Effect of Predators on Population Dynamics of Green Peach Aphid

on Flue-Cured Tobacco in Virginia

by

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(ABSTRACT)

The effects of indigenous predators on green peach aphid (GPA), *Myzus persicae* (Sulzer), populations on flue-cured tobacco were evaluated in 1985 and 1986. The most common GPA predators found on tobacco were convergent lady beetle (CLB) (*Hippodamia convergens*), syrphid flies, *Geocoris* spp., *Jalysus wackhimi*, *Nabis* spp., *Chrysopa* spp., *Micromus* sp., and several other species coccinellids. However, CLB was the only predator that had a numerical response to increasing GPA density on tobacco. In the laboratory, the minimum number of GPA required to initiate reproduction in CLB, and the conversion rates were two factors that determined the oviposition rate of CLB. In fields, CLB demonstrated a sigmoid curve predator-prey relationship. CLB did not show a linear relationship until GPA populations reached a certain density. Furthermore, CLB did not show a response when GPA density was above the satiation point.

Although CLB were able to reduce GPA population growth, they were not able to maintain GPA populations below the economic injury level. Two factors probably limited the success of CLB to control GPA populations on flue-cured tobacco: 1.) the glandular trichomes of tobacco which produced gummy exudates, and 2.) the satiation point of CLB when GPA populations were very high. In addition, interplanting tobacco with clover increased the number of syrphid fly larvae on tobacco. Likewise, tobacco interplanted with sunflowers had increased big-eyed bug, populations, and tobacco-alfalfa and tobacco-tobacco plots had higher stilt bug populations on tobacco.

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GENERAL INTRODUCTION

Tobacco (*Nicotiana tabacum* L.) is the most important cash crop in Virginia. It is the key part of two billion dollars of Virginia's total agricultural industries (Farmer 1987). The importance of tobacco is further enhanced by the employment opportunity provided by tobacco-related industries. In 1983, 146,331 jobs, about 6% of total state employment, were created, which compensated more than $2.87 billion (Farmer 1987). Therefore, the role of tobacco to the Virginia state economy is very important one, especially when its sales tax is also included.

There are four types of tobacco grown in Virginia; flue-cured, burley, sun-cured, and dark-fired tobacco. Of these four types, 80% of total acreage were planted with flue-cured tobacco (Semtner 1982). In 1986, flue-cured tobacco was planted on 28,000 acres on 5,000 farms in Virginia (VCRS 1986).

Green peach aphid (GPA), *Myzus persicae* (Sulzer), is one of the most important tobacco insect pests in Virginia. In North America, it first caused economic damage on cigar-wrapper tobacco in 1946 (Chamberlain 1958). Through the 1950's to 1970's, it was considered a moderate pest. However, since the mid-1970's it became a consistent pest (Cheng and Court 1977, Semtner 1983, Cheng and Hanlon 1985).

Severe GPA infestations may result in 100% loss if early control is not obtained (Tappan 1963). Losses can result from reductions in yield and quality of tobacco. Yield is reduced due to stunting of plants and thinner leaves caused by the removal of important nutrients (Chamberlain 1958, Tappan 1963). Quality decreases as the result of alteration in chemical composition and change in texture of tobacco leaves (Cheng and Court 1977, Mistric and Clark 1979). Heavy GPA infestations also lower reducing sugar and alkoloid contents, but increase nitrogen and starch contents of tobacco leaves. These changes in chemical composition contribute to reductions in tobacco quality.

Furthermore, GPA feeding results in necrosis of leaves near the petiole, especially on bottom leaves (Dominick 1949). GPA also produces exuviae and honeydew that promotes the growth of sooty-mold (*Fumago vagans* Pers.). GPA exuviae and sooty mold alter the texture of cured leaves (Cheng and Hanlon 1985). Mistric and Clark (1977) and Cheng and Hanlon (1985) compared yield of uninfested tobacco to that with 100% of the plants infested with GPA. Although their numbers differed, both indicated that GPA cause more damage to bottom leaves than the upper leaves. In addition to these injury factors, GPA is also a potential vector of pathogenic viruses (Wallis and Turner 1969, Lucas 1975).

Insecticides are the only effective methods of controlling GPA outbreaks (Tappan 1963, Semtner 1983a). Although the use of a treatment threshold is recommended, i.e control should be initiated when 20% of the tobacco plants are infested with 50 or more of GPA per leaf on the upper leaves (Semtner, 1985), most farmers spray an insecticide for preventative control (Semtner 1982). As a result, some of applications are wasted when GPA populations are too low to justify treatments. This practice will not only increase the cost of tobacco production, but will also reduce the beneficial insects on tobacco (Semtner 1979). In addition, insecticides could result in insect pest resistance and resurgence. Insecticides can also cause replacement of one pest problem with another, contaminate the environment, and leave residue on tobacco leaves. Therefore, cultural practices that lead to reduction in pesticide usage should be emphasized.

There are several predators associated with GPA populations on tobacco. These include several species of lady beetles, mainly convergent lady beetle (CLB), *Hippodamia convergens* Guerin-Meneville, syrphid fly larvae (Diptera: Syrphidae), green lacewings (*Chrysopa* spp.), and stilt bugs (*Jalysus wackhimi* Van Duzee) (Dominick 1949, Kulash 1949, Elsey and Stinner 1971). Among these predators, CLB is believed to be the most abundant on tobacco (Belcher and Thurston 1983, Elsey and Chaplin 1978). However, in many cases, CLB are not able to regulate GPA populations effectively. The reasons for CLB's ineffectiveness against GPA are unknown. Hence, it is important to understand the ecology of CLB and other GPA predators on tobacco. Studies are also needed to determine which cultural practices could increase predator activity on tobacco. This information is very useful in designing a better pest management program to benefit Virginia tobacco farmers.

Based on these considerations, my research was conducted in 1985 and 1986. Its main objective was to identify the major insect predators of GPA, and to evaluate their impact on GPA population dynamics on flue-cured tobacco in Virginia. To achieve this objective four experiments with four sub-objectives were designed. My specific sub-objectives are:-

1. To study the relationship between GPA and their predators on flue-cured tobacco by examining their seasonal abundance, synchronization, and vertical distribution.

2. To investigate the numerical response of CLB to various GPA densities on flue-cured tobacco under both laboratory and field conditions.

3. To assess the impact of initial CLB to GPA ratios on the predation rates of CLB on GPA populations on flue-cured tobacco grown in field cages.

4. To determine the suitability of various crops planted in association with flue-cured tobacco for increasing the activity of predators on tobacco, without reducing tobacco yield and quality.

LITERATURE REVIEW

Life-cycle and Biology of Green Peach Aphid

The green peach aphid (GPA), *Myzus persicae* (Sulzer) (Homoptera: Aphididae) is a phytophagous insect with a wide host range (Leonard et al. 1970). However, *Prunus* sp. is considered its primary host (Blackman and Eastop 1984). GPA has two types of life cycles, holocyclic and anholocyclic (van Emden et al. 1969). The holocyclic cycle consists of overwintered eggs on the primary host. The eggs hatch in spring and the resulting young are known as fundatrices. The fundatrices may develop on the primary host or emigrate onto secondary hosts, and reproduce through parthenogenensis (van Emden et al. 1969, Tamaki et al. 1982). In contrast, the anholocyclic life-cycle consists of overwintered viviparous parthenogenetic females on weeds or vegetables such as mustard, kale, and turnip (Fusco and Thurston 1968, Wallis and Turner 1969). They are usually found in mild winters or warmer climates (van Emden et al. 1969). They develop parthenogenetically on their overwintering hosts. Unlike the GPA that produces holocyclically, they were susceptible to cold weather, but are able to reproduce faster (van Emden et al. 1969).

On tobacco, GPA begins to infest tobacco in plant bed (Kulash 1949, Dominick 1949). However, they first become serious in fields in late June or early July (Semtner 1983a). GPA populations are usually most serious at the field edge (Kulash 1949). Topping (removal of plant terminal bud) reduces GPA populations on tobacco drastically (Webster et al. 1983, Semtner 1987). In addition, high temperature, poor host quality and the presence of natural enemies also reduces GPA population development in fields (Dominick 1949, van Emden et al. 1969). In laboratory, at 24°C, GPA live an average of two weeks and begin reproducing after one week. Their net reproduction was 17 to 20 nymphs/adult (Throne and Lampert 1985).

Biology and Ecology of Insect Predators of the Green Peach Aphid on Tobacco.

Coccinellid beetles

Several species of coccinellid beetles (Coleoptera: Coccinellidae) have been found on tobacco. Adults are easily identified by their orange- or red- and black-marked, oval and convex bodies (Dietz et al. 1976), while larvae are black or dark blue with red or yellow spots, and an elongate body (Hodek 1973). The most commonly observed coccinellid beetles on tobacco are *Hippodamia convergens* Guerin-Meneville, *Coleomagilla maculata* (De Geer), *Hippodamia tridecipunctata* L., *Adalia bipunctata* L. and *Coccinella transversogutatta* Falderman (Dominick 1949, Cheng 1981). However, *H. convergens*, the convergent lady beetle (CLB) is the dominant species observed in tobacco fields (Kulash 1949, Dominick 1949, Belcher and Thurston 1983, Semtner 1983b). These coccinellid beetles are believed to significantly reduce green peach aphid (GPA), *Myzus persicae* (Sulzer) populations on tobacco (Chamberlain 1958, Cheng and Hanlon 1985, Avery and Pless 1987).

In the southeastern United States, CLB have one or two generations per year (Hagen, 1962). The overwintered adults begin to lay eggs in early spring if prey are abundant (Hagen 1962). On tobacco, CLB oviposites when GPA are abundant (Belcher and Thurston 1983). CLB deposit spindle-shaped eggs in compact clusters of 10 to 50, standing vertically on the substrate (Clausen 1962). It is estimated that each CLB female is capable of ovipositing 500 to 1000 eggs over period of 3 to 4 months (Clausen 1962). Eggs hatch 2 to 6 days. However, in California, Hagen and Sluss (1965) observed that overwintered CLB females produced an average of 1270 eggs per female in 2 months when fed on pea aphid *Acyrthosiphon pisum* (Harris), but only 349 eggs per female in 28 days when fed on spotted alfalfa aphid *Therioaphis trifolii* (Monell).

Like other coccinellid species, larvae of CLB stay on egg shells for an hour after hatching (Dixon 1959). They may eat the non-viable eggs, or the late hatching larvae before they disperse to search for normal foods (Dixon 1959, Pienkowski 1965). This adaptive behavior of larvae could increase their survival (Pienkowski 1965, Ng 1986). The larval stage which contains four instars averages 20 days (Clausen 1962). The fourth instar larvae become immobile, and do not feed before ecdysis. The average duration of the pupal stage is 6 days (Clausen 1962). The emerged adults lack of pattern, and have soft elytra. The hind wings protrude under the front wings. Their color pattern appears a few hours later, but the red color remains lighter for weeks or months (Hodek 1973). Thus, it is relatively easy to distinguish between overwintered adults and young adults in the field. The mating of young adults usually takes place 1 or 2 days after emergence, and oviposition begins 7 to 10 days later (Clausen 1962). The adults migrate to overwintering sites in response to limited food, shorter photoperiods, and cold weather (Hagen 1962). Fourth instar larvae and ovipositing females of CLB can consume 50 aphids per day (Clausen 1962).

The role of CLB in regulating aphid populations is very important on several crops. For example, CLB is the most important predator of the spotted alfalfa aphid *Therioaphis maculata* (Monell) on alfalfa in Utah and Kansas (Goodarzy and Davis 1958, Simpson and Burhadt 1960); GPA and potato aphid *Macrosiphum euphorbiae* (Thomas) on potato in Maine (Shands et al. 1972a, Shands et al. 1972b); and GPA on burley tobacco in Tennessee (Avery and Pless 1987).

Syrphid Flies

Several species of syrphid flies (Diptera: Syrphidae), mostly *Sphaerophoria cylindrica* (Say) are associated with GPA populations on tobacco (Kulash 1949, Dominick 1949, Rabb et al. 1959). Syrphid fly adults are brightly marked with spots or stripes of yellow and black (Dietz et al. 1976), and larvae are maggots (Clausen 1962). They were less abundant than CLB on tobacco (Roach 1980). However, on peach syrphid flies are the most abundant predators of GPA (Tamaki 1973). Female syrphid flies deposit their eggs singly in aphid colonies (Schneider 1969). Each female can oviposit up to 400 eggs, which hatch in 2 to 3 days. The larval stage lasts an average of 20 days. A larvae requires more than 400 aphids to complete development (Clausen 1962).

The seasonal abundance of syrphid flies is greatly influenced by environmental factors. Syrphid flies prefer a humid habitat (Honek 1983), and are more numerous on crops adjacent to hedge areas (Polard 1971). The presence of alternate food for adults in such areas might be the reason for this observation. Pollen is required for the development of syrphid fly eggs (Schneider 1969).

Big-eyed Bugs

Two species of big-eyed bugs (Hemiptera: Lygaeidae) are commonly found on tobacco, *Geocoris punctipes* (Say) and *G. uliginosus* (Say). The former is more abundant (Roach 1980). Big-eyed bugs are easily identified with their large compound eyes and robust body (Dietz et al. 1976). Big-eyed bugs have five nymphal instars. It takes big-eyed bugs 40 to 47 days to complete their life-cycle at 25.5 ^{0}C (Champlain and Sholdt 1966).

Big-eyed bugs are important predators for reducing GPA populations on the orchard floor (Tamaki 1972). However, on tobacco big-eyed bugs were a major predator of tobacco flea beetles [*Epitrix hirtipennis* (Melsheimer)] (Dominick 1943). Hence, in tobacco fields, the presence of tobacco flea beetles may be more important to big-eyed bugs than the presence of GPA.

Stilt bugs

Stilt bugs (Hemiptera: Berytidae) are the most numerous insect predators observed on tobacco (Roach 1980). Stilt bugs are slender brown insects with thread-like legs (Wheeler and Henry 1981). They have five nymphal instars. There are three to four generations per year.

Stilt bugs were considered phytophagous insects (Rabb et al. 1959, Wheeler and Henry 1981). Elsey and Stinner (1971) demonstrated that they are predators of GPA. In addition, stilt bugs are considered major predators of hornworm and budworm eggs on tobacco (Elsey and Stinner 1971, Elsey 1972, Semtner 1979).

Other Insect Predators

Other insect predators found on tobacco include damsel bugs (Hemiptera: Nabidae), green lacewings (Neuroptera: Chrysopidae) and brown lacewings (Neuroptera: Hemerobiidae) (Roach 1980, Kulash 1949, Dominick 1949). Although damsel bugs and lacewings are consistently present in tobacco fields, they are not abundant enough to be major GPA predators. In addition, carabid beetles (Coleoptera: Carabidae) and spiders are numerous in tobacco fields. In other crops, carabid beetles and spiders are very important GPA predators (Loughridge and Luff 1983, Shands et al. 1972b). However, information on their ecology and biology on tobacco is lacking.

Coccinellid Beetles and Biological Control

The importance of coccinellid beetles in biological control has long been recognized. The earliest reports on their importance of were made by Spencer in 1815 and 1856, and by Fitch in 1856 (as in DeBach 1964). However, the result of releasing vedalia beetles *Rodalia cardinalis* (Muls) to control cottony cushion scale *Icerya purchasi* Mask in 1888 established the economic importance of coccinellid beetles in biological control (DeBach 1964). Since then, extensive work has involved the utilization of coccinellid beetles as biological control agents of several important pests (Laing and Hamai 1976). However, control with coccidophagous coccinellids has been more successful than with aphidophagous coccinellids (Clausen 1978).

Factors Influencing the Effectiveness of Coccinellid Beetles to Regulate Aphid Populations.

Climatic factors

Temperature is the most important climatic factor that affects the predation rates of coccinellid beetles (Frazer and Gilbert 1976, Mills 1982a). Higher temperatures usually increase the predation rates of coccinellid beetles on aphid populations, and the rate of aphid mortality (DeLoach 1974). Thus, greater reductions in aphid populations occur at higher temperatures. Hodek et al. (1965) observed that warmer temperatures help improve control of *Aphis fabae* Scopoli by *Cocccinela septempunctata* L. on sugar beet.

Synchronization in Space and Time

The ability of coccinellid beetles to occur at the same time and in the same habitat with aphid populations, increases its chance to come into contact with aphid, and should increase their predation rates (Hodek 1970). Time synchronization refers to the timing of coccinellid beetle colonization and aphid population development, which can be divided into the initiation, increasing, peak, and declining phases (Hodek 1973). The ability of coccinellid beetles to colonize aphid populations in the initial stages should result in better control of aphid populations (Way et al. 1954, Sluss and Hagen 1965). The presence of coccinellid beetles in the increasing phase of the aphid can result in better control if aphid reproductive rate and beetle voracity are balanced (van Emden 1965). Both of these factors are governed by temperature. However, when aphid populations reach their peak, the presence of coccinellids or other predators thereafter made no economic impact (Hodek 1973). Instead, it may benefit the aphids because their intraspecific competition is reduced (Way 1965). Space synchronization refers to the ability for coccinellid beetles to exist in the same microhabitat with aphid populations, i.e on the same part of the plant (Hodek 1970). Aphids are known to prefer the young parts of the plant (Kennedy et al. 1950, van Emden et al. 1969). Thus, it is important for coccinellid beetles to spend more time on this part of the plant so that more of their progeny survive, and increase their predation rate.

Voracity of Coccinellid beetles

Voracity is defined as the capability of predators to consum or kill their prey in a given time (van Emden 1965). It depends on appetite and number of predators. Hence, voracity is determined by the functional and numerical response of predators (Solomon 1949, Holling 1959). To ensure that coccinellids control aphid populations effectively, they have must be able to respond numerically and functionally to increasing aphid densities (Holling 1959).

Cultural Practices and Chemical Controls

The selection of certain crop varieties influence coccinellid-aphid interactions (Messenger et al. 1976). For example, tobacco and eggplant with trichomes were harmful to coccinellids larvae (Elsey 1974, Belcher and Thurston 1982, Quilici and Iperti 1986). Likewise, application of certain insecticides is detrimental to coccinellids, and can result in a resurgence of aphid populations (Goodarzy and Davis 1958). Kalushkov and Zeleny (1986) found that sublethal dosages of methomyl reduced the fecundity of *Propylea quatuordecimpunctata* L., while its use at the labeled rate kills all coccinellids. However, pirimicab did not affect coccinellids.

The presence of certain crops adjacent to protected crops can increase predator activity in protected crops (Shands et al. 1972b, Fye 1972, Burleigh et al. 1973, Stechmann 1986). Fye (1972) observed that alfalfa planted adjacent to cotton serves as a reservoir for natural enemies which control insect pests on cotton. Burleigh et al. (1973) also observed that sorghum which was planted adjacent to cotton attracted significantly more *H. convergens* than corn planted adjacent to cotton. Later in the season, when the sorghum matured, *H. convergens* moved into cotton fields, and helped reduce of several major cotton pests. Likewise, Ruzicka et al. (1986) observed that crop diversification helped coccinellid beetles to control aphids on garden crops.

Impact of Coccinellid Predation Rate on Aphid Populations.

Predators, mainly coccinellids, are very important in regulating aphid populations (Hagen and van den Bosch 1968, Mackeur 1986). Several methods have been employed to evaluate the impact of coccinellids on aphid populations. Hodek et al. (1972) and Kiritani and Dempster (1973) have outlined in detail both the indirect and direct methods.

Indirect methods involve monitoring of coccinellid beetle and aphid populations in the field. Their numbers are compared or analyzed, i.e correlation and regression, to determine their relationship (Shands et al 1972b, Allen 1986). The disadvantage this method is the possibility of coincidence. Unless there is evidence of direct causal relationship between coccinellids and aphids, the results are not very useful (Kritani and Dempster 1973). Another popular indirect method to evaluate the impact of coccinellids on aphid populations is modelling. Mack and Smilowitz (1982) used computer simulation CMACSIM to evaluate the impact of *C. maculata* predation rate on green peach aphid populations on potato. Likewise, Gutierrez and Baumgaertner (1984) used a simulation model to study the impact of predators on pea aphids [*Acyrthosiphon pisum* (Harris)] and blue alfalfa aphids (*A. kondoi* Shinji) in an alfalfa ecosystem. Their model indicated that *H. convergens* is the most important predator in the California alfalfa agroecosystem. Computer modelling may be the least expensive method, however it requires a thorough understand of biology and ecology of the species involved, and programming skills.

Direct methods involve field experiments where aphid population growth is compared for treatments with and without coccinellids (Hodek et al 1972). Aphid populations without coccinellids can be established through exclusion techniques such as the application of selective insecticides, their removal by hand, or the use of cages (Atwal and Sethi 1963, Hodek et al. 1965, Shands et al. 1972a, Chambers et al. 1983, Kring and Gilstrap 1984, Liao et al. 1985). The advantage of such techniques is that they provide the quantitative observation for each predator and prey system, under the field conditions. However, they may alter the habitat from natural conditions (Grant and Shepard 1985).

SEASONAL ABUNDANCE AND VERTICAL DISTRIBUTION OF GREEN PEACH APHID (HOMOPTERA: APHIDIDAE) AND ITS PREDATORS ON TOBACCO IN VIRGINIA

Introduction

The green peach aphid (GPA), *Myzus persicae* (Sulzer), is a pest of tobacco in most tobacco producing countries in the world. In North America, it first caused economic damage to tobacco in 1946 (Chamberlain 1958). Since then, it has become one of the most important insect pests of tobacco (Mistric and Clark 1979, Semtner 1983a, Cheng and Hanlon 1985). Severe GPA infestations reduce yield and quality of tobacco by stunting plants and causing thinner leaves (Dominick 1949, Chamberlain 1958). GPA feeding removes important plant nutrients, reduces cured leaf quality by lowering the levels of reducing sugars and phenolic compounds (Cheng and Court 1977), increases necrotic leaf tissue (Mistric and Clark 1979), and contaminates the leaves with honeydew and exuviae (Dominick 1949, Kulash 1949, Tappan 1963).

Several insect predators help regulate GPA populations on field, vegetable, and fruit crops. They include several species of lady beetles (Coleoptera: Coccinellidae), syrphid fly larvae (Diptera: Syrphidae), green lacewings (Neuroptera: Chrysopidae), brown lacewings (Neuroptera: Hemerobiidae), big-eyed bugs (Hemiptera: Lygaeidae), damsel bugs (Hemiptera: Nabidae), minute pirate bugs (Hemiptera: Anthocoridae), stilt bugs (Hemiptera: Berytidae), and carabid beetles (Coleoptra: Carabidae) (Van Emden et al. 1969, Elsey and Stinner 1971, Shands et al 1972b, Tamaki 1973, Mack and Smilowitz 1979, Loughridge and Luff 1983, Hussein 1985). On tobacco the most common GPA predators are lady beetles, syrphid fly larvae, green lacewings and stilt bugs (Dominick 1949, Kulash 1949, Elsey and Stinner 1971).

Two factors that determine the effectiveness of these predators in regulating GPA populations are their seasonal abundance and synchronization (in time and space) with GPA populations (Van Emden 1965). Seasonal abundance is determined by monitoring populations in the field, while synchronization in time is determined by correlating the seasonal abundance of predators with seasonal abundance of GPA (Huffaker and Kennet 1969). In addition, their synchronization in space is determined by examining whether the predator and its prey co-exist on the the same part of the plant.

This study was conducted to determine the relationship between GPA and its predators on flue-cured tobacco by examining their seasonal abundance, synchronization, and vertical distribution.

Materials and Methods

The experiments were conducted at Virginia Polytechnic Institute and State University - Southern Piedmont Agriculture Experiment Station, Blackstone, Virginia in 1985 and 1986. Each year, two tobacco plots (ca. 0.075 ha) were selected and planted in 'Coker 319' flue-cured tobacco. In each year one plot was located at the edge of the field (close to a wooded area), and a second was established near the middle of the field. The first and second plots were named PLOT-1 and PLOT-2, respectively. Tobacco was transplanted in both plots on 2 May 1985. In 1986, tobacco were transplanted on 12 and 16 May for PLOT-1 and PLOT-2 respectively. Tobacco production practices followed Virginia Cooperative Extension Service recommendations (Jones 1985). *Bacillus thuringiensis* Berliner (Dipel®) was applied to control hornworms (*Manduca* spp.) when necessary. No insecticides were applied to control GPA. In 1985, tobacco in PLOT-1 was topped (plant terminal bud was removed) in late flower stage (12 July), while tobacco in PLOT-2 were topped in early flower stage (8 July), and no chemical sucker control was used. However, in 1986, tobacco in both plots were topped in early flower stage (16 July) and treated with sucker control agent (Off Shoot T®).

In each field, 50 plants were randomly selected and populations of GPA and their predators were monitored on these plants at least once a week at ca. 9:00 a.m. For GPA, the underside of the top eight leaves at least 8 cm long, were examined. The numbers of GPA presence between the fourth and sixth lateral veins on the right side of the midrib of these leaves were recorded. The top four leaves were considered the upper leaf position (TOP), and the next four lower leaves as the middle leaf position (MID). GPA populations on the remaining lower leaves were not sampled because their number were negligible.

GPA predators (including eggs and larvae of convergent lady beetles) were identified and counted. All lady beetle eggs and larvae found on the sample plants were considered as convergent lady beetle eggs and larvae, since other species of lady beetles were very rare. Those predators that consistently had high numbers were classified as major predators, and counted on each of three leaf positions: 1) the four uppermost leaves (TOP), 2) the next four lower leaves (MID), and 3) the remaining lower leaves (BOT). The number of leaves for BOT position varied according to tobacco stage. Other predators that were inconsistently present and less numerous were sampled on the whole plant. Predators were identified in situ, at least to family.

Insect counts were transformed to $\log_{10}(x+1)$ for statistical analysis. The synchronization of major predators with GPA populations was determined with Pearson correlation analysis between total predators/plant and total GPA sampled/plant, before and after tobacco was topped. Adult and larva convergent lady beetles were combined for the statistical analysis. The vertical distribution of major GPA predators was compared by analysis of variance (ANOVA) on the means/plant position. A randomized complete block design model, with plant positions representing the treatments and plant numbers the replications, was used for the analysis. ANOVA was conducted for four different periods for each plot. The early period occurred between 30 to 50 days after transplanting (DAT); the Pre-topping period was 50 DAT to topping date (ca. 70 DAT); the Post-topping period occurred from topping date to ca. 80 DAT; and the Final period was from ca. 80 DAT to the end of the season. These periods were divided by tobacco growth stage. Statistical analyse were done with programs provided by SAS (SAS Institute 1985). Proc Corr was used for Pearson correlation analysis, and Proc GLM was used for ANOVA vertical distribution of GPA on tobacco. The significant means were separated using Duncan's multiple range test ($\alpha = 0.05$)

Result and Discussion

Green peach aphid (GPA)

The seasonal abundances of GPA for 1985 and 1986 are shown in Figs. 1 and 2, respectively. GPA populations were more abundant in 1986 than in 1985. In each year, tobacco in PLOT-1 (located at field edge) was infested earlier by GPA than PLOT-2 (located at middle field), and peak GPA populations were higher in PLOT-1 than PLOT-2.

