Population Dynamics of Three Coccinellids in Flue-Cured Tobacco and Functional Response of *Hippodamia convergens* (Coleoptera: Coccinellidae) Feeding on Tobacco Aphids (Homoptera: Aphididae)

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ABSTRACT The seasonal abundance of 3 species of coccinellids was observed on flue-cured tobacco, *Nicotiana tabacum* L., during 1997 and 1998 in Tift County, GA. The most abundant coccinellid during both seasons was the convergent lady beetle, *Hippodamia convergens* Guérin-Méneville, which was present from mid-May, when tobacco aphids, *Myzus nicotianae* Blackman, colonized the crop, until late July when sampling ended. The sevenspotted lady beetle, *Coccinella septempunctata* L., and the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas), were also observed. *C. septempunctata* was most abundant early in the season and maintained low population levels during June and July. Conversely, *H. axyridis* was absent in tobacco until late May and remained abundant until sampling was discontinued. Populations of *H. convergens*, *H. axyridis*, and *C. septempunctata* were linearly related to tobacco aphid populations during 1998. In functional response experiments, 4th-instar larvae and adult *H. convergens* exhibited a type II functional response to aphid density. Fourth-instar larvae had a higher search rate and a longer handling time than adult *H. convergens.* Two other coccinellid species were observed at low population densities on flue-cured tobacco, *Coleomegilla maculata* (Mulsant) and *Cycloneda munda* (Say). Collectively, coccinellids may be important biological control agents of tobacco aphids on Georgia flue-cured tobacco.

KEY WORDS Coccinellidae, *Coccinella septempunctata,* functional response, *Harmonia axyridis, Hippodamia convergens,* population dynamics

THE TOBACCO APHID, *Myzus nicotianae* Blackman, is an important economic pest of flue-cured tobacco, *Nicotiana tabacum* L., in Georgia (Douce and McPherson 1988). Direct feeding by adults and nymphs can cost growers over $2 million annually in insecticide costs as well as yield and quality losses (McPherson 1989). A better understanding and utilization of the natural enemies of tobacco aphids could help to reduce these costs. Aphidophagous coccinellids occur in most cropping systems, where they contribute to the suppression of various pests. Coccinellid population establishment is often unpredictable (Elliott and Kieckhefer 1990). This can lead to a high variability in the effectiveness of coccinellids as biological control agents (Kindlmann and Dixon 1993). Very little is known about the coccinellid populations in tobacco or their impact on tobacco aphid population densities.

Three of the most abundant lady beetle species occurring in Georgia tobacco are the convergent ladybeetle, *Hippodamia convergens* Guérin-Méneville, the sevenspotted lady beetle, *Coccinella septempunctata* L., and the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas). *H. convergens* is a native coccinellid and is known to prey on several aphid species, whereas *C. septempunctata* and *H. axyridis* are exotic natural enemies of several arthropod pests (Obrycki and Kring 1998). *H. convergens* is a common predator of aphids in a number of cropping systems and has been shown to reduce economic damage caused by tobacco aphids (Norowi and Semtner 1990). *C. septempunctata* has been permanently established in every state of the continental United States. This species is widely distributed in the Palearctic and Oriental Region and is considered an important aphid predator in numerous cropping systems (Phoofolo and Obrycki 1995).

Harmonia axyridis is an arboreal species and preys mainly on aphids, but has also been reported to feed on other arthropods, including scales and 2 species of chrysomelids (Tedders and Schaefer 1994). This species is polymorphic, very prolific, and individuals may live up to 3 yr (Hodek 1973). A native of Asia, it was released in California in 1916, 1964, and 1965. Additional releases of this species have been conducted in various states since that time. Releases of *H. axyridis* in Georgia were first made in Byron in pecan, *Carya illinoensis* (Wangengheim), orchards from 1978 to 1981 (Tedders and Schaefer 1994).

This study examined the seasonal abundance of these 3 common lady beetle species on flue-cured tobacco to determine the relationship between lady beetle populations and tobacco aphid densities, and to evaluate the efficiency of adult and 4th-instar *H. convergens* as predators of tobacco aphids through functional response experiments. The functional response is often considered to be an important component of predator–prey interactions (Holling 1959). The shape of the relationship of the number of prey eaten versus the number of prey available determines the type of functional response, which can influence the dynamics of predator and prey populations and can contribute to the stability of predator-prey systems (Hassell 1978).

