squares means for number of *H. virescens* eggs per plant for the four treatments. Means with dates followed by the same letter are not significantly different (PROC MIXED, LSD, $P > 0.05$, $n = 368$, SE = 0.0823, df = 203). B. Mean (± SE) percent *H. virescens* larvae parasitized by *T. nigriceps*, infected by *Ascovirus*, and these natural enemies combined in tobacco.

compared with *H. virescens* has been reported for other states, including North Carolina, SC, and Tennessee (Neunzig 1969, Roach 1976, Bidlack et al. 1991). Because the majority (~97%) of heliothine larvae on tobacco were *H. virescens*, both heliothine species were included in the description of seasonal occurrence of tobacco budworm eggs on this plant for this year. The first generation of *H. virescens* on vegetative tobacco and cotton in June was low (Fig. 3A). Peak density for the second generation occurred on 30 July on reproductive tobacco and was 6.12 heliothine eggs per plant (Fig. 3A). There was a significant date × treatment interaction for the number of *H. virescens* eggs per plant between the two trap crop treatments ($F = 2.29$; df = 11, 24; $P = 0.0439$) (Fig. 3B). On 2 and 9 July, the number of *H. virescens* eggs per plant was significantly lower in cotton fields with tobacco trap crops compared with that in cotton fields without these trap crops. For the other ten sampling dates, the number of eggs of this pest was not significantly different between these two treatments. Also, economic threshold for *H. virescens* was not reached in cotton fields with tobacco trap crops, but this threshold was met in control cotton fields with no trap crop on 9 July and 6 August.

It was concluded from the small plot experiments in 1996 and 1997 that *H. virescens* preferred tobacco over cotton as an ovipositional site because generally abundance of tobacco budworm eggs was greater on tobacco than on cotton. Previous field trials demonstrated that *Toxoneuron nigriceps* females also exhibit an ovipositional preference for tobacco over cotton (Tillman and Mullinix 2003). In the large-scale field experiment, density of *H. virescens* eggs was significantly lower in cotton fields with tobacco trap crops compared with control cotton fields without tobacco trap crops for two sampling dates but never significantly higher in cotton with trap crops compared with control fields. Also, economic threshold was not reached for this pest in any cotton with tobacco trap crops except for the occasion when natural enemies were killed in the 1996 experiment. Thus, tobacco served as a trap crop for *H. virescens* in cotton in this study.

Life table studies. Percent total real mortality for *H. virescens* in tobacco was highest for the egg stage for both generations of this pest for the 3 yrs of the study (Tables 1-3). In all three locations, *H. virescens* eggs were not parasitized on tobacco. Very low parasitization of *H. virescens* eggs on tobacco has been previously reported (Neunzig 1969, Gentry et al. 1973, Martin et al. 1981). Rabb and Bradley (1968) determined that *Trichogramma minutum* Riley adults became stuck in the gummy exudates of the trichomes on tobacco leaves and suggested that this was the reason why eggs of the tobacco hornworm, *Manduca sexta* (Johannson), were not parasitized in the field by this parasitoid.

Because parasitism of *H. virescens* eggs was not detected on tobacco in this study, predation must have been a major factor contributing to egg mortality. Therefore, it was assumed that percent apparent mortality in the "unknown fate" category for the *H. virescens* eggs was due in part to predation. Teetes et al. (1992) also presumed that predation accounted for some level of the major mortality for eggs classified as "disappeared". The big-eyed bug, *G. punctipes,* and the stilt bug, *Jalysus spinosus* (Say), were observed to feed on *H. virescens* eggs on tobacco. The big-eyed bug has been reported to be one of the most predominant and effective predators of heliothines in cotton (Bell and Whitcomb 1963, Lingren et al. 1968, Lopez et al. 1976). Elsey (1972) reported that predation of *H. virescens* eggs glued to the undersides of tobacco leaves ranged from 1-46% after 48 h and was correlated with the number of *J. spinosus* per unit area of foliage. *Geocoris punctipes* also preyed on