Observations of GPA distribution on the upper part of tobacco plants showed that GPA generally preferred the TOP position (four most upper leaves) early in the season (Table 1). In 1985, the numbers of GPA sampled on the TOP position were significantly (α = 0.05) higher than those sampled on the next four lower leaves during Early and Pre-topping Period. Later in the season (Post-topping and Final Period), GPA populations were reduced drastically, and the numbers on the upper leaves were not significantly different from those sampled from the next four lower leaves (except during Post-topping and Final periods of PLOT-2). In 1986, however, the GPA numbers on the upper leaf position were not significantly different from the next four lower leaves during Early and Pre-topping periods, except during Pre-topping period of PLOT-1. Later in the season, only Post-topping period of PLOT-1 had significantly more GPA on four lower leaves (MID).

Convergent lady beetle larvae and adults (CLBLA)

The seasonal abundance of CLBLA also varied between years and plots (Figs. 3 and 4). CLBLA were more abundant in 1986 than 1985. In each year, more CLBLA were observed in PLOT-1 in early season, while late in season more CLBLA were observed in PLOT-2. Compared

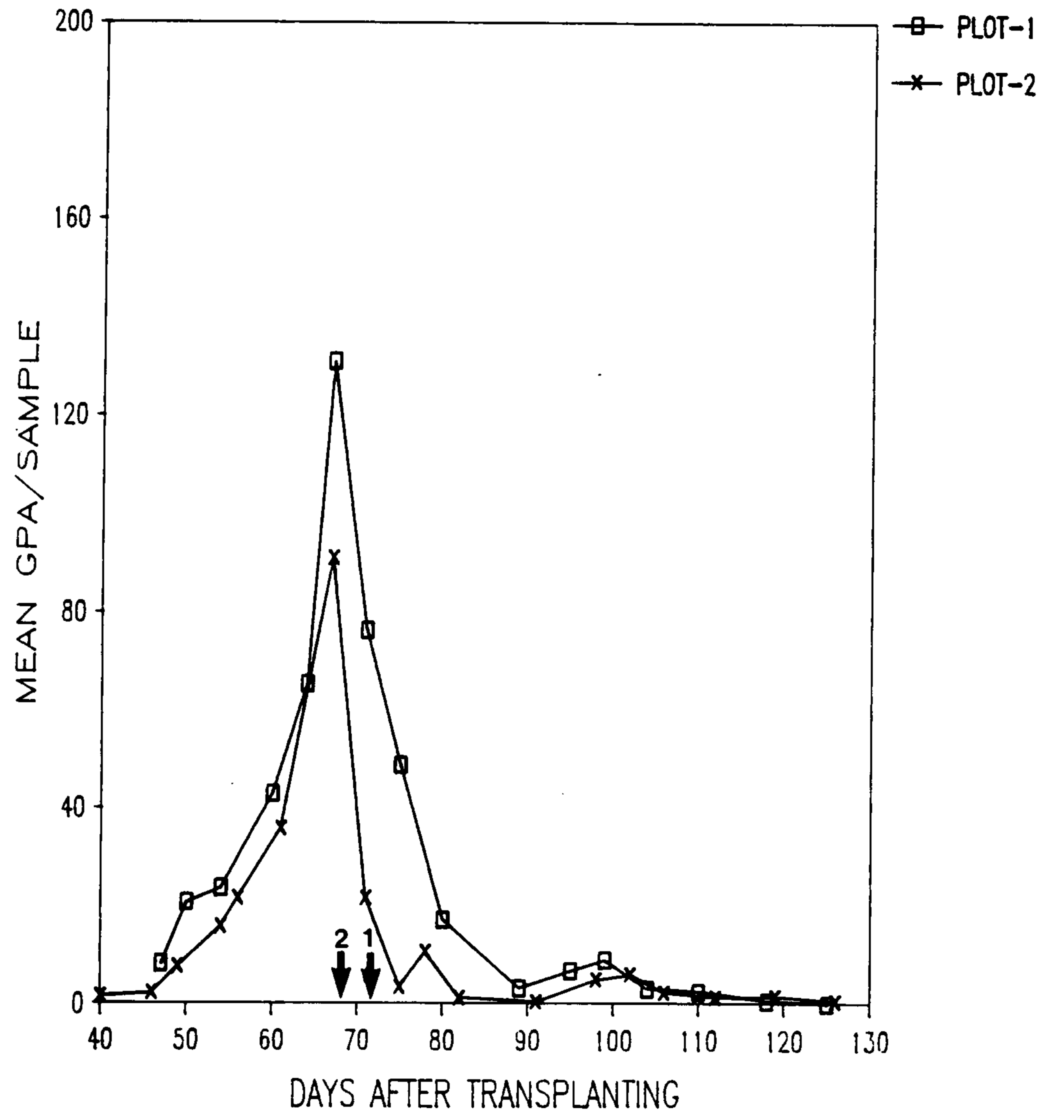

Fig. 1. **Seasonal abundance of green peach aphid (GPA) on flue-cured tobacco, Blackstone, Va., 1985. (Arrows 1 and 2 indicate topping time for PLOT-1 and PLOT-2, respectively).**

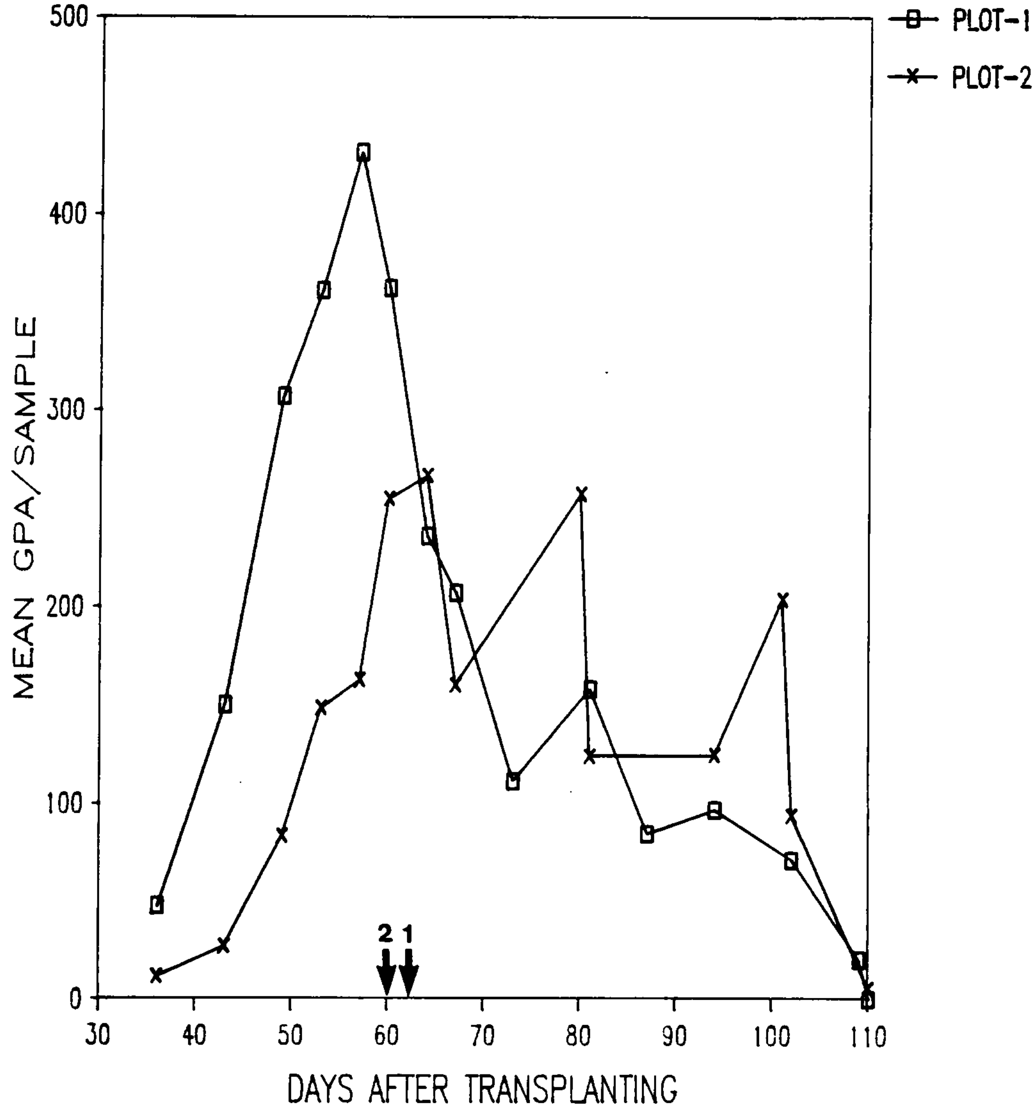

Fig. 2. Seasonal abundance of green peach aphid (GPA) on flue-cured tobacco, Blackstone, Va., 1986. (Arrows 1 and 2 indicate topping time for PLOT-1 and PLOT-2, respectively).

Table 1. The seasonal vertical distribution of green peach aphid on tobacco, Blackstone, Va., 1985-1986.

Period	Sampling duration	No. of plants sampled	No.of plants[1] with aphids	Mean/plant positions[2,3] (aphids/4 leaves) TOP	MID
1985					
		PLOT-1 [4]			
Early	18 Jun.-25 Jun.	150	40	47 a	19 b
Pre-topping	26 Jun.-12 Jul.	179	76	111 a	75 b
Post-topping	13 Jul.-31 Jul.	147	59	40 a	18 a
Final	1 Aug.- 4 Sep.	294	84	6 a	6 a
		PLOT-2 [5]			
Early	11 Jun.-20 Jun.	150	24	16 a	7 b
Pre-topping	21 Jun.- 2 Jul.	150	28	89 a	41 b
Post-topping	7 Jul.-23 Jul.	246	65	52 a	46 b
Final	24 Jul.- 5 Sep.	343	92	3 b	6 a
1986					
		PLOT-1 [4]			
Early	17 Jun.- 4 Jul.	200	113	217 a	165 a
Pre-topping	5 Jul.-15 Jul.	150	116	274 a	169 b
Post-topping	16 Jul.- 1 Aug.	149	101	159 a	75 b
Final	2 Aug.-29 Aug.	200	156	38 a	49 a
		PLOT-2 [5]			
Early	18 Jun.- 7 Jul.	200	62	106 a	112 a
Pre-topping	8 Jul.-14 Jul.	100	56	164 a	208 a
Post-topping	15 Jul.-28 Jul.	150	128	161 a	105 a
Final	29 Jul.-03 Sep.	250	196	73 a	66 a

[1] Total plants where insects were observed in each period (number of replications).
[2] TOP = Top four leaves on stalk.
MID = Middle leaf position (leaves #5 - leaves #8).
[3] Means within rows followed by the same letter for each field are not significantly different at 5% level using Duncan's multiple range test (the test was done on using $\log_{10}(x+1)$ transformation, but the actual means were shown.
[4] Plots located at the edge of field.
[5] Plots located at the middle of field.
Note: GPA populations on the remaining lower leaves were not sampled because their number were negligible.

to other predators, CLBLA populations were highly correlated with GPA populations on tobacco (Table 2).

Tables 3 and 4 summarize the vertical distributions of CLB eggs, larvae, and adults during four different periods for 1985 and 1986, respectively. In both years, significantly (α = 0.05) lower populations of CLB eggs, larvae, and adults were observed on the four uppermost leaves. Most of the time, the bottom leaf position (BOT) had the highest CLB egg, larva, and adult populations. Belcher and Thurston (1983) obtained similar results for CLB oviposition on burley tobacco.

Syrphid fly larvae (SFL)

Several species of syrphid fly larvae, mostly *Sphaerophoria cylindrica* (Say) were associated with GPA populations on flue-cured tobacco. Their seasonal abundance for 1985 and 1986 is shown in Figs. 3 and 4. SFL populations did not show a numerical response to change in GPA intensities. Correlation analysis between SFL and GPA populations showed differences between years (Table 2). SFL were more highly correlated with GPA populations in 1985. Dry weather conditions in 1986 season may have limited SFL development (Honek 1983). SFL did not show a vertical plant preference (Tables 5 and 6). ANOVA of vertical distribution was significantly different only for the Pre-topping period for both plots of 1985 and the Final period for both plots in 1986. However, their preferred distribution on the plant was inconsistent.

Stilt bugs (SB)

Seasonal abundance of SB on tobacco is presented in Figs. 3 and 4. SB populations increased in late season. GPA populations did not affect the seasonal abundance of SB, and there were very low correlation coefficients between SB and GPA populations in the field (Table 2). SB were most abundant on the upper four leaves, especially late in the season (during Post-topping and Final periods) (Table 5 and 6). Thus, the presence of other hosts (i.e hornworm and budworm

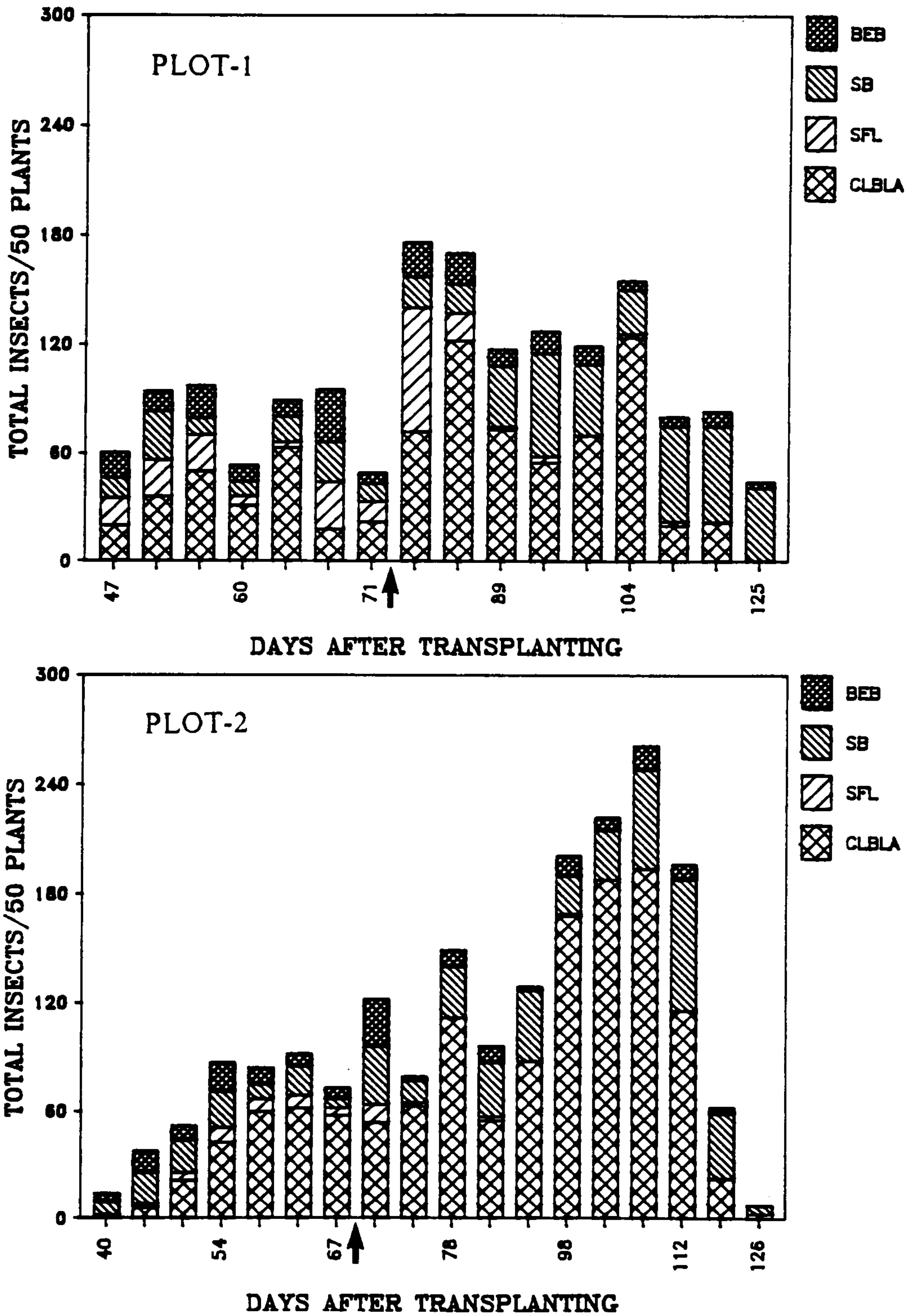

Fig. 3. Seasonal abundance of major GPA predators in flue-cured tobacco fields, Blackstone, Va., 1985. (BEB = big-eyed bugs, SB = stilt bugs, SFL = syrphid fly larvae, CLBLA convergent lady beetle larvae and adults. Arrows indicate topping time).

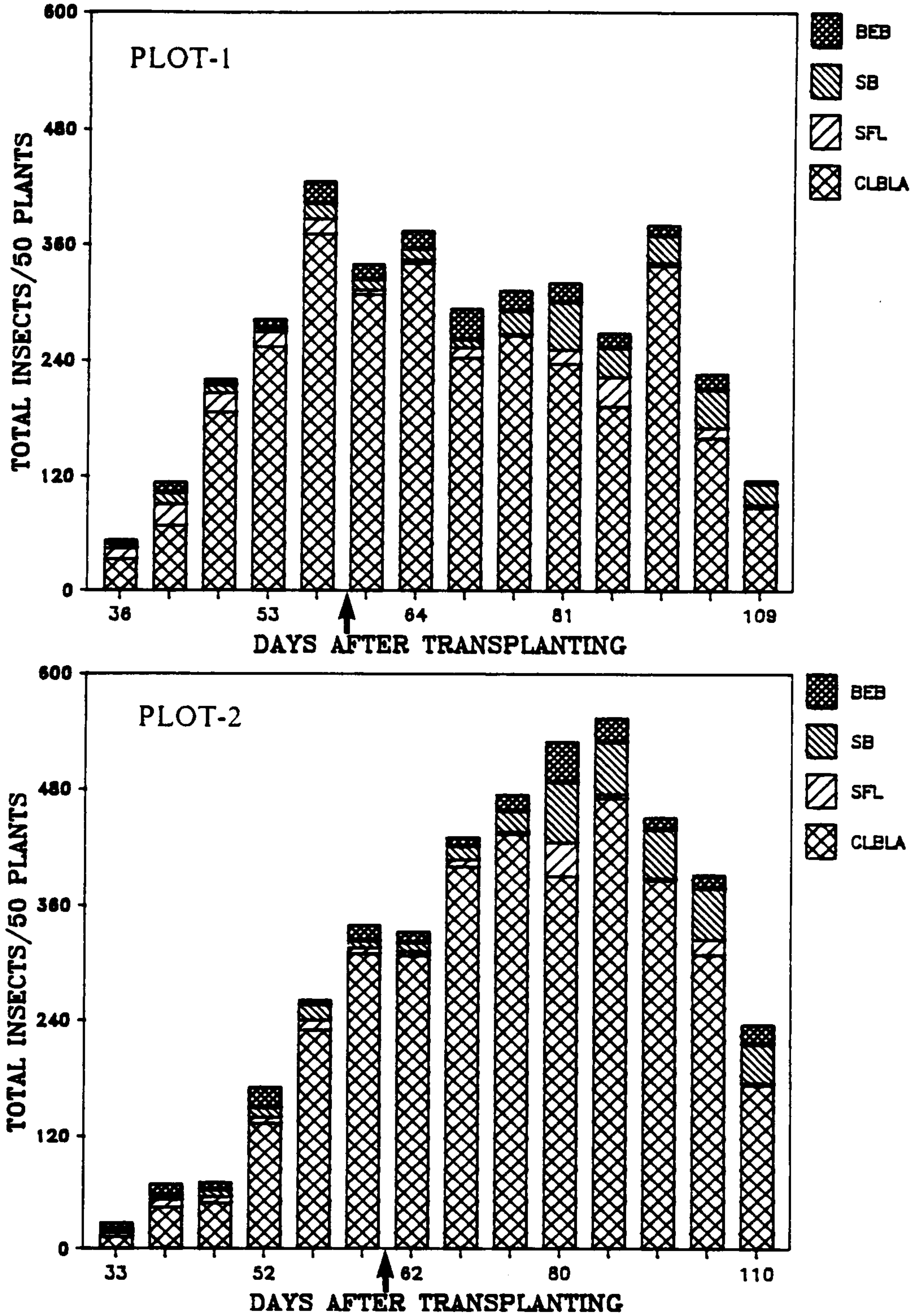

Fig. 4. Seasonal abundance of major GPA predators in flue-cured tobacco fields, Blackstone, Va., 1986. (BEB = big-eyed bugs, SB = stilt bugs, SFL = syrphid fly larvae, CLBLA convergent lady beetle larvae and adults. Arrows indicate topping time).

Table 2. Correlation coefficient (r) between log intensity of GPA and log intensity of the most common predators observed on tobacco, Blackstone, Va., 1985 and 1986.

	BEFORE TOPPING					AFTER TOPPING				
Plots	n	CLBLA [1]	SFL [2]	SB [3]	BEB [4]	n	CLBLA [1]	SFL [2]	SSB [3]	BEB [4]
1985										
PLOT-1[5]	329	0.59**	0.56**	0.33**	0.39**	441	0.41**	0.17**	0.05	0.14**
PLOT-2[6]	300	0.71**	0.71**	0.36**	0.50**	589	0.41**	0.36**	0.16**	0.16**
1986										
PLOT-1[5]	350	0.75**	0.39**	0.24**	0.36**	349	0.67**	0.23**	0.07	0.20*
PLOT-2[6]	300	0.70**	0.38**	0.12*	0.35**	400	0.53**	0.15**	0.15	0.09*

** $p < 0.01$ of Pearson correlation test
* $P < 0.05$
[1] convergent lady beetle larvae + adults
[2] syrphid fly larvae
[3] stilt bugs
[4] big-eyed bugs
[5] located at field edge
[6] located at middle field

Table 3. The vertical distribution of convergent lady beetle (CLB) stages on tobacco, Blackstone, Va., 1985.

CLB stage	Period [1]	No. of plants[2] with CLB	Mean/plant position[3,4] TOP	MID	BOT
		PLOT-1 [5]			
Eggs					
	Early	10	13.30 a	9.10 a	8.40 a
	Pre-topping	26	3.23 b	7.38 b	12.85 a
	Post-topping	13	4.00 b	4.23 b	9.23 a
	Final	33	4.27 b	2.33 b	12.06 a
Larvae					
	Early	4	5.75 a	7.25 a	0.00 a
	Pre-topping	14	1.21 a	2.36 a	2.71 a
	Post-topping	46	0.39 b	0.48 b	2.54 a
	Final	54	0.20 b	0.30 b	0.61 a
Adults					
	Early	19	0.42 b	1.58 a	0.84 ab
	Pre-topping	31	0.06 b	0.22 b	1.19 a
	Post-topping	53	0.32 b	0.30 b	1.49 a
	Final	76	0.22 b	0.35 b	1.03 a
		PLOT-2 [6]			
Eggs					
	Early	2	24.50 a	2.50 a	10.00 a
	Pre-topping	13	4.38 a	15.00 a	9.39 a
	Post-topping	30	4.67 b	3.37 b	10.03 a
	Final	66	2.05 b	1.38 b	13.08 a
Larvae					
	Early		-	-	-
	Pre-topping	6	3.83 a	9.00 a	7.67 a
	Post-topping	50	0.40 c	0.94 b	3.18 a
	Final	127	0.20 b	0.46 b	3.20 a
Adults					
	Early	8	1.25 a	2.00 a	0.05 a
	Pre-topping	15	0.47 a	1.40 a	0.93 a
	Post-topping	53	0.19 b	0.41 b	1.0 a
	Final	163	0.23 b	0.31 b	1.23 a

[1] Refer to Table 1 for the duration and total no. of plants sampled in each period.
[2] Total plants where insects were observed in each period (number of replications).
[3] TOP = Top four leaves on stalk.
MID = Middle leaf position (leaves #5 - leaves #8).
BOT = The remaining leaves (Varied according to growth stages).
[4] Means within rows followed by the same letter for each field are not significantly different at 5% level using Duncan's multiple range test (the test was done on using a $\log_{10}(x+1)$ transformation, but the actual means were shown.
[5] Plots located at the edge of field.
[6] Plots located at the middle of field.

Table 4. The vertical distribution of convergent lady beetle (CLB) stages on tobacco, Blackstone, Va., 1986.

CLB stage	Period [1]	No. of plants with CLB [2]	Mean/plant position[3,4] TOP	MID	BOT
			PLOT-1 [5]		
Eggs					
	Early	36	3.56 b	20.19 a	11.89 b
	Pre-topping	66	5.23 b	10.46 a	13.86 a
	Post-topping	76	7.57 a	14.41 a	9.87 a
	Final	63	8.89 b	8.10 b	16.51 a
Larvae					
	Early	51	1.24 b	2.98 a	4.59 a
	Pre-topping	89	0.58 c	1.43 b	4.99 a
	Post-topping	58	1.12 b	1.22 b	2.21 a
	Final	113	1.44 b	.84 b	1.81 a
Adults					
	Early	43	0.51 b	1.00 a	0.67 ab
	Pre-topping	86	.58 b	0.90 b	3.14 a
	Post-topping	100	1.24 b	1.52 ab	2.06 a
	Final	124	.90 a	.75 a	0.91 a
			PLOT-2 [6]		
Eggs					
	Early	37	2.92 b	5.70 b	13.03 a
	Pre-topping	45	2.44 c	8.67 b	19.11 a
	Post-topping	90	8.17 b	9.06 b	13.44 a
	Final	135	8.15 b	12.78 a	11.44 a
Larvae					
	Early	30	.30 b	.63 b	3.13 a
	Pre-topping	62	.06 b	1.19 b	5.57 a
	Post-topping	108	1.45 b	1.19 b	3.67 a
	Final	205	1.35 b	1.57 b	2.48 a
Adults					
	Early	51	.27 b	.59 b	1.43 a
	Pre-topping	35	.23 c	.69 b	1.89 a
	Post-topping	110	.85 b	1.18 b	2.14 a
	Final	183	1.30 a	1.10 ab	0.99 b

[1] Refer to Table 1 for the duration and total no. of plants sampled in each period.
[2] Total plants where insects were observed in each period (number of replications).
[3] TOP = Top four leaves on stalk.
MID = Middle leaf position (leaves #5 - leaves #8).
BOT = The remaining leaves (Varied according to growth stages).
[4] Means within rows followed by the same letter for each field are not significantly different at 5% level using Duncan's multiple range test (the test was done on using a $\log_{10}(x+1)$ transformation, but the actual means were shown.
[5] Plots located at the edge of field.
[6] Plots located at the middle of field.

Table 5. The vertical distribution of syrphid fly larvae, stilt bugs, and big-eyed bugs on tobacco, Blackstone, Va., 1985.

