MODELING SEASONAL DEVELOPMENT OF SQUASH BUGS (HETEROPTERA: COREIDAE) AND SQUASH

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PREFACE

Research was conducted from 1986-1989 to quantify the damage potential and model the phenology of squash bug populations in summer squash for the development of a pest management program. Results of these investigations are presented in four separate and complete manuscripts to be submitted to scientific journals. Each chapter in this thesis was prepared following guidelines for manuscript preparation as established by the Entomological Society of America.

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CHAPTER 1

INTRODUCTION

Introduction

Today growers must be able to produce a quality crop to be competitive in the vegetable industry. However, it is difficult to produce vegetables profitably unless pests are controlled efficiently. The squash bug, <u>Anasa</u> <u>tristis</u> (De Geer), has long been considered a serious indigenous pest of cucurbits throughout much of the United States. Early literature on the biology of the bug is limited to investigations of life-history and regional control. Recent studies have examined developmental rate, reproductive bionomics, seasonal reproduction, reproductive diapause, field population dynamics and the effects of pesticides on the life stages of squash bug.

The primary reason for conducting this research was to quantify the interactions of the squash bug and squash, to develop a model of squash bug population dynamics, and the vegetative growth of squash. Integrated pest management is based upon a thorough understanding of the underlying ecologies of the host and pest species. There is already a considerable body of information pertaining to the demographics of the squash bug. However, in order for an integrated pest management program to be realized, greater knowledge of insect-plant interactions was needed. These studies examine how plant phenology is affected by insect feeding and how plant responses to feeding impact on insect mortality and fecundity.

Using basic biological and ecological data, a systems approach, utilizing detailed system conceptualization and iterative simulation model development, was employed in examining the population dynamics in this agro-ecosystem. This approach offers a structured format within which complexities of the squash bug-squash interactions can be considered, future needs identified, alternative solutions evaluated, and programs implemented.

CHAPTER 2

LITERATURE REVIEW

Literature Review

The squash bug attacks all plants in the cucurbit family (Cucurbitales: Cucurbitaceae). First described by De Geer (1773) under the name Cimax tristis, it has long been found wherever cucurbits are grown in North America (Elliot 1935, Beard 1940). Overwintered squash bugs attack plants soon after the insects emergence, which may vary from early spring in the south to late June in the north (Chittenden 1908). Squash bug prefers squash and pumpkin (Balduf 1950, Bonjour & Fargo 1989) however, it is also found on other cucurbit species such as cucumber and watermelon.

Adult squash bugs vary in size from 13.0 to 16.5 m in length and from 4.5 to 6.0 mm in width (Wadley 1920, Beard 1940). Balduf (1950) noted that on average the female was 1.39 mm longer than the male. He also noted that adult size diminished gradually as the food availability decreased.

The majority of information available on the squash bug deals with life history and bionomics (Chittenden 1908, Briton 1919, Wadley 1920, Beard 1935, 1940, Elliot 1935, Haseman 1937, Nechols 1987, Fargo et al. 1988, Palumbo 1989). They conclude that temperature is the primary influence on oviposition, bionomics, and developmental rate. Beard (1940) reported that mated females lived significantly longer when separated from males, 81 vs. 43 days. When squash bugs were maintained as mating pairs Al-Obaidi (1987) found that males lived ca. 538 degree days and females ca. 901 degree days, using 15.6°C as a threshold.

Generally, the reproductive activity of the squash bug is limited by weather conditions (temperature, humidity, and day length). Oviposition by <u>Anasa tristis</u> is thought to be favored by higher temperatures and decreases with the onset of cool weather (Beard 1935 & 1940, Fargo et al. 1988). Al-Obaidi (1987) reported that fecundity, egg viability, and egg development rate generally decreases with increasing temperatures. Eggs are usually deposited in regular rows which may be aggregated or dispersed. Egg masses are generally deposited on the lower surface of the squash leaves (Palumbo 1989), but may occur on the upper leaf surface, petioles and stems. Average egg mass size is given by various authors as: 15, 15.4, 16.9, 14.2, and 33.4 eggs per mass (Wadley 1920, Beard 1935, Elliot 1935, Beard 1940, Al-Obaidi 1987, respectively). Total egg production per female has been reported as 150 (Girault 1904), 356 (Wadley 1920), 409 (Beard 1940), and 442.3 eggs (Al-Obaidi 1987). Squash bugs lay an average of ten eggs per day (Wadley 1920, Beard 1940), Al-Obaidi (1987) reported that the number of eggs laid per day increased with increasing temperature.

The naturally occurring combination of photoperiod and thermoperiod is considered to be significant in squash bug reproductive diapause. Fargo et al. (1988) reported finding adult squash bugs as early as 30 April in Oklahoma. Nechols (1987) found adult squash bugs on 27 May in Kansas. This time difference in founding the population greatly influences the population dynamics of the squash bug. Fargo et al. (1988) found 2.5 - 3.0 generations per year in Oklahoma, while Nechols (1987) found 1.5 in Kansas. Fargo et al. (1988) reported that immigration of overwintering adults to fields was completed in ca. two weeks. In Kansas 17 percent of the adult females were found diapausing on 7 August and all were in reproductive diapause on 5 September. Reproductive diapause was defined as females not mating and containing only small under developed ovaries devoid of eggs. No physiological changes were noted in male squash bugs however, sexual behavior was repressed. The sex ratio of the squash bug was found to be 1:1 (Beard 1940) and 1.2:1 (Fargo et al. 1988) in Oklahoma.

Normal plant phenology can be radically altered by damage to tissues caused by herbivores or other events. The removal of leaves from a plant represents a loss of nutrients and a reduction in photosynthetic capacity. The effects of squash bug feeding on squash has received little attention to date. Fargo et al. (1988) recently investigated squash bug-squash interactions in Oklahoma. The study showed that squash plant development in terms of leaf area followed a sigmoid growth curve over time. Additionally, they found that leaf area was highly correlated with yield indicating that a reduction in the vegetative growth rate may lead to reduction in yield or failure to meet a market window.

Squash bug feeding appears to reduce yield by decreasing the photosynthetic capacity of the plant. Beard (1935) noted that seedling plants are especially vulnerable to damage by all stages of squash bug but that as the plants become larger they appear to be able to withstand some feeding pressure. Balduf (1950) attributed the plant response to large amounts of plant material being removed. Fargo et al. (1988) attributed the plant response to a reduction in photosynthetic capacity. It follows that a reduction in plant material would lead to a reduction in photosynthesis. What remains unclear is whether the squash bug is removing photosynthetic organs (eg. chloroplasts), the raw material for photosynthesis (eg. sap) or both.

Another question is why are some squash plants attacked while others remain relatively free of bugs. Benepal & Hall (1966) reported significant preferential feeding when plants were deficient in phosphorus, potassium, and sulfur, while plants deficient in nitrogen were least preferred. Squash bug density was found to increase with increasing total free amino acids, total free amino acids, total soluble nitrogen, particularly with the percentage of amide nitrogen in the leaves.

How these changes in plant chemistry effect the squash bug is unknown, however, changes in leaf quality have been shown to limit herbivores in terms of the timing of events in their life-cycle. Pullin (1986) reported that the grazing of _Urtica_ _dioica_ L. by _Aglais_ _urticae_ L. shifted the plants chemistry in favor of the insect, thereby allowing it to escape these limitations. The advantages of improved feeding efficiency, faster development, and possibly increased fecundity (Cook 1961, Hough & Pimentel 1978) on regrowth leaves may allow reproduction at times of the year when it would otherwise be unfavorable (Pullin 1986).

Squash bugs make many preliminary attempts at finding a feeding site before settling down on a definite area (Novero et al. 1962, Bonjour 1988). Once a site has been chosen feeding may last an hour or longer (Novero et al. 1962). Preferred feeding areas in mature plants appear to be the veins of leaves, whereas on seedlings the preferred areas are veins, petioles, and stems.

In order to study how the squash bug effects plant growth, a measure of growth is needed. The measurement must be done in a non-destructive manner so that the effects of feeding over time can be determined. Portmouth (1937) used leaf area in describing the effects of light on the growth of cucumber. Sugg et al. (1960) used leaf area in describing the physical properties of tobacco leaves. Menke (1974) simulated the soybean (*Glycine max* (L.) Merr.) and velvetbean caterpillar (*Anticarsia gemmatalis* Hubner) agroecosystem using leaf area estimates.

A method of estimating leaf area is required which is nondestructive, inexpensive, and fast. Leaf area has been calculated from linear measurements of leaves for some plants. Gregory (1921) described a method of estimating cucumber leaf area from measurements taken of the length and width of the leaf between various lateral points, together with the angles subtended at the base by lines joining these points. Fargo et al. (1986) estimated leaf area of squash (*Cucurbita pepo* var. *melopepo*, 'Hyrific') using the midrib length and tertiary lobe width. Using stepwise regression analysis they derived the equation:

$$\text{AREA} = -5.25 + 0.67(\text{ML} * \text{TD}) + 1.48(\text{ML}) + 0.74(\text{TD})$$

where ML is the midrib length and TD is the distance between the tertiary lobes. This equation was shown to provide an accurate and easily obtainable estimate of squash leaf area in the laboratory and field.

In a sense, any equation that is supposed to represent a living phenomenon can be called a model of that phenomenon. Regarding plant growth, many growth equations have been suggested to account for changes, observed over time, in a plant. In the simplest case, growth rate is assumed to be constant, $dx/dt = a$, where x is a measure of some plant organ. This leads to a straight line, $x = x_0 + at$. An example is the growth of the primary root of Zea, which grows in length linearly at ca. 2mm/hr during its early development (Erickson 1976).

Advancing this theory was Blackman's (1919) proposal of the compound interest law of plant growth. Assuming that the rate of growth in some measure x is proportional to its size, then $dx/dt = r * x$ or on integrating is $x = x_0e^{rt}$, x_0 being the size at time $t = 0$, e the base of natural logs, and r the relative growth rate. This type of exponential equation has been found to fit the early phases of weight and length growth in many plants (Erickson 1976, Hunt 1982).

Systems analysis has often been proposed as a mechanism for developing and implementing integrated pest management programs (Botrell 1979, Zadoks & Schein 1979, Allen & Bath 1980, Haynes et al. 1980, Getz & Gutierrez 1982, Onstad et al. 1984, Carruthers et al. 1986, Haith et al. 1987). These proposals are based upon two observations: 1) pest control is a complex process that requires an integrated approach and 2) systems analysis has been shown to be an effective means for managing large, complex problems. Combining these two technologies is a difficult task. Systems analysis is a highly structured, quantitative approach to decision making that relies on mathematical modeling and optimization techniques. Pest management, on the other hand, requires control of biological processes, which are often poorly defined and sparsely quantified. In spite of these obstacles, mathematical models have been developed for many aspects of insect control (Ruesink 1976, Kranz & Hau 1980).

These models seldom result in precise predictive tools for farm management. Their primary value has been in directing future research and conceptual evaluation. An understanding of system response to various man-induced and environmental stimuli is necessary to develop and implement pest management strategies in the field. Simulation of these conditions can provide insight into the system response at a fraction of the cost of large scale field evaluations. Such insight may be useful for management and for the development of hypotheses to be tested under field conditions.

Although there is considerable biological information available on the squash bug, only preliminary work has been done in simulating it's population dynamics (Fargo & Woodson 1989). Hughes & Gilbert (1968) and later Gilbert & Hughes

(1971) developed simulation models for aphids which concentrated on the inter-relationships between the aphid and it's natural enemies. The model used discrete time steps to simulate the continuous processes and integrated the effects of time and temperature by using heat unit accumulations. Carter (1985) described a simulation model of the grain aphid-wheat agro-ecosystem that included aphid population growth, effects of natural enemies, and crop development components. Wilkerson et al. (1986) developed a simulation model of the velvetbean caterpillar that extended the von Foerster (1959) model, in that an age structure was maintained within each developmental stage. Onstad et al. (1984) developed a model of the potato leafhopper-alfalfa interaction based solely on data from the literature. Their model provides an excellent example of how systems analysis may be used as a tool to understand complex interactions.

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CHAPTER 3

INTERACTIONS OF TEMPERATURE AND SQUASH BUG DENSITY (HETEROPTERA: COREIDAE) ON SEEDLING SQUASH GROWTH

ABSTRACT A laboratory study was conducted to quantify the relationship of adult squash bug, Anasa tristis (DeGeer), density to summer squash (Cucurbita pepo L. var Hyrific) plant damage. Five temperatures (20.0, 22.5, 25.0, 27.5, and 30.0°C), four adult squash bug densities (0, 2, 4, 6) and fifteen replicates were used in the study. Plant growth rates and ovulate flower productivity decreased with increasing squash bug density; staminate flower productivity was not significantly affected by squash bug density. Growth rates and, ovulate and staminate flower productivity increased with increasing temperatures. Squash bug mortality was highest at 25.0°C and lowest at 22.5°C. Female squash bug mortality was significantly higher when there were only two squash bugs per plant. Mean eggs per squash bug female increased with temperature and was unaffected by squash bug density.

KEY WORDS Insecta, Anasa tristis, Cucurbita pepo, insect-plant interactions

THE SQUASH BUG, _Anasa_ _tristis_ (DeGeer), has long been recognized as a serious indigenous pest of cucurbits throughout much of the United States (Britton 1919, Beard 1940, Gould 1943, Davidson & Lyon 1979). The effect of squash bug feeding on seedling squash has received only qualitative attention to date (Beard 1935, 1940, Britton 1919). Feeding injury is usually characterized by a general wilting of the leaves. Plant destruction may occur in the seedling stage as a result of relatively few feeding insects. Death of the plant is also possible later in the season when the insect population has reached higher levels (Fargo et al. 1988).

Insect feeding early in the development of cucurbits may have a significant impact on subsequent fruit production. Several variables can influence the amount of plant damage that may occur, eg., temperature, insect density, and the compensation ability of the plant. Brewer et al. (1987) illustrated the importance of early season defoliation by cucumber beetles in reducing the production of zucchini squash. Unlike cucumber beetles squash bugs reduce the growth rate of the plant by removing plant fluids.

This project was initiated to provide a quantitative description of the effects of temperature and insect density on the early growth of squash. The specific objectives were to determine how squash bug feeding influenced squash growth rate. We were also interested in the affects of insect density and ambient temperature on insect fecundity and mortality.

Materials and Methods

Insect culture. A laboratory colony of squash bugs was established using field collected fourth and fifth instar nymphs from Payne Co., Okla. during the summers of 1986 and 1987. Squash plants and fruit were provided for food and ovipositional material. Squash bugs were kept in plastic boxes 30 x 10 x 5 cm lined with paper toweling to absorb feces and excess moisture. Insects were maintained in a walk-in bio-chamber at 20.0-30.0°C and 50-70% RH with a photoperiod of 16:8 (L:D). Copulating adults were randomly selected for use in the study.

Plant culture. Yellow straight necked bush squash, Cucurbita pepo L. 'Hyrific', was grown in 5 cm square plastic pots containing a commercial soil-less growth media, PRO-MIX BX (Premier Brands Inc., New Rochelle, NY 10801). Plants were grown in a walk-in bio-chamber at 20.0-30.0°C and 50-70% RH with a photoperiod of 16:8 (L:D). Seedlings at the two true leaf stage were transplanted into 15 cm round plastic pots and seedlings were watered as needed.

Experimental Design and Procedure. A factorial arrangement of treatments in a split plot design was used in this study. The main plot was temperature and insect density the subplot. Each run in a chamber represented a group of 20 plants that were planted the same day, received equal amounts of water and were exposed to the same environmental conditions. The 20 plants were split into 4 treatment combinations with 5 plants. This procedure was repeated 3 times for each temperature giving a total of 15 replications for each treatment combination.

