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 lady beetle, *Hippodamia convergens* Guérin-Méneville, the sevenspotted lady beetle, *Coccinella septempunctata* L., and the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas). *H. convergens* 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 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.

**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
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 1981).

**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’ blue-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 1978). 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 two-way analysis of variance (ANOVA) with coccinellid species and date as main effects. A linear two-way analysis of variance (ANOVA) with coccinellid species and date as main effects.

**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-
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 tobacco plots after tobacco flower heads were removed.

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 + 0.2973*x*; *P* = 0.0006) than during 1997 (*R*² = 0.50; *y* = 0.7397 + 0.6727*x*; *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 + 0.6442*x*; *P* = 0.003) and 1998 (*R*² = 0.78; *y* = -0.0752 + 0.2804*x*; *P* = 0.0001). *C. septempunctata* populations did not appear to be linearly related to tobacco aphid populations during

![Table 1. Mean numbers of lady beetles per 100 plants ± SD and R² values for linear regression of each species’ abundance (log transformed) with tobacco aphid abundance (log transformed) during the 1997 and 1998 growing seasons.](image)

<table>
<thead>
<tr>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. axyridis</em></td>
<td>11.0 ± 9.34</td>
<td>2.58 ± 3.85</td>
<td>0.5969</td>
<td>0.7830</td>
<td></td>
</tr>
<tr>
<td><em>H. convergens</em></td>
<td>66.25 ± 44.08</td>
<td>88.33 ± 96.15</td>
<td>0.5028</td>
<td>0.7087</td>
<td></td>
</tr>
<tr>
<td><em>C. septempunctata</em></td>
<td>14.25 ± 16.40</td>
<td>9.08 ± 16.54</td>
<td>0.1765</td>
<td>0.3672</td>
<td></td>
</tr>
</tbody>
</table>

Large standard deviations are the result of large sampling date variations in ladybeetle densities throughout the growing seasons.
were negative (i.e., the proportion of aphids eaten
regression because estimates of the linear coef-
ficents of Type II functional response were also suggested by logistic
II functional response for both beetle stages. Type II
with initial aphid density (Table 2), indicating a type
adults and 4th-instar larvae declined monotonically
were conducted as a step in this direction.
work is needed to confirm this hypothesis and our
integrated pest management (IPM) programs. More
species were good candidates for tobacco aphid
aphidabundance during 1998 could indicate that these
strong linear relationship was observed between C.
species was more closely correlated with tobacco
aphid populations than C. septempunctata (Figs. 2, 3,
and 4). Population levels of each of the 3 coccinellid
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
life stage on the propor-
number 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

\begin{align*}
\text{Table 2. Mean numbers} & \pm \text{SD and mean proportions} \pm \text{SD of tobacco aphids consumed by H. convergens larvae and adults at each tobacco aphid density} \\
\hline
\text{Tobacco aphid density}^a & \text{Mean number} & \text{Mean proportion} \\
\hline
2 & 2.0 \pm 0.0 & 2.0 \pm 0.0 \quad 100 \pm 0.0 & 100 \pm 0.0 \\
6 & 7.66 \pm 0.52 & 8.0 \pm 0.0 \quad 98.3 \pm 6.45 & 100 \pm 0.0 \\
16 & 13.07 \pm 3.86 & 13.83 \pm 4.28 \quad 81.6 \pm 24.22 & 86.5 \pm 26.67 \\
32 & 25.6 \pm 6.13 & 23.9 \pm 8.77 \quad 90.07 \pm 19.23 & 71.92 \pm 27.37 \\
64 & 33.4 \pm 13.46 & 52.92 \pm 10.14 \quad 52.13 \pm 21.98 & 82.67 \pm 15.95 \\
\hline
\end{align*}

\text{Number of aphids per 100 by 15 mm petri dish arena.}

Fig. 2. Linear regression of H. axyridis abundance (log transformed) versus tobacco aphid abundance (log transformed) \((R^2 = 0.78; y = -0.0752 + 0.2604x; P = 0.0001)\).

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

Fig. 4. Linear regression of adult C. septempunctata abundance (log transformed) versus tobacco aphid abundance (log transformed) \((R^2 = 0.37; y = 0.1307 + 0.2771x; P = 0.04)\).
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, *Thioaphis 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 1989). 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 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 fluctuated 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.

### 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

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>Parameter</th>
<th>Estimate (SE)</th>
<th>t-ratio</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fourth-instar</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Linear</td>
<td>-0.5667 (0.2471)</td>
<td>12.30</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>0.0272 (0.0079)</td>
<td>11.90</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Linear</td>
<td>-3.4421 (0.0090)</td>
<td>22.26</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>0.1050 (0.0003)</td>
<td>18.29</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

### 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

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>Model</th>
<th>$a$ (95% CI)</th>
<th>$T_H$ (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fourth-Instar</td>
<td>Type II</td>
<td>0.0088 (0.003-0.0145)</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>Type II</td>
<td>0.0037 (0.002-0.005)</td>
</tr>
</tbody>
</table>

*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.

**Acknowledgments**

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