Predators	Period [1]	No. of plants [2] with predator	Mean/plant position[3,4] TOP	MID	BOT
			PLOT-1 [5]		
Syrphid fly larvae					
	Early	19	1.16 a	1.21 a	0.53 b
	Pre-topping	23	0.30 b	1.09 a	0.57 ab
	Post-topping	28	1.04 a	1.07 a	0.89 a
	Final	7	0.00 a	0.43 a	0.57 a
Stilt bugs					
	Early	33	0.91 a	0.39 b	0.12 b
	Pre-topping	36	0.33 b	0.81 a	0.36 b
	Post-topping	47	0.89 a	0.13 c	0.43 b
	Final	146	1.07 a	0.38 b	0.38 b
Big-eyed bugs					
	Early	30	0.20 b	0.40 ab	0.83 a
	Pre-topping	33	0.00 b	0.03 b	1.58 a
	Post-topping	35	0.00 b	0.11 b	1.36 a
	Final	34	0.18 b	0.26 b	0.82 a
			PLOT-2 [6]		
Syrphid fly larvae					
	Early	3	0.67 a	1.00 a	0.33 a
	Pre-topping	14	0.79 a	0.57 a	0.21 a
	Post-topping	11	0.55 a	0.82 a	0.27 a
	Final	1	0.00	1.00	0.00
Stilt bugs					
	Early	33	1.00 a	0.30 b	0.03 b
	Pre-topping	33	0.33 b	0.76 a	0.24 b
	Post-topping	63	0.68 a	0.51 a	0.52 a
	Final	142	0.68 a	0.49 a	0.62 a
Big-eyed bugs					
	Early	21	0.81 a	0.14 b	0.24 b
	Pre-topping	22	0.14 b	0.32 b	1.00 a
	Post-topping	40	0.12 b	0.22 b	0.95 a
	Final	35	0.09 b	0.11 b	1.06 a

[1] Refer to Table 1 for the duration and total no. of plants sampled in each period.
[2] Total plants where insects were observed in each period (number of replications).
[3] TOP = Top four leaves on stalk.
MID = Middle leaf position (leaves #5 - leaves #8).
BOT = The remaining leaves (Varied according to growth stages).
[4] Means within rows followed by the same letter for each field are not significantly different at 5% level using Duncan's multiple range test (the test was done on using a $\log_{10}(x+1)$ transformation, but the actual means were shown.
[5] Plots located at the edge of field.
[6] Plots located at the middle of field.

Table 6. The vertical distribution of syrphid fly larvae, stilt bugs, and big-eyed bugs on tobacco, Blackstone, Va., 1986.

Predators	Period [1]	No. of plants [2] with predator	Mean/plant position[3,4] TOP	MID	BOT
		PLOT-1 [5]			
Syrphid fly larvae					
	Early	34	0.47 b	1.09 a	0.44 b
	Pre-topping	15	0.20 a	0.73 a	0.60 a
	Post-topping	13	0.38 a	1.31 a	0.23 a
	Final	15	1.53 a	1.33 ab	0.13 b
Stilt bugs					
	Early	21	0.38 ab	0.76 a	0.14 b
	Pre-topping	25	0.48 a	0.48 a	0.56 a
	Post-topping	42	1.02 a	0.45 b	0.45 b
	Final	62	0.87 a	0.50 b	0.56 ab
Big-eyed bugs					
	Early	32	0.25 a	0.50 a	0.50 a
	Pre-topping	37	0.00 b	0.11 b	1.46 a
	Post-topping	53	0.17 b	0.13 b	1.07 a
	Final	36	0.44 ab	0.22 b	0.58 a
		PLOT-2 [6]			
Syrphid fly larvae					
	Early	9	0.89 a	1.22 a	0.56 a
	Pre-topping	10	0.10 a	0.40 a	1.10 a
	Post-topping	12	0.50 a	0.25 a	0.33 a
	Final	20	2.30 a	0.20 b	0.30 b
Stilt bugs					
	Early	18	0.56 a	0.33 a	0.44 a
	Pre-topping	19	0.16 a	0.63 a	0.42 a
	Post-topping	31	0.58 a	0.16 b	0.68 a
	Final	104	0.75 a	0.68 a	1.08 a
Big eye bugs					
	Early	32	0.00 c	0.38 b	1.00 a
	Pre-topping	18	0.00 b	0.06 b	1.11 a
	Post-topping	29	0.07 b	0.31 b	0.90 a
	Final	80	0.15 b	0.30 b	0.96 a

[1] Refer to Table 1 for the duration and total no. of plants sampled in each period.
[2] Total plants where insects were observed in each period (number of replications).
[3] TOP = Top four leaves on stalk.
MID = Middle leaf position (leaves #5 - leaves #8).
BOT = The remaining leaves (Varied according to growth stages).
[4] Means within rows followed by the same letter for each field are not significantly different at 5% level using Duncan's multiple range test (the test was done on using a $\log_{10}(x+1)$ transformation, but the actual means were shown.
[5] Plots located at the edge of field.
[6] Plots located at the middle of field.
tobacco

eggs), are probably more important factors than GPA alone (Elsey and Stinner 1971, Semtner 1979).

Big-eyed bugs (BEB)

BEB was most numerous early in the tobacco growing season (Fig. 3 and 4.). Their populations had low correlations with GPA populations (Table 2). BEB preferred the lower leaves of tobacco plants (Tables 5 and 6). Thus, BEB were probably more attracted to insects other than to GPA on tobacco. The BEB is an important predator of tobacco flea beetles, *Epitrix hirtipennis* (Melsheimer), which are more abundant in early season and on the lower part of plant (Dominick 1943). Thus, they may also be important predators for suppressing GPA populations on the lower part of plants (Tamaki 1972).

Other minor GPA predators

Other predators that were less numerous or sporadic in occurrence, were considered as minor GPA predators. This included two species of lady beetle [*Coccinella septempunctata* L. and *Coleomagilla maculata* (De Geer)], damsel bugs (*Nabis* spp.), green lacewings (*Chrysopa* spp.), and brown lacewings (*Micromus* sp.). Their seasonal abundances for 1985 are presented in Fig. 5. Since very few of *C. septempunctata* and *C. maculata* occurred in 1985, they were combined as were green and brown lacewings. Damsel bugs on the other hand, were consistently present, but they were not abundant enough to be considered important GPA predators.

The minor predators were more abundant in 1986 than in 1985 (Fig. 6). Higher GPA populations in 1986 probably attracted more predators into tobacco fields. The seasonal abundance of two minor species of lady beetle were observed. *C. septempunctata* was most abundant in early and late tobacco season. Hagen (1962) reported that *C. septempunctata* is uncommon in the middle of the season because it aestivates during the hot summer months. In contrast, *C. maculata*

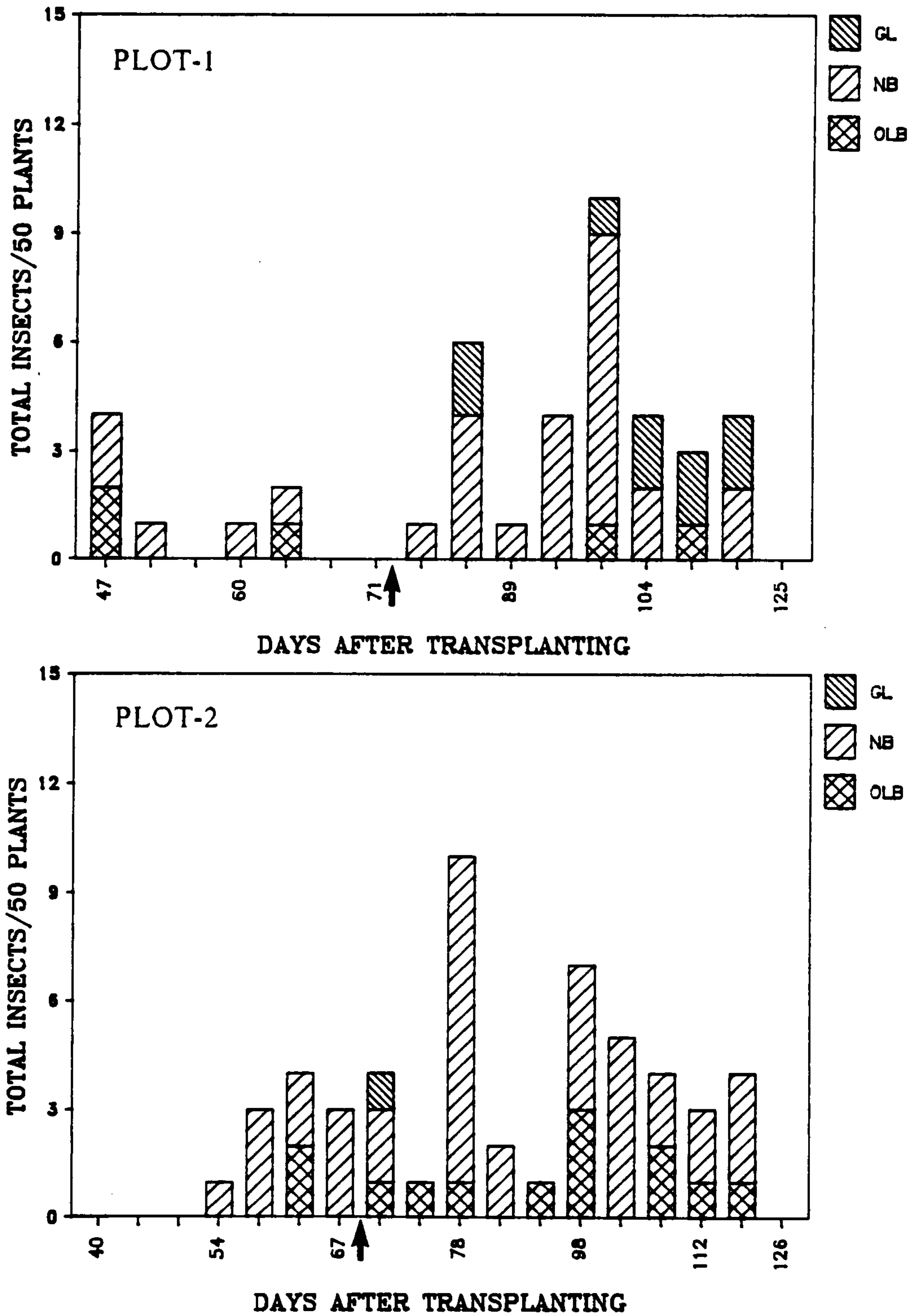

Fig. 5. Seasonal abundance of minor GPA predators in flue-cured tobacco fields, Blackstone, Va., 1985. [GL = green lacewings, NB = damsel bugs, OLB = other lady beetle species (see text). Arrows indicate topping time].

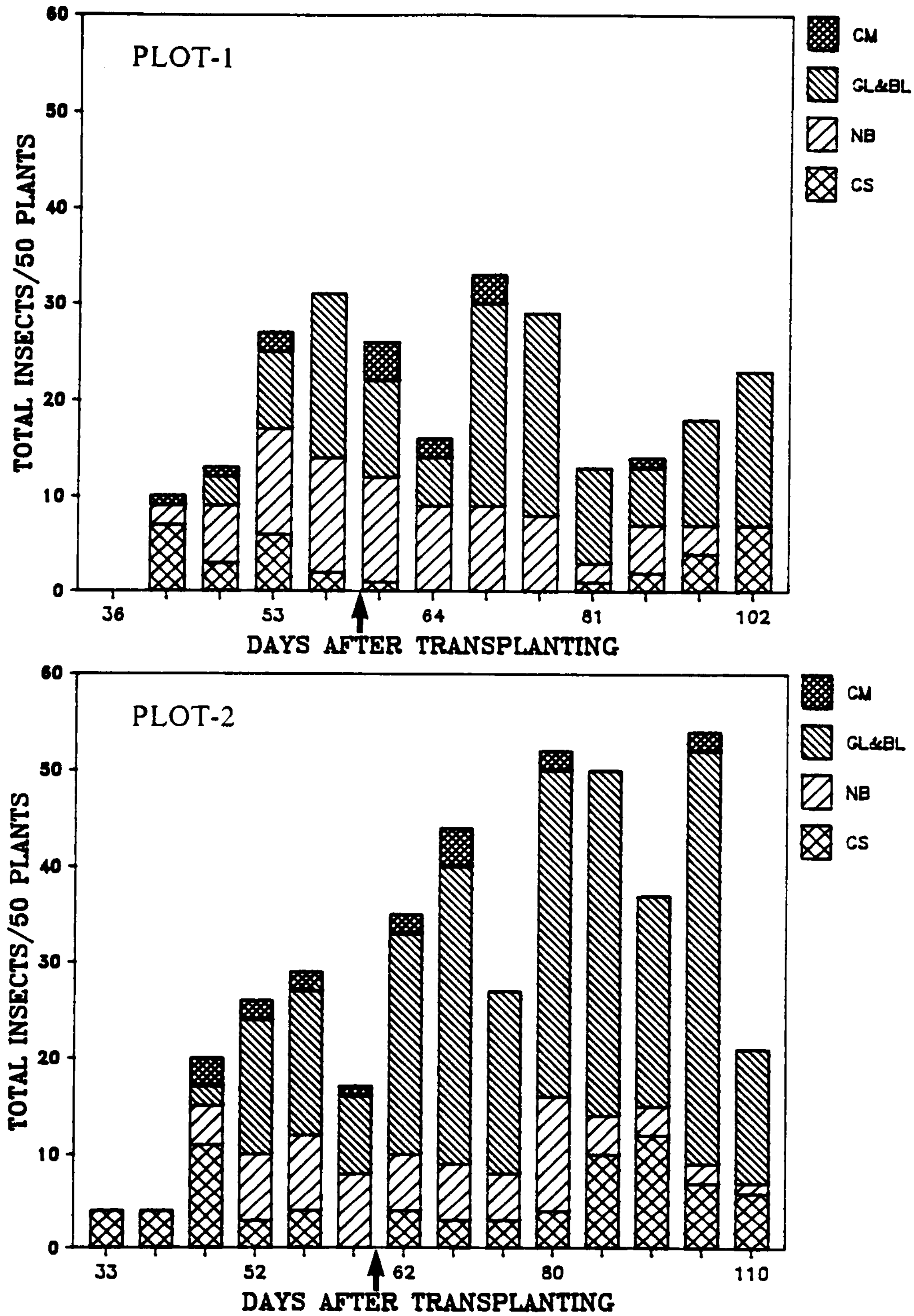

Fig. 6. Seasonal abundance of minor GPA predators in flue-cured tobacco fields, Blackstone, Va., 1986. (CM = *Coleomagilla maculata* GL&BL = green lacewings and brwon lacewings, NB = damsel bugs, CS = *Coccinella septempunctata*. Arrows indicate topping time).

was most numerous in the middle of the season since it requires high temperature to become active (Obrycki and Tauber 1978). Lacewings showed a delayed response to increasing GPA populations. They were most abundant in the middle of the season (Fig. 6).

Results from this study indicated that GPA counts differed between years and plots. The factors that contributed to difference in years is unknown. However, the difference between the plots was probably related to their location. PLOT-1 was infested earlier in the season than PLOT-2. This may be related to their distances from wooded areas which may serve as overwintering sites for GPA (Davis and Landis 1951). In addition, the wooded areas produced a shading effect that favored GPA population growth (Kulash 1949). The difference in GPA abundance between plots and years affected the abundance of GPA predators. GPA predators were more abundant in 1986 than 1985. In addition, early in the season of both years, more predators were observed in PLOT-1 probably in response to early GPA population development in these plots. Late in the season, more GPA predators were observed in PLOT-2 because they were attracted to high GPA populations that developed later than in PLOT-1.

The difference in vertical plant preference between GPA and CLBLA may be due to tobacco characteristics. GPA probably preferred the upper four leaves of tobacco because the young growing tip of tobacco is more nutritious than other parts of the plants (Kennedy et al. 1950). On the other hand, CLB did not prefer the four upper leaves although GPA were more abundant at this leaf position. This observation is contrast to observation on corn and cotton (Ewert and Chiang 1965, Cosper et al. 1983). According to Ewert and Chiang (1965), CLB preferred the upper part of corn because they are negatively geotactic and positively phototactic. On cotton, Cosper et al. (1983) sampled more CLB adults from the terminal part of cotton plants. The difference in vertical distribution of CLB between these crops (corn and cotton) and tobacco can be attributed to differences in their leaf characteristics. The uppermost tobacco leaves contain higher densities of glandular trichomes which produces gummy exudates (Barrera and Wernsman 1969), that probably repel CLB and reduce time they spend searching for prey. Tobacco trichomes are detrimental to CLB and other coccinellid larvae (Elsey 1974, Belcher and Thurston 1982). Furthermore, Elsey and Chaplin (1978) observed that CLB are more abundant on tobacco introductions with fewer trichomes than on flue-cured tobacco with many trichomes and high populations of GPA.

Several species of predators were found in tobacco fields. However, only CLB and SFL seemed to utilize GPA as their main source of food on tobacco. Only CLB had a numerical response to changes in GPA intensity. In addition, CLB were more abundant than SFL. Thus, CLB (larvae and adults) was the important GPA predator in tobacco fields. But, they were still not able to effectively control GPA populations on tobacco, especially before topping. Their inability to spend more time in search of GPA on the upper leaves of tobacco plants, where GPA were most abundant, probably reduced their effectiveness. The higher trichome densities on the upper leaves could be the main factor affecting CLB abundance on that region of the plant.

THE NUMERICAL RESPONSE OF HIPPODAMIA CONVERGENS GUERIN-MENEVILLE (COLEOPTERA: COCCINELLIDAE) TO VARIOUS DENSITIES OF MYZUS PERSICAE (SULZER) (HOMOPTERA: APHIDIDAE) ON TOBACCO IN VIRGINIA

Introduction

The green peach aphid (GPA), *Myzus persicae* (Sulzer), is one of the most important pests of tobacco in North America (Dominick 1949, Chamberlain 1958, Semtner 1983a). GPA infestations reduce yield and quality of tobacco. Plants may be stunted because GPA withdraw important nutrients from them (Cheng and Hanlon 1985). GPA also produces exuviae that contaminate tobacco leaves, and honeydew which reduces the quality of cured leaves (Mistric and Clark 1979).

The convergent lady beetle (CLB), *Hippodamia convergens* Guerin-Meneville, is one of the most widely distributed aphid feeding coccinellids in North America (Hagen 1962). It is the most important aphid predator in alfalfa fields (Gutierrez and Baumgaertner 1984), and in cotton fields (Fye 1979). Its quick response (i.e. smaller time lag) to change in aphid populations and its ability to reproduce at low aphid densities are important traits which enhance its effectiveness in regulating aphid populations (Hagen and Van den Bosch 1968). In the laboratory, Hagen and Sluss (1965) noted that overwintered CLB must eat ca. 90 pea aphids [*Acyrthosiphon pisum* (Harris)], to initiate oviposition, but after that an egg was oviposited for each subsequent aphid eaten.

On tobacco, CLB is also believed to be the most important predator associated with GPA populations (Dominick 1949, Kulash 1949, Chamberlain 1958, Semtner 1983b, Belcher and Thurston 1983). It is estimated that the late instar and adult CLB are capable of consuming 50 aphids per day (Clausen 1962). However, in tobacco fields, CLB are unable to effectively regulate GPA populations. One important trait that enhances CLB effectiveness for regulating GPA populations is its ability to increase predation rates in response to increasing GPA populations. Thus, it is important to study its response to various GPA densities on tobacco.

Two basic components of predation are the numerical and functional response (Solomon 1949). Functional response refers to change in number of prey consumed by a predator per unit time in response to the change in prey density. Numerical response, on the other hand, is the change in predator number in response to the change in prey number (Solomon 1949). The two main factors that influence the numerical response are predator dispersal and reproduction.

The purpose of this study was to investigate the numerical response of CLB to various GPA intensities on flue-cured tobacco under both laboratory and field conditions.

Materials and Methods

Laboratory Studies

The experiment was conducted in 1986, in the greenhouse at Virginia Polytechnic Institute and State University, Blacksburg Virginia. CLB adults used in this experiment were obtained from Carolina Biological Supply Company, maintained in an environmentally controlled growth chamber at ca. 5 ^{0}C, and provided with 10 % sucrose solution. Initially, mated CLB females were selected and placed individually in small vials. The vials were placed in growth chamber at ca. 23 ^{0}C, 70$\pm$ 5% R.H., and 16:8(L:D) photoperiod for at least 24 hours period. GPA used in the experiment were reared on tobacco in the greenhouse. Host tobacco plants were changed at least once a week.

Various intensities of adult or late instar GPA were placed in a confined experimental arena with a volume of ca. 573 cm^3. Each arena was constructed from a clear plastic container (473 cm^3), extended at the bottom with one-third of clear picnic cup (ca. 100 cm^3) (Fig. 7). A 1-month old tobacco plant growing in a peat pot was infested with the desired number of aphids and placed in each arena. A mated, female adult CLB was released into each experimental arena. The arenas were placed into environmental chambers at ca. 23 ^{0}C, 70$\pm$ 5% R.H., and 16:8(L:D). Every 24 hours, CLB were transferred into new experimental arenas with the same numbers of aphids/plant. The numbers of live GPA and CLB eggs laid were counted in each arena after the CLB had been removed. A randomized complete block design with seven treatments and five

Fig. 7. The experimental arena used in the laboratory study.

replications was used. Treatments were 0, 5, 10, 20, 30, 40, 50, and 100 GPA/plant/day. The test was conducted for 10 days. The number of nymphs produced by GPA left in experimental arena were not counted. It was reported that at 25 ^{0}C, the adult GPA could produce at average two nymph/day (Reed 1987).

Field Studies

Field experiments were conducted at Virginia Polytechnic Institute and State University Southern Piedmont Agricultural Experiment Station, Blackstone, Virginia in 1985 and 1986. Each year, two tobacco plots (ca. 0.075 ha.) were selected and planted in 'Coker 319' flue-cured tobacco. In each year one plot was located at the edge of the field (close to wooded area), and a second plot was established near the center of a field. The first and second plots were named PLOT-1 and PLOT-2 respectively. Tobacco was transplanted in both plots on 2 May, 1985. In 1986, tobacco was transplanted on 12 and 16 May for PLOT-1 and PLOT-2 respectively. Virginia Cooperative Extension Service recommendations for cultural practices were followed (Jones 1985). *Bacillus thuringiensis* (Berliner) (Dipel ®) was applied to control hornworms and budworms when necessary. Insecticides were not used for GPA control. In 1985, tobacco in PLOT-1 was topped (removal of plant terminal bud) in late flower stage (12 July), while PLOT-2 was topped in early flower stage (8 July). Suckers were controlled by hand. However, in 1986, tobacco in both plots was topped in early flower stage (16 July), and treated with sucker control agent (Off Shoot T®).

In each field, 50 plants were selected at random for monitoring GPA and CLB populations. At least once a week throughout the growing season, GPA and CLB eggs, larvae, and adults were sampled on selected plants. The eggs and larvae of other species of lady beetles were grouped with CLB since they were rare. The underside of the top eight leaves at least 8 cm long were examined for GPA. The number of GPA present between the fourth and sixth lateral veins on the right side of the midrib of each leaf was recorded. CLB eggs, larvae and adults were counted on the entire plant

Statistical Analysis

The percent hatchability of eggs in the laboratory experiment was transformed to arcsine, and field counts were transformed to $\log_{10}(x + 1)$ for statistical analysis. However, the actual means of percentages and counts are presented in the tables and figures. Statistical analysis included Pearson correlation procedure for the correlation analysis, Proc NLIN for least square analysis of non-linear model, and Proc GLM for simple linear regression analysis, and analysis of variance (SAS Institute 1985). Significantly different means in the laboratory experiment were separated using Duncan's multiple range test.

Results and Discussion

Laboratory experiment

The relationship between the number of eggs produced and feeding rates, and GPA intensities are summarized in the Table 7. CLB exhibited a linear numerical response. The first equation reflects CLB egg production at a particular feeding rate. This was determined by two factors, maintenance requirement and conversion rates. The maintenance requirement, which is estimated by the 'X' intercept, refers to the number of GPA consumed/day to meet metabolic requirements (Dixon 1959), (at least 6.3 GPA). The conversion rate, i.e., the slope of the line, is the number of eggs produced for each GPA consumed/day above the maintenance requirement. The conversion rate was 0.44 egg/GPA. Equation 2 explains the relationship between CLB egg production and GPA intensities CLB egg production increased linearly with increasing GPA intensity. The 'X' intercept (6.92 GPA) in the equation represents the minimum number of GPA required to initiate CLB oviposition.

Table 7. Relationship of convergent lady beetle (CLB) egg production (Y) with feeding rates (aphids consumed/day) (X), and GPA intensity (X) on tobacco in laboratory

Independent variables	Equations	r^2	X intercept
Feeding rates	$Y = -2.75 + 0.44X$	0.95*	6.25
GPA/plant/day	$Y = -1.80 + 0.26X$	0.97*	6.92

* $p < 0.001$

The effect of GPA intensities on the hatchability of CLB eggs, number eggs oviposited, and days to oviposition for CLB are tabulated in the Table 8. Analysis of variance (ANOVA) showed that there were no significant effects due to GPA intensities on CLB egg hatchability ($P < 0.41$) and days to oviposition ($p < 0.33$), but there was a significant ($\alpha = 0.05$) effect of GPA intensity on CLB oviposition rate. CLB that were provided with 100 GPA/pant/day oviposited more than CLB provided with other GPA intensities. Thus, under laboratory conditions, the number of GPA available above the CLB metabolic maintenance requirement appears to determine its reproductive rate. The same relationship was observed on *Coccinella undecimpunctata aegyptiaca* (Beddington et al. 1975).

Field Studies

The seasonal abundance of GPA and CLB populations in tobacco fields for the 1985 season are presented in Figs. 8 through 11. GPA and CLB populations were higher in 1986 than in 1985. The higher GPA intensities in 1986 appeared to encourage higher CLB populations. In both years GPA populations were drastically reduced by topping.

In 1985, GPA populations peaked between 60 and 70 days after transplanting. Plants were topped on 72nd and 68th days after transplanting for PLOT-1 and PLOT-2 respectively. The rapidly developing GPA populations before topping encouraged CLB adults to immigrate and oviposit in both fields (Figs 9 and 11). There was a considerable fluctuation in CLB adult populations in response to increasing GPA populations before the tobacco was topped. CLB egg numbers closely followed GPA populations. A sudden decrease in GPA populations after topping affected CLB populations. CLB adult populations decreased slightly, while egg numbers decreased drastically immediately after topping, and increased again 28-35 days later. The late season increase in egg numbers was evidently contributed by young CLB adults that had emerged just before that time. Since GPA populations were low, these young adults oviposited and then emigrated. The

Table 8. Effect of green peach aphid intensities and number of GPA consumed/day on days to oviposition, ovipositional rates, and hatchability of convergent lady beetles.