Five temperatures were used in the study: 20.0, 22.5, 25.0, 27.5, and 30.0°C, which correspond to average temperatures encountered by squash bugs during the growing season in Oklahoma. Four squash bug adult densities also were used in the study: 0, 2, 4, and 6 copulating adults (0 - 3 pairs) per plant. Adults were allowed to remain on the plants for 12 d. Treatments then consisted of 20 combinations of squash bug density (4) and temperature (5) replicated 15 times. These 20 treatments were chosen to bound observed squash bug field populations. Typical field densities of squash bugs seldom exceed two per plant early in the season however, individual plants often have more (Fargo et al. 1988).

Plants that attained ca. 400 cm^2 of leaf area were placed into 15 liter plastic containers with nylon-screen covers. Preliminary experiments revealed plant mortality was likely at higher insect densities with smaller plants. Plants for the study were selected for uniform height and leaf development.

Plants were infested with an appropriate number of copulating squash bugs from the laboratory colony for 12 d. Insect variables measured included mortality and the number of eggs laid. Dead or moribund squash bugs were replaced from the laboratory colony. Eggs were counted and removed every 48 h.

Plant variables monitored included leaf area and number of flower buds. Vegetative growth was determined by leaf area and reproductive growth by counts of ovulate and staminate flower buds > 1 cm long from stem to tip. Leaf area was estimated by the method of Fargo et al. (1986). Most insect and plant variables were monitored every 48 h. Flower bud counts were taken at the conclusion of each study to reduce handling damage to buds.

Data analysis. Analysis of variance was used for growth rate, flower production, number of eggs, and squash bug mortality. Means were separated using a protected Duncan's (1955) multiple range test. Standard statistical software (SAS Institute 1985) was used for these analyses.

Results

Vegetative growth. Estimates of mean daily growth rate increased significantly ($F = 29.12$; df = 4,10; $P = 0.0001$) with temperature for all insect densities. However, growth was less at 30.0°C than at 27.5°C when averaged over all insect densities. Mean daily growth rate estimates decreased significantly ($F = 77.22$; df = 3, 270; $P = 0.0001$) with increasing squash bug density when averaged over all temperatures. Plants infested with two, four and six squash bugs had ca. an 8, 17 or 28% reduction in mean growth rate compared with controls, respectively.

The influence of the interaction of squash bug density by temperature on mean daily growth rate ($F = 2.24$; df = 12, 270; $P = 0.0106$) was significant. Significant (Table 1) differences in plant growth rates were found between insect densities at all temperatures. The plants tolerated an infestation of 2 squash bugs for the duration of this study as evidenced by the lack of significant differences between these plants and the controls for temperatures $<$ 30.0°C. The mean growth rate was reduced when there were more than 2 squash bugs per plant. Plants at 20.0 and 30.0°C with 4 squash bugs had higher mean growth rates than those with 6 squash bugs. At other temperatures plants with 4 or 6 squash bugs were equally affected.

Reproductive growth. Significant differences in staminate flower productivity were found between temperatures (*F* = 16.76; df = 4, 10; *P* = 0.0002) averaged over all insect densities. However, the number of staminate flowers was less at 30.0°C than at 27.5°C, indicating a reduction in plant growth when temperatures exceeded 27.5°C (Table 2). The number of staminate flowers decreased significantly (*F* = 4.37; df = 3, 270; *P* = 0.0050) with increasing squash bug density only at 30.0°C (Table 2). This indicates that staminate flower productivity is more influenced by temperature than by squash bug density. The interaction of squash bug density by temperature (*F* = 1.73; df = 12, 270; *P* = 0.0607) was not significant.

Ovulate flower productivity increased significantly with temperature (*F* = 9.15; df = 4, 10; *P* = 0.0022) averaged over all insect densities. The mean number of ovulate flowers decreased significantly (*F* = 28.54; df = 3, 270; *P* = 0.0001) when insect density exceeded 2 per plant indicating that ovulate flower productivity was influenced more by squash bug density than by temperature. There were no significant differences found between 0 and 2 squash bugs at any temperature (Table 3). At 27.5°C there were no significant differences between squash bug densities for either staminate or ovulate flower production, indicating that 27.5°C is the optimal temperature for plant growth.

The trend in plant response above and below 27.5°C is decreasing ovulate flower productivity with increasing insect density.

Insect responses. Female mortality was highest at 25.0°C and the lowest at 22.5°C (Table 4). Plants with more than 2 squash bugs had significantly less female mortality than other insect densities (Table 5). The interaction of temperature and squash bug density on female mortality was not significant (*F* = 0.60; df = 2, 200; *P* = 0.7797). Highest male mortality also occurred at 25.0°C and the lowest at 22.5°C (Table 5). Male mortality was not significantly effected by squash bug density (*F* = 0.35; df = 2, 200; *P* = 0.7025) (Table 5). The interaction of temperature and squash bug density on male mortality was not significant (*F* = 0.89; df = 2, 200; *P* = 0.5297).

Significantly more eggs per female per day (Table 4) were found at 30.0°C than at 20.0°C. The average daily number of eggs laid per female (Table 5) was not significantly affected by squash bug density (*F* = 0.46; df = 2, 200; *P* = 0.6351). The interaction of temperature and squash bug density on oviposition was not significant (*F* = 1.43; df = 2, 200; *P* = 0.1843). The cumulative number of eggs per female was significantly affected by time (*F* = 24.97; df = 5, 1050; *P* = 0.0001) and its interaction with temperature and time (*F* = 3.30; df = 20, 1050; *P* = 0.0001).

The number of egg masses per female increased with time until 8 d after which there were no significant differences.

Discussion

Mean daily growth rate and ovulate flower productivity were both maximized at 27.5°C irrespective of squash bug density. Staminate flower productivity was not greatly affected by squash bug density but was influenced by temperature. Examination of plant growth rate at 25.0 and 30.0°C shows that the feeding rate of the squash bugs increased at 30.0°C while the growth rate of the plant was inhibited. The implication is that at sufficiently high temperatures and squash bug densities the squash plant will not be able to compensate for squash bug feeding.

Squash bug mortality was highest at 25.0°C indicating that squash bugs may be most active at this temperature. This agrees with Al-Obaidi (1987) who found squash bug longevity was shorter at 26.7°C than at 31.1°C or 23.3°C. The daily mean number of eggs per female generally increased with temperature. Since female mortality decreased with increasing squash bug density there may be a shift in plant chemistry that somehow favors the squash bug under increased density. All other insect variables were not affected by squash bug density.

Normal plant phenology can be radically altered by damage to tissues caused by the squash bug. The removal of assimilates from a plant represents a loss of nutrients and concomitant reduction in growth rate. Squash bug feeding appears to reduce yield by decreasing the photosynthetic capacity of the plant. Beard (1935) noted that seedling plants are especially vulnerable to damage by all stages of squash bug, but as plants become larger they appear to be able to withstand some feeding pressure. Balduf (1950) attributed the plant damage to removal of large amounts of plant material. Fargo et al. (1988) ascribed the plant damage to a reduction in photosynthetic capacity. It follows that a reduction in plant material would lead to a reduction in photosynthesis. These authors determined that leaf area was correlated with yield, indicating that a reduction in leaf area may lead to a reduction in yield or failure to meet a market window due to slower fruit production.

This study has shown that early season control of the squash bug is imperative due to the reduction in plant growth rate and number of ovulate flowers. Reduced plant vigor can contribute to yield loss. Vegetable growers often attempt to produce an early crop to market at higher early season prices. Plants stressed early in their development may result in the loss of early season yield, even though the reduction in total yield may not be appreciable.

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Table 1. Mean daily growth rates by temperature and squash bug density. Units are cm^2/d.

Squash Bugs	Temperature				
	20.0°	22.5°	25.0°	27.5°	30.0°
0	55.61Ca	58.89Ca	83.83Ba	104.33Aa	81.57Ba
2	52.10Da	54.27Da	79.78Ba	98.10Aa	66.61Cb
4	46.56Db	44.73Db	75.10Bab	86.76Ab	64.43Cb
6	41.09Cc	40.75Cb	67.07Bb	80.35Ab	48.65Cc

Means within rows followed by the same uppercase letter are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

Means within columns followed by the same lowercase letter are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

Table 2. Mean staminate flower productivity by temperature and squash bug density.

Squash Bugs	Temperature				
	20.0°	22.5°	25.0°	27.5°	30.0°
0	16.47Ca	17.67Ca	25.47Ba	31.33Aa	25.87Ba
2	17.07Da	17.27Da	25.40Ba	31.27Aa	22.60Cbc
4	16.20Ca	17.27Ca	25.33Ba	29.20Aa	23.87Bab
6	16.33Da	17.40Da	24.87Ba	28.73Aa	20.33Cc

Means within rows followed by the same uppercase letter are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

Means within columns followed by the same lowercase letter are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

Table 3. Mean ovulate flower productivity by temperature and squash bug density.

Squash Bugs	Temperature				
	20.0°	22.5°	25.0°	27.5°	30.0°
0	4.67Aa	4.73Aa	4.20Aab	4.33Aa	4.73Aa
2	3.93Aa	4.13Aa	4.60Aa	4.80Aa	4.47Aab
4	2.53Cb	2.87BCb	4.60Aa	4.73Aa	3.53Bb
6	1.87Cb	2.27Cb	3.53ABb	4.20Aa	2.53BCc

Means within rows followed by the same uppercase letter are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

Means within columns followed by the same lowercase letter are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

Table 4. Mean daily insect response by temperature.

Temperature	Mortality		
	Female	Male	Eggs
20.0°	0.096ab	0.031cb	3.890b
22.5°	0.067b	0.015c	5.598ab
25.0°	0.129a	0.098a	10.862ab
27.5°	0.091ab	0.067ab	9.355ab
30.0°	0.095ab	0.052abc	13.209a

Means within columns followed by the same letter are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

Table 5. Mean daily insect response by squash bug density.

Squash	Mortality		
bugs	Female	Male	Eggs
2	0.120a	0.058a	9.036a
4	0.084b	0.048a	8.346a
6	0.082b	0.053a	8.367a

Means within columns followed by the same letter are not significantly different (P = 0.05; Duncan's [1955] multiple range test).

CHAPTER 4

DEVELOPMENT OF SQUASH SEEDLINGS FOLLOWING SQUASH BUG (HETEROPTERA: CORIEDAE) DAMAGE

ABSTRACT Influence of feeding by adult squash bug, Anasa tristis (De Geer), on squash, Cucurbita pepo var. melopepo L. 'Hyrific', was investigated. When two or more squash bugs were placed on plants at the two true leaf stage for 200 degree days, seedling mortality was the primary cause of yield reduction. Plants infested at the two true leaf stage produced lower yields than plants infested at the 6 true leaf stage. Plants infested at the four or six true leaf stages were unable to compensate for growth delays caused by seedling damage.

THE SQUASH BUG, Anasa tristis (De Geer), has long been recognized as a serious indigenous pest of cucurbits in the United States east of the Rocky Mountains. Although squash bugs will feed on most cucurbits (Bonjour & Fargo 1989), it prefers new world varieties (Beard 1935). Eggs are typically laid on the abaxial leaf surface, with nymphs developing on the leaves and petioles and adults feeding on foliage, stems, and petioles (Beard 1940). Plantings of cucurbits have been devastated by squash bugs within a few days after emergence of seedlings (Fargo et al. 1988). Adult feeding may kill young seedlings, and stunt or kill older plants. Poor stand development is the most serious damage incurred by squash bug feeding. This study investigated the relationship between seedling age of squash and adult squash bug feeding at several insect densities. An understanding of the ability of squash to tolerate and compensate for seedling damage is necessary to manage squash bug populations effectively.

Materials and Methods

Experiments were conducted during the summer of 1988 and 1989 at the Oklahoma State University Landscape and Horticulture Nursery Farm near Stillwater, Payne Co., Okla. 'Hyrific' squash (Ferry-Morse Seed Co. Fulton, KY), a straightnecked yellow bush cultivar, were transplanted at the cotyledon stage on two beds 1 m apart on 26 July and 10 August 1988 and 28 May and 12 June 1989. Beds were prepared using standard cultivation practices. Drip irrigation was used as needed throughout the growing season. After transplanting, plants were covered with screened cages made from a plastic container (15 l). The centers of the lids were cut out and replaced with fiber glass fabric (1 mm mesh) to permit aeration and exposure to the sun. The fabric was secured to the lids by using hot glue. Bottoms of the containers were removed and the containers secured to the ground using 38 cm steel stakes.

The experimental design in 1988 was a randomized complete block arranged in a three by four factorial. Copulating pairs of squash bugs were confined on individual plants at three levels of maturity: second leaf, fourth leaf, sixth leaf. Each stage refers to the oldest fully expanded true leaf. The experimental design in 1989 was a randomized complete block arranged in a two by four factorial. The two leaf stage plants suffered high plant mortality in 1988 and were not included in the 1989 study. When plants reached the appropriate maturity (2, 4, or 6 leaf stage), four insect densities (0, 2, 4, and 6 adult squash bugs) were released onto individual plants for a duration of ca. 200 degree days. Each treatment combination was replicated 10 times each year.

Adult insects were field collected as needed from squash in the vicinity of the study. They were temporarily maintained in the laboratory on squash foliage and released within 24 hrs. Plants and squash bugs were examined every 48 h for dead or moribund bugs which were replaced with one of the same sex collected from squash in the vicinity. At the end of the feeding period all bugs and cages were removed. A systemic insecticide (carbofuran (15 % AI) at a rate of 6.6 kgs/ha) was then applied to prevent further plant injury by resident insect populations.

Plant variables measured were mortality, leaf area at the beginning and end of infestation and 28 d after the first fruit, staminate and ovulate flower production, and fruit counts as the season progressed. Leaf area was measured by the method of Fargo et al. (1986). Plant mortality data were taken at the end of the infestation period. Counts of flowers and mature fruit were made every 48 h after first occurrence. Harvestable fruit (fruit > 15 cm long) were picked every 48 h for 28 d.

An analysis of variance was used to compare plant mortality and vegetative and reproductive growth among treatments. Contrasts constructed within the analysis of variance (Steel & Torrie 1980) were used to study the trends across insect density for each plant stage (interaction) and paired comparisons of means for separate plant and insect treatment effects (main effects). Regression analysis using a common intercept model (Neter et al. 1985) was used to determine if linear trends across density differed between pairs of plant stages.

Results

Infestation at the two-leaf stage caused higher plant mortality than at the four- or six-leaf stage. Within each plant stage mortality tended to increase with insect density. At the two-leaf stage in 1988, mortality of 50, 100, and 100% occurred at the 2-, 4- and 6-insect densities, respectively. In 1988 the four-leaf stage plants suffered mortality of 40, 80, and 90% at the 2-, 4-, and 6-insect densities, respectively. At the four-leaf stage in 1989, mortality of 30, 60, and 70% occurred at the 2-,4-, and 6-insect densities, respectively. In 1988, the six-leaf stage plants had mortality of 20, 20, and 30% for the 2-, 4-, and 6-insect densities, respectively. At the six-leaf stage in 1989, mortality of 20 and 30% occurred at the 4- and 6-insect densities, respectively. No mortality occurred at the 2-insect density in 1989.