Materials and Methods

Field studies were conducted throughout the 1997 and 1998 growing seasons at 2 sites at the University of Georgia Coastal Plain Experiment Station (CPES) in Tift County, GA. 'K-326' flue-cured tobacco was transplanted on 1 April 1997 and 21 April 1998 at the Bowen Research Farm (0.5-ha field) and on 27 March 1997 and 26 March 1998 at the CPES campus (0.30-ha field). Tobacco plots were maintained according to Georgia Cooperative Extension Service Guidelines (Moore 1998) and no foliar insecticides were used in the sampling area.

During the 1997 growing season, samples were obtained every 7–10 d from 30 April to 22 July. During the 1998 growing season, sampling was conducted every 7–10 d from 5 May to 21 July. All adult lady beetles were recorded from 10 consecutive plants at 10 random locations within each field on each sampling date. These lady beetles were collected in plastic bags and returned to the laboratory for positive identification. Representative specimens were held at the entomology departmental collection at UGA-CPES. Aphid population samples were taken from 4 consecutive plants within 1 row in each of 4 random sites on each sampling date by counting all aphids observed on the surface of each plant. The data from each site were pooled separately each year. Data were analyzed using two-way analysis of variance (ANOVA) with coccinellid species and date as main effects. A linear regression of the abundance of each coccinellid species versus tobacco aphid abundance was conducted to evaluate the parameters of the relationships between the 3 species of coccinellids and tobacco aphids (SAS Institute 1985). Data for the linear regression were log transformed.

Functional response experiments were conducted to examine the effectiveness of the native *H. convergens* as a predator of tobacco aphids. *H. convergens* pupae were collected from tobacco plants at the CPES Bowen Research Farm. Upon eclosion, 30 female *H. convergens* were isolated without food for 24 h. Adult tobacco aphids were provided to individual lady beetles on tobacco foliage placed in 100 by 15-mm petri dishes lined with wet filter paper at densities of 2, 8, 16, 32, and 64 aphids per prey arena. Each density was replicated 12 times and individual lady beetles were exposed to the aphids for 24 h and the number of prey consumed during the feeding period was recorded. One replication of each density was conducted to determine mortality of tobacco aphids in the artificial environment in the absence of predators. Experiments were conducted in an environmental chamber at 27°C and a photoperiod of 16:8 (L:D) h. Predation of tobacco aphids by 4th-instar *H. convergens* larvae was examined as well. These larvae were derived from laboratory stocks maintained for 3 generations on a diet of tobacco aphids also collected from tobacco plants at the Bowen Research Farm. Experimental procedures for examining *H. convergens* larvae were similar to those for examining adults, and each density was replicated 15 times.

A two-stage analysis was used to analyze the *H. convergens* functional response (Juliano 1993). The shape of the functional response was determined by performing a logistic regression of the proportion of aphids eaten as a function of initial density. Logistic regression has been shown to provide a more powerful and accurate means of distinguishing between type II or type III functional responses compared with analysis of the typical functional response curve (Trexler et al. 1988). The shape of the curve is determined by fitting polynomial regression to observed proportions of prey eaten versus numbers of prey offered, and then determining the shape of the polynomial fit. For a type II response, the proportion of prey eaten declines monotonically with prey density. If the proportion eaten initially increases with number of prey provided, this is sufficient to identify a type III functional response.

Once the shape of the functional response was determined, a nonlinear least-squares regression procedure was performed to estimate and compare parameters of the functional response for *H. convergens* larvae and adults using the "random-predator" equation (Rogers 1972):

$N_e = N_o(1 - \exp[a(T_h N_e - T)])$, where N_e = the number of aphids eaten, N_o = the initial aphid density, a = the attack coefficient or instantaneous searching rate, T_h = time spent handling each prey caught, and T = the total time available for search. This is the appropriate model to use for this analysis, rather than the Holling disk equation (Holling 1959), because aphid prey were depleted during the experiment (Juliano 1993). A two-way ANOVA was also used to test the effects of prey density and beetle stage on the proportions of prey consumed.