GPA/plant	Mean no. no. GPA consumed/day	Mean [1] days to oviposition	Mean[1] oviposition rate	Hatchability[1]
0	0	ND	-	-
5	3.91	ND	-	-
10	7.84	ND	-	-
20	14.92	5.33 a	3.98 b	91.5 a
30	25.09	5.00 a	5.42 b	88.72 a
40	28.45	3.40 a	7.60 b	85.89 a
50	32.82	3.33 a	10.84 b	76.61 a
100	65.46	2.67 a	28.72 a	71.98 a

[1] Number with same letter within the same column is not significant at $\alpha \leq 0.05$ under Duncan's multiple range test
ND = No data

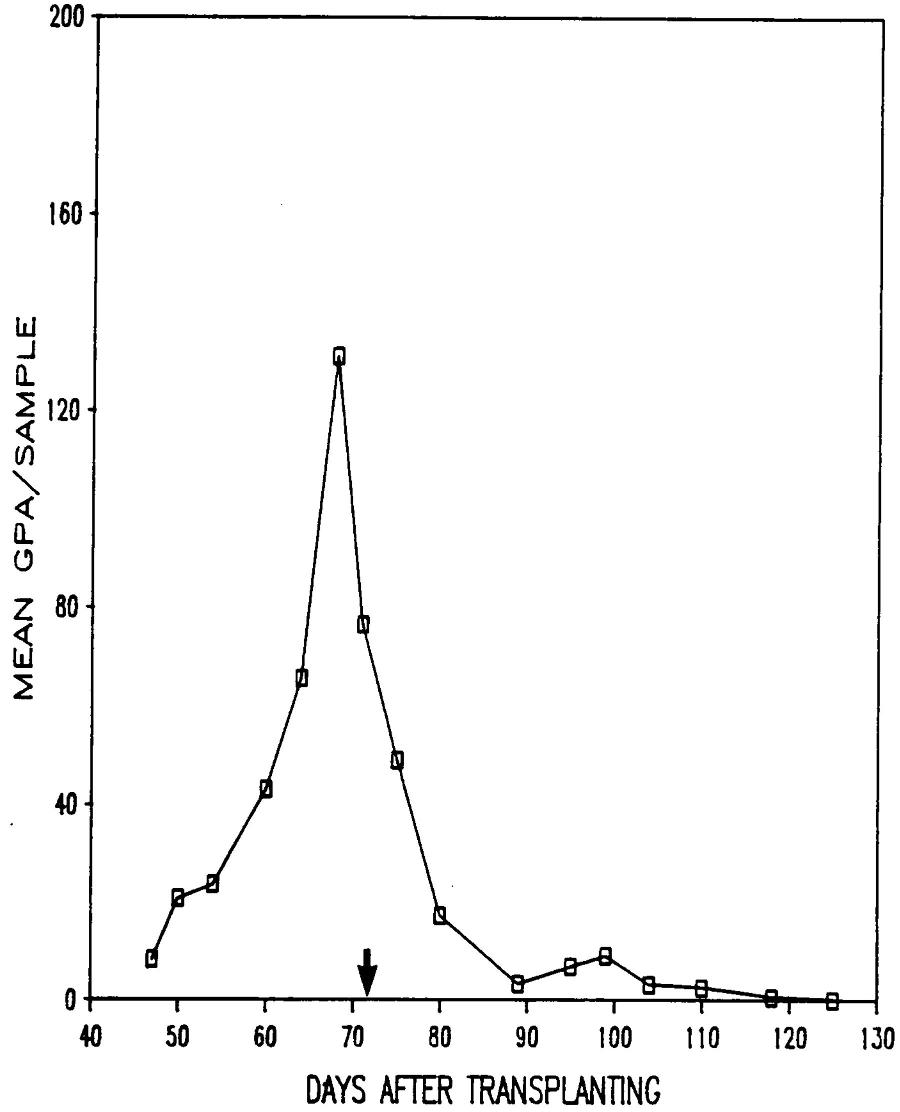

Fig. 8. Seasonal abundance of green peach aphid (GPA) on flue-cured tobacco in PLOT-1, Blackstone, Va., 1985. (Arrow indicates topping time)

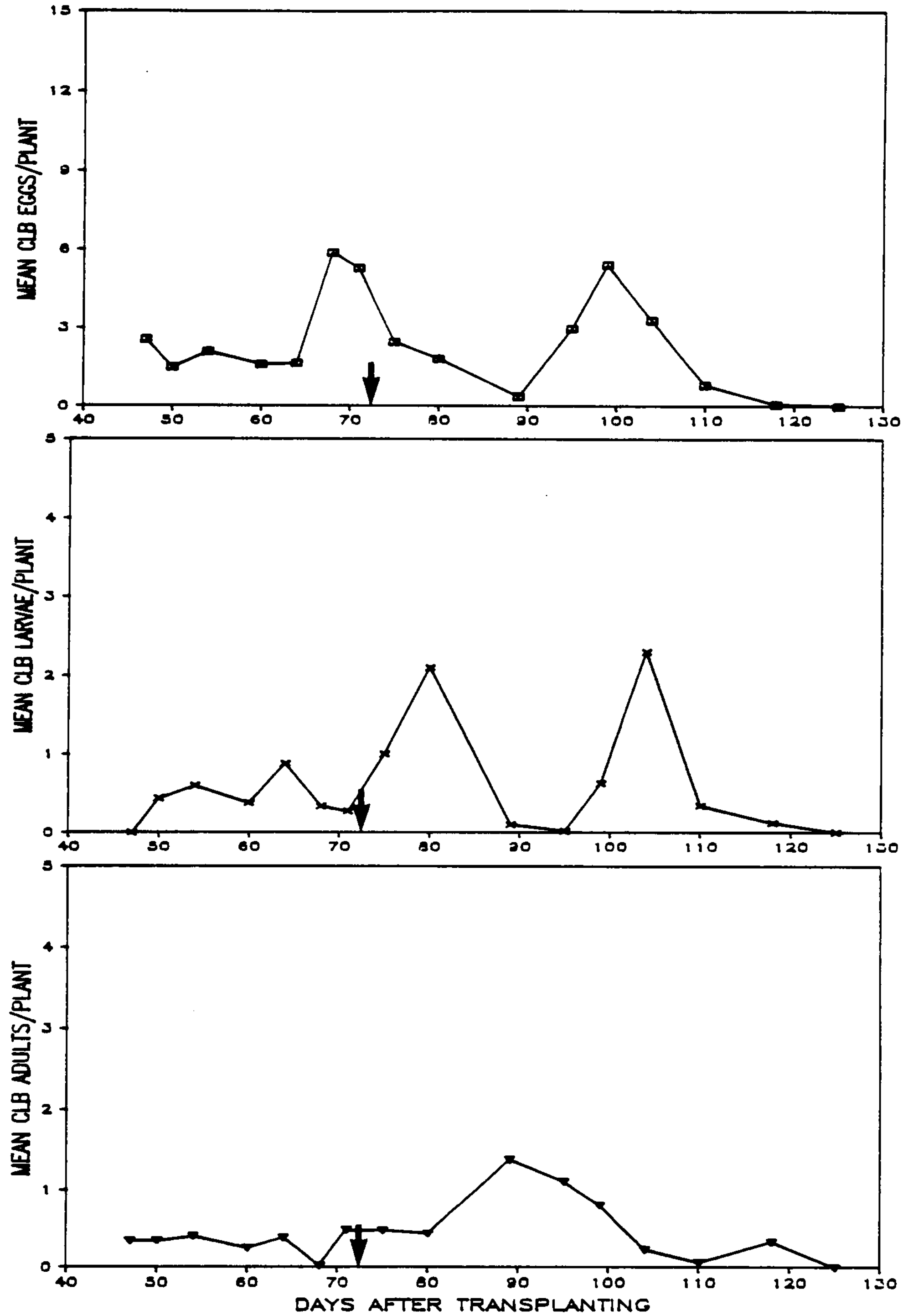

Fig. 9. Seasonal abundance of convergent lady beetle (CLB) eggs, larvae, and adults on flue-cured tobacco in PLOT-1, Blackstone, Va., 1985. (Arrows indicate topping time)

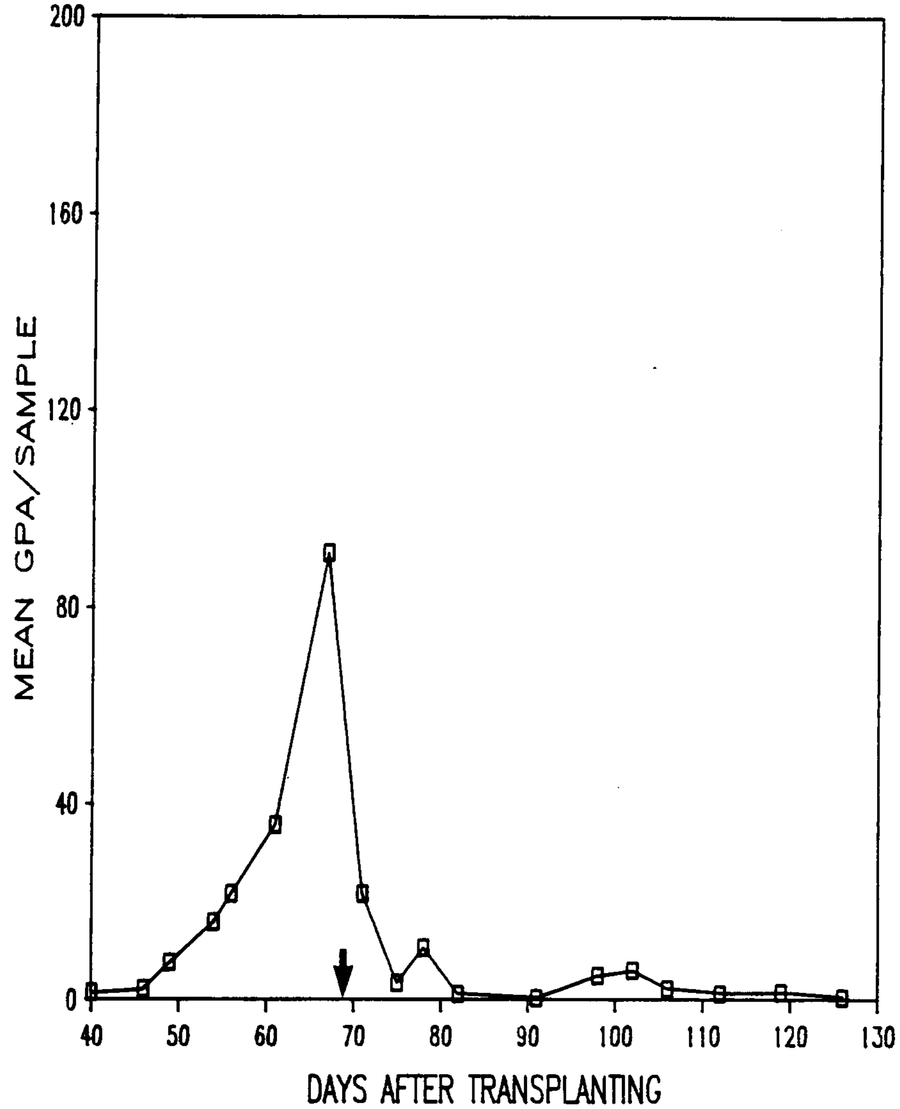

Fig. 10. **Seasonal abundance of green peach aphid (GPA) on flue-cured tobacco in PLOT-2, Blackstone, Va., 1985. (Arrow indicates topping time)**

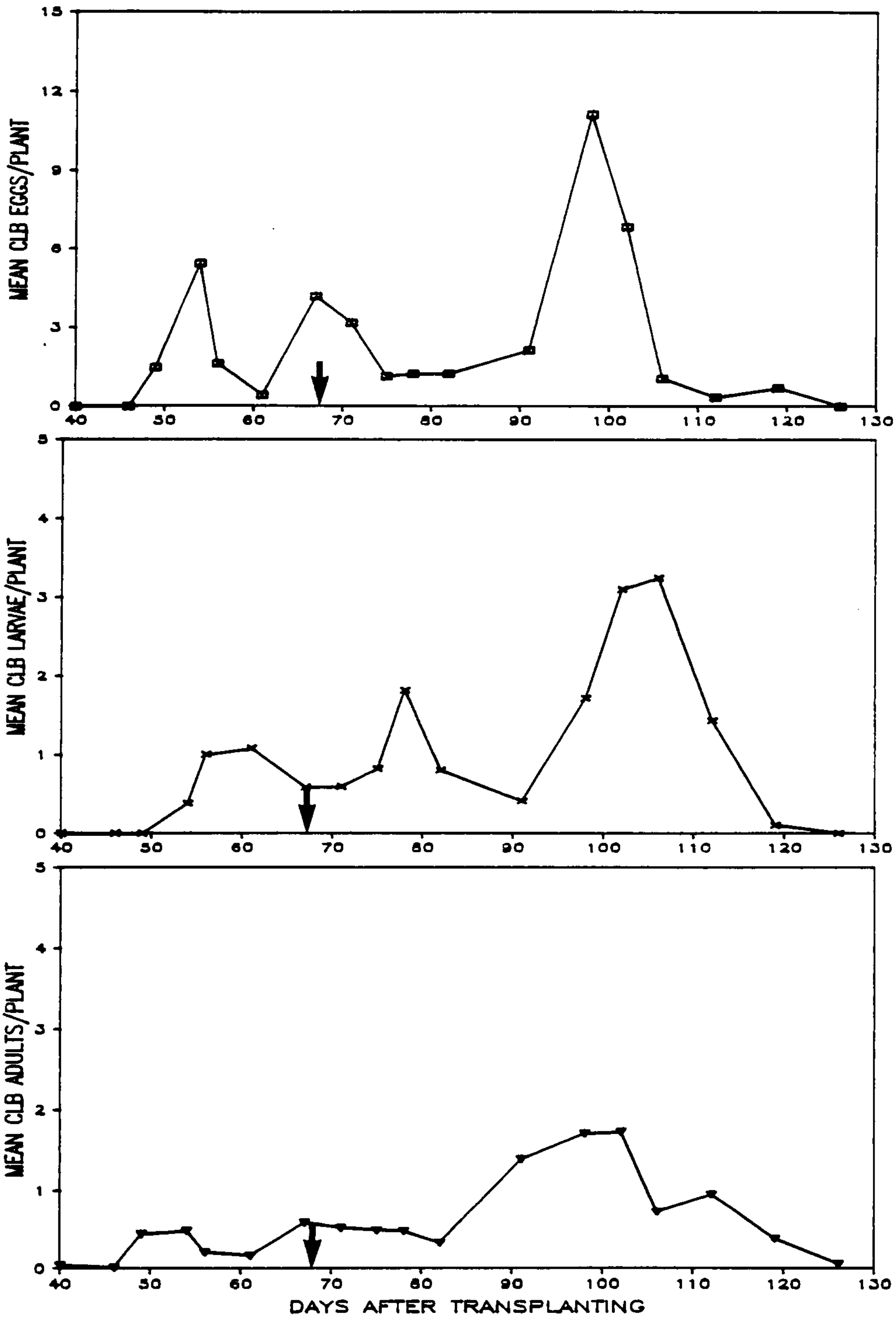

Fig. 11. Seasonal abundance of convergent lady beetle (CLB) eggs, larvae, and adults on flue-cured tobacco in PLOT-2, Blackstone, Va., 1985. (Arrows indicates topping time)

second generation larvae were not able to complete their life cycle because the population intensity of their GPA prey were low at the end of the growing season.

Similar population trends were observed in 1986 season (Figs. 12-15). GPA populations peaked 62 days after transplanting. The tobacco in both fields was topped 60-61 days after transplanting. Populations of CLB adults steadily increased in response to changes in GPA intensity until ca. 65 days after transplanting. GPA populations in the PLOT-2 increased again after topping. The second increase in GPA populations coincided with the emergence of young CLB adults. For this reason, the number of CLB eggs increased after topping, and CLB adult populations remained at almost the same level from 65 to 96 days after planting. In PLOT-1, on the other hand, GPA populations did not increase after topping. This resulted in a lower rate of oviposition, and more emigration by young CLB adults.

CLB adult, egg, and larval populations were more highly correlated with change in GPA intensities in the early season (before topping) than later in the season (after topping). Table 9 shows the correlation coefficients (r) between log intensity of CLB adults, eggs, and larvae, and log intensity of GPA on tobacco before and after topping. The higher correlation coefficients before topping indicate that immigrant adult CLB were more sensitive to change in GPA intensity than adults produced in the field, which represented the majority of CLB adults after topping. A positive numerical response was noted because CLB adults were able to increase in number through immigration. Thus, they were able to respond to GPA population change in a short time (Crawley 1975).

CLB adult immigration and reproduction in response to change in GPA intensity differed between 1985 and 1986. Regression analysis of log intensities of GPA with log intensities of CLB adults before topping revealed the differences in the immigration of CLB adults between years (Table 10). The relationship was non-linear in 1985, while a linear relationship was observed in 1986. Likewise, CLB adult reproduction (number of egg per adult) also varied between years. The log number of CLB egg/adult was more highly correlated with the log GPA intensity in 1985 than 1986 (Table 11).

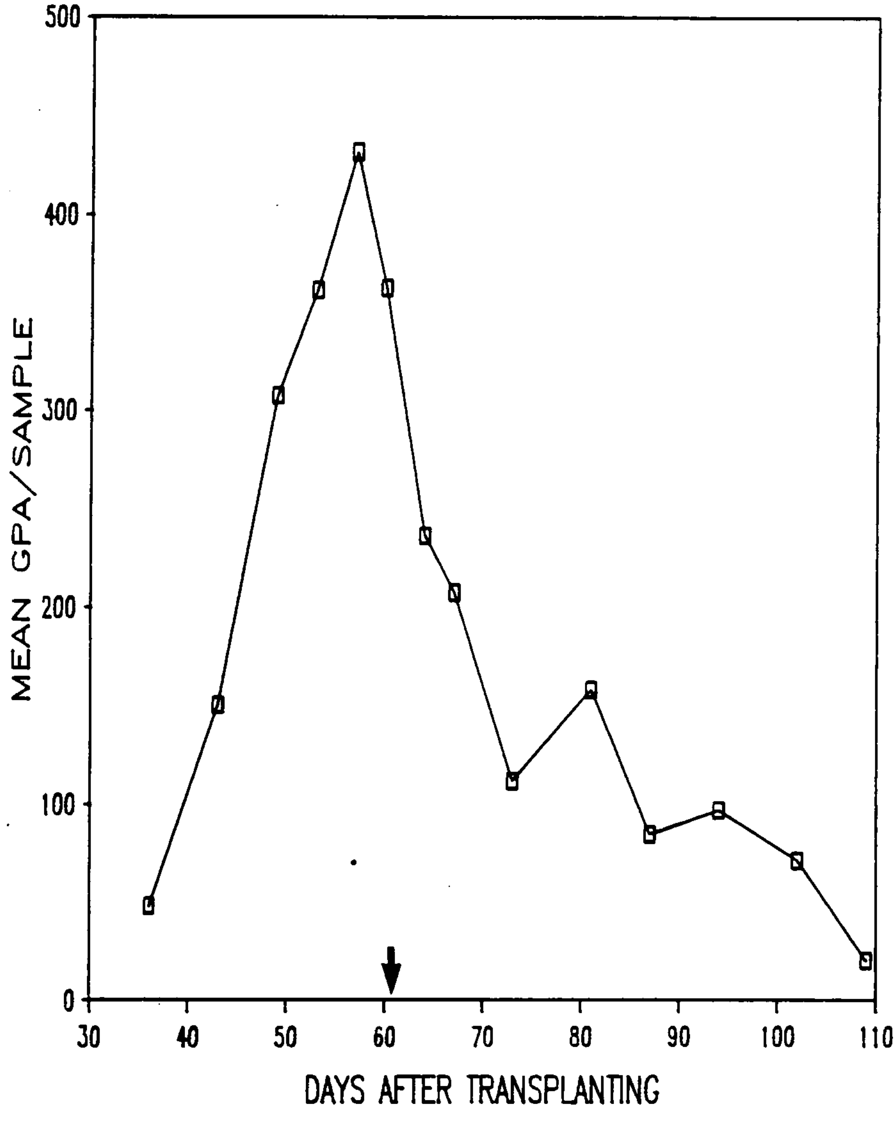

Fig. 12. Seasonal abundance of green peach aphid (GPA) on flue-cured tobacco in PLOT-1, Blackstone, Va., 1986 (Arrow indicates topping time)

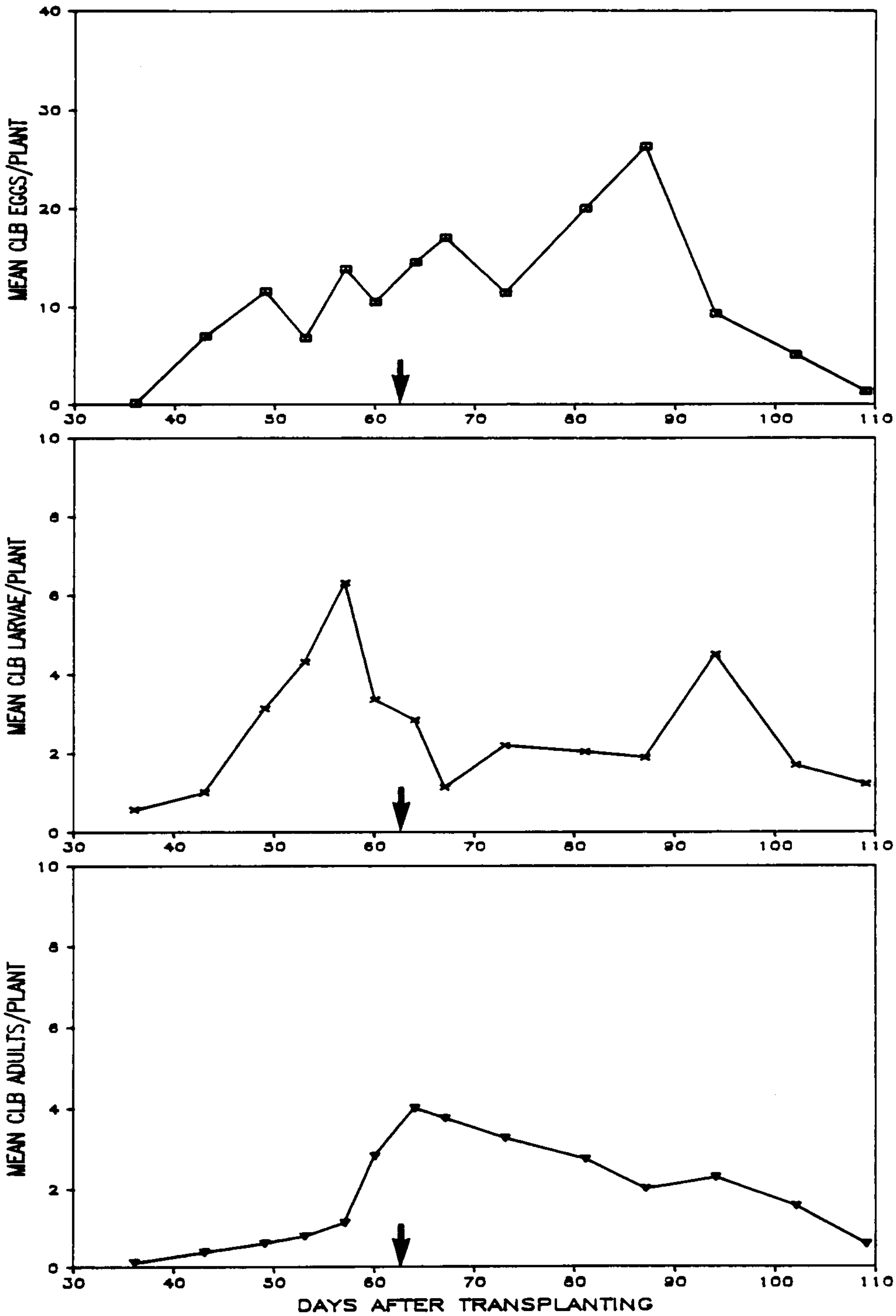

Fig. 13. Seasonal abundance of convergent lady beetle (CLB) eggs, larvae, and adults on flue-cured tobacco in PLOT-1, Blackstone, Va., 1986. (Arrows indicate topping time)

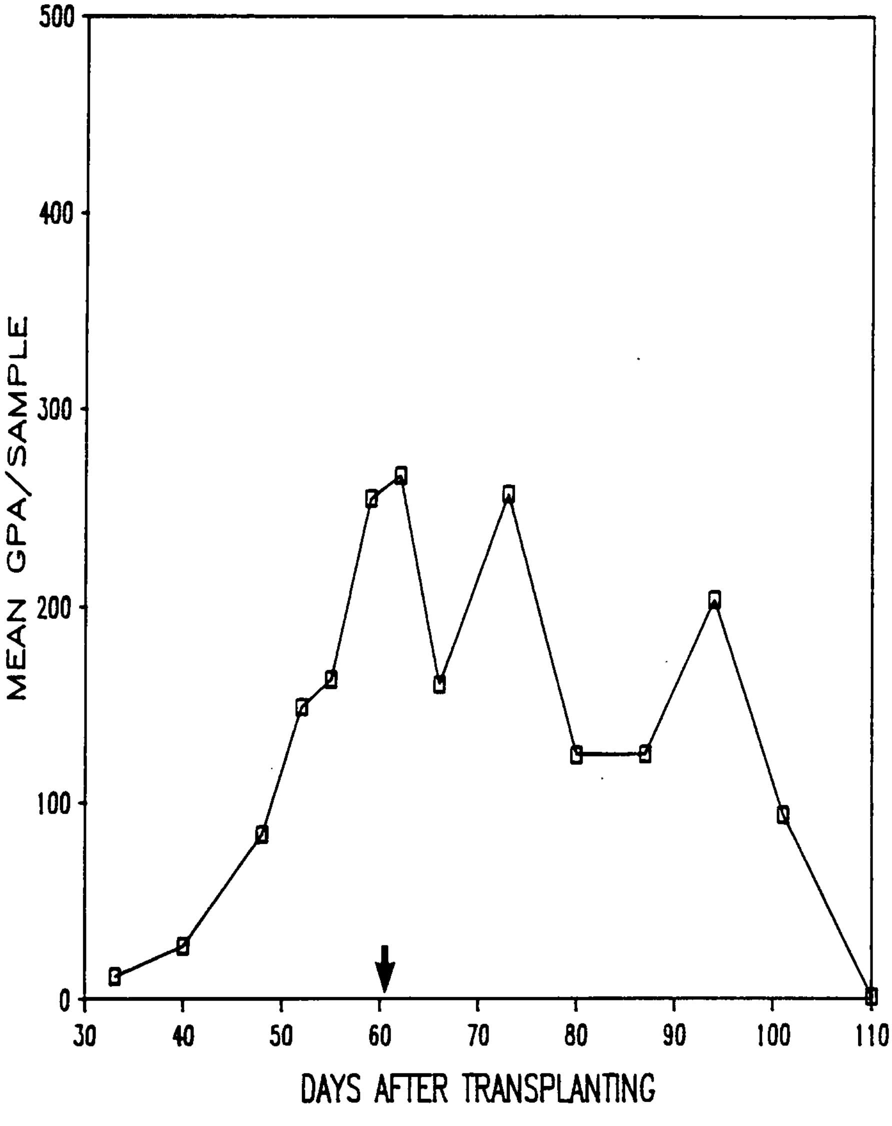

Fig. 14. Seasonal abundance of green peach aphid (GPA) on flue-cured tobacco in PLOT-2, Blackstone, Va., 1986 (Arrow indicates topping time)

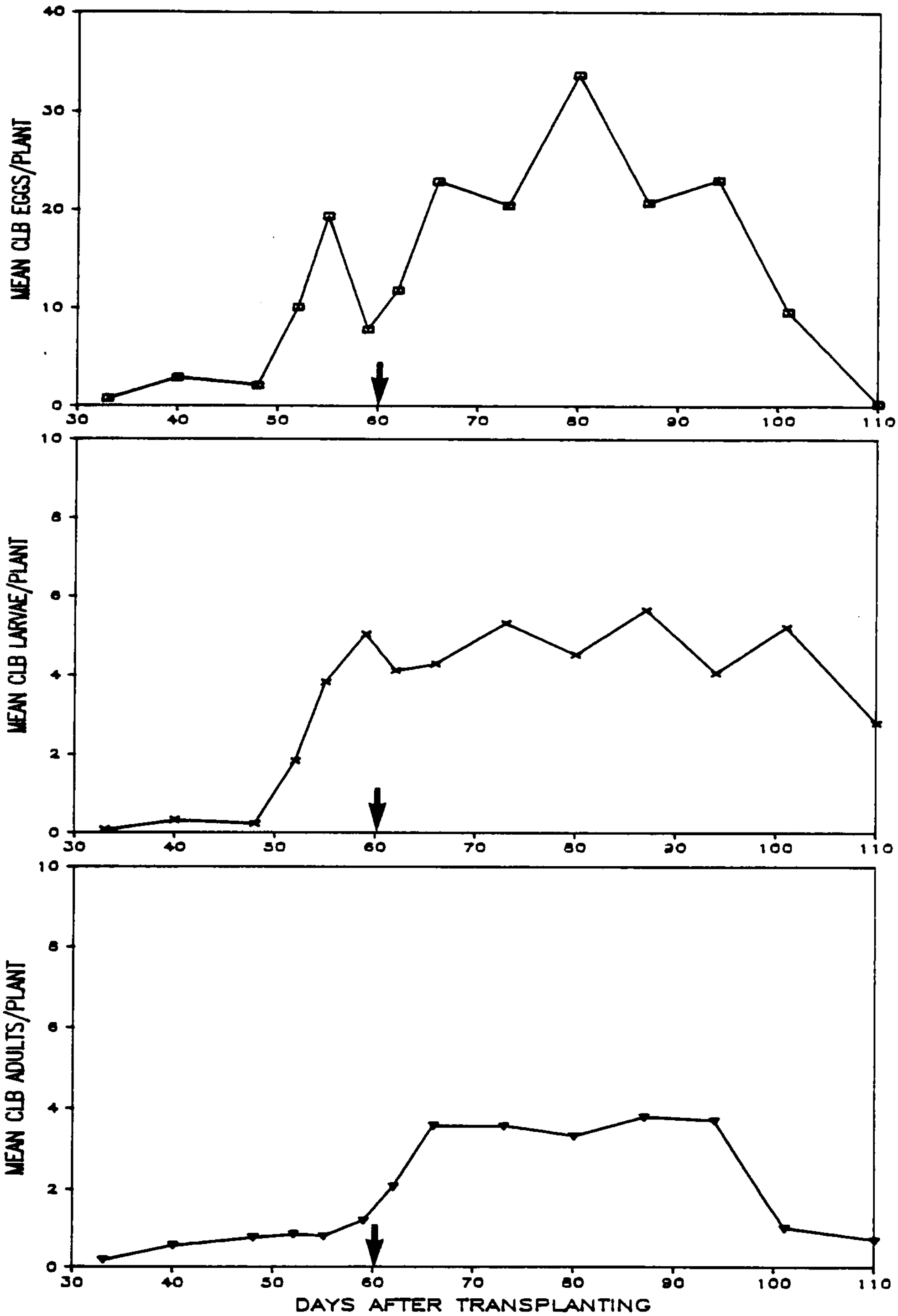

Fig. 15. Seasonal abundance of convergent lady beetle (CLB) eggs, larvae, and adults on flue-cured tobacco in PLOT-2, Blackstone, Va., 1986. (Arrows indicate topping time)

Table 9. Correlation coefficients (r) between log intensity of CLB eggs, larvae, and adults, and log intensity of GPA on tobacco, before and after topping, Blackstone, Va., 1985-1986.