The analysis of leaf area after 200 degree days of infestation revealed a similar pattern (Fig. 1). Response differences between treatment combinations in both years were detected. Main-effect paired comparisons of plant stages were the greatest contributors to the treatment variability. The total plant insect interaction was not significant for either year (*F* = 2.165 and 1.274; df = 6, 107 and 3, 71; *P* = 0.052 and = 0.290 for 1988 and 1989, respectively). A negative linear trend in leaf area was evident as the insect densities increased within all plant infestation periods (Fig. 1). In 1988, the slopes for each plant stage differed, with a greater reduction in leaf area as insect density increased at the two-leaf stage compared with the four-leaf stage (*F* = 12.611; df = 1, 107; *P* < 0.001) and a greater reduction at the four-leaf stage compared with the six-leaf stage (*F* = 65.469; df = 1, 107; *P* < 0.001). In 1989, the same trend of progressively decreasing slopes occurred, with a greater reduction in leaf area as insect density increased at the four-leaf stage compared with the six- leaf stage (*F* = 36.151; df = 1, 71; *P* < 0.001).

Analysis of leaf area at the end of the study showed that squash bug damage to seedling plants varied by the interaction of the age of the seedlings at infestation and the number of bugs per plant. There was a greater reduction in foliar productivity as bug density increased at the younger plant stages (Fig. 2). A negative linear trend in foliage production was evident as insect density increased for two- and four-leaf stage plants; however, the slopes were not significantly different (*F* = 1.474; df = 1, 107; *P* = 0.227). Plants infested at the six-leaf plant stage showed a trend of reduced foliage production in 1989, but not in 1988. A smaller decrease in foliage productivity was detected at the six-leaf stage compared with the four-leaf stage in both years (*F* = 7.336 and 20.753; df = 1, 107 and 1, 71; *P* < 0.001 for 1988 and 1989, respectively). Treatment differences were significant in both years (*F* = 8.674 and 7.627; df = 11, 107 and 7, 71; *P* < 0.001 for 1988 and 1989, respectively). These differences were largely a result of reduced foliage production of plants infested at the two- and four-leaf stage.

Analysis of reproductive growth as measured by staminate flower production revealed significant differences between treatments in each year (*F* = 8.836 and 7.247; df = 11, 107 and 7, 71; *P* < 0.001 for 1988 and 1989, respectively). The trend in mean staminate flower production decreased as the number of insects increased for plants infested at the two-, four- and six-leaf stage (Fig. 3). Comparing rates of decline of flower production between plant stages in both years, a greater decrease in flower productivity by density was detected at the four-leaf stage compared with the six-leaf stage (*F* = 3.602 and 10.198; df = 1, 107 and 1, 71; *P* = 0.029 and < 0.001 for 1988 and 1989, respectively). In 1988, plants infested at the six-leaf stage displayed no significant linear trend in flower production across insect density.

Analysis of reproductive growth as measured by ovulate flower production revealed significant differences between treatments in both years (*F* = 8.282 and 8.386; df = 11, 107 and 7, 71; $P < 0.001$ for 1988 and 1989, respectively). Mean ovulate flower production decreased as the number of insects increased for both plant stages in 1989 (Fig. 4). In 1988, plants infested at the six-leaf stage displayed no significant linear trend in flower production across insect density. Comparing rates of decline of flower production between plant stages in both years, a greater decrease in flower productivity by density was detected at the four-leaf stage compared with the six-leaf stage (*F* = 7.817 and 10.416; df = 1, 107 and 1, 71; *P* = 0.006 and 0.002 for 1988 and 1989, respectively). A negative linear trend in ovulate flower production as insect density increased was evident for two- and four-leaf stage plants, however the slopes were not significantly different (*F* = 2.861; df = 1, 107; *P* = 0.094).

The analysis of fruit production revealed treatment differences in both years (*F* = 10.130 and 8.543; df = 11, 107 and 7, 71; $P < 0.001$ for 1988 and 1989, respectively). Fruit production decreased as the number of insects increased for plants infested at the two-, four- and six-leaf stage but more so at the earlier plant stages (Fig. 5). Comparing rates of decline of fruit production between plant stages in both years, a greater decrease in fruit productivity by density was detected at the four-leaf stage compared with the six-leaf stage (*F* = 6.794 and 16.936; df = 1, 107 and 1, 71; *P* = 0.010 and < 0.001 for 1988 and 1989, respectively). In 1988, plants infested at the six-leaf stage displayed no significant linear trend in fruit production across insect density.

Discussion

Seedling mortality was a function of both seedling age and density of the squash bug infestation. Our study provides evidence that as seedlings mature their susceptibility to squash bug feeding decreases. This confirms earlier work by Beard (1935) and Eichmann (1945). Brewer et al. (1987) found squash had a decreasing susceptibility to cucumber beetle damage as seedlings matured. This increased tolerance may be a function of the dilution of injury per bug as the foliar surface area increases. Stand reduction due to adult feeding on seedlings should be of primary concern in management of this pest. Infestations at the two- and four-leaf stages may lead to poor stand development. At the two-and four-leaf stages, yield reductions were caused primarily by stand loss. The ability of squash bugs to destroy a planting within a few days after emergence can not be over-stressed, as indicated by the severity of stand reduction at the two-leaf plant stage.

Reductions in plant vigor can also contribute to yield loss. Vegetable producers often attempt to produce an early crop to market at higher prices. Plants stressed in their development can reduce early season yield, even though the reduction in total yield averaged through the season may not be noticeable. Palumbo (1990) found that in mature plants yield losses were directly related to the duration and magnitude of the squash bug infestation. In our study, plants that survived the infestation period had both reduced vegetative growth and decreased flower production. In 1989, plots were planted ca. 2 mo earlier and yield reductions were not as severe as 1988. This difference may be due to the more favorable abiotic factors for plant growth found in May-June compared with July-August in Oklahoma. Plants infested at the later growth stages with low bug densities were able to compensate for growth delays by the end of the study.

Seedling damage by the squash bug indicates that to prevent stand reduction, the greatest concern should be directed toward protection of the crop as it emerges from the soil until the first six true leaves are formed. Preventive or critically timed pesticide applications are necessary when the seedlings emerge if squash bugs are active. Squash bugs typically become active in the early spring when cultivated cucurbits are emerging; hence, frequent sampling to detect the first arrival of the squash bugs is required.

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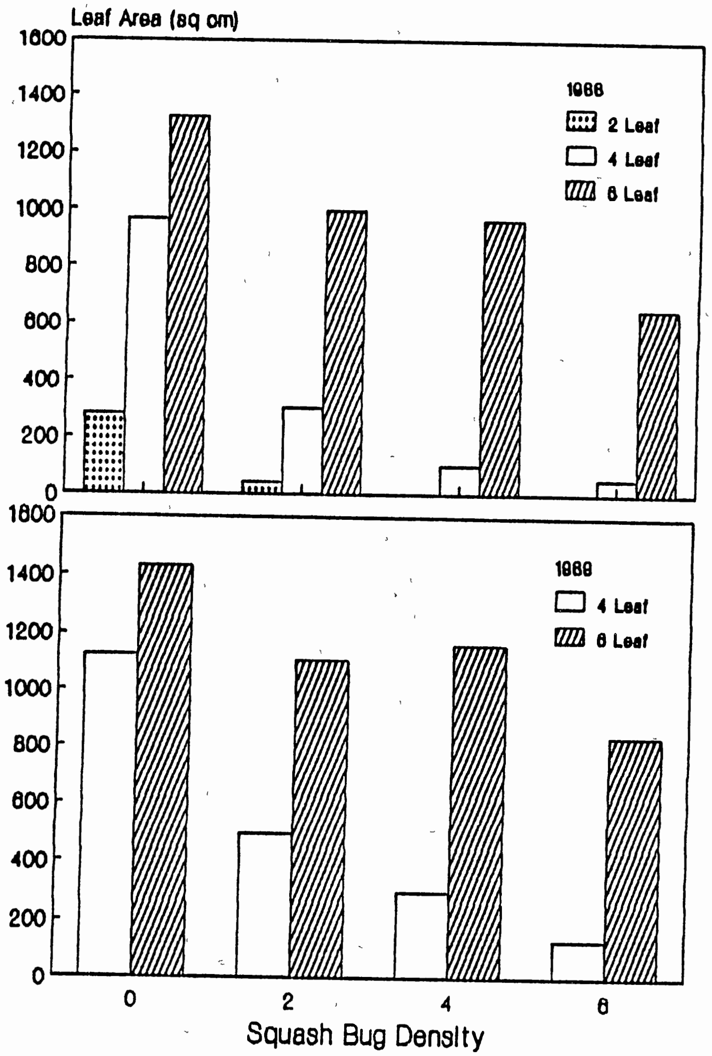

Figure 1. Leaf area of three stages of squash seedlings after 200 degree days of feeding by squash bugs.

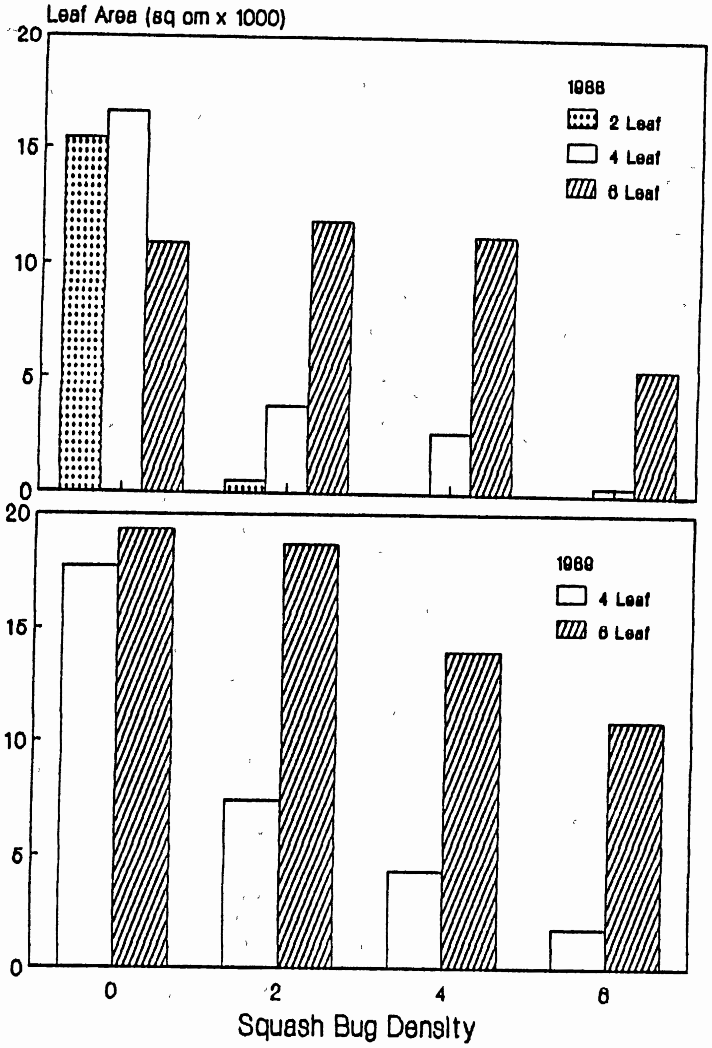

Figure 2. Leaf area of three stages of squash seedlings at the end of harvest after 200 degree days feeding period by squash bugs.

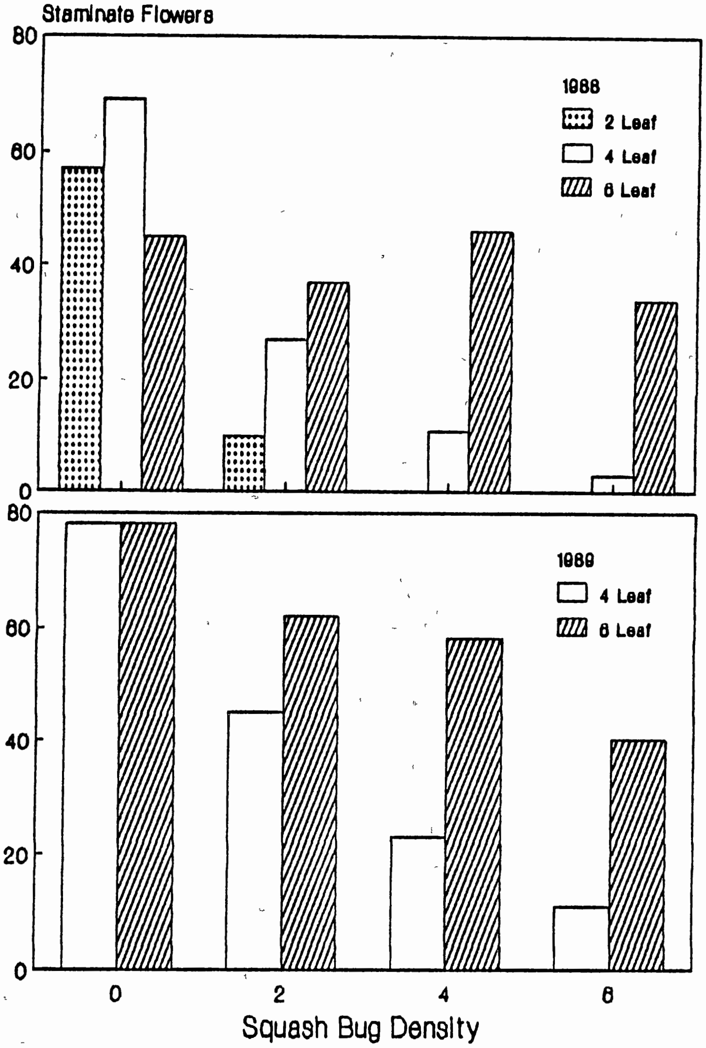

Figure 3. Staminate flower productivity of plants after 200 degree days of feeding by squash bugs.

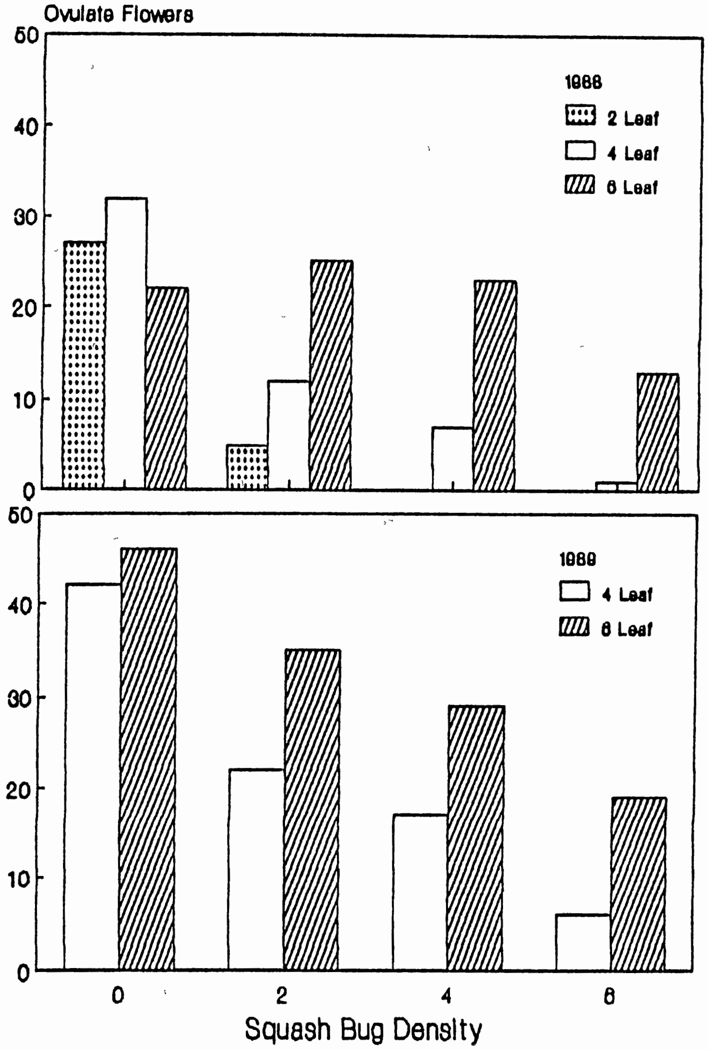

Figure 4. Ovulate flower productivity of plants after 200 degree days of feeding by squash bugs.