Results and Discussion

Hippodamia convergens was the most abundant coccinellid during the 1997 growing season ($F = 20.14$; df = 2, 22; $P < 0.05$) with populations peaking on 23 May 1997. Population levels remained relatively high throughout the entire season (Fig. 1A). Mean population levels of *C. septempunctata* and *H. axyridis* were similar to each other (Table 1), but were lower than *H. convergens* levels. Date did not have a significant effect ($F = 2.01$; df = 11, 22; $P > 0.05$) on coccinellid abundance during 1997. *C. septempunctata* was the 1st species to appear during the 1997 growing season, but *H. convergens* was the dominant species on all follow-

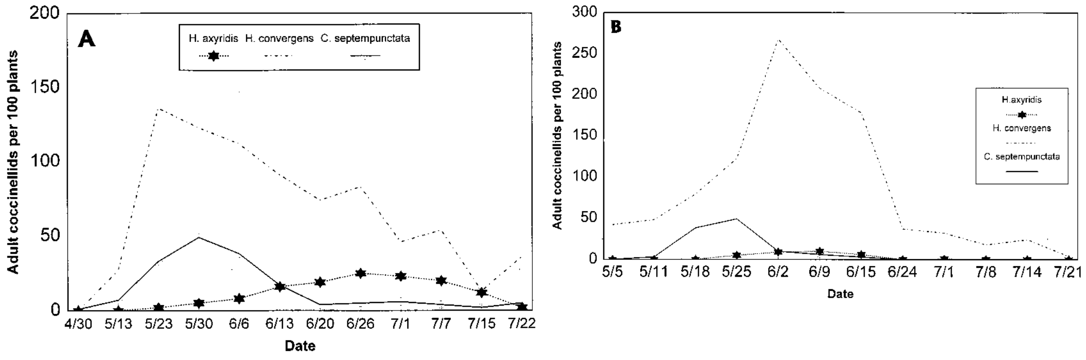

Fig. 1. Seasonal abundance curves for 3 species of coccinellids in Georgia flue-cured tobacco during the 1997(A) and 1998(B) growing seasons.

ing sampling dates. Population levels of *C. septempunctata* began to decrease with the advent of increasing *H. axyridis* population levels in mid-June (Fig. 1A).

Hippodamia convergens was the most abundant coccinellid during the 1998 growing season ($F = 11.68$; df = 2, 22; $P < 0.05$), with populations peaking on 2 June at higher population intensities than were observed in 1997 (Table 1). As in 1997, population levels remained high relative to the other 2 species throughout the 1998 tobacco season (Fig. 1B). Both *C. septempunctata* and *H. axyridis* population levels were lower during 1998 than during the previous year. Date did not have a significant effect ($F = 1.29$; df = 11, 22; $P > 0.05$) on coccinellid abundance during 1998. The population peak for *C. septempunctata* was similar during both years, but ≈1 wk earlier in 1998. *C. septempunctata* appeared earlier during the 1998 growing season than *H. axyridis.* Population levels of *C. septempunctata* began to decrease with increasing *H. axyridis* population levels in early June (Fig. 1B). These data show that *H. axyridis* populations are at low levels in tobacco early in the season when tobacco aphid densities are low. *C. septempunctata* and *H. convergens* populations appear capable of increasing when tobacco aphid populations are at low levels. This may support the findings of Norowi and Semtner (1990), who suggest that *H. convergens* is capable of suppressing tobacco aphid populations during the first 40 d after tobacco aphids become established.

Coleomegilla maculata (Mulsant) and *Cycloneda munda* (Say) were also observed during the study but these species occurred in such low numbers that individual analysis was not undertaken. *C. maculata* is reported as 1 of the most abundant coccinellids on tobacco (Reich 1991). Several studies have indicated the importance of pollen as an alternate food source for *C. maculata* (Hodek et al. 1978, Hazzard and Ferro 1991). During the course of this study, *C. maculata* was observed at relatively high numbers in a corn field adjacent to the tobacco plots; however, these coccinellids failed to become abundant in tobacco. *C. maculata* may have remained in the corn field as a result of the lack of pollen in the tobacoo plots after tobacco flower heads were removed.

Table 1. Mean numbers of lady beetles per 100 plants ± SD and R^2 values for linear regression of each species' abundance (log transformed) with tobacco aphid abundance (log transformed) during the 1997 and 1998 growing seasons

Species	1997	1998	R^2	
			1997	1998
H. axyridis	11.0 ± 9.34	2.58 ± 3.85	0.5969	0.7830
H. convergens	66.25 ± 44.08	88.33 ± 86.15	0.5028	0.7087
C. septempunctata	14.25 ± 16.40	9.08 ± 16.54	0.1765	0.3672

Large standard deviations are the result of large sampling date variations in ladybeetle densities throughout the growing seasons.