	BEFORE TOPPING			AFTER TOPPING		
Fields	Eggs	Larvae	Adults	Eggs	Larvae	Adults
1985						
PLOT-1 [1]	0.52	0.46	0.72	0.33	0.32	0.37
PLOT-2 [2]	0.55	0.40	0.53	0.28	0.33	0.31
1986						
PLOT-1 [1]	0.58	0.66	0.62	0.35	0.44	0.60
PLOT-2 [2]	0.55	0.58	0.68	0.49	0.36	0.55

All numbers are significant ($p < 0.001$) under Pearson Correlation test
[1] Plots located at the edge of field
[2] Plots located at the middle of field

Table 10. Coefficient of determination (r^2) analysis between log intensity of CLB adults and log intensity of GPA before topping, Blackstone, Va., 1985-1986

Plots	Linear Model	Non-linear Model	Mean ± S.E GPA/Plant
1985			
PLOT-1 [1]	0.11	0.80	51.11 ± 7.50
PLOT-2 [2]	0.005	0.83	14.01 ± 3.60
1986			
PLOT-1 [1]	0.58*	0.85	271.05 ± 21.18
PLOT-2 [2]	0.83*	0.98	114.49 ± 15.82

* $p < 0.05$
[1] Plots located at the edge of field
[2] Plots located at the middle of field

Table 11. Correlation coefficient (r) between log number of convergent lady beetle egg/adult and log intensity of green peach aphid, and number (mean ± S.E) of CLB adult/plant, egg/adult, and GPA/plant in tobacco fields, Blackstone, Va., 1985-1986

YEAR	*1985*		*1986*	
Plots [1]	PLOT-1	PLOT-2	PLOT-1	PLOT-2
r	0.53*	0.65**	0.44	0.16
Mean± S.E CLB Adult/plant	0.54± 0.004	0.54± 0.04	1.85± 0.20	1.85± 0.10
Mean± S.E Egg/Adult	25.37± 19.22	3.82± 0.82	7.63± 1.59	7.57± 2.73
Mean± S.E GPA/Plant	28.70± 9.08	12.66± 5.14	188.75± 35.75	136.75± 23.68

* and ** are Significant at $P < 0.05$ and $P < 0.01$ respectively under Pearson Correlation test

[1] PLOT-1 was located at the edge of field and PLOT-2 was located at the middle of field

The difference in GPA intensity between years may have resulted in a different response by CLB adult. The immigration of CLB adults in 1985 had a non-linear relationship with GPA intensity probably because GPA intensities for this year was low and fell within Region 1 of a sigmoid curve which describes predator-prey relationships (Hassel and May 1974). This predator behavior enhanced the survival of predators progeny as intraspecific competition was avoided (Frazer and Raworth 1985). However, GPA intensities in 1986 probably fell within Region 2 of the sigmoid curve, which explains a linear relationship between predator immigration and prey intensities. Hence, predators stay and reproduce in response to prey intensities, in Region 2. In Region 3, on the other hand, more predators emigrate due to overcrowding. A better improvement in coefficient of determination (r^2) of 1985 observations was noted when the model was changed from linear to non-linear (Table 10).

However, the number of CLB egg/adult was only correlated with GPA intensities in 1985 and may have resulted from the satiation point of CLB. In 1985, the GPA intensities probably fell below the satiation point of CLB. Consequently, any increase in GPA intensities would automatically increase the number of CLB eggs produced as more GPA were eaten. However, GPA intensities in 1986 were probably above the satiation point of CLB. As a result, CLB populations did not respond to increasing GPA intensities. This resulted in no correlation between the number of eggs/adult and GPA intensities. This observation is in agreement with a model described by Mills (1982a). The satiation point of CLB may also explain the high number of eggs/adult for CLB in PLOT-1 of 1985. Predators are become inactive when they are satiated (Dixon 1959, Mills 1982a, Frazer and Raworth 1985, Evans and Dixon 1986). As the GPA intensities in 1985 fell below the satiation point, CLB adults were very active. This increased their probability of being miscounted. Thus, the number of CLB eggs/adult in the PLOT-1 of 1985 season may have been overestimated. Meanwhile, GPA populations in PLOT-2 of were too low to stimulate more CLB oviposition. However, GPA intensities in 1986 were above the satiation point which reduced adult CLB activity. Thus the number of CLB eggs/adult in that year more closely approximated the actual number of CLB eggs/adult in the field.

The ability of CLB females to increase activity when prey populations are low enables them to find areas of higher GPA densities for oviposition. This increases the survival of their progeny (Evans and Dixon 1986), and enhances their rates of predation. GPA, and CLB egg, larva and adult populations in fields before and after topping are summarized in Table 12. PLOT-1 had higher GPA numbers in early season attracted more CLB adults, which oviposited more eggs, and yielded more larvae. Hence, predation rates increased, and reduced GPA populations later in the season. In contrast, fields with lower GPA numbers in early season attracted fewer CLB adults. Therefore the numbers of eggs and larvae were reduced, which in turn, reduced predation rates, and allowed relatively higher GPA numbers in the fields. Although CLB were attracted to areas of higher GPA densities, they were not able to maintain GPA populations below the economic threshold.

This study has shown that immigration and satiation point are the main factors affecting the numerical response of CLB populations to GPA on tobacco. The linear numerical response in the laboratory was probably related to the following factors: 1) confinement -- CLB females were forced to eat and reproduce in the experimental arena; 2) the highest GPA intensity used was still below the satiation point of CLB; and 3) the seedlings used in the experiment had fewer trichomes, and lower levels of exudates than tobacco plants in the field. These factors increase the predation rates by CLB. However, under fields conditions, CLB demonstrated a numerical response that followed a sigmoid curve. CLB did not show a linear response until populations of their prey reached the intensity that supported their metabolic need, and the development of their progeny. The prey intensities above the optimum range resulted in no response in predator populations. The plateau in the curve resulted from the satiation point of the predator as reported by Mills (1982a) and Frazer and Raworth (1985). However, Holling (1961) suggested that the plateau is a result of other limiting factors besides food. The typical numerical response of CLB, coupled with short tobacco growing season, may account for the lack of effective control of GPA populations by CLB on tobacco. The satiation point characteristic is exhibited by most of the aphidophagous coccinellids, which are less effective biological control agents than the coccidophagous coccinellids, which showed no prey satiation point (Mills 1982b).

Table 12. Number (mean ± S.E) of GPA and CLB eggs, larvae, and adults per plant, before and after topping in tobacco fields, Blackstone Va., 1985-1986

	BEFORE TOPPING				AFTER TOPPING			
		CLB [1]				CLB [1]		
Plot	GPA [2]	Eggs	Larvae	Adults	GPA	Eggs	Larvae	Adults
1985								
PLOT-1[3]	51.11 ± 7.50	2.79 ± 0.59	0.42 ± 0.13	0.30 ± 0.06	10.10 ± 2.00	1.91 ± 0.33	0.74 ± 0.10	0.53 ± 0.05
PLOT-2[4]	14.01 ± 3.60	1.49 ± 0.77	0.41 ± 0.20	0.24 ± 0.07	12.01 ± 2.86	2.77 ± 0.35	1.21 ± 0.18	0.69 ± 0.05
1986								
PLOT-1[3]	271.05 ± 21.18	9.23 ± 1.03	3.06 ± 0.36	1.40 ± 0.15	106.78 ± 10.38	12.97 ± 1.48	2.08 ± 0.23	2.28 ± 0.18
PLOT-2[4]	114.49 ± 15.85	7.20 ± 1.02	1.88 ± 0.27	0.72 ± 0.09	153.21 ± 10.11	17.82 ± 1.22	4.41 ± 0.28	2.70 ± 0.15

[1] convergent lady beetles
[2] green peach aphid
[3] located at field edge
[4] located at middle field

IMPACT OF INITIAL CONVERGENT LADY BEETLE TO GREEN PEACH APHID RATIOS ON GREEN PEACH APHID POPULATIONS ON FLUE-CURED TOBACCO

Introduction

The convergent lady beetle (CLB), *Hippodamia convergens* Guerin-Meneville, is the most common predator of the green peach aphid (GPA), *Myzus persicae* (Sulzer), on tobacco (Dominick 1949, Kulash 1949). Its seasonal abundance is closely synchronized with GPA populations (see Chapter 3). However, CLB alone is not able to keep GPA populations below the economic injury level on tobacco. In sorghum fields, two main factors limiting CLB effectiveness in regulating greenbug [(*Schizaphis graminum* (Rondani)] populations are its late arrival into the fields and its highly mobile behavior (ARS-USDA 1975). It is desirable to determine whether the same factors limit the success of CLB in the regulation of GPA populations on tobacco. Hence, the predation rates of CLB on GPA populations on tobacco were examined when these two factors were eliminated.

Cages have been used in several studies to investigate predation in the field. For instance, van den Bosch et al. (1969) used cages to evaluate the effectiveness of bollworm [*Heliothis zea* (Boddie)] predators on cotton. Richman et al. (1980) used cages to study the predation rates of several predators on soybean loopers [*Pseudoplusia includens* (Walker)] in soybean fields. In addition, several researchers used cages to study various factors affecting predation rates. Reed et al. (1984) studied the effect of predator and prey densities on predation rates of noctuid larvae by the predator complex in soybean fields. In another study, Abdul-Satar and Watson (1982) used cages to investigate the effect of *Bacillus thuringiensis* (Berliner) on the predation rates of *Geocoris punctipes* (Say) on cotton pests. Hodek et al. (1965) studied the effect of initial ratios of *Coccinella septempunctata* L. to *Aphis fabae* Scop on the efficacy of *C. septempunctata* for the control of *A. fabae* populations on sugar beets. They found that cage studies are useful for examining predator/prey relationships under field conditions.

A disadvantage of using field cages is that they alter several environmental conditions, i.e. temperature and humidity (Fye et al. 1969). The predator/prey relationship may also be affected because immigration and emigration are prevented. However, the major advantage of the cage technique is that it provides a quantitative assessment of potential predation by each predator (Grant and Shepard 1985).

The objective of this study was to assess the impact of CLB to GPA initial ratios on development of GPA and CLB populations on flue-cured tobacco grown in field cages.

Materials and Methods

Research was conducted at Virginia Polytechnic Institute and State University, Southern Piedmont Agricultural Experiment Station, Blackstone, Virginia in 1985 and 1986. Experimental plots consisted of six flue-cured tobacco plants (cv 'Coker 319') (2 rows of 3 plants spaced 51 cm apart), grown in 1.8 m X 1.8 m X 1.8 m cages covered with saran screen (32 X 32 mesh) (Chicopee, Gainesville, Georgia). In 1985, tobacco was transplanted on 2 May, and cages were placed on tobacco 60 days (1 July) after transplanting. In 1986, tobacco was transplanted on 16 May, and cages were placed on tobacco 38 days (24 June) after transplanting. Tobacco production practices followed Virginia recommendations (Jones 1985), but no chemical sucker control was applied after topping (removal of plant terminal bud).

The cage plots were arranged in a randomized complete block design containing six treatments of initial ratios of CLB:GPA and controls, with four replications. In 1985, the treatments were A - no CLB or GPA present (control to determine cage effect), B - 1 CLB:50 GPA, C - 1 CLB:100 GPA, D - 1 CLB:200 GPA, E - 1 CLB:300 GPA, and F - GPA alone (control for CLB effect). In 1986 the CLB:GPA ratios were changed to B - 1:25, C - 1:50, D - 1:100, and E - 1:200; treatments A and F were the same as in 1985.

GPA introductions

One week before releases were made, tobacco in all cages was sprayed with pirimicarb (Pirimor®) at the rate of 0.28 kg a.i/ha to eliminate early GPA infestations. GPA were collected from adjacent tobacco fields for release on the test tobacco. GPA were uniformly distributed by placing aphid infested tobacco leaves with a specific number of GPA on each plant. One or to days later, GPA populations were examined and a second infestation was made if GPA populations were not established.

CLB introductions

CLB were introduced into the cages after GPA colonies had become established. CLB adults were collected from adjacent fields, and introduced into cages on the same day. The numbers of CLB released into each cage varied according to total number of aphids present and the predetermined initial ratio for each cage (see Table 13 for the actual initial numbers of CLB and GPA released into each cage). In 1985, all releases of CLB were made on the same day for all treatments. However, in 1986, CLB introductions into cages were varied according to treatments. CLB were introduced 2-3 days after GPA introductions in cages with treatments B (1:25) and C (1:50), and 6 - 7 days after GPA introductions in cages with treatments D(1:100) and E(1:300).

Data collection and statistical analysis

GPA and CLB populations in each cage were monitored at least once a week, until all tobacco leaves had been harvested. Insect counts were started on the day of CLB introductions. GPA population development was monitored by counting the number of GPA present between the fourth and sixth lateral veins on the right side of the midrib of the top eight leaves of each plant. CLB population development was monitored by counting the number of eggs and larvae on each

Table 13. The initial numbers of GPA and CLB released into each cage, Blackstone, Va., 1985-1986.

		1985			1986		
Cage #	Treatment	Initial CLB:GPA ratios	No. of CLB released	No. of GPA released	Initial CLB:GPA ratio	No. of CLB released	No. of GPA released
1	F	GPA only	0	4715	GPA only	0	2100
2	A	No CLB, no GPA	0	0	No CLB, no GPA	0	0
3	D	1:200	30	5860	1:100	35	3540
4	B	1:50	55	2790	1:25	52	1283
5	C	1:100	31	3100	1:50	19	942
6	E	1:300	16	4738	1:200	20	4075
7	D	1:200	8	1554	1:100	13	1270
8	B	1:50	38	1898	1:25	151	3768
9	C	1:100	26	2584	1:50	9	445
10	F	GPA only	0	2118	GPA only	0	1950
11	E	1:300	10	3194	1:200	16	3190
12	A	No CLB, no GPA	0	0	No CLB, no GPA	0	0
13	B	1:50	60	3025	1:25	21	504
14	E	1:300	25	7500	1:200	7	1270
15	F	GPA only	0	2780	GPA only	0	2800
16	D	1:200	20	3900	1:100	32	3130
17	A	No CLB no GPA	0	0	No CLB, no GPA	0	0
18	C	1:100	28	2750	1:50	28	1375
19	C	1:100	46	4530	1:50	12	595
20	D	1:200	13	2590	1:100	22	2170
21	A	No CLB, no GPA	0	0	No CLB, no GPA	0	0
22	E	1:300	18	5310	1:200	21	4150
23	B	1:50	42	2115	1:25	9	220
24	F	GPA only	0	1580	GPA only	0	1200

plant. The egg and larval populations on screen were not sampled. Meanwhile, CLB adult populations were determined by counting the number in each cage (those found on plants and screen).

The cumulative proportional population growth rates of GPA, and CLB egg, larval, and adult populations for each treatment were determined with simple regression analysis of logit cumulative proportion against number of days after GPA introductions. The logitP's were calculated using the formula:

$$\text{LogitP} = \ln(P/1\text{-}P)$$

where P = cumulative proportional development of GPA or CLB egg, larval, and adult populations. Zero and 1.0 cumulative proportion value were discarded from the analysis since only cumulative proportion greater than 0, but less than 1.0 can be transformed to logit value. Furthermore, the proportional growth between last two observations is not independent of the preceding proportional development. The slope estimates in this analysis represented the cumulative proportional growth rates of each population in each treatment. Significant effects of treatments on slopes were determined with analysis of covariance (ANACOVA). If ANACOVA tests showed significant (α = 0.05) differences between slopes, then Tukey's procedure was used to separate the different slopes (Zar 1984). In addition, the cumulative proportional growth rate of GPA populations to reach 37,500, and 110,000 (where GPA population in one of the treatments did not show any further increase) for 1985 and 1986 respectively, were also calculated.

Tobacco leaves were harvested and cured as they ripened. A USDA marketing service grader placed standard commercial grades on cured-leaves for each priming from each plot. Yield (kg/ha), returns ($/ha), and quality index (0 - 100, 0 = the lowest quality, and 100 = the highest quality) using a modification of Wernsman and Price (1975) were determined. The percent reductions in yield, returns and quality index were compared to treatment A (No GPA or CLB present), in each replicate. Likewise, the percent reductions in GPA populations in each treatment were compared to GPA numbers in treatment F (GPA only) of each replication. Analyses of variance (ANOVA) were performed on arcsine transformation of these parameters. Significant means were separated with Duncan's multiple range test (α = 0.05) (Steel and Torrie 1980).

The influences of cage on the sunlight, temperature, and humidity were examined using simple linear regression analysis between information obtained inside and outside the cages during the 1986 study. Sunlight inside the cages was recorded with a Li-Cor Inc. Quantum Sensor, Lincoln, Nebraska. Humidity and temperature were recorded with DATAPOD 220® (Omnidata International, Logan, Utah) and POLYCORDER® (Omnidata International, Logan, Utah). Climatological data outside cages were obtained from a weather station (Courtesy Dr. S.D. Steel) located ca. 100 m from the experimental site. Comparisons were made for relative humidity, temperature, and sunlight (PAR - photosynthetically action rate). Statistical analyses were performed with Proc GLM of SAS (SAS Institute 1985).

Results and Discussion

Impact of initial CLB:GPA ratios on GPA populations

Figs. 16 and 17 demonstrate the cumulative development of GPA populations for each treatment of the 1985 and 1986 experiments. In 1985 (Fig. 16), all curves were similar in slope with the standard line in the early part of the season (which means that the counts on succeeding dates were similar). In the middle of the season (ca. 20 - 42 days after GPA introduction), GPA populations in treatments B(1:50), C(1:100), and D(1:200) continued to parallel the standard line, but GPA populations in treatments E(1:300) and F(GPA only) developed at a faster rate than standard line. Ca. 42 days after GPA introductions, all curves leveled off except GPA populations in treatment F(GPA only), which continued to increase but at a slower rate than standard line. Cumulative GPA counts during the experiment had inverse linear relationships with initial CLB:GPA initial ratios. GPA counts were highest in Treatment F(GPA only) followed by Treatments E(1:300), D(1:200), C(1:100), and B(1:50). In 1986, the results followed almost the

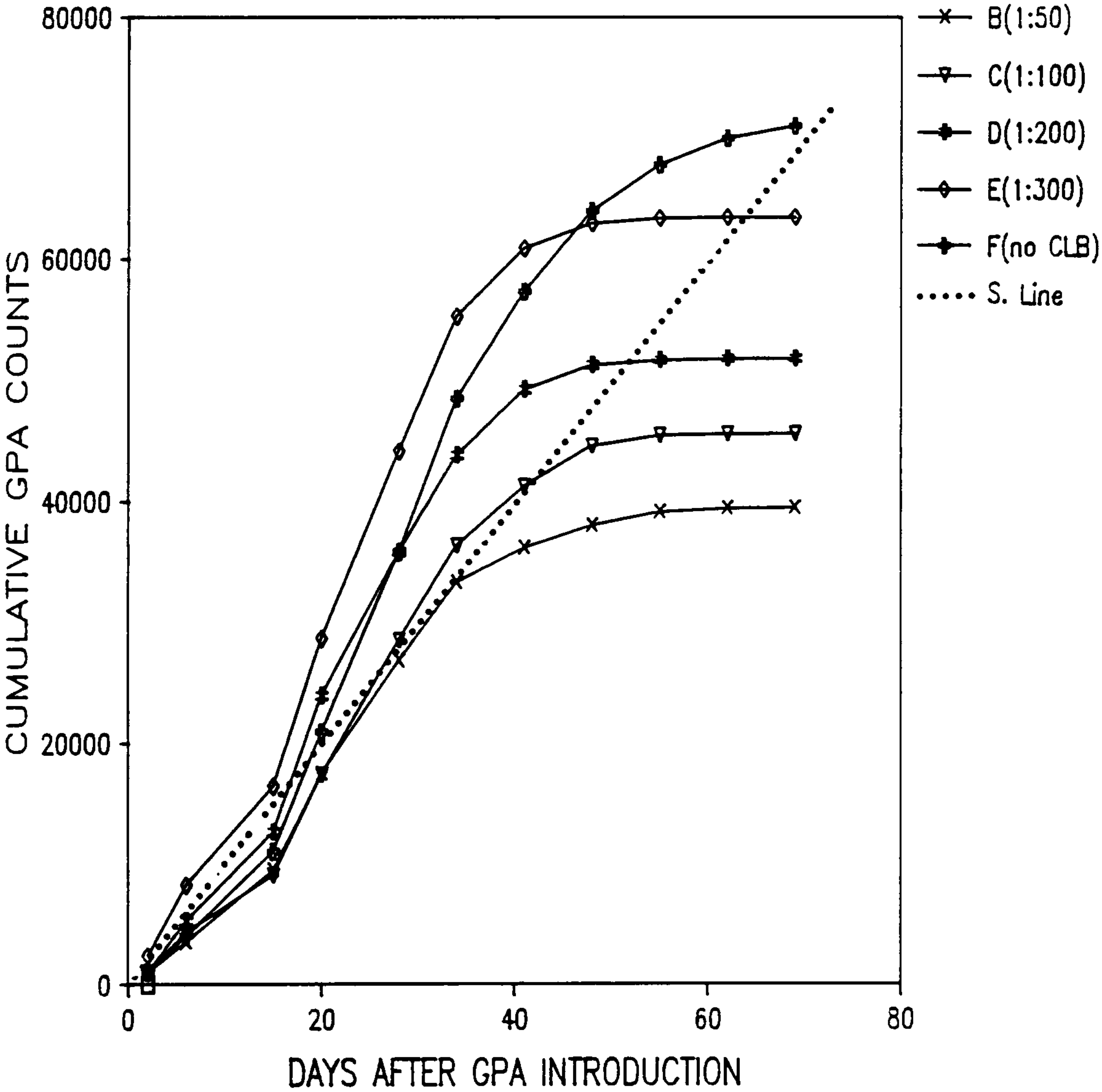

Fig. 16. Cumulative green peach aphid counts on tobacco (total of four cages) receiving different initial CLB to GPA ratios, Blackstone, Va., 1985 [(S.Line is a standard line to show if GPA populations accumulated at the same rate each day (250 GPA/day)].