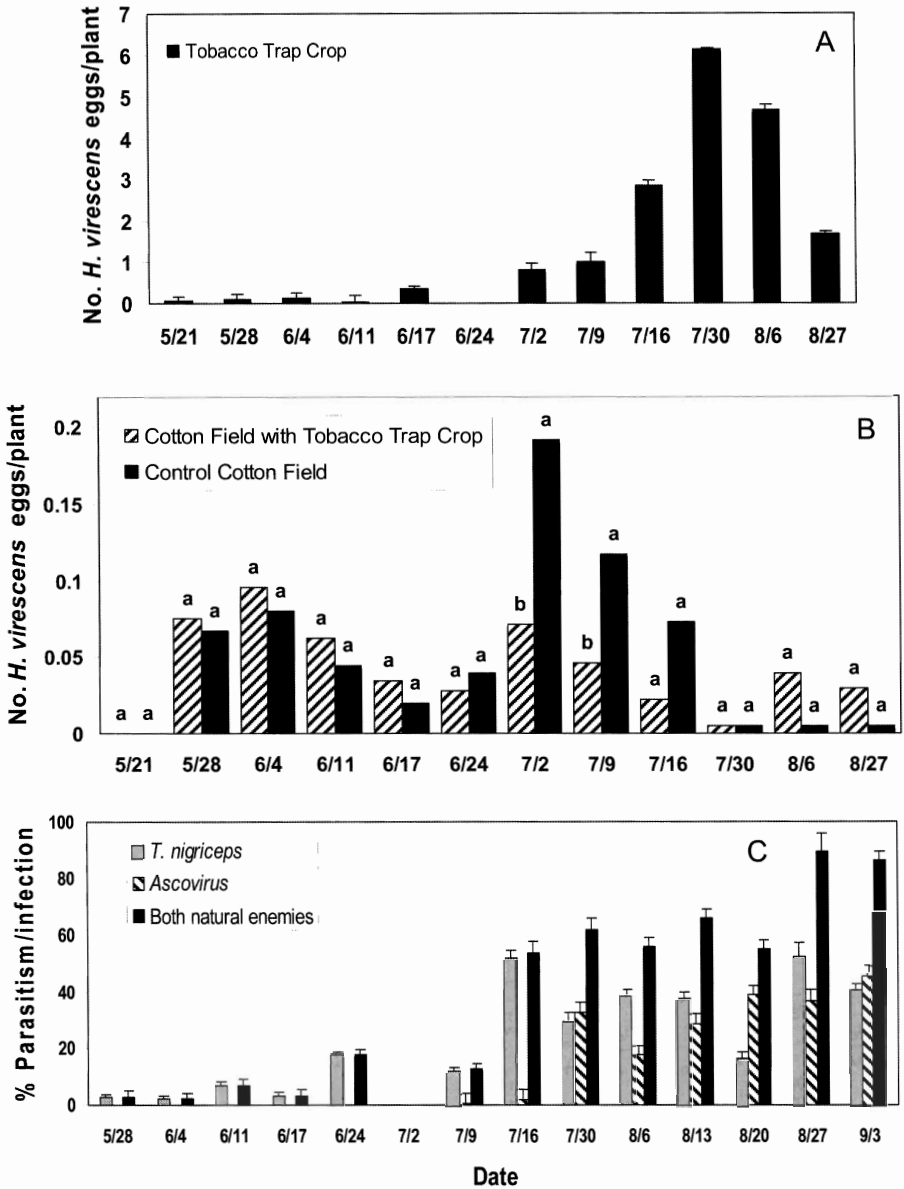

Fig. 3. Trap crop experiment in Funston, GA in 1998. A. Mean (± SE) for number of *H. virescens* eggs per tobacco plant. B. Least squares means for number of *H. virescens* eggs per plant in a cotton field with a tobacco trap crop and a control cotton field without a tobacco trap crop. Means with dates followed by the same letter are not significantly different (PROC MIXED, LSD, $P > 0.05$, $n = 108$, SE = 0.027, df = 24). C. Mean (± SE) percent *H. virescens* larvae parasitized by *T. nigriceps*, infected by *Ascovirus*, and these natural enemies combined in tobacco.

Table 1. Partial life table for first and second generation *H. virescens* on tobacco in tobacco trap crop strips in cotton field plots in Starkville, MS in 1996

				% Apparent mortality (q_x)			
Generation	Life stage (x)	No./ha entering stage (l_x)	% Real mortality (r_x)	Total	Parasitized	Disease	Unknown fate
first	Egg	156,885.3	59.5	59.5	0	—	59.5
	1st	63,574.9	21.9	54.1	30.8	0	23.3
	2nd	29,152.5	1.7	9.0	4.2	0.3	4.5
	3rd	26,519.8	14.1	83.4	45.5	2.2	35.7
	4th	4,409.1	1.9	66.9	27.5	2.5	36.9
	5th/6th	1,461.5	0.1	—	33.3	0	—
	Total		99.2				
second	Egg	170,340.3	76.3	76.3	0	—	76.3
	1st/2nd	40,365.0	7.0	29.4	6.2	7.7	15.5
	3rd	28,497.7	13.6	81.5	29.8	33.8	17.9
	4th	5,278.5	0.9	31.4	12.6	12.8	6.0
	5th/6th	3,618.9	0.1	—	56.5	21.8	—
	Total		97.9				