The establishment of exotic organisms often has a detrimental effect on native species (Elliott et al. 1996). Although we have no record of *H. convergens* population levels in Georgia tobacco before invasion by *C. septempunctata* and *H. axyridis,* these exotic coccinellids do not as yet appear to have had any adverse effects on *H. convergens* populations in Georgia tobacco. *H. axyridis* may be more efficient predators of other prey species such as cotton aphids or pecan aphids than of tobacco aphids. Both species have been observed in cotton, *Gossypium hirsutum* (L.), when aphids are present on this crop (Knutson and Ruberson 1996). *H. axyridis* is 1 of the most abundant coccinellids in pecan and has been considered to be an efficient biological control agent of pecan aphids (Tedders and Schaefer 1994). The availability of alternate prey may cause these predators to move to and from a diet of tobacco aphids, depending on the presence of more suitable prey on other crops; however, this hypothesis needs to be examined in more detail.

Linear regressions of the log transformed data revealed that *H. convergens* populations had higher correlations with tobacco aphid populations during 1998 ($R^2 = 0.71$; $y = 1.3016 + 0.2979x$; $P = 0.0006$) than during 1997 ($R^2 = 0.50$; $y = 0.7397 + 0.6727x$; $P = 0.01$). A significant linear relationship was observed between *H. axyridis* populations and aphid populations during 1997 ($R^2 = 0.60$; $y = 0.0133 + 0.6442x$; $P = 0.003$) and 1998 ($R^2 = 0.78$; $y = -0.0752 + 0.2804x$; $P = 0.0001$). *C. septempunctata* populations did not appear to be linearly related to tobacco aphid populations during

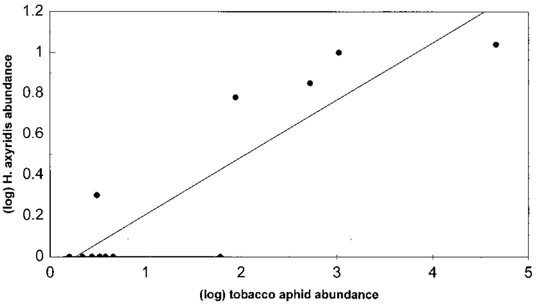

Fig. 2. Linear regression of *H. axyridis* abundance (log transformed) versus tobacco aphid abundance (log transformed) ($R^2 = 0.78$; $y = -0.0752 + 0.2804x$; $P = 0.0001$).

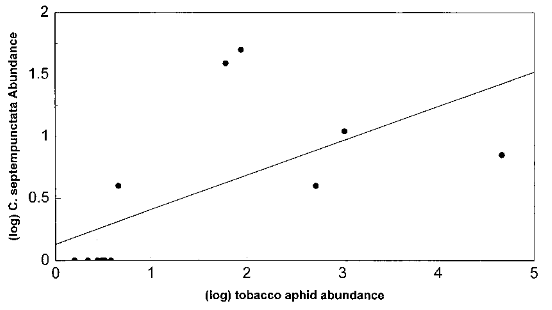

Fig. 4. Linear regression of adult *C. septempunctata* abundance (log transformed) versus tobacco aphid abundance (log transformed) ($R^2 = 0.37$; $y = 0.1307 + 0.2771x$; $P = 0.04$).

1997 ($R^2 = 0.18$; $y = 0.5581 + 0.3042x$; $P = 0.17$). A weak linear relationship was observed between *C. septempunctata* populations and tobacco aphid populations during 1998 ($R^2 = 0.37$; $y = 0.1307 + 0.2771x$; $P = 0.04$). *H. convergens* and *H. axyridis* populations appeared to be more closely correlated with tobacco aphid populations than *C. septempunctata* (Figs. 2, 3, and 4). Population levels of each of the 3 coccinellid species was more closely correlated with tobacco aphid population levels during 1998 than 1997 (Table 1). Hagen and van den Bosch (1968) suggested that synchronization with prey is 1 of the main factors to be taken into account in determining a predator's effectiveness. Although these coccinellid populations could simply be tracking tobacco aphid populations, their significant linear relationships with tobacco aphid abundance during 1998 could indicate that these coccinellids are good candidates for tobacco aphid integrated pest management (IPM) programs. More work is needed to confirm this hypothesis and our functional response experiments with *H. convergens* were conducted as a step in this direction.