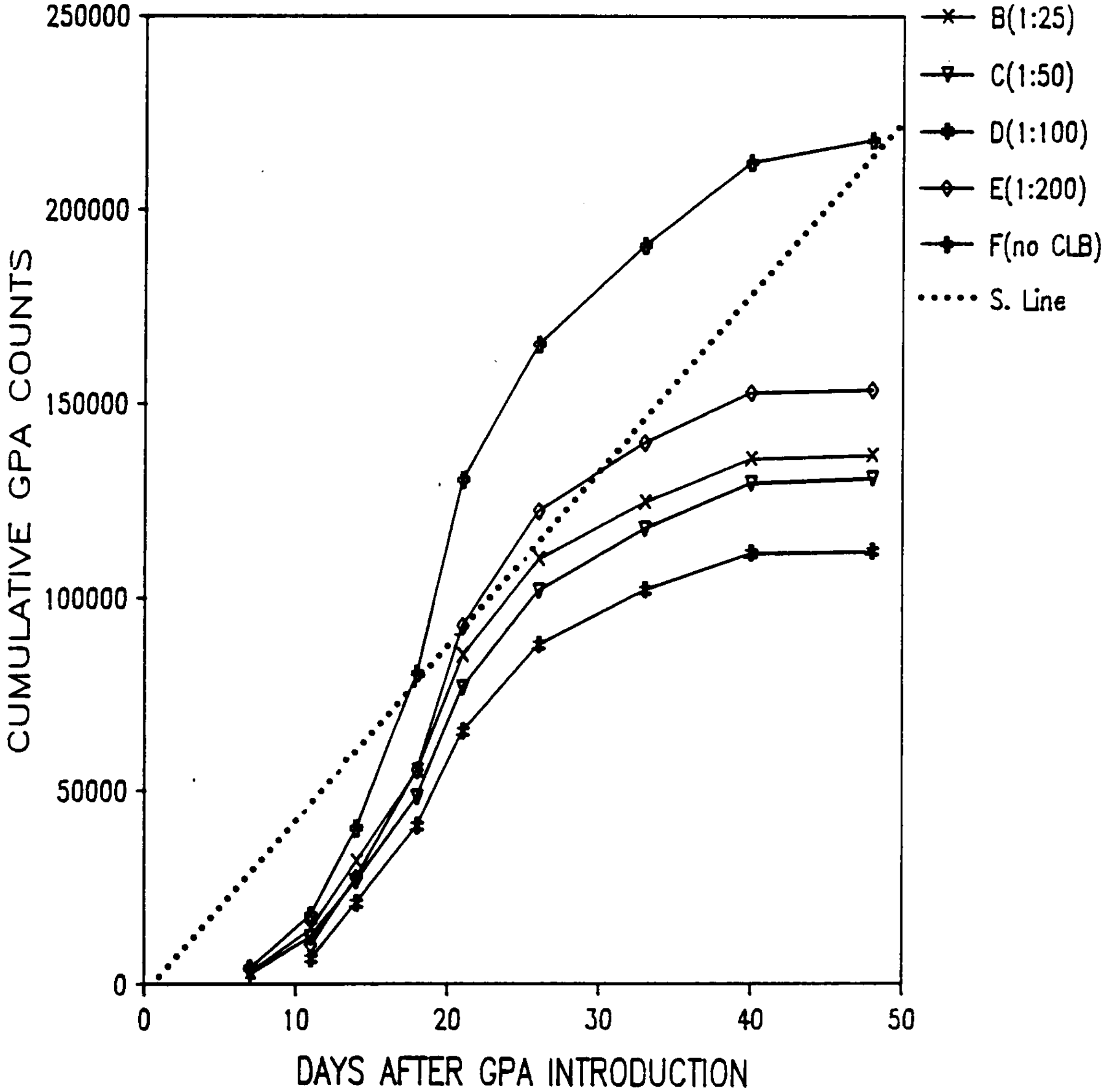

Fig. 17. Cumulative green peach aphid counts on tobacco (total of four cages) receiving different initial CLB to GPA ratios, Blackstone, Va., 1986. [(S.Line is a standard line to show if GPA populations accumulated at the same rate each day (460 GPA/day)].

same pattern as those in 1985 (Fig. 17). All slopes of GPA cumulative population development were higher than slope of standard line except at the beginning of the experiment (7 - 11 days after GPA introduction). They were paralleled with the Standard line between ca. 17 - 25 days after GPA introductions. After this point, all slopes of GPA cumulative populations were lower than slope of the Standard line, but slope for GPA populations in Treatment E(GPA only) was higher than slopes for GPA populations in other treatments. However, cumulative GPA counts during the experiment were not related to initial CLB:GPA ratios. GPA populations in Treatment F(GPA only) were the highest, followed by populations from Treatments E(1:200), B(1:25), C(1:50), and D(1:100).

Results from analyses on rates of cumulative proportional growth of GPA populations for the entire season, and to reach 37,500 and 110,000 (for 1985 and 1986 respectively) are shown in Table 14. There were significant ($\alpha = 0.05$) differences in cumulative proportional growth rates of GPA populations receiving different initial CLB:GPA ratios in 1985 (over entire season), but not in 1986. In 1985, the cumulative proportional growth rates for the entire season of GPA populations in cages with 1:200 (CLB:GPA) initial ratios were significantly higher than GPA populations in cages with 1:50 (CLB:GPA) initial ratio, and GPA populations without CLB. When the cumulative proportional growth rates of GPA populations to reach 37,500 and 110,000 (for 1985 and 1986 respectively) were compared, significant ($\alpha = 0.05$) treatment effects occurred both years. In 1985, the rate of cumulative proportional growth rate for GPA populations without CLB was higher than for GPA populations receiving 1:50 and 1:300 of CLB:GPA initial ratios. Similar trends were also observed in 1986. The cumulative proportional growth rates of GPA populations without CLB, and GPA population receiving the 1:300 CLB:GPA initial ratio were significantly ($\alpha = 0.05$) higher than cumulative proportional rates of GPA populations that were treated with other initial CLB:GPA ratios.

The percent reduction of GPA populations in each treatment for 1985 and 1986 are tabulated in Table 15. The effect of initial CLB:GPA ratios were more pronounced in 1985. Treatment B which received the highest initial ratio showed highest predation rates. There were significantly ($\alpha = 0.05$) greater reductions in GPA populations in treatment B(1:50) than in treatment E(1:300),

Table 14. Slope estimates for cumulative proportional growth of GPA populations receiving different initial CLB:GPA ratios, on flue-cured tobacco in field cages, Blackstone, Va., 1985-1986.

	Entire season		Early season[1]	
Initial CLB:GPA ratios	Estimate[2] of slope	r^2	Estimate[2] of slope	r^2
1985				
1:50	0.14 b	0.99 **	0.17 a	0.99 **
1:100	0.15 bcd	0.98 **	0.20 b	0.96 **
1:200	0.17 d	0.98 **	0.23 b	0.97 **
1:300	0.16 cd	0.99 **	0.18 a	0.99 **
GPA only	0.13 a	0.99 **	0.23 b	0.97 **
1986				
1:25	0.23 a	0.98 **	0.32 b	0.99 **
1:50	0.24 a	0.98 **	0.31 b	0.99 **
1:100	0.22 a	0.97 **	0.23 a	0.97 **
1:200	0.22 a	0.97 **	0.38 c	0.98 **
GPA only	0.21 a	0.96 **	0.38 c	0.99 **

** $p < 0.001$

[1] Analysis were done on cumulative proportion of GPA populations to reach 37,500 and 110,000 in 1985 and 1986 respectively.

[2] The estimates for the slope of simple linear regression analysis between logit cumulative proportions of GPA populations and number of days after GPA inoculations. Slopes within a column followed by the same letter are not significantly different ($P < 0.05$) as indicated by Tukey's test.

Table 15. Mean percent of reduction of cumulative GPA counts in treatments receiving different initial CLB:GPA ratios, on flue-cured tobacco in field cages, Blackstone, Va., 19

Years	1985		1986	
Treatment	Initial CLB:GPA ratios	Mean % reduction[1,2]	Initial CLB:GPA ratios	Mean % reduction[1,2]
B	1:50	35.75 a	1:25	33.75 a
C	1:100	30.75 ab	1:50	39.50 a
D	1:200	18.50 ab	1:100	47.25 a
E	1:300	2.00 b	1:200	27.00 a
F	GPA only	0.00 b	GPA only	0.00 b

[1] Means followed by the same letter in each column are not significantly different ($\alpha \leq 0.05$) under Duncan's multiple range test (analysis was done using arcsine of percentage transformation)
[2] Mean percent reduction, (GPA counts in treatment B - GPA counts in each treatment) X 100 / GPA counts in treatment B

but there were no significant ($\alpha = 0.05$) differences among the other treatments. In 1986, the initial CLB:GPA ratios did not significantly affect GPA populations in cages.

Impact of initial CLB:GPA ratios on CLB egg, larva, and adult populations

The cumulative growth of CLB egg, larva, and adult populations for the experiment are presented in Figs. 18 to 20 and Figs. 21 to 23 for 1985 and 1986, respectively. In 1985, the population growth curves were very similar to each other, but treatment E(1:300) consistently showed higher cumulative numbers for eggs, larvae and adults. Likewise, the slopes of each curve for CLB egg, larval, and adult populations to reach their peaks were almost similar in the slope of the standard line, except the slope for GPA populations in Treatment E(1:300) consistently developed higher than slope of standard line, especially between 20-40 days after GPA introduction. However, no distinct difference was observed in 1986 experiment. Their cumulative growth curves were also almost similar to each other. Their slopes were lower than the slope of Standard line in early part of experiment (before ca. 14 and 25 days after GPA introduction for larval, and egg and adult populations, respectively), but higher during the later part of experiment, until they reached the plateau. ANOVA on their cumulative population counts (Table 16) showed no significant ($\alpha = 0.05$) effects of initial CLB:GPA ratios, except in 1985, when significantly more CLB larvae were found in treatment E(1:300) than in treatment C(1:50). In 1986, initial CLB:GPA ratios had no significant effect on the cumulative population counts of CLB eggs, larvae, and adults. In fact, the numbers between treatments were almost identical.

Analysis of cumulative proportional growth rates of CLB egg, larval, and adult populations (Table 17) showed that initial CLB:GPA ratios did not influence the cumulative proportional growth rate of CLB egg populations in either year, but it did influence the cumulative proportional growth rates of CLB larval populations in 1985, and CLB adult populations for both 1985 and 1986. It consistently showed that rates for CLB populations treated with the lowest CLB:GPA initial ratios, were higher than the populations treated with highest CLB:GPA ratios.

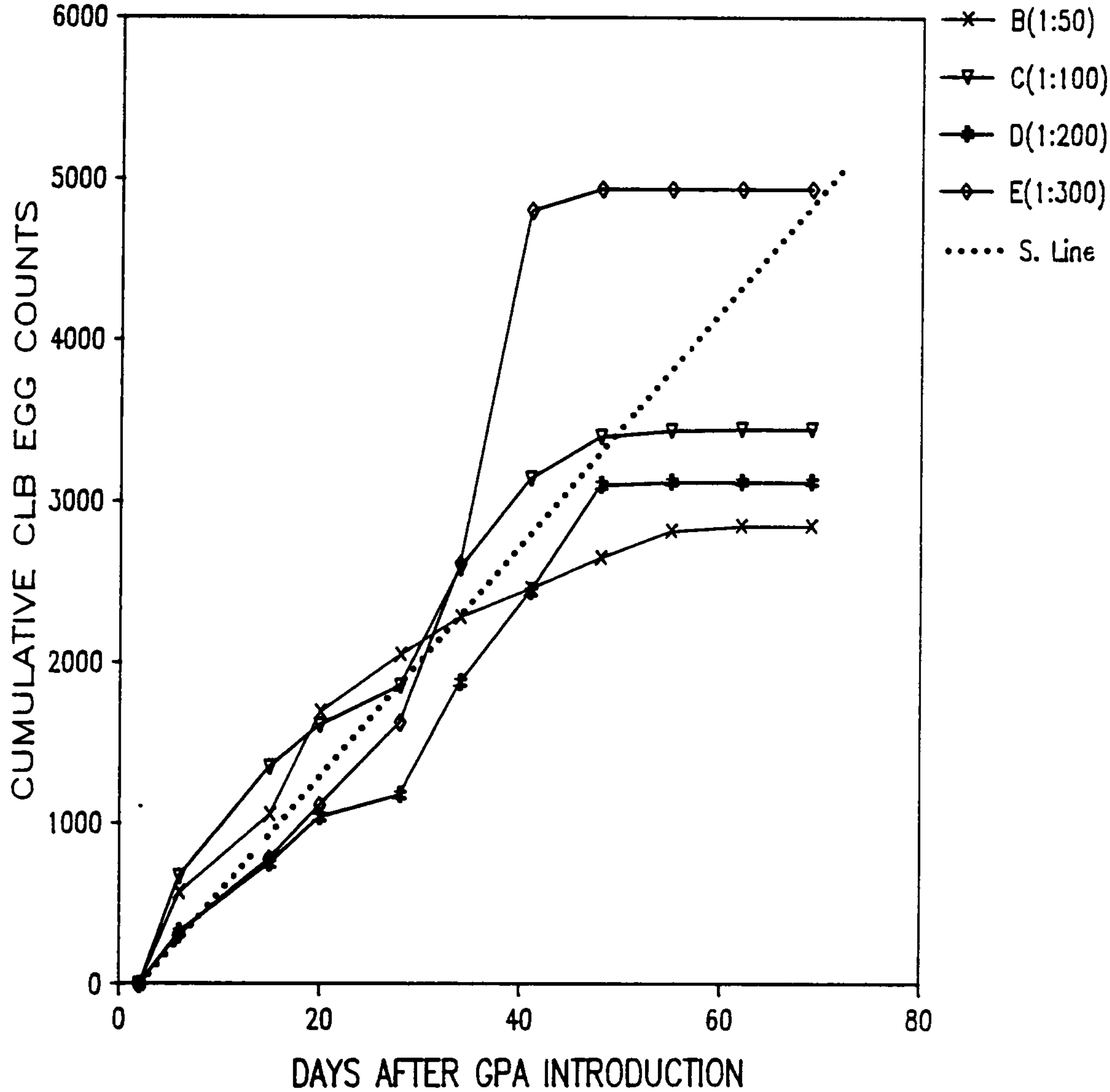

Fig. 18. Cumulative convergent lady beetle egg counts on tobacco (total of four cages) receiving different initial CLB to GPA ratios, Blackstone, Va., 1985. [(S.Line is a standard line to show if egg populations accumulated at the same rate each day (75 eggs/day)].

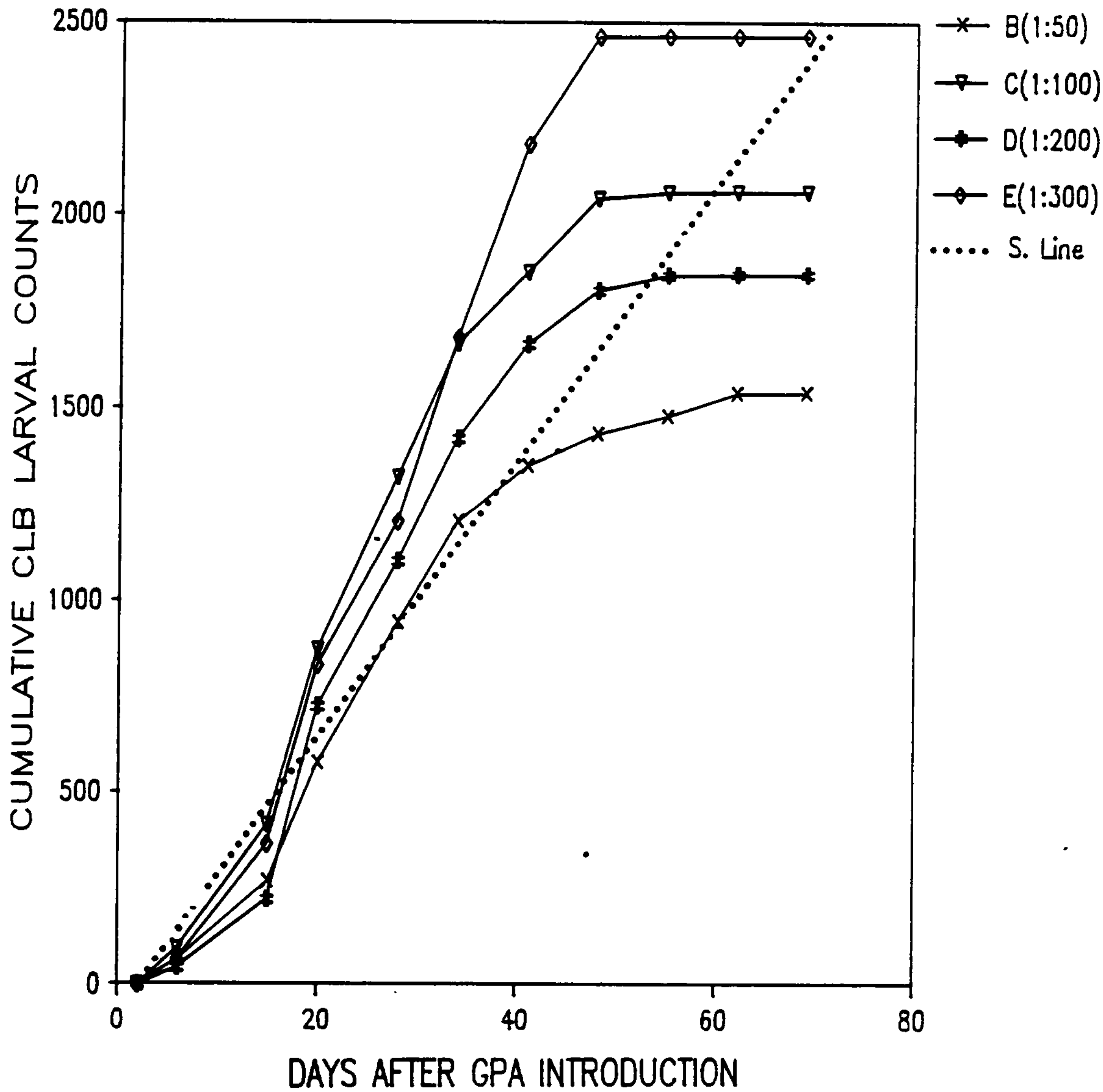

Fig. 19. Cumulative convergent lady beetle larval counts on tobacco (total of four cages) receiving different initial CLB to GPA ratios, Blackstone, Va., 1985. [(S.Line is a standard line to show if larval populations accumulated at the same rate each day (36 larvae/day)].

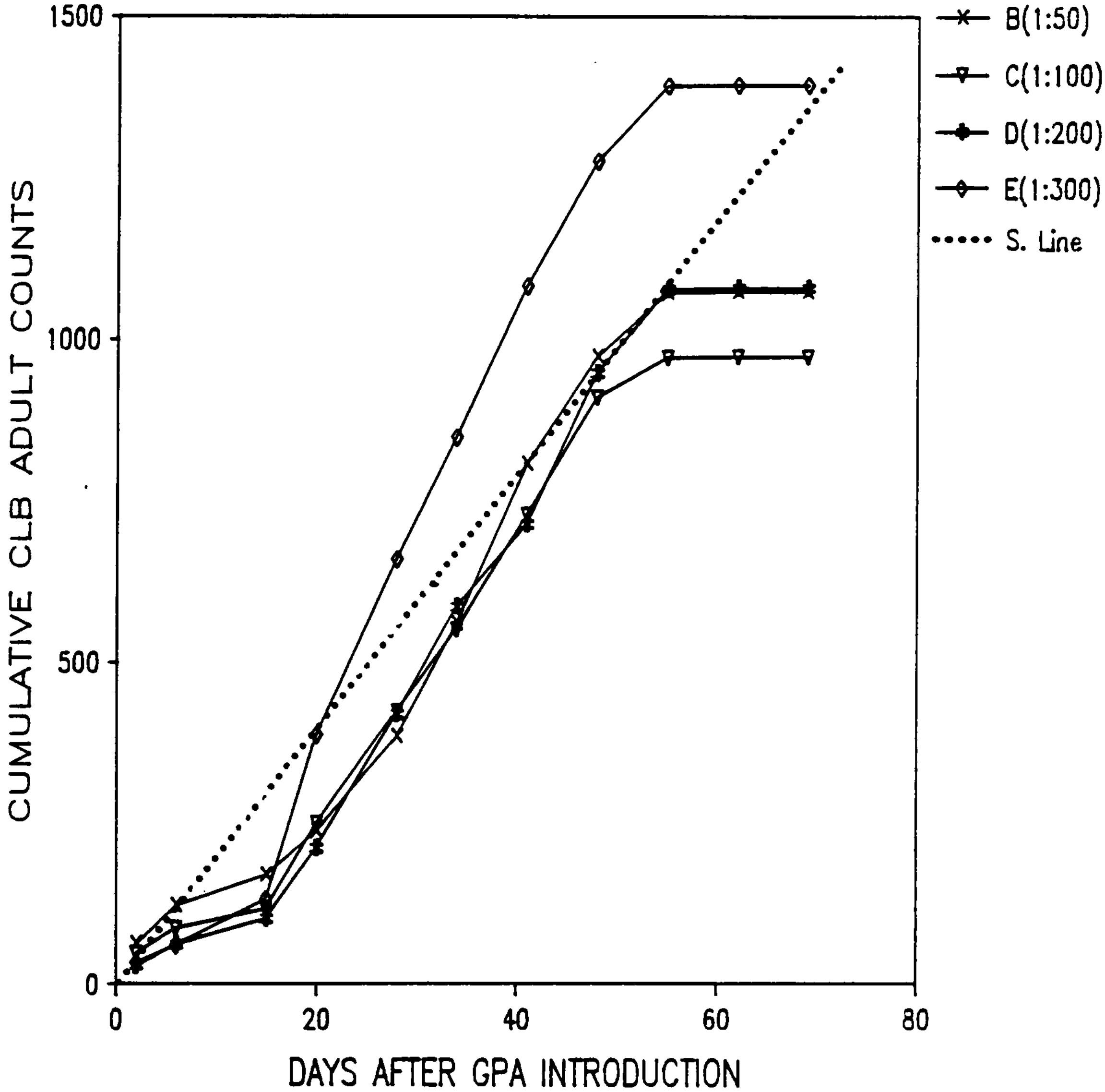

Fig. 20. Cumulative convergent lady beetle adult counts on tobacco (total of four cages) receiving different initial CLB to GPA ratios, Blackstone, Va., 1985. [(S.Line is a standard line to show if adult populations accumulated at the same rate each day (20 adults/day)].

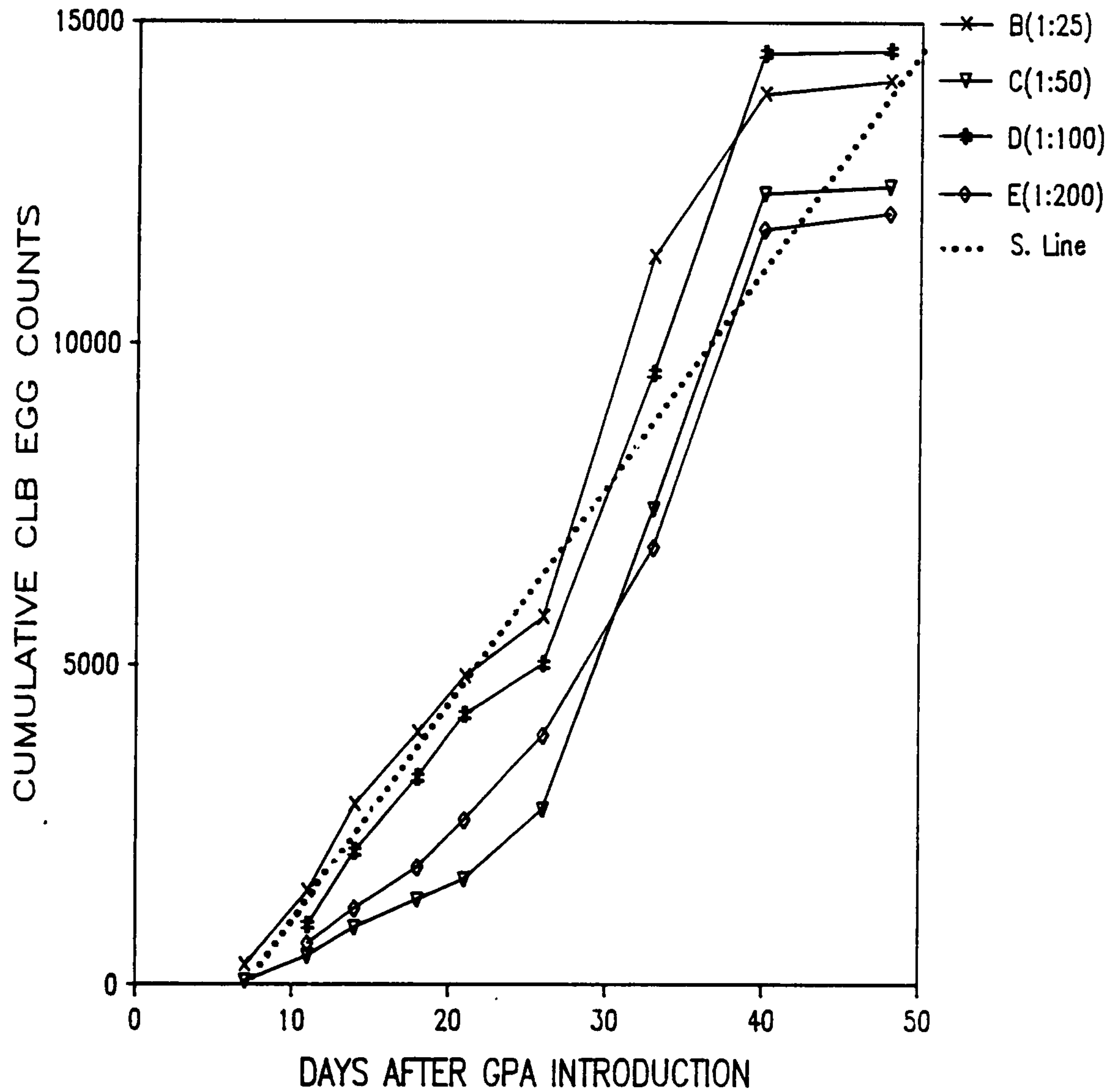

Fig. 21. Cumulative convergent lady beetle egg counts on tobacco (total of four cages) receiving different initial CLB to GPA ratios, Blackstone, Va., 1986. [(S.Line is a standard line to show if egg populations accumulated at the same rate each day (330 eggs/day)].

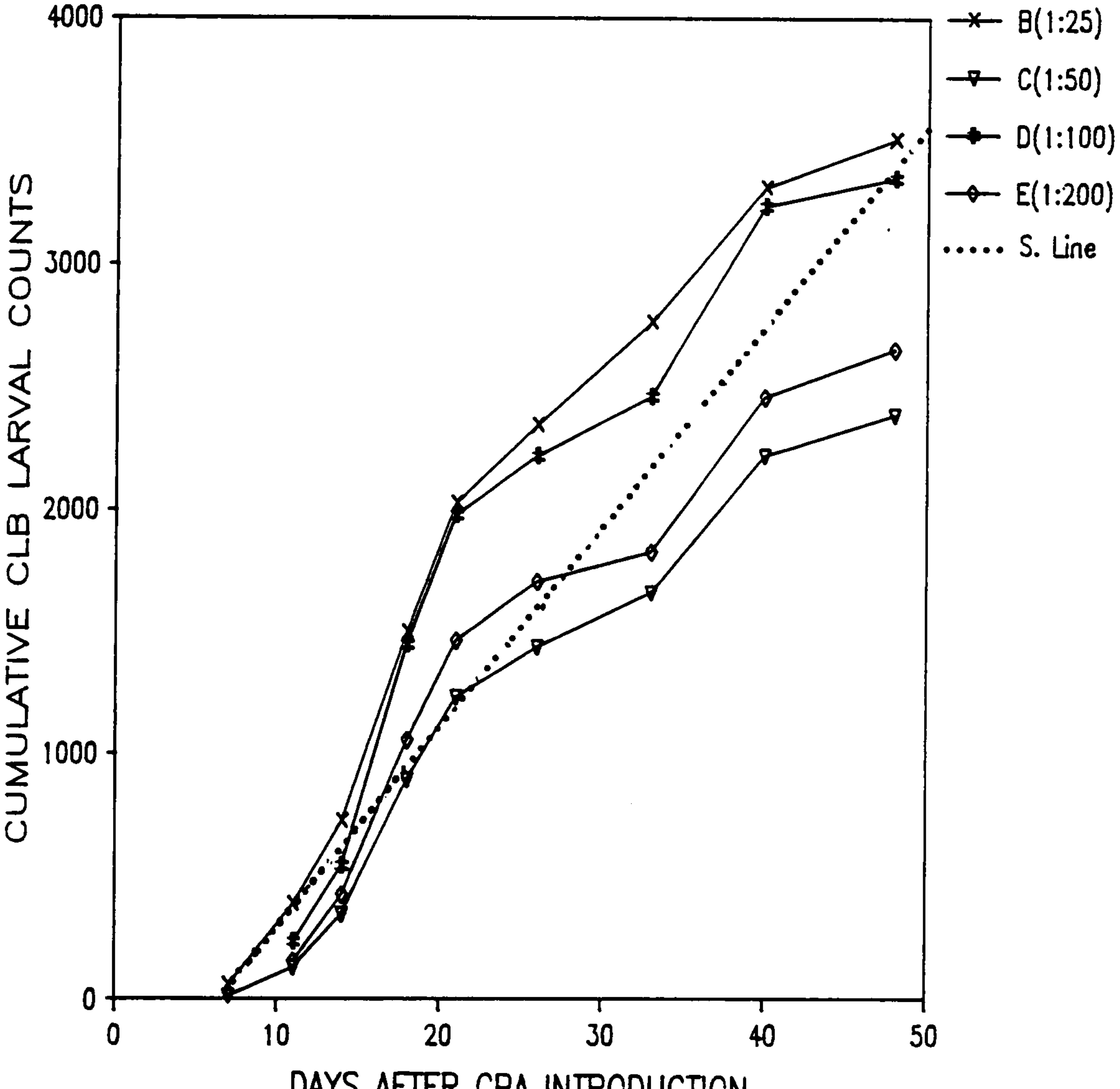

Fig. 22. Cumulative convergent lady beetle larval counts on tobacco (total of four cages) receiving different initial CLB to GPA ratios, Blackstone, Va., 1986. [(S.Line is a standard line to show if larval populations accumulated at the same rate each day (80 larvae/day)].