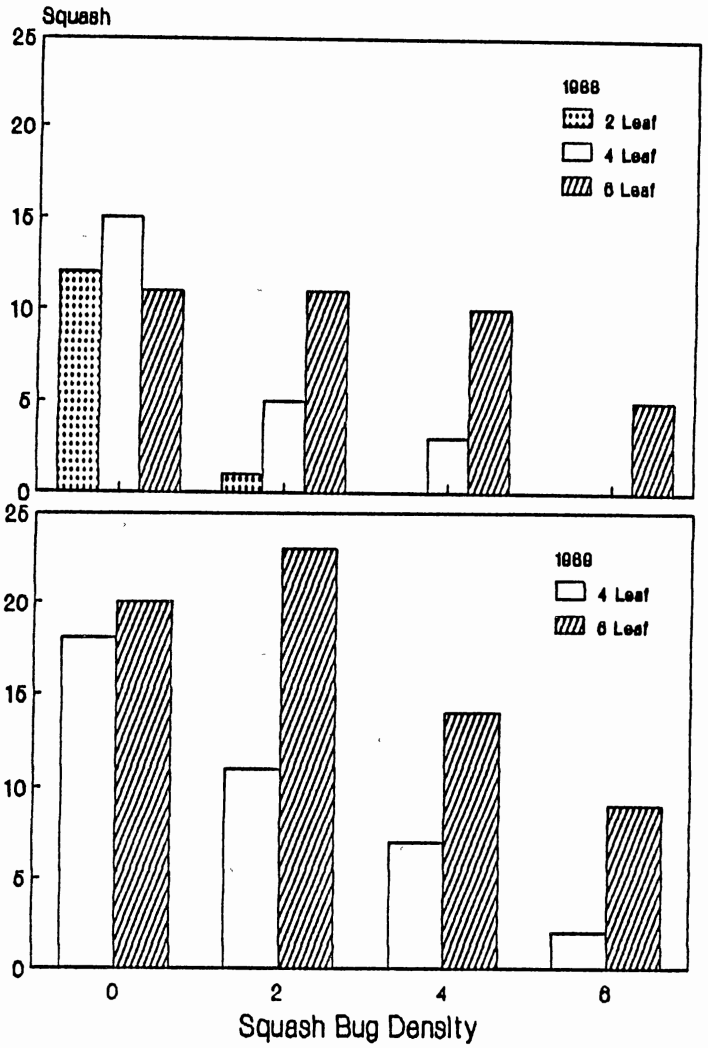

Figure 5. Fruit productivity during a 1-mo period after 200 degree days of feeding by squash bugs.

CHAPTER 5

MODELING SQUASH BUG (HETEROPTERA: COREIDAE) POPULATIONS IN CUCURBITS

ABSTRACT A stochastic model of squash bug, _Anasa tristis_ (De Geer), population dynamics was developed and used to investigate the functional response parameters of this insect. The processes of oviposition, development, and stage specific mortality are modeled at the individual level (the level at which they operate). Inter-individual variation in physiology is easily represented and the results of such variation are explicit in the model output.

Information from the literature as well as laboratory and field data were used to set the parameters of the model. Simulated populations were compared with 2 years of field population data. Using the first non-zero sampling date as a start time for the model, adequate fits (within ± 2 SE of field means) were obtained for both years. Effects of host type on developmental rate and mortality were modeled using watermelon, pumpkin, and squash. Population growth rates were faster for insects developing on pumpkin than squash. Populations developing on either pumpkin or squash, new world cucurbits, had faster growth rates when compared with those on watermelon, an old world cucurbit.

KEY WORDS: Insecta, _Anasa tristis_, simulation, population dynamics

THE SQUASH BUG, Anasa tristis (De Geer), has long been recognized as the most important pest of cucurbits in the United States east of the Rocky Mountains (Beard 1935, Fargo et al. 1988, Bonjour & Fargo 1989). High populations have been observed to completely destroy fields when left unchecked (Beard 1935, Eichmann 1945, Palumbo 1989). Because squash bug populations can vary markedly from year to year, the species is an ideal candidate for directed management (Palumbo 1990) where the aim is to maintain pest densities below economically important levels. In this approach to pest management, systems modeling is used to evaluate compatibility of control measures and to predict their consequences. Population models developed for this purpose must take into account the effects of suppressive tactics on pests.

Over the past ten years much ecological information has been collected for the squash bug (Al-Obaidi 1987, Bonjour & Fargo 1989, Fargo et al. 1988, Fargo & Bonjour 1988, Fielding 1988, Fielding & Ruesink 1988, Nechols 1987). There has been one preliminary attempt to model the population dynamics of the squash bug (Fargo & Woodson 1989). That model was not intended for pest management and did not include the detail necessary for studying insect control alternatives.

The model described in this paper is stochastic. The input independent values, where appropriate (e.g. the time that an insect spends in a specific instar) are described in terms of probability distributions. Each time the model is run, the specific outputs from the model will have different numerical values even though the input probability distributions are unchanged. When a large number of simulations from the model are examined, the results themselves will form probability distributions. The states of nature describing a real agroecosystem are random variates (probabilistic). A realistic model prescribes a stochastic approach in order to simulate not only the relations observed in nature but their variances, which are often large.

The purpose of this paper is to describe a squash bug population dynamics model developed for use in a management framework. This model will be one component of a larger system model that integrates crop growth, and economic models.

Materials and Methods

First, a theoretical model of squash bug population dynamics was developed that included the processes of development, oviposition, and mortality. The parameters of the model were set from information available in the literature and the computer simulation model was developed. Model parameters for which there was no information available were estimated.

Simulated squash bug populations were compared with those observed by Fargo et al. (1988) at the Oklahoma State University Horticultural Research Station near Perkins, Payne County, Okla. in a field of 'Hyrific' summer squash planted 15 May 1984 and 1985 to validate the ability of the model to simulate squash bug population dynamics. Simulation model data reported herein is the mean of 20 runs for each set of simulation conditions. Random number streams required for the model were reseeded before each run. Simulations were made using the first nonzero adult count from data collected in 1984 and 1985 to initialize the populations.

Following model validation, a number of simulations were made in which the effects of the host on simulated adult populations were investigated. Development and mortality parameters used in these simulations are given in Bonjour & Fargo (1989).

The simulation model was programmed in SLAM II (Pritsker & Associates, West Lafayette, Ind.). A copy of the source code for the base model is listed in the appendix.

Model Description. Squash bug populations are divided into ten stages: eggs, five instars, males, premated females, preovipositional females and ovipositing females. A stochastic network model of squash bug population dynamics was developed that included processes of development, oviposition, time since last oviposition, time since mating and mortality. Egg and nymphal stage durations were obtained from Fargo & Bonjour (1988). Reproductive bionomics and adult survivorship were obtained from Al-Obaidi (1987). Egg mass parameters were estimated from laboratory studies (WDW data). Stage durations and mortality for squash, watermelon and pumpkin were obtained from Bonjour & Fargo (1989).

These simulations model the development of the insect population per plant using a 10 degree day time step. Time was measured in degree days using 15.6°C as a reference temperature (Fargo & Bonjour 1988). Figures 1, 2, and 3 are the SLAM network model of the insect dynamics. The model is initiated by allowing one overwintered, mated female to arrive on the plant. Her longevity is drawn from a normal distribution ($\mu = 394.8$, $\sigma = 94.0$).

Oviposition. Upon arrival the female may or may not lay an egg mass; 63% of the time she will go on to lay an egg mass. If she does lay an egg mass the number of eggs in that egg mass will be drawn from a triangular distribution

(Low = 1.0, Mode = 13.0, High = 37.0). At this point, the age of the female is checked at G1, a goon node. If she has reached her assigned longevity she is routed to a collect node, FDTH, before being terminated. If she is not terminated, she is routed back along Activity 9 to G1, a goon node, to determine if she lays another egg mass. The delay time between egg masses is drawn from a normal distribution (μ = 14.1, σ = 13.6). In the event she does not lay an egg mass, her age is checked and she is routed back to G1 along Activity 9 before it is determined if she will lay an egg mass.

Development. The egg masses are routed along Activity 6 to MASS, an unbatch node, where the individual eggs are separated from the egg mass. Each of these eggs are then each assigned the current simulation time, at the assignment node EGGS (Fig. 2), as their time of oviposition. Next, 97% of the eggs are routed along Activity 12 to N1, a goon node, with the other nonviable 3% being sent along Activity 11 to EDTH, a collect node, before termination. The length of time spent in Activity 12 is the time required for the eggs to hatch, and is drawn from a normal distribution (μ = 97.4, σ = 3.6). At the end of Activity 12 the individual eggs encounter N1, a goon node, where 5% are routed to N1D, a collect node before being terminated. The other 95% of the first instars are sent along Activity 13 which corresponds to the duration of the first instar drawn from a normal distribution ($\mu = 29.4$, $\sigma = 1.1$). At the end of Activity 13, the first instar nymphs encounter N2, a goon node, where 11% are routed along Activity 16 to N2D, a collect node, before termination. The remaining second instar nymphs continue along Activity 15, which has a duration drawn from a normal distribution ($\mu = 62.6$, $\sigma = 3.1$), the time spent in the second instar. At N3, another goon node, 7% of the third instar nymphs are route along Activity 18 to N3D, a collect node before termination. The other 93% are routed along Activity 17, whose duration is drawn from a normal distribution ($\mu = 42.0$, $\sigma = 2.4$), the time spent in the third instar. At N4 (Fig. 3), a goon node, 5% of the nymphs are routed along Activity 20 to N4D, a collect node, before termination. The other 95% are routed along Activity 19, which has a duration drawn from a normal distribution ($\mu = 53.0$, $\sigma = 2.7$), the time spent in the fourth instar. At N5, a goon node, 16% of the nymphs are routed along Activity 22 to N5D, a collect node, before termination. The other 84% are routed along Activity 21, which has a duration drawn from a normal distribution ($\mu = 92.3$, $\sigma = 9.9$), the time spent in the fifth instar.

Adults. The new adults are routed through SEX, a collect node, to determine their total nymphal development time. Here 50% of the adults are assumed to be males and follow Activity 24. The duration of Activity 24 is taken from a normal distribution (μ = 1803.0 ,σ = 783.0), and represents the remainder of the male's lifespan. The remaining 50% are routed along Activity 23 and assumed to be females. The duration of Activity 23 is drawn from a normal distribution (μ = 75.8, σ = 18.9), and corresponds to premating time. At the end of Activity 23 the unmated females encounter PREM, a goon node, and proceed along Activity 25 which represents the preovipositional period that occurs after first mating. The duration is taken from a normal distribution (μ = 41.6, σ = 21.9). When the females reach OVIP, an assignment node, they are given an adult longevity time taken from a normal distribution (μ = 902.0 , σ = 318.0). The adults are then directed to G1 (Fig. 1), a goon node, to enter the fecundity cycle.

The population of live and dead insects is continuously monitored. The number of insects in any activity at any time may be collected when needed. For example, the number of viable eggs is given by the number currently in Activity 12, while statistics are collected on nonviable eggs by the collect node, EDTH. Immature development for each instar is collected in an analogous manner. The collect nodes allow the user to collect time of death, total deaths, or time between deaths and will automatically compute statistics and construct histograms if desired, which greatly simplifies the verification process.

Results and Discussion

Validation. Insect population numbers for the Perkins 1984 experiment were much lower than the numbers for the 1985 experiment. Simulated values consistently overestimated the numbers for immatures during the buildup of the population. The model estimated the number of eggs in 1984 (Fig. 4.) quite well; most of the simulated values lie within ± 2 SE (standard error of the mean) of the field means over the season. First instars (Fig. 5) were overestimated during the first 150 degree days but were within ± 2 SE thereafter. The second and third instars (Figs. 6 and 7) were overestimated between degree days 120 and 300 but otherwise followed the observed data well. Fourth and fifth instars (Figs. 8 and 9) were overestimated by the model between degree days 250 and 400 and 300 and 400, respectively. Adult males (Fig. 10) were within ± 2 SE of the field means during the first 450 degree days. Simulated adult female numbers (Fig. 11) matched very well for the first 450 degree days and then overestimated the number present.

In 1985, simulated and field sample populations overall matched well for immatures and adults during the buildup of the population. The model underestimated the number of eggs in 1985 (Fig. 12) during the mid and late season but was adequate during the early season. First instars (Fig. 13) were overestimated during the first 200 degree days but were within ± 2 SE of the field means thereafter. The second instars (Fig. 14) were overestimated between degree days 180 and 300 but otherwise followed the observed data well. Third instars (Fig. 15) were overestimated between degree days 180 and 300 but later were within ± 2 SE of the observed field means. Fourth instars (Fig. 16) followed the field means well and were only overestimated by the model during the initial build up, between degree days 220 and 320. Fifth instars (Fig. 17) were estimated very well with simulated numbers being within ± 2 SE of the observed field means. Adult males (Fig. 18) were within ± 2 SE of those reported during the first 550 degree days and overestimated thereafter. Adult females (Fig. 19) matched very well over the entire season.

Sensitivity Analysis. In order to evaluate the importance of a particular process within the model, survivorship, fecundity, sex ratio, and stage duration parameters were fluctuated by ± 10 and 20 %. Changes in survivorship were found to have the greatest impact on population change. Decreasing survivorship by 10 and 20 percent reduced the cumulative total number of bugs by 32.8

and 55.3 percent after 600 degree days, respectively. Conversely, increasing survivorship by 10 and 20 percent increased the cumulative total number of bugs by 38.5 and 87.2 percent, respectively. The implication is that the squash bug population may recover quickly from population crashes due to external factors such as pesticide applications.

Increasing and decreasing the total number of eggs per mass impacted squash bug population growth rates. Increasing oviposition by 10 and 20 percent increased the cumulative total number of bugs by 14.2 and 25.4 percent, respectively. Decreasing the ovipositional rate by 10 and 20 percent led to an 11.3 and 23.7 percent reduction in the cumulative total number of bugs.

The effects of changing the sex ratio and stage durations were linear. Sex ratio variation in the form of increasing and decreasing the number of females has a significant impact on squash bug population growth rates. Increasing the number of females by 10 and 20 percent increased the cumulative total number of bugs by 9.5 and 21.6 percent, respectively. Decreasing the number of females by 10 and 20 percent led to an 8.9 and 19.5 percent reduction in the cumulative total number of bugs. Changes in stage duration were found to have an impact on the degree of population change. Decreasing the stage durations by 10 and 20 percent increased the cumulative total number of bugs by 8.4 and 15.3 percent, respectively. Conversely, increasing the stage duration by 10 and 20 percent decreased the cumulative total number of bugs by 8.7 and 17.3 percent, respectively.

Host Effects. Bonjour & Fargo (1989) found significant differences in the mortality of squash bug nymphs reared on different cucurbit hosts. There were also differences in the mean developmental time, though these were not as distinct as those for mortality. How these two processes interact to change the population dynamics over the season is a problem well suited to simulation modeling.

The rate increase for eggs was greatest for insects using the parameters for pumpkin (Fig. 20). During the first 450 degree days the differences between the number of eggs on the different hosts was insignificant; thereafter, populations feeding on pumpkin and squash rapidly increased the number of eggs laid. Pumpkin and squash had similar patterns of increase in the number of eggs up to degree day 550 when the number of eggs on pumpkin increased above that of squash and remained higher through the rest of the simulation.