The proportion of aphids eaten by *H. convergens* adults and 4th-instar larvae declined monotonically with initial aphid density (Table 2), indicating a type II functional response for both beetle stages. Type II functional responses were also suggested by logistic regression because estimates of the linear coefficients were negative (i.e., the proportion of aphids eaten declined even at lower aphid densities) and the quadratic coefficient was positive for *H. convergens* larvae and adults (Table 3). The model fit observed data reasonably well for both larvae and adults, but was better for adults; the raw R^2 (=1-residual sum of squares/total sum of squares) = 0.94 for adults and 0.89 for 4th-instar larvae.

The estimate of T_h was significantly larger for *H. convergens* larvae than for adults because larvae consumed significantly fewer aphids at the highest aphid density than did adults (Table 2). This may indicate that *H. convergens* adults may be more effective than larvae at suppressing tobacco aphid populations when aphid populations are high and the predator is likely to be limited primarily by handling time. The estimate of a was larger for larvae as well, although the difference was not significant (Table 4). Because *H. convergens* larvae took longer to process aphids, but were more efficient searchers, we may conclude that *H. convergens* larvae require fewer aphids to reach satiation than do adults. Additionally, we may conclude that *H. convergens* larvae may be more effective predators of tobacco aphids when aphid populations are low and the predator is likely to be limited by searching efficiency.

The effect of *H. convergens* life stage on the proportion of aphids consumed was significant ($F = 9.70$; df = 1, 4; $P = 0.0023$). As expected, initial aphid density had a highly significant ($F = 154.7$; df = 4, 4; $P = 0.0001$) effect on the proportion of aphids consumed as well. The interaction between *H. convergens* life

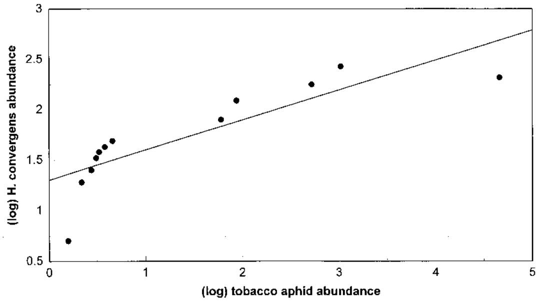

Fig. 3. Linear regression of *H. convergens* abundance (log transformed) versus tobacco aphid abundance (log transformed) ($R^2 = 0.71$; $y = 1.3016 + 0.2979x$; $P = 0.0006$).

Table 2. Mean numbers ± SD and mean proportions ± SD of tobacco aphids consumed by *H. convergens* larvae and adults at each tobacco aphid density

Tobacco aphid density[a]	Mean number		Mean proportion	
	Larvae	Adults	Larvae	Adults
2	2.0 ± 0.0	2.0 ± 0.0	100 ± 0.0	100 ± 0.0
8	7.86 ± 0.52	8.0 ± 0.0	98.3 ± 6.45	100 ± 0.0
16	13.07 ± 3.86	13.83 ± 4.28	81.6 ± 24.22	86.5 ± 26.67
32	25.6 ± 6.13	23.0 ± 8.77	80.07 ± 19.23	71.92 ± 27.27
64	33.4 ± 13.46	52.92 ± 10.14	52.13 ± 21.08	82.67 ± 15.95

[a] Number of aphids per 100 by 15 mm petri dish arena.

Table 3. Maximum likelihood estimates from logistic regressions of the proportion of tobacco aphids eaten by *H. convergens* 4th-instar larvae and adults as a function of initial aphid density

H. convergens Life Stage	Parameter	Estimate (SE)	*t*-ratio	*P*
Fourth-instar	Constant	9.4119 (2.1926)	18.43	<0.01
	Linear	−0.8667 (0.2471)	12.30	<0.01
	Quadratic	0.0272 (0.0079)	11.90	<0.01
Adult	Constant	33.835 (0.0690)	24.04	<0.01
	Linear	−3.4421 (0.0090)	22.26	<0.01
	Quadratic	0.1050 (0.0003)	18.29	<0.01

stage and initial aphid density was also significant ($F = 12.41$, df = 4, 125; $P = 0.0001$).