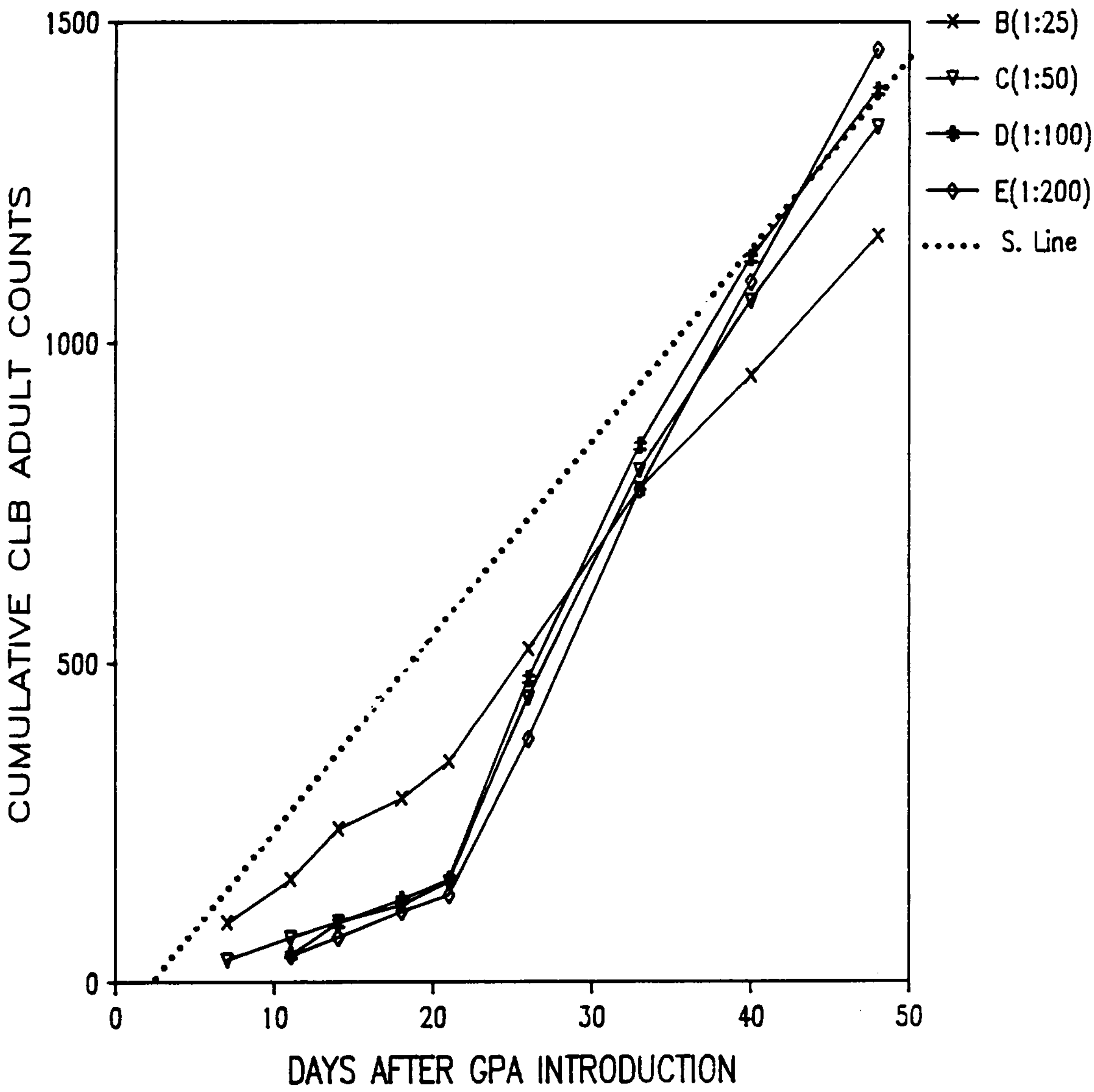

Fig. 23. Cumulative convergent lady beetle adult counts on tobacco (total of four cages) receiving different initial CLB to GPA ratios, Blackstone, Va., 1986. [(S.Line is a standard line to show if adult populations accumulated at the same rate each day (40 adults/day)].

Table 16. Mean cumulative CLB egg, larvae, and adult populations in each treatment receiving different initial CLB:GPA ratios, Blackstone, 1985-1986

Initial CLB:GPA ratios	CLB stage [1]		
	Eggs	Larvae	Adults
1985			
1:50	712.0 a	384.5 b	268.3 a
1:10	862.5 a	515.0 ab	243.3 a
1:20	781.0 a	461.3 ab	269.8 a
1:30	1235.3 a	616.3 a	348.5 a
1986			
1:25	3522.0 a	877.0 a	291.5 a
1:50	3111.5 a	595.0 a	334.0 a
1:100	3637.3 a	836.5 a	348.0 a
1:200	3006.3 a	661.5 a	364.0 a

[1] Means within a column (each year), followed by the same letter are not significantly different ($P \leq 0.05$)as indicated by Duncan's multiple range test

Table 17. Slope estimates for cumulative proportional growth of CLB egg, larval, and adult populations receiving different initial CLB:GPA ratios, on flue-cured tobacco in field cages, Blackstone, Va., 1985 - 1986.

1985			1986		
Initial CLB:GPA ratios	Estimate[1] of slope	r^2	Initial CLB:GPA ratios	Estimate[1] of slope	r^2
Eggs					
1:50	0.11 a	0.95 **	1:25	0.22 a	0.93 **
1:100	0.13 a	0.90 **	1:50	0.24 a	0.88 **
1:200	0.14 a	0.84 **	1:100	0.14 a	0.95 **
1:300	0.15 a	0.84 **	1:200	0.21 a	0.88 **
Larvae					
1:50	0.13 a	0.98 **	1:25	0.18 a	0.92 **
1:100	0.16 bc	0.97 **	1:50	0.17 a	0.91 **
1:200	0.17 c	0.98 **	1:100	0.18 a	0.92 **
1:300	0.15 abc	0.98 **	1:200	0.21 a	0.91 **
Adults					
1:50	0.10 a	0.97 **	1:25	0.11 a	0.99 **
1:100	0.11 a	0.97 **	1:50	0.15 b	0.98 **
1:200	0.11 a	0.99 **	1:100	0.17 c	0.99 **
1:300	0.13 b	0.99 **	1:200	0.16 cb	0.99 **

** $p < 0.001$

[1] The estimates for the slope of simple linear regression analysis between logit cumulative proportions of CLB egg, larva, and adult populations and number of days after GPA inoculations. Slopes within a column followed by the same letter are not significantly different ($P < 0.05$) as indicated by Tukey's test.

Impact of initial CLB:GPA ratios on quality index of tobacco

The percent reduction in yield (kg/ha), returns ($/ha), and quality index in each treatment for 1985 and 1986 are presented in Table 18. The initial CLB:GPA ratios did not affect the yields and returns in 1985, but they affect the yield and returns in 1986. In 1986, Treatment D(1:100) had significantly less yield reduction than Treatment F(GPA only). Likewise, Treatment D(1:100) significantly (α = 0.05) lower reduction in returns than Treatments B(1:25), E(1:200), and F(GPA only). The percent reductions in quality index of tobacco leaves were significantly (α = 0.05) affected by the initial CLB:GPA ratios in both years. In 1985, Treatment B(1:50) was significantly lower than in Treatment E(1:300) and Treatment F(GPA only). In 1986, there was no direct relationship between percent reduction in quality index and CLB:GPA initial ratios. Treatment D(1:100) had significantly less reduction in quality index than Treatments B(1:25) and F(GPA only). Hence, Treatment B(1:25) was not as effective as expected. Although Treatment B(1:50) of 1985, and Treatment D(1:100) of 1986, had less reductions in quality index, their lowest percent reductions were still too high (65.25% and 51.50% for 1985 and 1986 respectively). Thus, the reduction of GPA populations by CLB was not enough to reduce the injury that the GPA caused.

The cages had significant effects on relative humidity, temperature, and light intensity (Table 19). The complete data for the analysis are presented in the Appendix A. The reduction in light intensity may have exerted a significant effect on the results, because it affected tobacco performance.

The duration of the experiment were differed between years (ca. 69 and 48 days after GPA introduction for 1985 and 1986 respectively). The drought season in 1986 probably caused the tobacco to mature earlier. Furthermore, higher GPA densities in 1986 caused tobacco leaves to mature early. Consequently, tobacco leaves were harvested earlier in 1986 than in 1985 (ca. 73 and 97 days after transplanting in 1986 and 1985 respectively).

Although length of the experiment differed between years, results were similar. The initial CLB:GPA ratios used in this experiment failed to produce a pronounced effect on GPA populations. However, it did demonstrate that CLB (larvae and adults) were able to suppress the

Table 18. Mean percent reductions in yield (kg/ha), returns ($/ha), and quality index of flue-cured tobacco receiving different initial CLB:GPA ratios, Blackstone, Va., 1985-1986

Treatment	initial ratios	Reduction in yield	Reduction in returns[1]	Reduction in quality index[1]
1985				
A	No CPA, no CLB	0.00 b	0.00 b	0.00 d
B	1:50	12.75 ab	24.25 a	65.25 c
C	1:100	20.75 a	36.00 a	82.50 abc
D	1:200	9.75 ab	24.25 a	73.75 bc
E	1:300	20.25 a	26.25 a	91.25 ab
F	GPA only	24.00 a	28.25 a	95.25 a
1986				
A	No GPA, no CLB			
present	0.00 c	0.00 c	0.00 c	
B	1:25	39.50 ab	63.75 a	79.50 a
C	1:50	32.25 b	53.50 b	57.25 b
D	1:100	29.75 b	51.50 b	51.50 b
E	1:200	42.00 ab	64.25 a	72.75 ab
F	GPA only	49.00 a	69.25 a	79.00 a

[1] Means within a column (each year), followed by the same letter are not significantly different ($P \leq 0.05$) separated by Duncan's multiple range test (Percentages were transformed to arcsine before analysis)

Table 19. The simple linear regression analysis between temperature (^{o}C), sunlight (photosyntheticaly available rates) and humidity recorded inside and outside of experimental cages, Blackstone, Va., 1986.

	Intercept	slopes	r2	df
Temperature (^{0} C)	- 3.68 **	1.13 **	0.97 **	290
Sunlight(PAR)	114.57 **	0.84	0.64 **	291
Humidity				
day	-18.50 **	1.15 **	0.84 **	114

** and * are $p < 0.001$ and $p < 0.05$ respectively number and cumulative proportional growth rates (in early season) of GPA populations. Although GPA populations were reduced, reductions were not enough to prevent economic damage. The cage conditions appeared to favor GPA development. Kulash (1949) reported that shading during part of the day favors GPA population development. In addition, the cages reduced the impact of rainfall and storms on tobacco plants. These two climatic factors are considered the most important aphid mortality factors (Walker et al. 1980). Cages also prevented the emigration of aphids, and the emigration or immigration of CLB.

The initial CLB:GPA ratios did not affect the cumulative proportional rates of CLB egg populations. Thus, the initial CLB:GPA ratios used in this experiment did not seem to influence the ovipositional rate of CLB adults. This was probably because GPA density inside the cages were above the satiation point of CLB. Hence, their rate of oviposition was at maximum. Therefore, any increase in GPA density did not influence CLB oviposition rate (Mills 1982a).

However, the cumulative proportional rates of CLB adult populations were affected by the initial CLB:GPA ratios used. The GPA population growth in each treatment probably affected the population growth rates of immature stages of CLB. Higher numbers of GPA resulted in more aphids eaten by the larval stage and speeded the development of CLB (Murdoch 1977). Thus, its speeded up adult emergence.

In these studies the CLB alone was not able to maintain GPA populations on tobacco below the economic injury level. However, the shading produced by the cages not only favored GPA population growth, but also enhanced GPA injury to tobacco. For instance, lack of sunlight causes a reduction in reducing sugars (Tso et al. 1970). GPA infestations also remove significant amounts of reducing sugar from tobacco leaves (Cheng and Hanlon 1985). Thus, the use of cages increased the possibility of producing low quality cured leaves. The use of cages also increased the incidence of sooty mold fungus (*Fumago vagans* Pers.) because more honeydew accumulated and ventilation was reduced. More honeydew accumulated because the insects that feed on honeydew were eliminated, and rain impact was reduced. Sooty mold also reduced the leave's ability to recover sunlight. Furthermore, sooty mold itself resulted in lifeless leaves when cured (Mistric and Clark 1979).

Despite the negative effect of cages on this experiment, their use is useful for the study of predator/prey relationships in the field. The treatment effects would be more apparent if the effect of cages on tobacco were reduced. The cage effects may be reduced if a wider plant spacing, or larger cages were used.

INFLUENCE OF INTERPLANTING OF VARIOUS CROPS WITH FLUE-CURED TOBACCO ON THE ABUNDANCE OF THE GREEN PEACH APHID AND ITS PREDATORS.

Introduction

The green peach aphid (GPA), *Myzus persicae* (Sulzer) is one of the most important tobacco insect pests in Virginia (Semtner 1983a). Severe GPA infestation may result in 100% loss if early control is not obtained (Tappan 1963). GPA serves as a host to several predators such as lady beetles (Coleoptera: Coccinellidae) - mainly convergent lady beetle (CLB), *Hippodamia convergens* Guerin-Meneville, syrphid fly larvae (Diptera: Syrphidae), lacewings [green lacewings (Neuroptera: Chrysopidae) and brown lacewings (Neuroptera: Hemerobiidae)], big-eyed bugs (Hemiptera: Lygaeidae), stilt bugs (Hemiptera: Berytidae), and damsel bugs (Hemiptera: Nabidae) (Dominick 1949, Kulash 1949, Elsey and Stinner 1971, Tamaki and Long 1978, Hussein 1985). In many cases, these predators are not able to suppress GPA populations on tobacco to sub-economic levels.

The lack of appropriate alternate hosts for these predators when hosts are scarce early and late in the season is considered one of the primary factors limiting their success as a biological control agent in transitory cropping systems (Eikenbary and Rogers 1973). Thus, to develop a successful pest management program in transitory crops such as tobacco, alternate hosts and shelter for beneficial insects should be provided, especially in early spring and late summer or early fall. This practice increases the survival of beneficial insects when prey populations on primary crops are limited (Dout et al. 1966).

A polyculture ecosystem is more stable than a monoculture ecosystem (Pimentel 1961), and it can result in a reduction in insect pest abundance (Root 1973, Perrin and Phillips 1978, Risch et al. 1983). An advantage of the polyculture ecosystem is that it enhances the activity of beneficial insects. For example, in Georgia the pecan aphid (*Norellia* sp.) is controlled without insecticides by planting clover and vetch under pecan trees to increase the populations of non-injurious aphid species that serve as an initial food source for the development of predators (Trible 1985). Likewise, alfalfa planted adjacent to cotton fields serves as a reservoir for natural enemies of insect pests on cotton (Fye 1972). In other studies, nectar produced by crops such as cotton and sunflower increased the longevity of beneficial insects (Lingren and Lukefahr 1977, DeLima and Leigh 1984).

However, the presence of certain crops adjacent to other crops can also reduce the rate of predation. Risch et. al. (1982) noted that certain combinations of crops lead to a more dense environment that results in a reduction in predation rates of *Coleomagilla maculata* (De Geer).

This experiment was conducted to determine the suitability of various crops planted in association with flue-cured tobacco for increasing the activity of predators on tobacco, without reducing tobacco yield and quality.

Materials and Methods

This study was conducted at Virginia Polytechnic Institute and State University, Southern Piedmont Agriculture Experiment Station, Blackstone, Virginia in 1986. The treatments consisted of four crops - alfalfa (*Medicago sativa* L.), crimson clover (*Trifolium incarnatum* L.), tall fescue (*Festuca elatior* L. cv 'Kentucky 31') , sunflower (*Helianthus annuus* L.), and tobacco (*Nicotiana tabacum* L. cv 'Coker 319'), the control. Crops were planted in 2-row strips (1.2 m row spacing) 12.2 m long on each side of three rows (3.7 m) of flue-cured tobacco (cv 'Coker 319') 12.2 m long (see Fig. 24 for plot size and arrangement). Tobacco was transplanted on 16 May; alfalfa and clover were planted on 9 April; and sunflower was planted on 1 May. Fescue was established in October, 1984. The treatments were arranged in a randomized complete block design replicated 4 times. Tobacco production practices followed Virginia Cooperative Extension Service recommendations (Jones 1985). *Bacillus thuringiensis* (Berliner) (Dipel®) was applied on 9 July to control hornworms (*Manduca* spp.). Other insecticides were not used to control GPA. Tobacco leaves were harvested, and cured as they ripened. The cured leaves were graded to standard commercial grades by a USDA marketing service grader (USDA 1984).

Populations of GPA and its predators were counted once a week on 15 tobacco plants per plot (five randomly sampled plants from each of three rows). GPA populations were rated on each

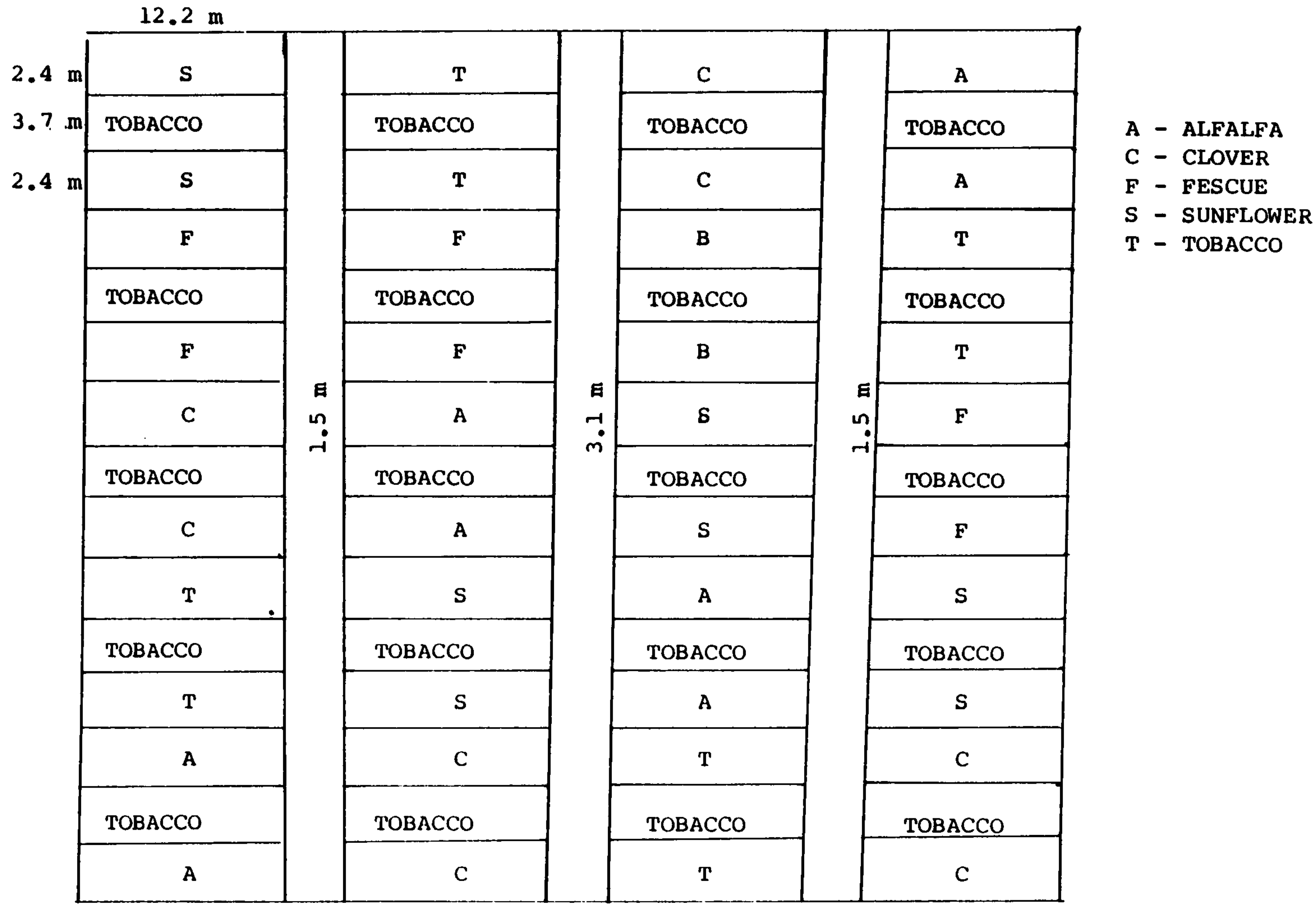

Fig. 24. Experimental plots layout and arrangement in strip-croping study, Blackstone, Va., 1986.

sampled plant using a scale of 0 to 5 where 0 = no aphids and 5 = very high GPA infestations. These ratings were converted to a seasonal GPA infestation index using the formula:

$$\text{GPA index} = \frac{(\Sigma \text{ RC X NPRC}) \text{ X } 100}{5 \text{ X TPS13}}$$

where

RC = Rating classes (0 -5)

NPRC = No. plants rated in each class

TPS13 = Total no. of plants sampled in 13 weeks.

All GPA predators were counted on each plant.

In addition, predator numbers in the strip crops were monitored by sampling each plot with a D-Vac (D-Vac company, P.O. Box 2095, Riverside, Ca. 92506) vacuum sampler (Roach 1980). Plots of alfalfa, clover, and fescue were sampled by randomly placing a 0.37 m diameter (0.11 m^2) D-Vac collecting head. Plots of sunflower and tobacco were sampled by randomly sucking a plant with the same D-Vac sampler. There were 20 samples/plot. Samples were taken on four dates: 24 July - when tobacco was topped (removal of terminal inflorescence), 27 August - after second priming, 15 September - at the completion of harvest, and 24 October - 39 days after the completion of harvest. The insect predators were collected, frozen, identified, and counted.

Statistical analysis

Statistical analysis were performed with Proc GLM of SAS (SAS Institute 1985). Analysis of variance (ANOVA) to test for treatment effects were conducted on GPA infestation index, yield, return, and quality index of flue-cured tobacco. Analysis of covariance (ANACOVA) were performed on the cumulative counts of insect predators, with GPA infestation index as the covariate. Lady beetles, syrphid fly larvae, and lacewings were closely associated with GPA populations. Thus, they were considered primary GPA predators. Results from ANACOVA were used to test for significant effects (Lentner and Bishop 1986). Stilt bugs (Hemiptera: Berytidae), big-eyed bugs (Hemiptera: Lygaeidae) and damsel bugs (Hemiptera: Nabidae) had weak or no associations with GPA populations. Thus they were considered as secondary GPA predators and ANOVA were performed on their cumulative counts to determine significant treatment effects.

Significant means ($\alpha = 0.05$) in ANOVA and adjusted means for significance ($\alpha = 0.05$) in ANACOVA were separated with Duncan's multiple range test ($\alpha \leq 0.05$) (Cochran and Cox 1957). Statistical analysis was not performed on insect predator counts from the strip crops since there were too many zero observations. Their means and standard error (SE) were calculated.

Results and Discussion

The GPA infestation indices are compared in Table 20. There were no significant differences ($\alpha = 0.05$) among the crops. Analysis on weekly observations of GPA infestation index also did not significantly differ among the crops. However, plots of tobacco-tobacco had a numerically higher GPA infestation index, followed by tobacco-sunflower, tobacco-clover, tobacco-alfalfa, and tobacco-fescue.

The total cumulative counts of primary GPA predators are presented in Table 21. Tobacco-clover plots had significantly more ($\alpha = 0.05$) syrphid fly larvae than tobacco-alfalfa, tobacco-sunflower, and tobacco-tobacco plots. There were no significant differences among the other treatments. The adjusted means of cumulative counts of eggs, larvae, and adults of CLB were not significantly ($\alpha = 0.05$) different among treatments, but there were higher cumulative numbers recorded in plots of tobacco-sunflower. In addition plots of tobacco-clover had numerically more, but not significantly ($\alpha = 0.05$) higher numbers of other lady beetles and lacewings.

Table 22 shows the cumulative counts of secondary GPA predators. Plots with tobacco-alfalfa and tobacco-tobacco had significantly ($\alpha = 0.05$) more total stilt bugs than tobacco-sunflower plots. However, tobacco-sunflower plots had significantly ($\alpha = 0.05$) higher numbers of big-eyed bugs than plots of tobacco-clover and tobacco-fescue.

Table 20. Mean GPA infestation indices for tobacco planted in strip with other crops, Blackstone, Va., 1986.

Crops	GPA infestation index[1,2]
Alfalfa	20.56 a
Clover	22.14 a
Fescue	20.54 a
Sunflower	24.38 a
Tobacco	25.32 a

[1] Refer to the text for the calculation of this index
[2] Means are not significantly different ($\alpha \leq 0.05$) as indicated by Duncan's multiple range test.

Table 21. Cumulative means[1,2,3] convergent lady beetle (CLB) eggs, larvae, and adults, syrphid fly larvae, other lady beetle species, and lacewings counted on flue-cured tobacco planted in strips with other crops, Blackstone, Va., 1986.

Crop	CLB eggs	CLB larvae	CLB adults	Syrphid fly larvae	Other[4] lady beetle species	Lacewings[5]
Alfalfa	528.1 a	160.1 a	114.8 a	13.5 b	7.7 a	16.1 a
Clover	459.8 a	168.1 a	148.5 a	29.3 a	9.0 a	23.0 a
Fescue	397.1 a	124.3 a	91.7 a	20.7 ab	8.0 a	15.5 a
Sunflower	639.5 a	171.4 a	148.6 a	11.6 b	5.4 a	21.6 a
Tobacco	474.0 a	104.3 a	102.3 a	13.6 b	5.1 a	20.3 a

[1] Adjusted means, obtained through analysis of covariance with GPA index as the covariate.
[2] Total insects on 15 tobacco plants for 13 weeks.
[3] Adjusted means followed by the same letter within a column are not significantly ($\alpha \leq 0.05$) different as indicated by Duncan's multiple range test (Cochran and Cox, 1957).
[4] Primarily spotted lady beetles (*Coleomagilla maculata*) and seven spotted lady beetles (*Coccinella septempunctata*)
[5] Consisted of green lacewings (Neuroptera: Chrysopidae) and brown lacewings (Neuroptera: Hemerobiidae).