There was a similar pattern observed in the adults. Males (Fig. 21) on squash and pumpkin began to increase at an exponential rate about degree day 375, with those on pumpkin increasing faster than squash. Males on watermelon did not begin to increase until well after degree day 500. The difference between squash and pumpkin was more pronounced for females than males (Fig 22). The number of females on pumpkin was greater than on squash. Watermelon again had the smallest increase in numbers of females.

The differences between these hosts are twofold: first, the time of year when they are typically grown, and second, their native origins. Squash, a native crop, is traditionally grown early season, watermelon mid season, and pumpkin late season. Control of squash bug populations in squash is most effective when directed at small populations of young nymphs (Criswell 1987). This occurs early in the season before any new adults have developed and effectively delays the build-up of large populations. Watermelon is a non-native crop that is thought to come from Africa (Beard 1940). Although squash bugs are considered economically damaging to watermelon, the results of the simulation using watermelon show that the squash bug population builds up very slowly on this crop. The damage sustained by watermelon may be due to either being attacked when very small, a higher susceptibility to squash bugs (relative to squash) or to higher numbers of adults immigrating into the field. For this crop the pest manager should be more concerned with controlling the immigrating adults rather than controlling any nymphs that occur. Simulation results indicate that squash bugs will rapidly increase on pumpkin, a native crop.

The squash bug population dynamics model in general simulates the field dynamics well. The laboratory-determined development rates worked well for the field populations in 1984 and 1985. The model simulates development and survival of the immature stages and adults, but it consistently underestimates the number of eggs late in the season. Palumbo (1989) found that egg masses were the best stage to scout for in the field to estimate population densities. Population studies have shown that nymphal populations begin increasing rapidly after plants begin flowering (Fargo et al. 1988). The model could be used in conjunction with a scouting program to predict if the population is likely to cross into an economically damaging area before the next scheduled scouting date early in the crop cycle. When joined with crop, economic, and pesticide effects models, the squash bug model can be used to evaluate proposed control strategies. Those found to be robust could then be field tested.

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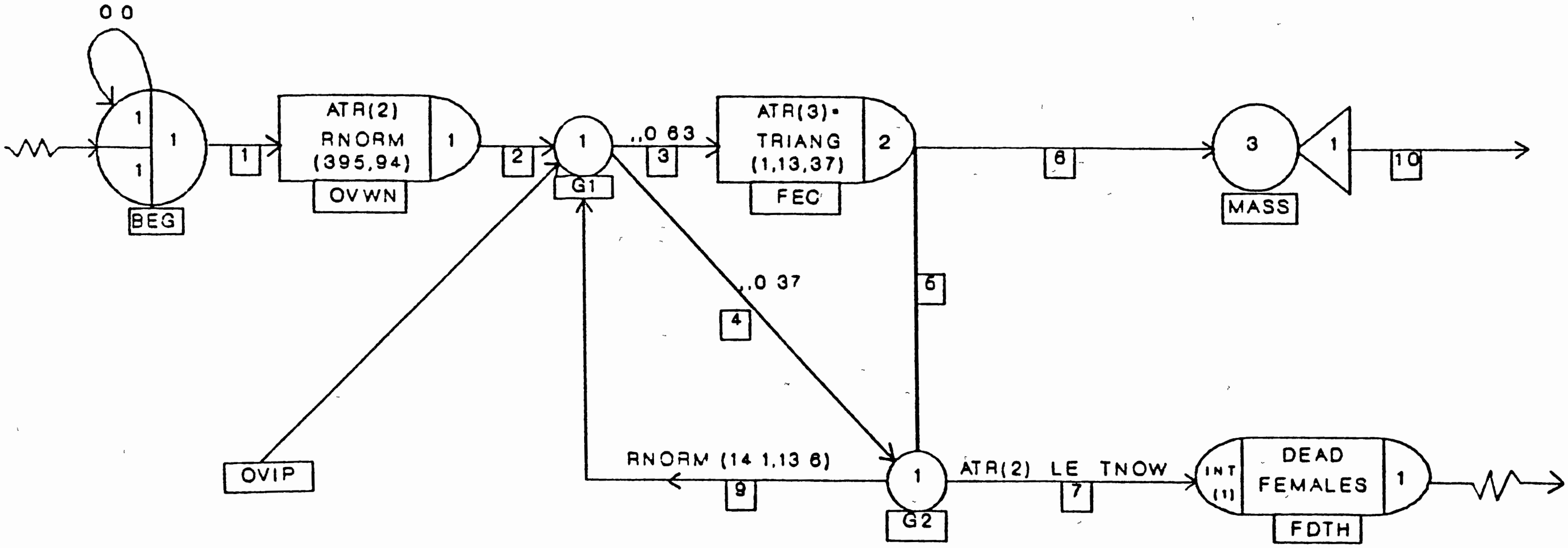

Figure 1. Part 1 of SLAM network flowchart of squash bug model.

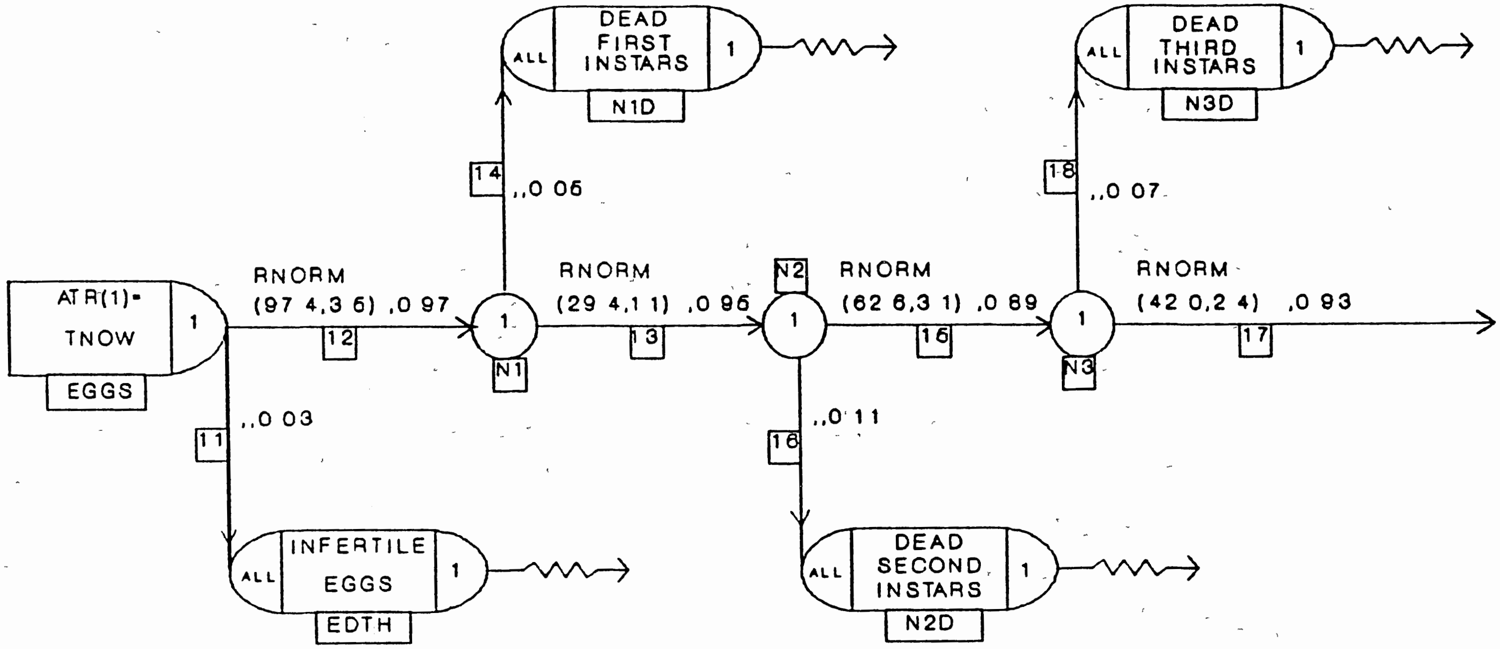

Figure 2. Part 2 of SLAM network flowchart of squash bug model.

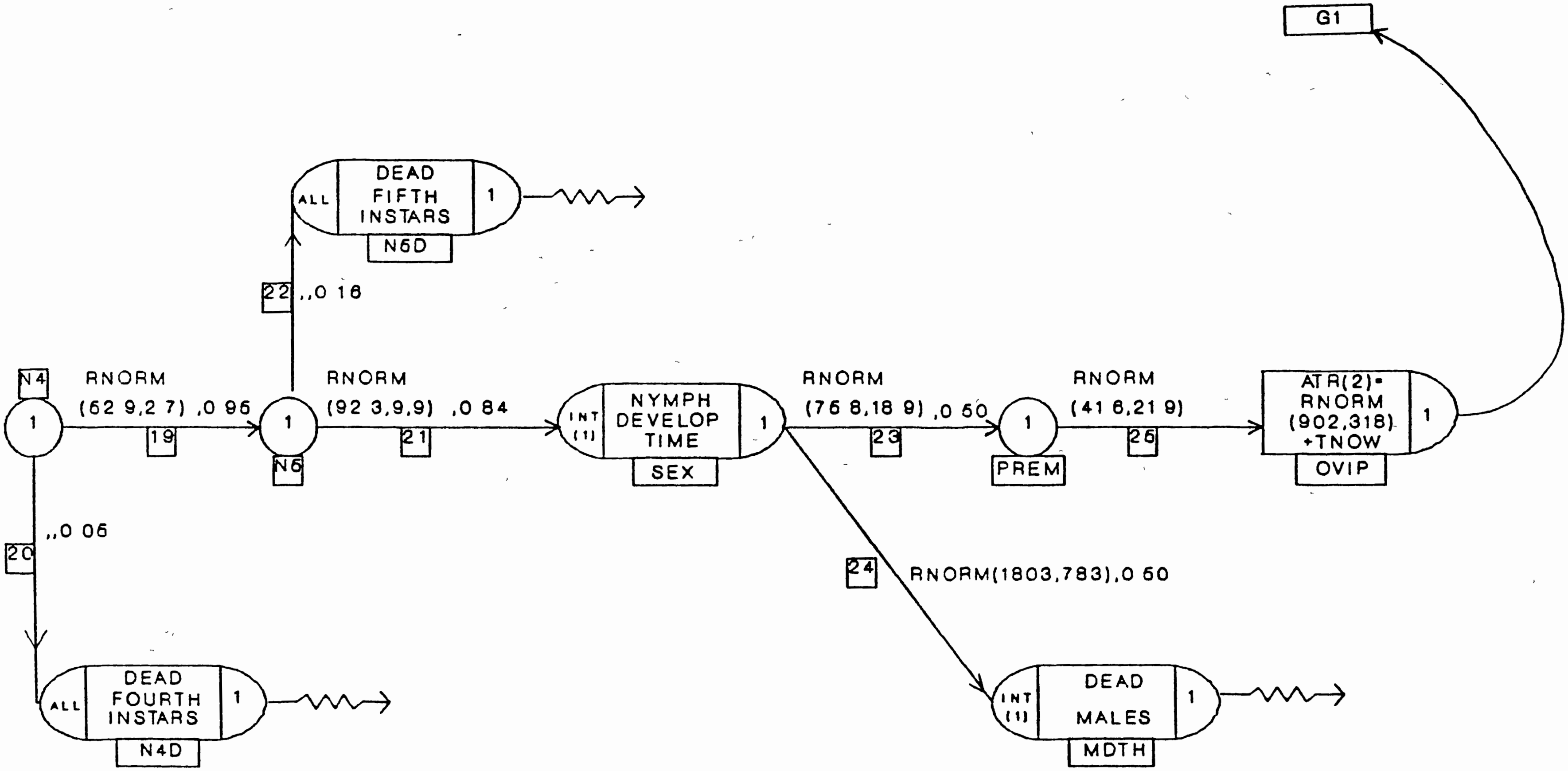

Figure 3. Part 3 of SLAM network flowchart of squash bug model.

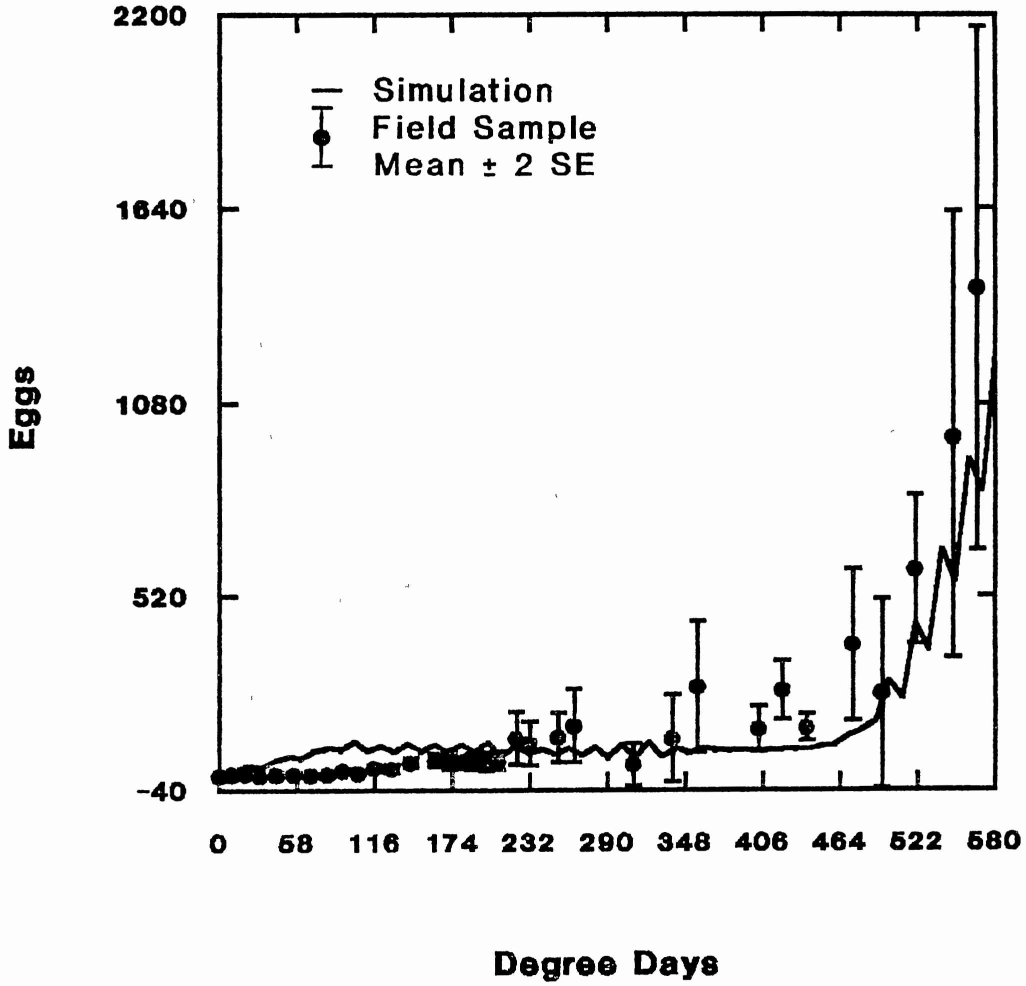

Figure 4. Comparison of simulated and field sampled squash bug egg population for Perkins in 1984.