Chedester (1979) indicates that 4th-instar *H. convergens* larvae consumed no <82% of spotted alfalfa aphids, *Therioaphis maculata* (Buck), presented at densities of up to 50 aphids per arena. In the current study, 4th-instar larvae did not consume such high proportions of tobacco aphids at the highest initial aphid density (Table 2). Adults still consumed >82% of the aphids at the highest aphid density. The increased consumption by adults relative to larvae may be caused by digestion or handling time differences. The greater mobility of the adult lady beetle most likely had very little effect on the consumption of aphids in the artificial environment of the petri dish because aphids were normally concentrated on the leaf provided during the study.

Searching efficiency declined with increasing aphid density for *H. convergens* larvae and adults, as indicated by the decline in the proportion of aphids consumed with increasing aphid density (Fig. 5). The decline in searching efficiency illustrates the effect of handling time on predator searching ability (Hassell 1978). The simplified environment provided by laboratory conditions may provide a poor estimate of the efficiency of *H. convergens* as a predator of tobacco aphids under field conditions. Searching efficiency is likely to be much lower in the field than in the laboratory because of interference from other predators and the impediments provided by plant architecture (Messina and Hanks 1998). Some prey species are often dispersed throughout the plant canopy and predators must search leaves to find prey (O'Neil 1989). Aphids however are often aggregated at certain locations on plant surfaces such as the undersides of leaves. Their concentration would make aphids a

Table 4. Attack coefficients *(a)*, handling time *(T_h)*, and their asymptotic standard errors from nonlinear regressions of the number of tobacco aphids eaten by *H. convergens* 4th-instar larvae and adults as a function of initial aphid density

H. convergens Life Stage	Model	*a* (95% CI)	T_h (95% CI)
Fourth-Instar	Type II	0.0088 (0.003–0.0145)	41.18* (35.97–46.38)
Adult	Type II	0.0037 (0.002–0.005)	19.38* (14.04–24.72)

Time units are minutes. Coefficients significantly different from 0 at $P \leq 0.05$.

*Indicates significant difference.

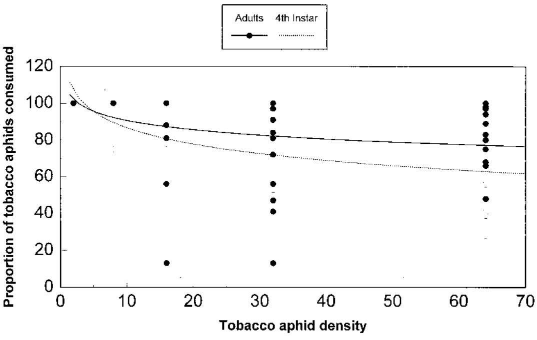

Fig. 5. Proportions of adult tobacco aphids consumed by 4th-instar and adult *H. convergens* as a function of initial tobacco aphid density.

highly efficient prey for most predators, particularly those that are less mobile.

The information gathered during this study would suggest that the native *H. convergens* appears to be an efficient predator of tobacco aphids in Georgia flue-cured tobacco. The abundance of *C. septempunctata* early in the growing season suggests an earlier emergence from diapause for this species than that of *H. axyridis*, or that *H. axyridis* may occupy a different habitat during this time. The early season abundance of *C. septempunctata* also suggests that this species may be more tolerant of early season conditions in tobacco than *H. axyridis*. However, *C. septempunctata* appears to emigrate from tobacco once *H. axyridis* populations become abundant. Tedders and Schaefer (1994) report emigration of *C. septempunctata* from pecan as *H. axyridis* becomes more abundant in pecan. Neither of these 2 introduced species are as abundant as the convergent lady beetle or persist as long during the growing season in tobacco. It is possible that *C. septempunctata* and *H. axyridis* are moving to other crops before *H. convergens*. *H. convergens* appears capable of consuming large numbers of aphids under the appropriate conditions. Collectively, these 3 coccinellids may be important in regulating tobacco aphids in Georgia tobacco; however, additional work is needed in this area to confirm the impact of these natural enemies on tobacco aphids. A better understanding of ladybeetle population dynamics and their interactions with pest species would advance biologically based pest management programs in tobacco.

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