Table 2. Partial life table for first and second generation *H. virescens* on tobacco in tobacco trap crop strips in cotton field plots in Aliceville, AL in 1997

Generation	Life stage (x)	No./ha entering stage (l_x)	% Real mortality (r_x)	% Apparent mortality (q_x)			
				Total	Parasitized	Disease	Unknown fate
1st	Egg	42,819.6	76.1	76.1	0	—	76.1
	1st	10,215.1	4.0	16.9	9.1	0	7.8
	2nd	8,489.3	3.4	17.1	4.9	2.7	9.5
	3rd	7,039.7	9.8	59.5	37.3	5.0	17.2
	4th	2,854.6	5.8	87.3	87.3	0	0
	5th	361.9	0.7	92.0	92.0	0	0
	6th	29.0	0.1	—	100.0	0	—
	Total		99.9				
2nd	Egg	35,263.2	30.0	30.0	0	—	30.0
	1st/2nd	24,674.9	4.2	6.0	2.6	1.1	2.3
	3rd	23,185.9	15.3	23.2	4.8	10.0	8.4
	4th	17,799.5	34.3	68.0	10.7	24.1	33.2
	5th	5,703.5	7.5	46.7	13.0	13.7	20.0
	6th	3,039.9	0.1	—	6.2	21.5	—
	Total		91.4				

Table 3. Partial life table for first and second generation *H. virescens* on tobacco in tobacco trap crops in cotton fields in Funston, GA in 1998

				% Apparent mortality (q_x)			
Generation	Life stage (x)	No./ha entering stage (l_x)	% Real mortality (r_x)	Total	Parasitized	Disease	Unknown fate
1st	Egg	11,141.2	64.0	64.0	0	—	64.0
	1st	4,012.7	4.9	13.7	4.0	0	9.7
	2nd	3,461.9	3.7	11.9	6.4	0	5.5
	3rd	3,050.4	12.1	44.3	27.5	0	16.8
	4th	1,699.5	13.5	88.5	57.4	0	31.1
	5th	195.3	1.0	53.5	37.8	0	15.7
	6th	90.8	0.1	—	100.0	0	—
	Total		99.3				
2nd	Egg	392,773.3	34.3	34.3	0	—	34.3
	1st/2nd	258,072.2	2.8	15.9	7.2	1.1	7.6
	3rd	247,013.1	29.4	39.4	12.3	11.4	15.7
	4th	131,428.0	23.9	71.4	27.4	24.6	19.4
	5th	37,603.9	7.7	76.9	35.6	22.3	19.0
	6th	7,520.8	0.1	—	18.6	20.8	—
	Total	—	98.2	—			

these artificial infestations of eggs, but this predator was less numerous on plants than the stilt bug.

Mortality of *H. virescens* larvae on tobacco was due in part to parasitism by parasitoids, infection by pathogens, predation, and probably cannibalism (Tables 1-3). Female *T. nigriceps* very effectively search for *H. virescens* larvae in tobacco (Tillman and Mullinix 2003). In these trap crop studies, they were observed parasitizing all of the various instars of *H. virescens* on tobacco. They were even observed parasitizing *H. virescens* 1st instars that recently (within 5 s) had emerged from their egg shells. *Campoletis sonorensis* parasitized young *H. virescens* larvae, but only very early in the tobacco growing season.

The predominant pathogen was an ascovirus of *H. virescens*. A nuclear polyhedrosis virus, known to be highly virulent against *H. zea* and *H. virescens* (Ignoffo 1965), occurred in *H. virescens* larvae at a very low rate of infection (0.9%) only near the end of the second generation of this pest in 1998.

Geocoris punctipes and *J. spinosus* were observed feeding on *H. virescens* young instars. The spined soldier bug, *Podisus maculiventris* (Say), a generalist predator feeding on a variety of insect prey in a diversity of crop and noncrop ecosystems (McPherson 1980), was observed to ingest late-instar *H. virescens* on tobacco. Therefore, percentage of apparent mortality in the "unknown fate" category for *H. virescens* larvae probably was due in part to predation.