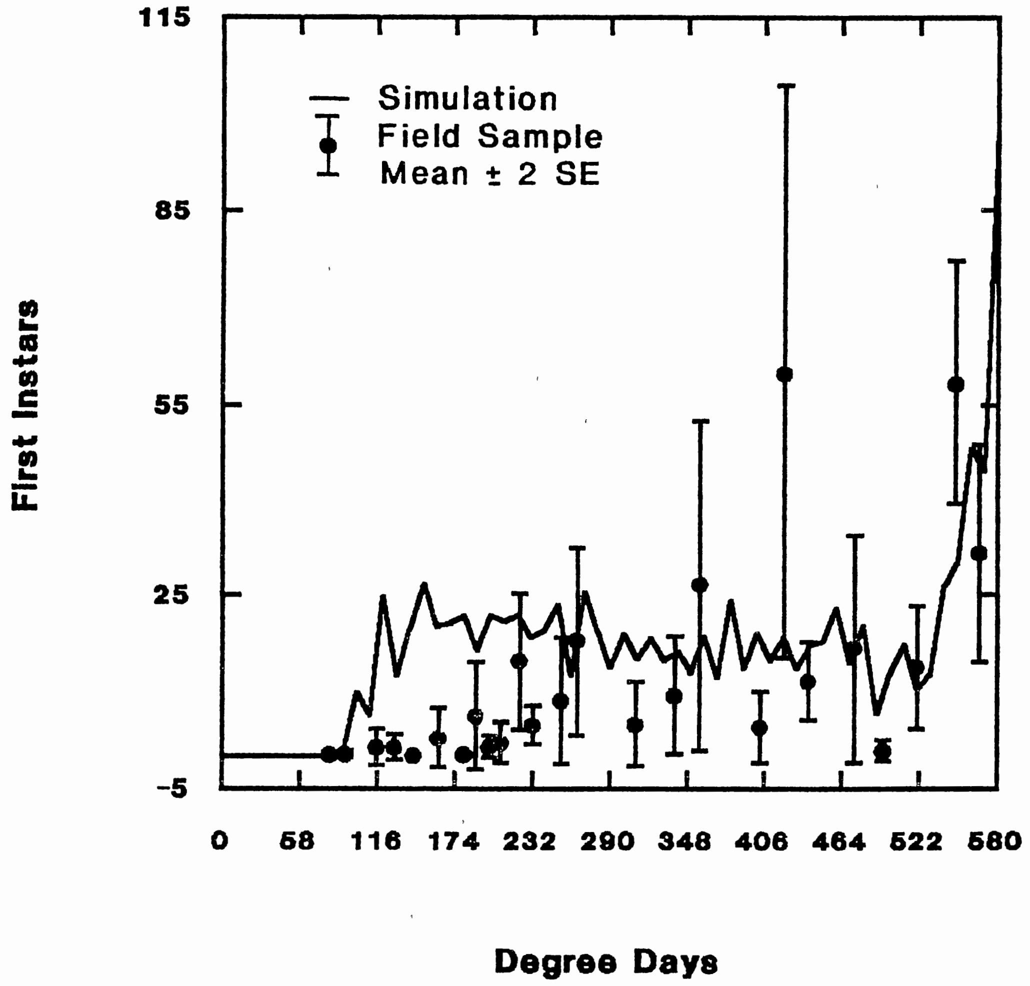

Figure 5. Comparison of simulated and field sampled squash bug first instar population for Perkins in 1984.

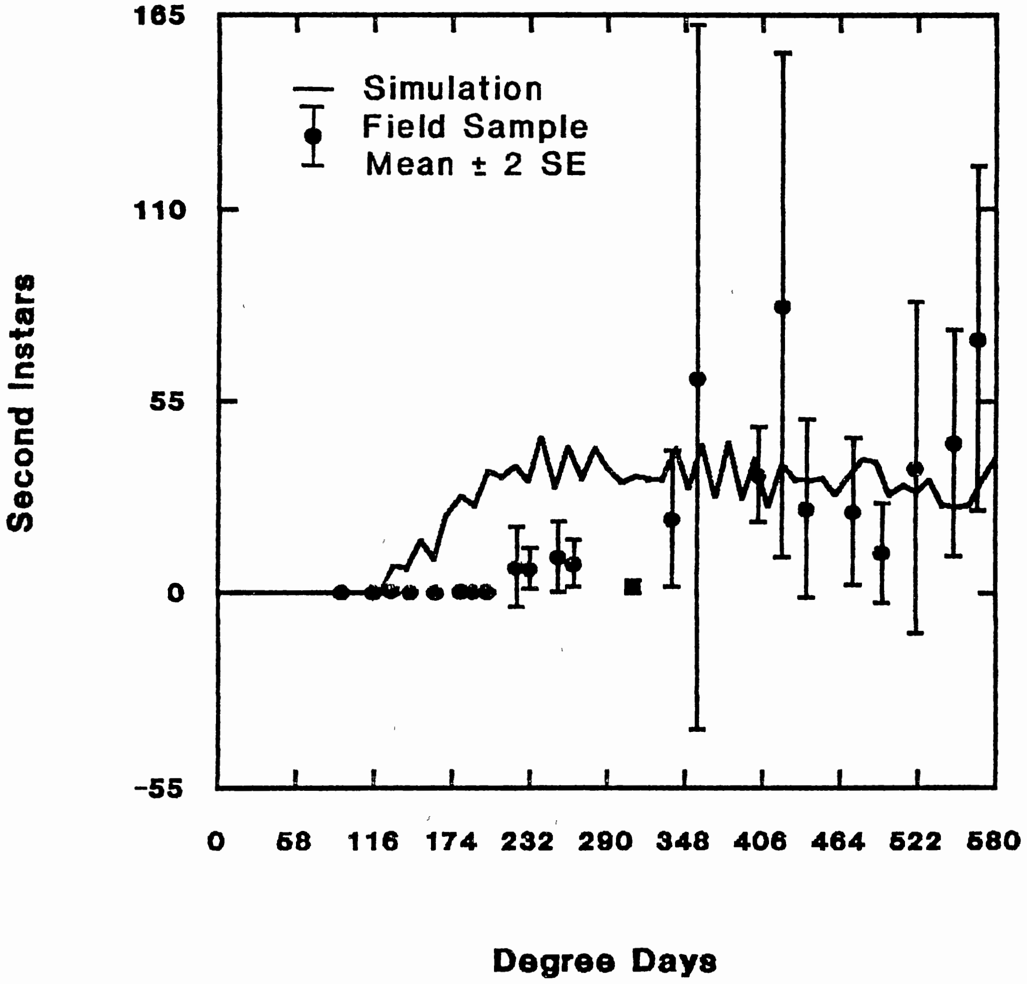

Figure 6. Comparison of simulated and field sampled squash bug second instar population for Perkins in 1984.

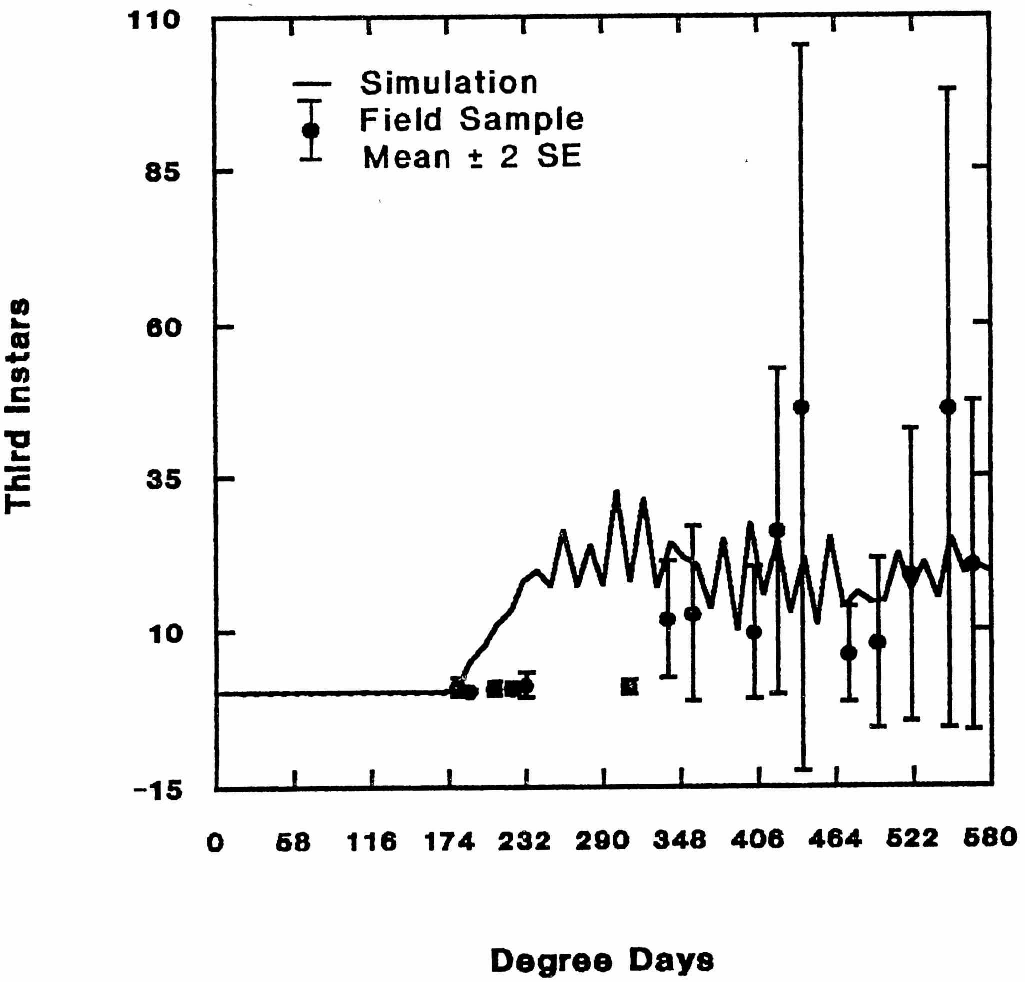

Figure 7. Comparison of simulated and field sampled squash bug third instar population for Perkins in 1984.

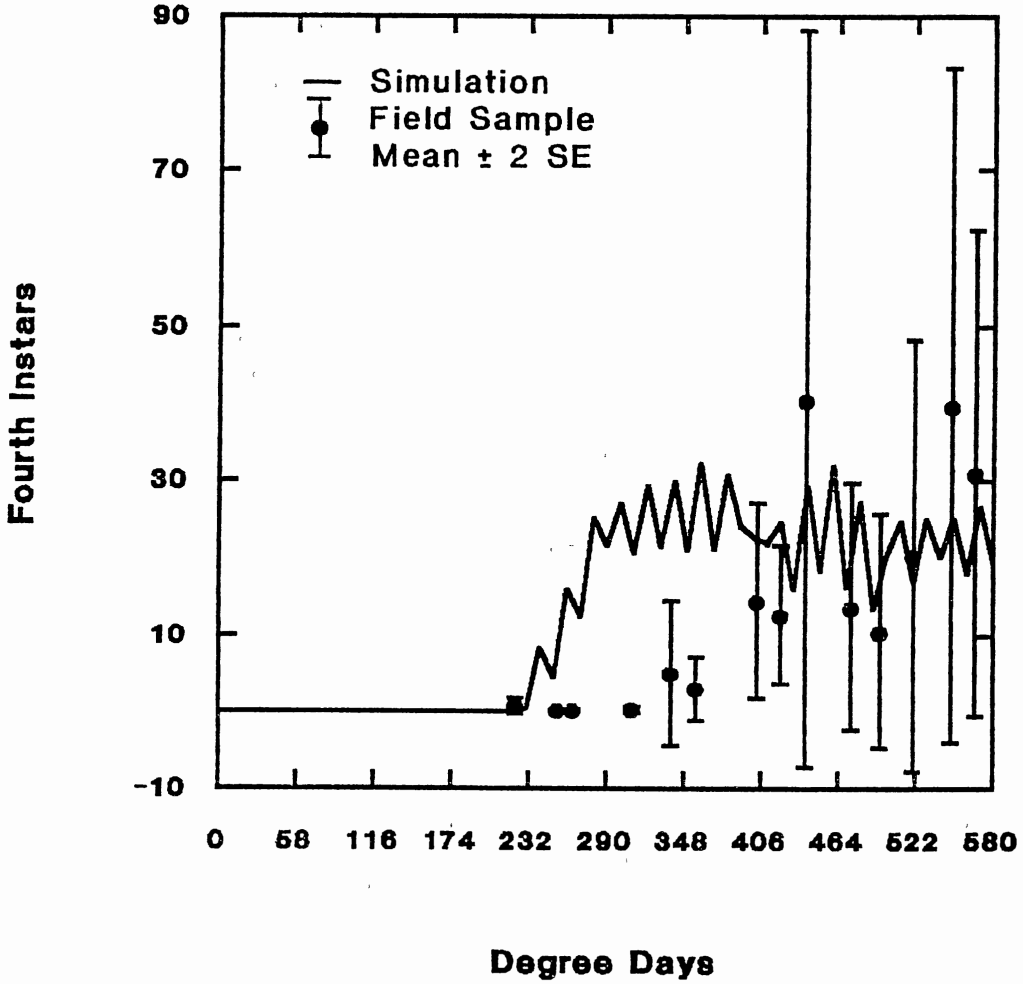

Figure 8. Comparison of simulated and field sampled squash bug fourth instar population for Perkins in 1984.

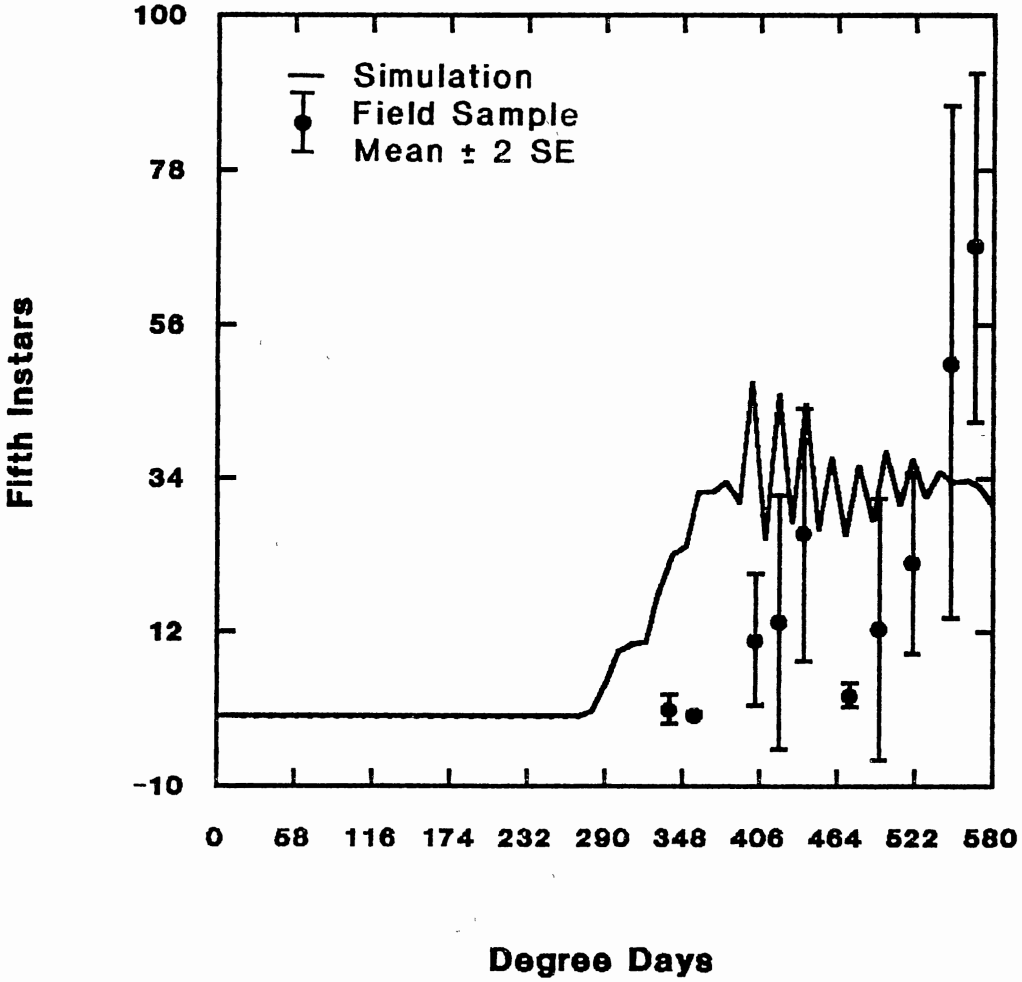

Figure 9. Comparison of simulated and field sampled squash bug fifth population for Perkins in 1984.