Table 22. Total[1] stilt bugs, big-eyed bug, and damsel bugs counted on tobacco planted in strip with other crops, Blackstone, Va., 1986

Crops	Insects[2]		
	stilt[3] bugs	Big-eyed[4] bugs	Damsel[5] bugs
Alfalfa	143.8 a	38.8 a	6.8 a
Clover	136.0 ab	27.5 bc	6.3 a
Fescue	116.0 ab	14.3 c	7.0 a
Sunflower	102.8 b	51.0 a	10.0 a
Tobacco	143.0 a	36.5 ab	8.5 a

[1] Total insect counts on 15 tobacco plants for 13 times (weeks).
[2] Means within a column followed by the same letter are not significantly different ($\alpha = 0.05$) as indicated by Duncan's multiple range test.
[3] Hemiptera: Berytidae
[4] Hemiptera: Lygaeidae
[5] Hemiptera: Nabidae

The numbers of primary and secondary GPA predators in strip crops are summarized in Tables 23 and 24, respectively. Except for one lady beetle, primary predators were not observe, on any of the strip crops after the tobacco season was over (24 October). In contrast, the secondary GPA predators, except stilt bugs, were still numerous. Silt bugs, when present, were more numerous on tobacco than in the other strip crops. Roach (1980) obtained similar results.

Table 25 indicates the yield (kg/ha), returns ($/ha), and quality index of flue-cured tobacco from this study. ANOVA on these parameters showed that there were no significant ($P < 0.05$) treatment effects. Thus, the crops selected for this experiment did not affect the yield and quality of flue-cured tobacco.

Results from this experiment were not conclusive. However, a few interesting observations were noted. Syrphid fly larvae were more numerous in tobacco-clover plots. Adult syrphid flies were probably attracted to clover flowers which were blooming in the early part of the season. Polard (1971) made a similar observation. In addition, although not significantly different (α = 0.05), more CLB eggs, larvae and adults were observed in tobacco-sunflower plots. This observation was in agreement with Rogers (1985) who observed that CLB is attracted to the extrafloral nectar produced by sunflowers. Tobacco-sunflower plots also had significantly more total big-eyed bugs. It is possible that CLB and big-eyed bugs were attracted to the nectar produced by sunflowers. According to DeLima and Leigh (1984) nectar produced by cotton influences the population development of big-eyed bugs, especially when prey populations are scarce.

There were several factors that contributed to these inconclusive results. The plots used in this experiment were probably too small to serve as discrete reservoirs for predators for one plot. to reduce insects movement from one plot to another. In addition, the strip crops were planted too late to attract predators or conserve their populations before GPA colonized tobacco plants. Thus, future studies should be conducted using larger plots and earlier planting of strip crops. In addition, the effects of strip planting should be observed for all the major pests and predators on tobacco instead of just a few.

Table 23. Mean ± SE of convergent lady beetles (CLB) and other lady beetle species, syrphid fly larvae and lacewings sampled with a D-Vac® sampler on different crops planted adjacent to flue-cured tobacco. Blackstone, Va., 1986

	Sampling date			
Crop	24 July	27 August	15 Sept.	24 Oct.
		CLB and other coccinellidae/sample		
Alfalfa	3.75 ± 1.75	0.75 ± 0.48	0.75 ± 0.48	0.00
Clover	0.75 ± 0.25	1.00 ± 0.41	0.25 ± 0.25	0.00
Fescue	0.33 ± 0.33	0.50 ± 0.29	1.00 ± 0.71	0.25 ± 0.25
Sunflower	1.25 ± 0.75	1.00 ± 0.41	0.75 ± 0.48	0.00
Tobacco	3.75 ± 2.78	11.75 ± 2.87	4.50 ± 1.50	0.00
		Syrphid fly[1] larvae		
Alfalfa	0.00	0.25 ± 0.25	1.00 ± 0.71	0.00
Clover	0.25 ± 0.25	0.75 ± 0.75	0.25 ± 0.25	0.00
Fescue	0.00	1.50 ± 0.96	2.00 ± 0.91	0.00
Sunflower	0.50 ± 0.29	0.00	0.75 ± 0.48	0.00
Tobacco	0.00	1.00 ± 0.41	0.75 ± 0.25	0.00
		Lacewings[2]		
Alfalfa	0.25 ± 0.25	0.50 ± 0.50	0.00	0.00
Clover	0.00	1.25 ± 0.75	0.25 ± 0.25	0.00
Fescue	0.00	0.25 ± 0.25	1.00 ± 0.41	0.00
Sunflower	0.75 ± 0.25	0.50 ± 0.29	0.25 ± 0.25	0.00
Tobacco	0.75 ± 0.75	1.25 ± 0.63	0.50 ± 0.50	0.00

[1] Diptera: Syrphidae
[2] Consisted of green lacewings (Neuroptera: Chrysopidae) and brown lacewings (Neuroptera: Hemerobiidae).

Table 24. Mean ± SE of stilt bugs, big-eyed bugs, and damsel bugs sampled with D-Vac® sampler on different crops planted adjacent to flue-cured tobacco, Blackstone, Va., 1986.

	Sampling date			
Crop	24 July	27 August	15 Sept.	24 Oct.
	Stilt bugs[1]			
Alfalfa	3.75 ± 3.12	0.25 ± 0.29	0.75 ± 0.48	0.00
Clover	0.50 ± 0.50	0.25 ± 0.25	0.00	0.00
Fescue	0.00	0.75 ± 0.48	1.25 ± 0.75	0.00
Sunflower	0.25 ± 0.25	1.75 ± 0.75	0.00	0.00
Tobacco	9.25 ± 5.38	22.50 ± 4.13	6.25 ± 2.23	0.00
	Big-eyed bugs[2]			
Alfalfa	8.25 ± 2.25	9.00 ± 1.96	2.25 ± 0.75	1.25 ± 0.75
Clover	6.00 ± 0.58	2.75 ± 1.11	1.50 ± 0.87	2.50 ± 0.85
Fescue	4.00 ± 2.00	2.50 ± 0.29	2.75 ± 1.11	1.75 ± 0.49
Sunflower	2.50 ± 0.87	1.25 ± 0.48	0.75 ± 0.48	0.00
Tobacco	5.00 ± 1.96	4.75 ± 3.09	0.50 ± 0.50	2.50 ± 1.55
	Damsel bugs[3]			
Alfalfa	0.25 ± 0.25	1.00 ± 0.58	0.75 ± 0.48	1.50 ± 0.65
Clover	0.00	1.00 ± 0.58	2.50 ± 1.89	2.00 ± 1.35
Fescue	0.67 ± 0.33	0.75 ± 0.75	1.00 ± 0.58	1.00 ± 1.00
Sunflower	0.00	0.00	0.25 ± 0.25	0.00
Tobacco	0.25 ± 0.25	1.50 ± 0.50	0.75 ± 0.48	2.00 ± 0.58

[1] Hemiptera: Berytidae
[2] Hemiptera: Lygaeidae
[3] Hemiptera: Nabidae

Table 25. Means of yield, return, and quality index of flue-cured tobacco planted in strip with other crops, Blackstone, Va., 1986

Crops	Yield (kg/ha)	Returns ($/ha)	Quality index
Alfalfa	2737 a	8776 a	60.75 a
Clover	2950 a	9508 a	59.75 a
Fescue	2518 a	7864 a	60.50 a
Sunflower	2790 a	8887 a	61.25 a
Tobacco	2665 a	8446 a	61.00 a

Means within the same column, followed by the same letter are not significantly different ($\alpha \leq 0.05$), by Duncan's multiple range test

SUMMARY AND CONCLUSIONS

The green peach aphid (GPA), *Myzus persicae* (Sulzer), is one of the most important insect pests of tobacco in the United States and in other tobacco producing countries. Uncontrolled infestations may result in significant crop loss. In Virginia GPA infestations vary considerably from year to year. Predators and high temperatures are the two main natural mortality factors of GPA on tobacco. Although several predators are associate with GPA on tobacco, in many cases they are not able to maintain GPA populations below the economic injury level. The factors that reduce the effectiveness of predators are not known. Thus the present research was conducted to identify major GPA predators on tobacco and to evaluate their effectiveness in regulating GPA populations in the field.

Seasonal abundance and vertical distribution of GPA and its predators on tobacco.

Several predators were associated with GPA populations on tobacco. They included several species of lady beetles, primarily convergent lady beetle (CLB), *Hippodamia convergens* Guerin-Meneville, syrphid fly larvae, two species of big-eyed bugs (*Geocoris* spp.), stilt bugs (*Jalysus wackhimi* Van Duzee), damsel bugs (*Nabis* spp.), and lacewings [(green lacewings (*Chrysopa* spp.) and brown lacewings (*Micromus* sp.)]. However, only CLB showed a numerical response to increases in GPA populations on tobacco. Thus, CLB was the most important GPA predator on tobacco. CLB did not effectively control GPA populations in the field probably because they could not co-exist with GPA populations on the same part of the plant. GPA preferred the upper leaves of tobacco since they were attracted to the most nutritious part of the plant. However, CLB were not common on this part of the plant. The high density of glandular trichomes on the upper leaves may have repelled CLB.

The numerical response of CLB to various GPA densities on tobacco.

The numerical response of CLB to various GPA densities on tobacco was investigated under laboratory and field conditions. In laboratory, CLB exhibited a linear numerical response to increasing GPA intensity. Two factors had determined oviposition of CLB were the minimum number GPA required to initiate CLB reproduction, and the conversion rates. In this experiment, it was found that at least 6.25 GPA were required to initiate GPA oviposition, and 0.44 eggs were oviposited for each GPA eaten thereafter. However, in the field CLB demonstrated a sigmoid curve predator-prey relationship, where CLB did not show a linear response until GPA population reached a certain intensity. Furthermore, CLB did not show a response when GPA populations were above its satiation point. CLB adults preferred to oviposit in areas of high GPA density, to increase the survival of their progeny. From this study, it seemed that the satiation point of CLB limited their success in regulating GPA populations effectively on tobacco.

Impact of initial CLB:GPA ratios on the development of GPA populations on field caged flue-cured tobacco.

The study was conducted by introducing several initial CLB to GPA ratios on field caged tobacco. Results showed that CLB could reduce the cumulative proportional growth rates and number of GPA on flue-cured tobacco, but were not able to reduce GPA populations to sub-economic levels. The initial ratios also influenced the population growth of CLB larvae, and adults. The lowest initial CLB to GPA ratio resulted in the slowest cumulative proportional growth rates of CLB populations. The humidity, temperature, and light intensity were altered inside cages. Alteration in light intensity was probably the most important factor because it enhanced tobacco injury by GPA. Therefore, from this exclusion study, CLB alone was not able to suppress GPA population on flue-cured tobacco to sub-economic level.

Influence of interplanting of various crops with flue-cured tobacco on abundance of GPA and its predators.

Populations of GPA and its predators were monitored on tobacco interplanted with alfalfa, clover, fescue, sunflower, and tobacco. Results showed that interplanting of selected crops with tobacco did not influence GPA infestations on tobacco. Only syrphid fly larvae, and big-eyed bugs populations were affected by the treatment crops. More syrphid fly larvae were observed on tobacco planted in strips with clover. Likewise, higher big-eyed bug populations were found on tobacco planted in strips with sunflower. Tobacco planted in strips with sunflower also had numerically higher (but not significantly different at $\alpha = 0.05$) CLB eggs, larvae, and adults. Thus, it was possible that CLB and big-eyed bug activities were influenced by sunflowers. The crops interplanted with tobacco in this experiment did not serve as alternate habitats to primary GPA predators when the tobacco season was over. The earlier establishment of interplanted crops, and larger plot sizes may have improved the results.

Conclusions

Results from this study showed that CLB is the most important predator of the GPA on tobacco. However, CLB success is limited by its reduced ability to search for aphids on the upper leaves of tobacco, and its satiation point which limited its predation rates when GPA intensity was very high. These two factors could interact with each other. For instance, the satiation point of CLB could be at higher GPA densities if CLB spent more time on the upper leaves of tobacco. Thus, in the future, the study on predation rates of CLB on GPA on several tobacco varieties with different glandular trichomes densities should be emphasized before use of CLB as a biological control agent of GPA on tobacco is implemented.

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Appendix a. The meteorological data obtained inside and outside cages, Blackstone, Va., 1986.

	Temperature (°C)		Sunlight (PAR)		Relative humidity[1]	
Observation	Inside cage	Outside cage	Inside cage	Outside cage	Inside cage	Outside cage
1	27.75	26.72	1603.31	896.94	44	55
2	27.40	27.28	906.34	736.13	45	49
3	25.18	25.67	622.59	356.91	45	45
4	20.75	22.28	0.00	74.32	44	39
5	18.25	20.39	0.00	2.47	41	44
6	16.50	18.33	0.00	2.47	39	48
7	16.30	18.00	0.00	2.47	38	51
8	16.53	18.44	0.00	4.94	37	45
9	15.20	16.72	0.00	2.47	36	50
10	14.75	16.28	0.00	2.47	36	43
11	13.75	16.06	0.00	2.47	35	50
12	12.95	15.11	0.00	2.47	36	47
13	12.43	14.67	0.00	4.94	35	42
14	12.33	14.56	0.00	12.35	35	44
15	15.33	15.78	1473.83	202.70	37	42
16	19.45	18.06	1914.60	554.26	38	46
17	22.80	21.22	1639.12	807.20	39	50
18	24.35	23.72	1619.83	1219.46	44	56
19	25.00	25.39	1404.96	1108.29	55	83
20	26.65	27.22	1388.43	1656.80	76	91
21	27.75	29.06	1173.55	1708.31	89	94
22	29.90	30.83	1104.68	1880.03	98	98
23	29.03	29.33	1735.54	1002.01	99	94
24	31.68	30.67	1101.93	1461.35	97	84
25	31.60	30.33	1371.90	1131.37	95	88
26	30.93	30.33	754.82	696.47	91	80
27	28.80	29.06	674.93	389.26	84	72
28	24.85	25.94	0.00	66.98	73	65
29	21.23	22.33	0.00	4.95	64	63
30	19.75	20.83	0.00	2.47	57	61
31	20.20	21.78	0.00	4.95	53	55
32	19.95	21.06	0.00	2.47	47	58
33	19.30	20.56	0.00	4.95	46	57
34	19.05	20.22	0.00	4.95	44	59
35	19.10	20.06	0.00	4.95	43	58
36	18.50	19.61	0.00	4.94	41	56
37	17.80	19.06	0.00	4.94	41	60
38	17.85	18.94	0.00	9.90	42	60
39	19.63	20.11	988.98	178.10	42	60
40	22.70	22.22	1377.41	507.77	42	61

(Appendix A continued)

41	25.30	24.94	1429.75	862.55	43	62
42	27.40	27.56	1526.17	1177.73	47	60
43	28.50	28.83	1292.01	1425.19	50	63
44	29.70	30.50	1187.33	1619.06	52	67
45	31.85	31.22	1217.63	1754.13	58	69
46	30.70	31.72	509.64	1195.89	63	74
47	32.55	33.17	1236.91	1672.26	70	78
48	30.50	31.78	534.44	617.58	80	82
49	32.68	32.78	831.96	1051.98	98	92
50	32.23	32.22	881.54	689.51	97	91
51	30.13	30.56	446.28	357.28	96	88
52	27.33	27.78	0.00	91.80	92	84
53	24.28	25.61	0.00	2.48	87	81
54	22.70	23.83	0.00	4.96	78	75
55	21.38	22.67	0.00	2.48	71	73
56	20.75	22.06	0.00	2.48	68	74
57	20.18	22.00	0.00	2.48	64	74
58	20.03	21.44	0.00	2.48	58	73
59	19.50	20.78	0.00	2.48	57	72
60	19.33	20.67	0.00	2.48	59	72
61	18.70	19.94	0.00	4.96	59	73
62	18.18	19.50	0.00	9.91	60	74
63	19.70	20.39	889.81	153.52	58	75
64	23.53	23.44	1427.00	525.11	57	75
65	26.68	26.56	1341.60	813.25	57	75
66	29.38	29.72	1586.78	1170.68	58	75
67	31.40	31.89	1203.86	1408.31	58	77
68	33.13	32.83	936.64	1570.53	59	77
69	34.60	34.44	741.05	1666.73	61	78
70	36.00	34.61	636.36	1725.68	65	79
71	35.55	34.94	840.22	1337.31	68	80
72	35.90	34.72	619.83	1118.60	72	85
73	36.45	35.11	539.94	1037.10	79	86
74	34.60	34.50	537.19	709.35	84	87
75	32.28	32.61	236.91	302.79	85	90
76	28.33	28.89	0.00	81.88	96	93
77	25.28	25.83	0.00	2.48	97	93
78	23.90	25.22	0.00	4.96	94	93
79	23.33	24.78	0.00	4.96	92	92
80	23.23	24.56	0.00	4.96	92	91
81	22.65	23.94	0.00	4.96	90	89
82	22.73	23.78	0.00	2.48	85	86
83	22.13	23.56	0.00	2.48	78	81
84	23.10	24.06	0.00	2.48	74	82
85	21.95	23.17	0.00	4.96	66	82
86	21.80	22.78	0.00	9.91	66	82
87	22.85	23.11	790.63	193.20	65	83
88	25.83	25.22	1148.76	535.38	65	83
89	29.15	28.50	1099.17	843.29	67	83

(Appendix A continued)

90	31.53	30.06	1008.26	1162.85	69	83
91	33.35	32.72	184.57	1171.01	67	81
92	29.23	29.11	415.98	493.22	66	82
93	27.58	27.94	8.26	175.09	71	83
94	26.55	27.17	0.00	73.98	71	82
95	24.33	25.39	0.00	2.46	73	82
96	24.08	24.89	0.00	4.92	73	84
97	23.85	24.67	0.00	4.92	75	86
98	23.73	24.50	0.00	2.46	79	86
99	23.15	24.00	0.00	4.92	82	84
100	23.18	24.06	0.00	0.00	82	86
101	22.95	24.00	0.00	4.92	85	90
102	22.70	23.72	0.00	2.46	90	93
103	22.75	23.78	0.00	2.46	97	94
104	23.08	23.94	0.00	4.92	98	94
105	23.40	24.06	0.00	73.86	97	95
106	24.08	24.33	730.03	243.82	96	96
107	24.35	24.39	592.29	224.04	97	97
108	25.78	25.39	920.11	438.38	96	96
109	28.05	27.50	1146.01	748.94	93	96
110	32.25	31.22	1046.83	1499.85	92	95
111	33.30	33.06	831.96	1576.72	90	91
112	31.83	32.33	484.85	1109.00	83	87
113	29.55	30.56	179.06	354.88	77	86
114	25.63	25.89	0.00	103.47	75	85
115	26.35	26.61	1264.46	753.87	72	83
116	25.58	26.00	490.36	231.65	72	85
117	25.10	25.22	0.00	76.34		
118	24.40	24.83	0.00	9.85		
119	23.58	24.61	0.00	4.92		
120	23.15	24.00	0.00	4.92		
121	22.50	23.39	0.00	4.92		
122	21.88	22.78	0.00	4.92		
123	21.85	22.67	0.00	2.46		
124	21.20	22.06	0.00	0.00		
125	20.88	21.78	0.00	2.46		
126	20.53	21.39	0.00	4.92		
127	20.28	21.33	0.00	4.92		
128	20.25	21.22	0.00	2.46		
129	20.48	21.11	0.00	63.93		
130	20.85	22.17	617.08	140.15		
131	22.98	22.50	1333.33	558.31		
132	23.45	23.28	1531.68	654.45		
133	27.43	27.28	1617.08	1284.73		
134	30.28	29.33	1236.91	1237.96		
135	31.85	31.50	1245.18	1629.83		
136	32.43	31.61	1220.39	1647.62		
137	33.00	32.83	1044.08	1494.93		
138	33.78	33.11	842.98	1290.94		

(Appendix A continued)

139	34.03	33.67	826.45	982.99
140	32.63	32.94	454.55	662.94
141	30.43	30.94	30.30	273.46
142	27.73	28.94	0.00	51.74
143	25.63	26.72	0.00	4.93
144	25.88	26.89	0.00	2.46
145	23.98	25.61	0.00	2.46
146	23.50	24.72	0.00	2.46
147	23.70	24.89	0.00	2.46
148	23.10	24.11	0.00	2.46
149	22.68	23.72	0.00	0.00
150	22.03	23.11	0.00	2.46
151	21.98	22.94	0.00	0.00
152	21.65	22.67	0.00	7.38
153	21.90	22.83	118.46	73.76
154	23.15	23.22	1005.51	324.66
155	25.25	24.83	1314.05	686.89
156	31.60	31.44	542.70	572.91
157	29.65	30.00	220.39	266.70
158	25.45	27.17	0.00	32.09
159	23.28	25.39	0.00	2.47
160	22.95	24.44	0.00	0.00
161	22.40	23.67	0.00	2.47
162	22.13	23.33	0.00	2.47
163	20.83	22.39	0.00	2.47
164	20.80	22.17	0.00	2.46
165	20.73	22.00	0.00	2.46
166	20.18	21.44	0.00	0.00
167	19.58	20.61	0.00	2.46
168	20.28	21.22	0.00	2.46
169	21.25	21.89	256.20	93.65
170	23.73	22.83	1033.06	377.19
171	27.20	26.17	1223.14	727.50
172	30.03	28.61	1366.39	989.58
173	32.25	30.67	743.80	1335.51
174	33.45	32.22	969.70	1502.87
175	34.58	33.06	991.74	1532.48
176	20.90	22.33	0.00	29.57
177	20.90	22.00	0.00	17.25
178	20.68	21.72	0.00	2.46
179	20.43	21.33	0.00	2.46
180	20.35	21.33	0.00	2.46
181	20.28	20.89	0.00	0.00
182	20.28	21.22	0.00	4.93
183	20.18	21.17	0.00	0.00
184	19.93	20.83	0.00	0.00
185	19.88	20.78	0.00	0.00
186	19.98	20.83	0.00	0.00
187	20.35	20.94	0.00	4.92

(Appendix A continued)

188	20.53	21.00	5.51	54.14
189	20.95	21.39	785.12	164.95
190	21.85	21.78	672.18	167.41
191	22.93	22.39	1269.97	433.45
192	23.15	22.94	1258.95	359.68
193	23.85	24.00	1804.41	953.42
194	26.35	24.39	1707.99	1118.48
195	26.58	24.83	1534.44	887.49
196	28.80	26.33	1732.78	1151.28
197	28.38	26.94	977.96	887.79
198	29.00	27.61	1341.60	1030.82
199	29.10	27.83	1002.75	816.27
200	27.10	26.50	719.01	350.06
201	24.23	24.33	0.00	56.69
202	22.40	23.11	0.00	4.92
203	21.53	22.11	0.00	7.38
204	20.98	21.83	0.00	7.38
205	20.28	21.39	0.00	4.92
206	20.08	20.94	0.00	7.38
207	19.73	20.50	0.00	0.00
208	19.38	20.44	0.00	2.46
209	19.85	20.33	0.00	7.38
210	19.15	19.83	0.00	0.00
211	19.15	20.22	0.00	4.92
212	19.33	20.00	719.01	76.22
213	20.58	20.67	1242.42	354.05
214	24.03	21.61	1391.18	711.51
215	27.28	24.94	1677.69	1063.93
216	29.78	27.17	1057.85	1323.42
217	31.03	28.39	1286.50	1540.29
218	30.65	29.61	1225.90	1619.69
219	31.13	29.56	1137.74	1552.61
220	30.53	29.83	1132.23	808.61
221	31.23	29.39	1038.57	1196.07
222	29.05	28.50	735.54	508.02
223	23.50	24.33	0.00	73.88
224	26.20	26.50	972.45	554.32
225	31.60	29.06	818.18	1339.77
226	29.88	30.06	895.32	808.07
227	28.88	29.72	336.09	593.93
228	28.95	29.33	418.73	473.18
229	24.60	25.50	0.00	49.26
230	23.20	24.44	0.00	2.46
231	21.98	22.83	0.00	2.46
232	22.05	23.44	0.00	2.46
233	22.23	22.44	0.00	2.46
234	21.98	23.67	0.00	2.46
235	21.33	22.11	0.00	0.00
236	21.25	22.39	0.00	0.00

(Appendix A continued)

237	21.55	23.22	0.00	2.46
238	21.23	22.11	0.00	2.46
239	20.50	21.89	0.00	2.46
240	21.90	22.39	0.00	41.81
241	21.70	22.33	501.38	150.03
242	25.93	25.39	1129.48	676.59
243	27.58	26.72	1234.16	800.14
244	29.55	28.11	1123.97	871.54
245	29.45	28.50	1234.16	780.45
246	29.13	28.44	826.45	620.63
247	28.30	28.39	462.81	470.24
248	28.50	28.06	1008.26	667.42
249	30.25	29.06	889.81	909.08
250	30.40	29.83	699.72	1004.82
251	29.75	29.83	468.32	657.57
252	28.13	28.61	247.93	379.27
253	24.30	25.06	0.00	27.10
254	23.23	24.50	0.00	2.46
255	22.70	23.94	0.00	2.46
256	22.83	24.00	0.00	4.92
257	22.58	23.72	0.00	4.92
258	22.83	23.94	0.00	2.46
259	22.65	23.61	0.00	2.46
260	22.58	23.33	0.00	4.92
261	22.60	23.22	0.00	7.38
262	22.10	23.22	0.00	4.92
263	22.45	23.22	0.00	4.92
264	22.23	22.78	24.79	81.19
265	24.75	23.94	831.96	398.57
266	27.18	26.33	1369.15	765.42
267	29.98	28.61	917.36	1087.83
268	32.35	30.33	1143.25	1383.63
269	33.85	31.94	942.15	1770.76
270	30.83	30.28	644.63	736.38
271	32.00	31.44	407.71	785.63
272	35.18	33.00	892.56	1672.24
273	24.58	25.83	330.58	246.28
274	26.48	28.11	650.14	477.78
275	27.38	28.33	347.11	270.91
276	26.78	27.22	597.80	369.30
277	25.33	26.06	0.00	32.00
278	24.30	25.17	0.00	7.38
279	23.60	24.17	0.00	2.46
280	23.78	24.39	0.00	2.46
281	23.15	23.72	0.00	4.92
282	22.35	23.06	0.00	2.46
283	21.95	22.67	0.00	4.92
284	21.65	22.44	0.00	4.92
285	22.08	22.89	0.00	2.46

(Appendix A continued)

286	22.10	23.11	0.00	0.00
287	22.13	23.11	0.00	4.92
288	22.60	23.39	0.00	78.71
289	25.43	24.61	1030.30	496.99
290	26.23	25.83	1093.66	494.69
291	28.80	26.89	1355.37	1088.19
292	28.80	27.50	1176.31	839.25

[1] Data recorded between 6:30 a.m to 9:30 p.m.
Note: Temperature and relative humidity inside cages were recorded with POLYCORDER® and DATAPOD 220® (Omnidata International, Logan, Utah) respectively, and sunlight (Photosyntheticaly action rate) inside cages was recorded with a Li-Cor Inc. Quantum Sensor, Lincoln, Nebraska. Meteorological data outside cages were obtained from a weather station (Courtesy Dr. S.D. Steel).

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