Although cannibalism was not specifically addressed in this study, it probably made a significant contribution to *H. virescens* population suppression and accounted for some of the apparent mortality listed in the "unknown fate" category for larvae. This assumption is based on the fact that cannibalism among late instars of *H. zea* can be a major factor in the reduction of the population of this pest (Barber 1936), and *H. armigera* eggs can be cannibalized by 1st instars of this pest on sorghum and pigeon pea (Sigsgaard et al. 2002).

In tobacco, *H. virescens* females laid eggs on plant leaves or on the outside of flowers, buds, or fruit. Newly-emerged 1st instars moved toward the main stem searching for terminal leaves or they fed through or crawled into the inside of a reproductive structure. These 1st instars began feeding and generally remained hidden in terminals of plants or reproductive structures until they were 2nd instars. Older instars (3rd-6th) of *H. virescens* generally were partially or fully exposed during some or most of their development. Type I host defenses, avoidance and concealment (Gross 1993), provided protection for young larvae of *H. virescens* against female parasitoids searching for hosts. For example, upon detecting a host hidden in a terminal, a *T. nigriceps* female would stretch her ovipositor far into the terminal, but she still sometimes was unable to reach the host with her ovipositor (Tillman and Mullinix 2003). This defensive behavior of 1st and 2nd *H. virescens* instars probably affected percentage apparent mortality attributed to parasitization because this mortality factor was generally lower for 1st and 2nd instars than for 3rd and sometimes 4th instars over each year of the study.

In 1996, a new ascovirus isolate was discovered in *H. virescens* larvae on tobacco (Tillman et al. 2004). When the ovipositor of a female *T. nigriceps* becomes contaminated with the ascovirus upon parasitizing a host with a full-blown ascovirus infection, she can transmit this pathogen to healthy tobacco budworm larvae. Because young immature parasitoids die in ascovirus-infected tobacco budworms, infected host larvae were not considered to be parasitized by this parasitoid. In 1996 and 1997, ascovirus infection was first detected in tobacco trap crops 4-7 d after first occurrence

of parasitization by *T. nigriceps*. However, this pathogen did not appear until 2 months after *T. nigriceps* began parasitizing *H. virescens* larvae in tobacco in 1998. This delay in occurrence of ascovirus during the last season of the study probably was due to the low density of first generation *H. virescens* on tobacco.

Larval mortality due to *T. nigriceps* parasitism generally was higher than that due to ascovirus infection for the first *H. virescens* generation in 1996 and 1997 (Figs. 1B and 2B). In 1998, parasitization by *T. nigriceps* was higher than ascovirus infection at the beginning of the second *H. virescens* generation (Fig. 3C). Regardless of when ascovirus infection began in tobacco, the infection rapidly increased over time finally reaching higher levels than *T. nigriceps* parasitism. In 1996 and 1997, *T. nigriceps* parasitism + ascovirus infection reached a moderately high level in tobacco for the second *H. virescens* generation. In 1998, a very high incidence of *T. nigriceps* parasitism + ascovirus infection occurred for the second generation of *H. virescens*. In the field, ascovirus infection never completely eliminated parasitization by *T. nigriceps* because there are two mechanisms for survival of immature parasitoids when ascovirus is prevalent in *H. virescens* in the field. Immature *T. nigriceps* can survive if they are at least 2nd instars when the host is inoculated by ascovirus or if the ascovirus infection is less than 48 h old in the host when the worm is parasitized (Tillman et al. 2004).

For each year of the study, percentage total real mortality of *H. virescens* on tobacco was very high, ranging from 99.2-99.9% for the first generation and from 91.4-98.2% for the second one (Tables 1-3), demonstrating that the tobacco trap crops were sinks for *H. virescens* in cotton. However, tobacco was not a sink for *T. nigriceps*, for females of this parasitoid also readily search in cotton for *H. virescens* even in the presence of host-infested tobacco (Tillman and Mullinix 2003). Even though some *H. zea* were found in the tobacco traps crops, in Georgia, sorghum can be an excellent trap crop for *H. zea* (Tillman and Mullinix 2004).

In conclusion, field studies conducted for 3 yrs demonstrated that tobacco was highly attractive to *H. virescens* females, and acted as a trap crop for this pest. From life table analyses it was determined that biological control by natural enemies of *H. virescens* on tobacco resulted in these tobacco trap crops becoming a sink for this pest. Therefore, tobacco served as a trap crop and sink for *H. virescens* in cotton.

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