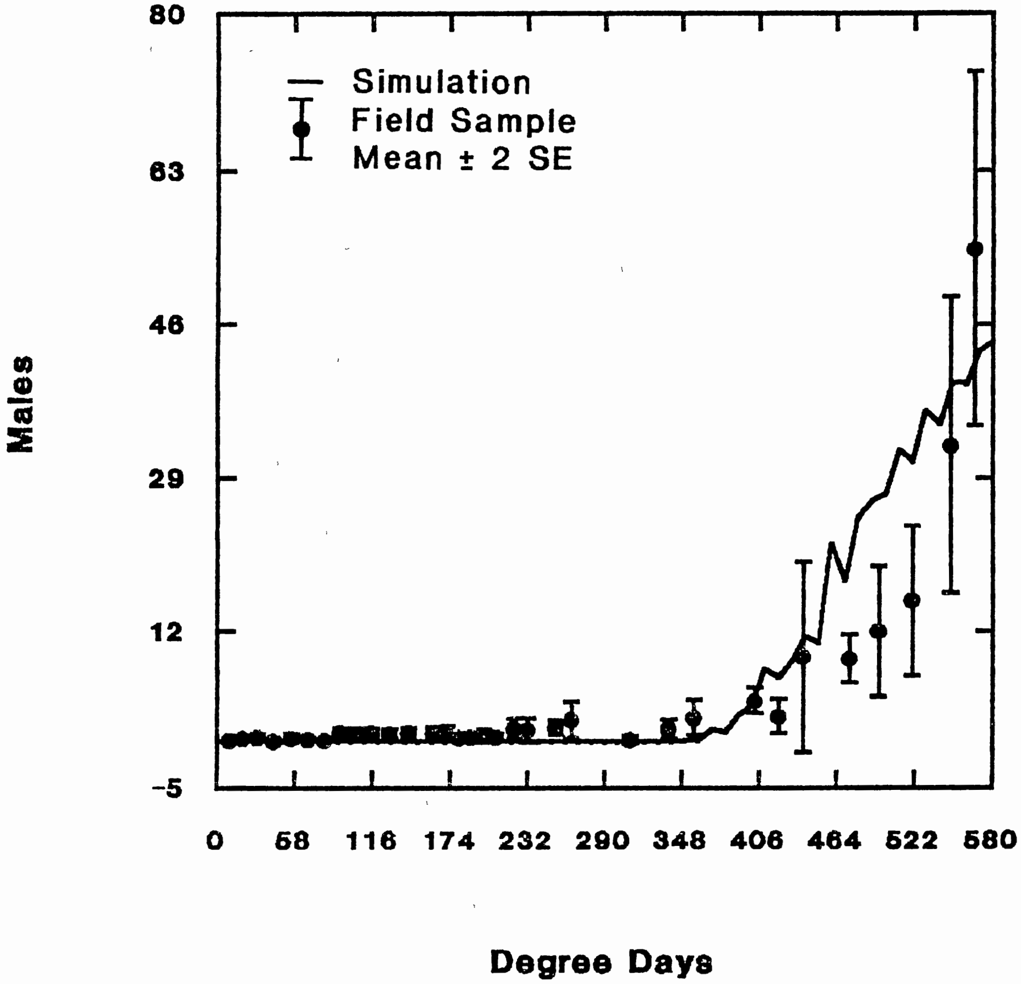

Figure 10. Comparison of simulated and field sampled squash bug male population for Perkins in 1984.

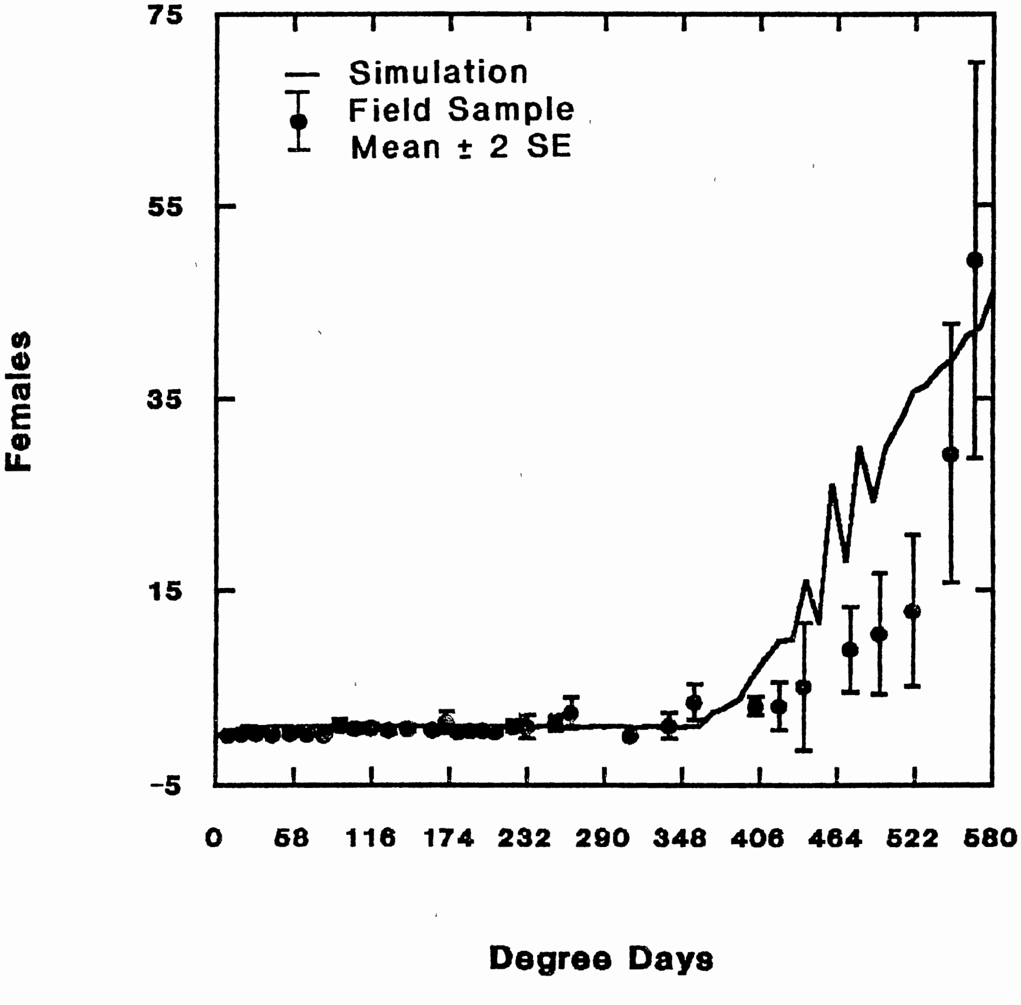

Figure 11. Comparison of simulated and field sampled squash bug female population for Perkins in 1984.

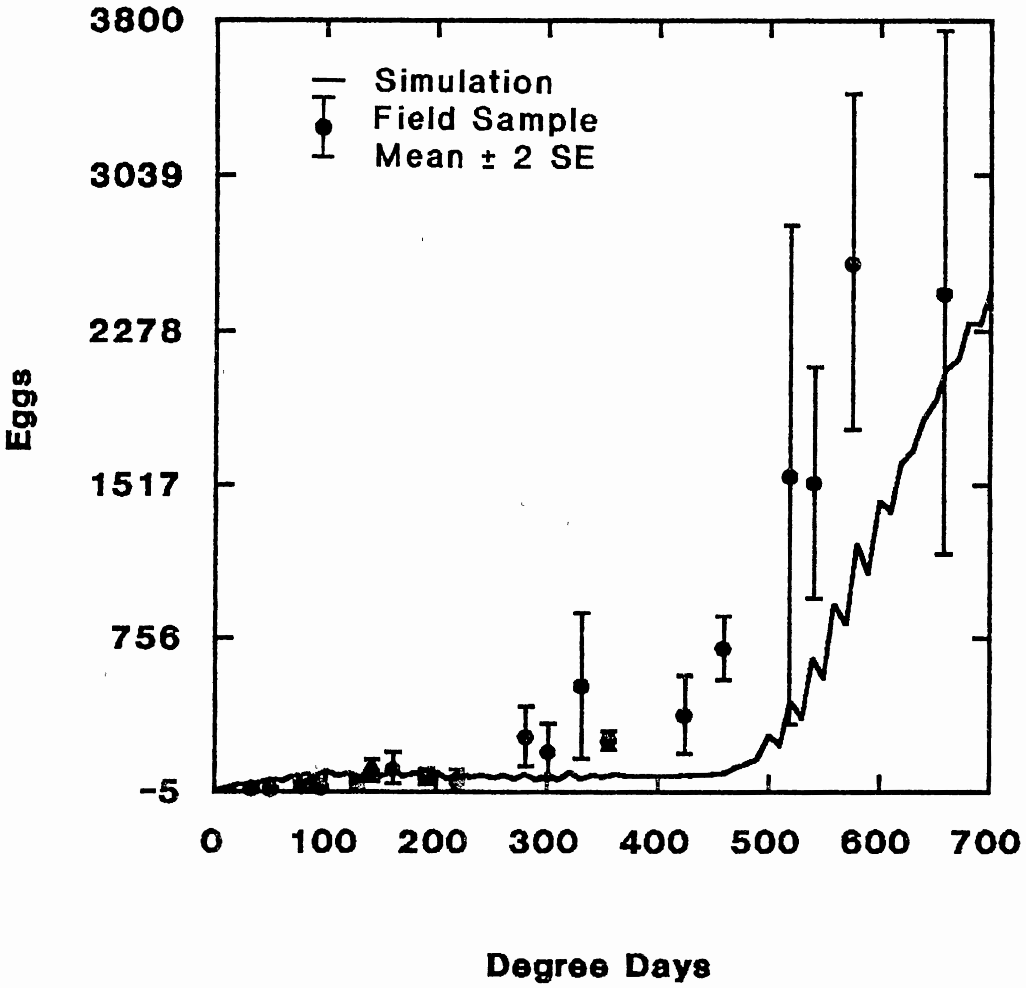

Figure 12. Comparison of simulated and field sampled squash bug egg population for Perkins in 1985.

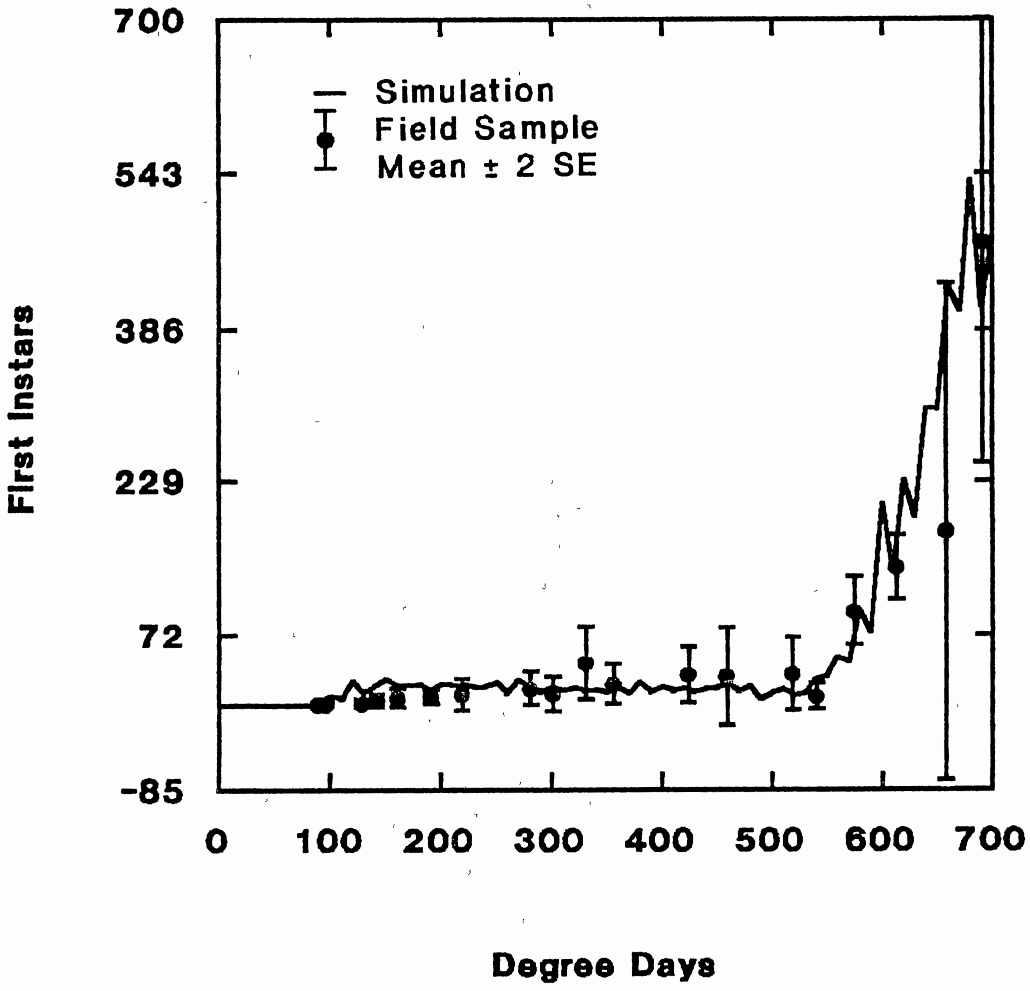

Figure 13. Comparison of simulated and field sampled squash bug first instar population for Perkins in 1985.

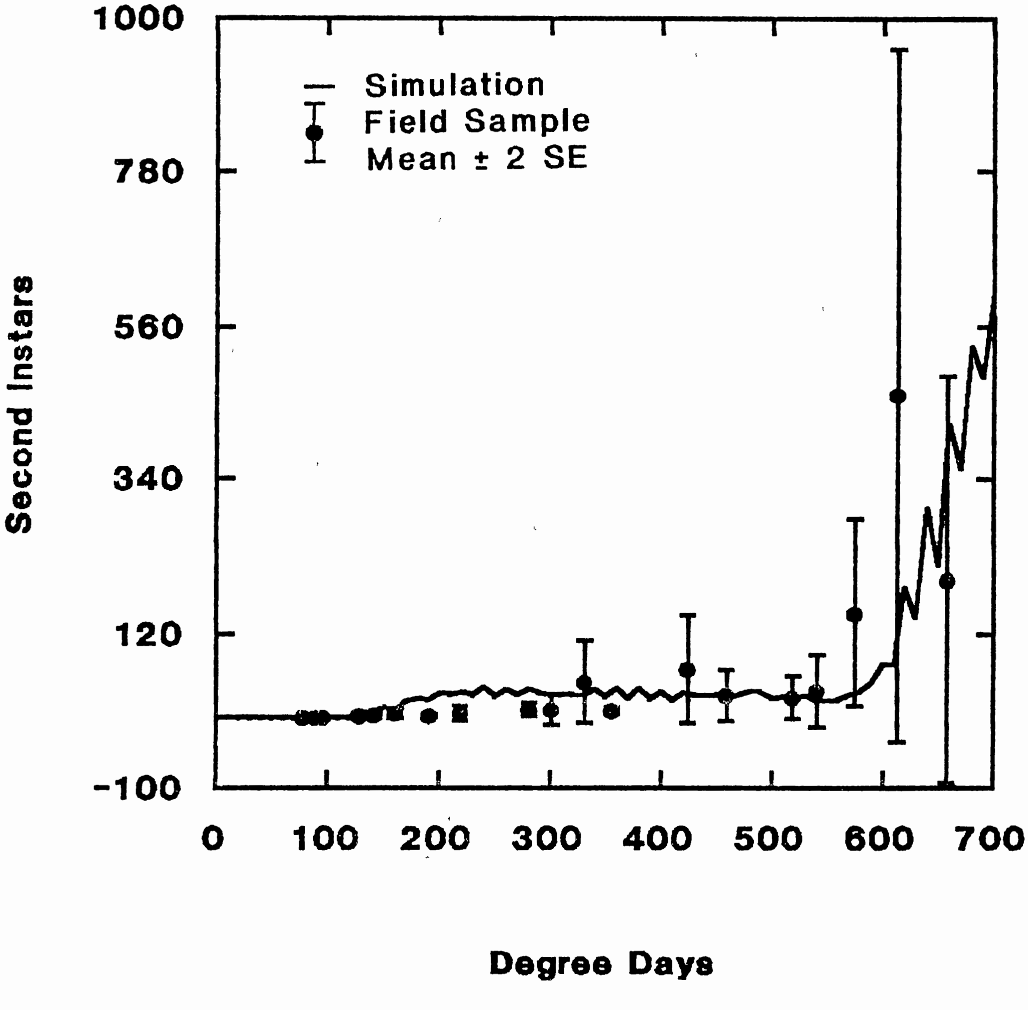

Figure 14. Comparison of simulated and field sampled squash bug second instar population for Perkins in 1985.

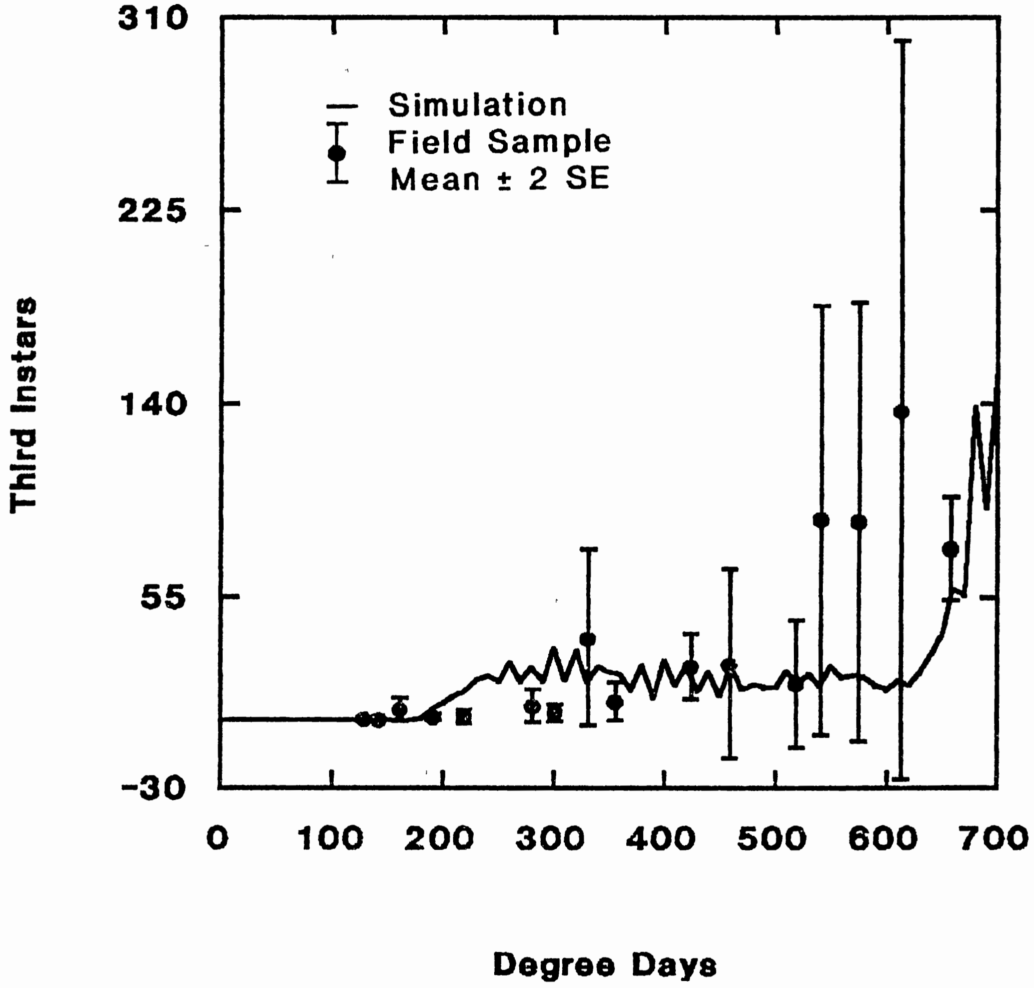

Figure 15. Comparison of simulated and field sampled squash bug third instar population for Perkins in 1985.

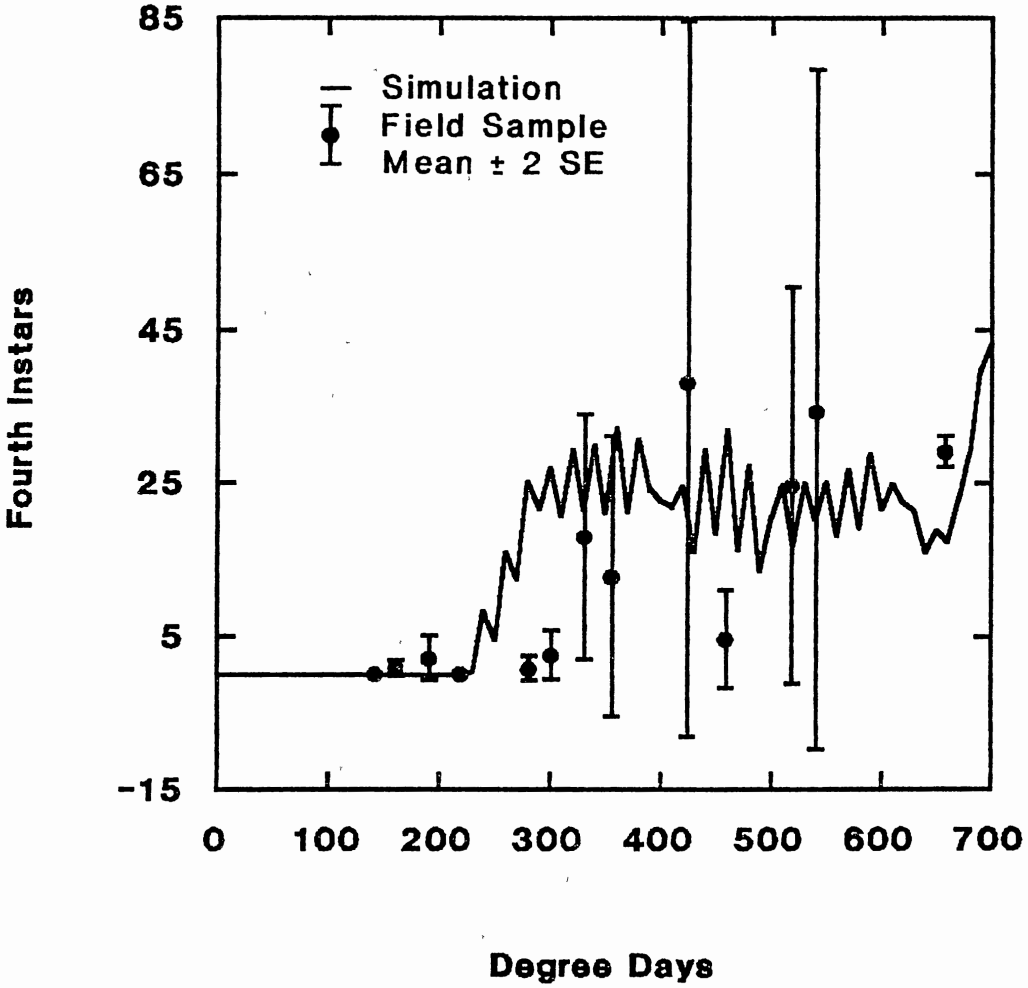

Figure 16. Comparison of simulated and field sampled squash bug fourth instar population for Perkins in 1985.

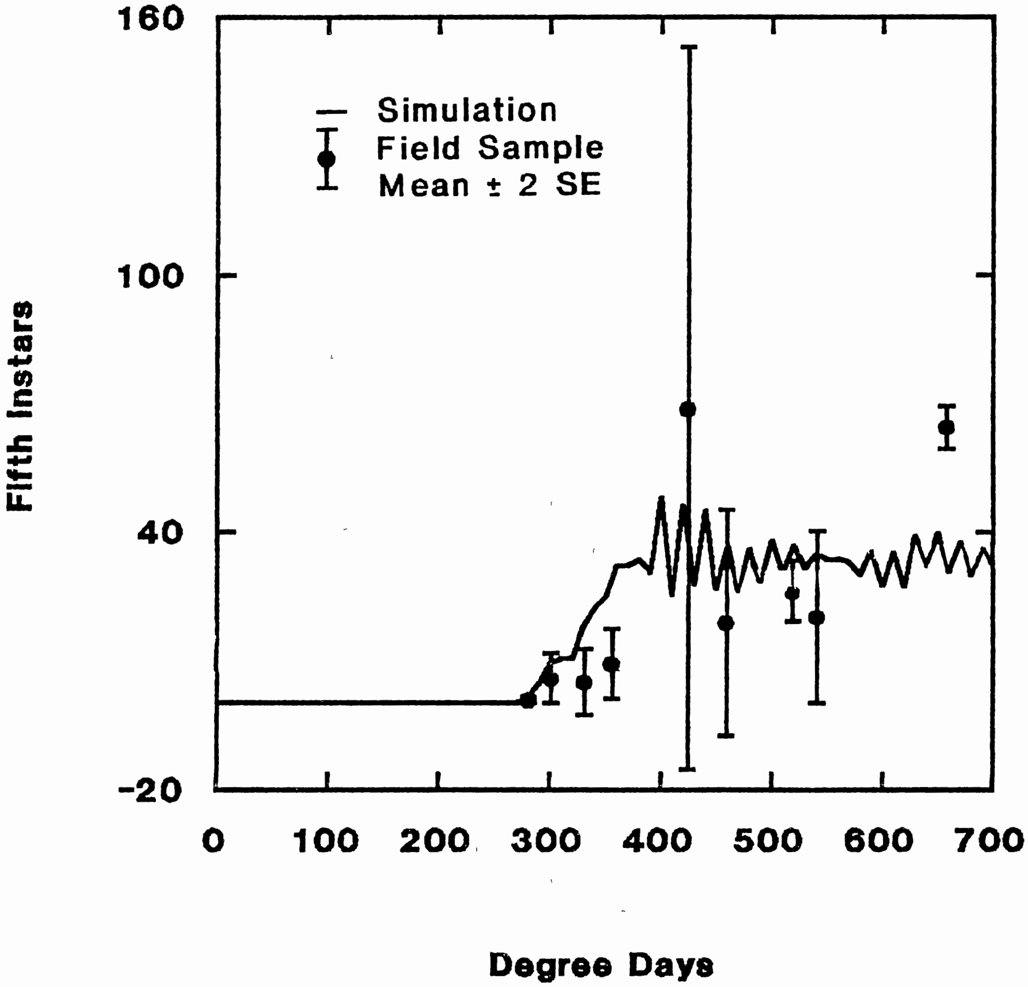

Figure 17. Comparison of simulated and field sampled squash bug fifth population for Perkins in 1985.

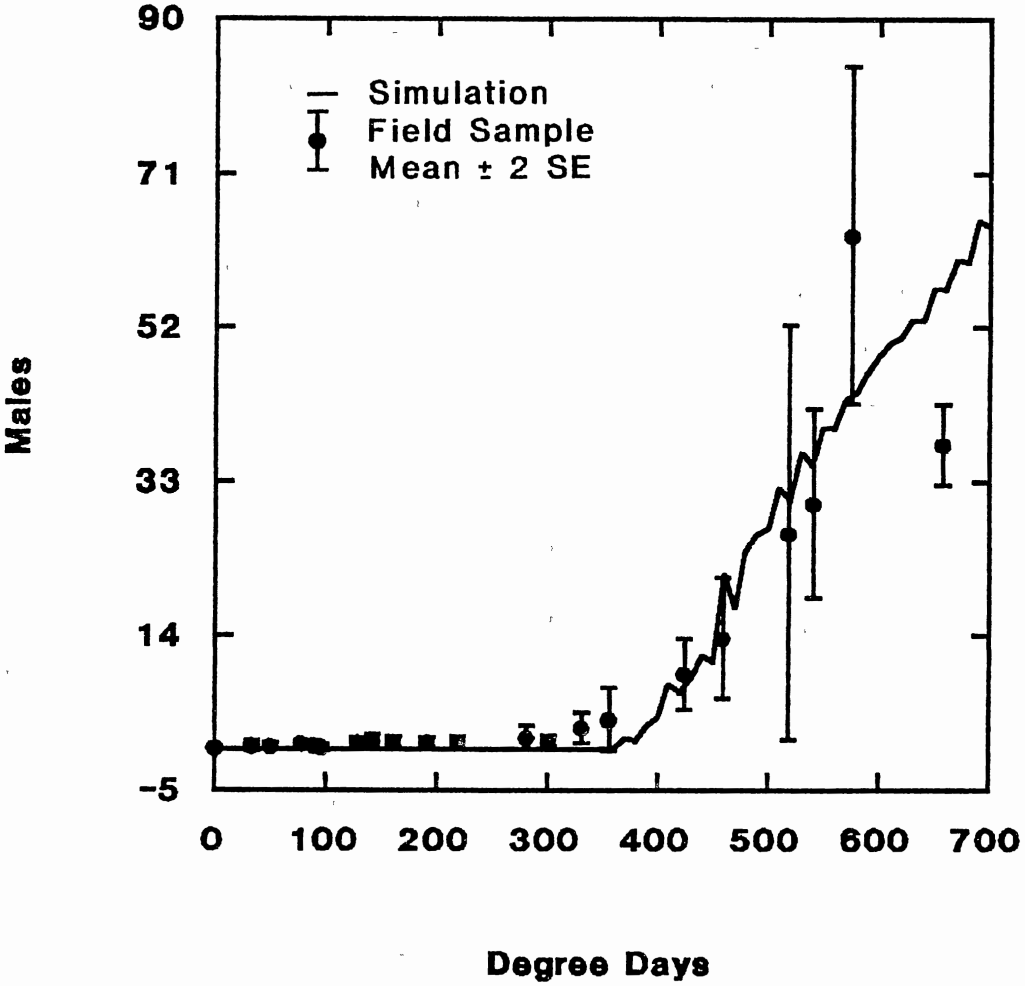

Figure 18. Comparison of simulated and field sampled squash bug male population for Perkins in 1985.

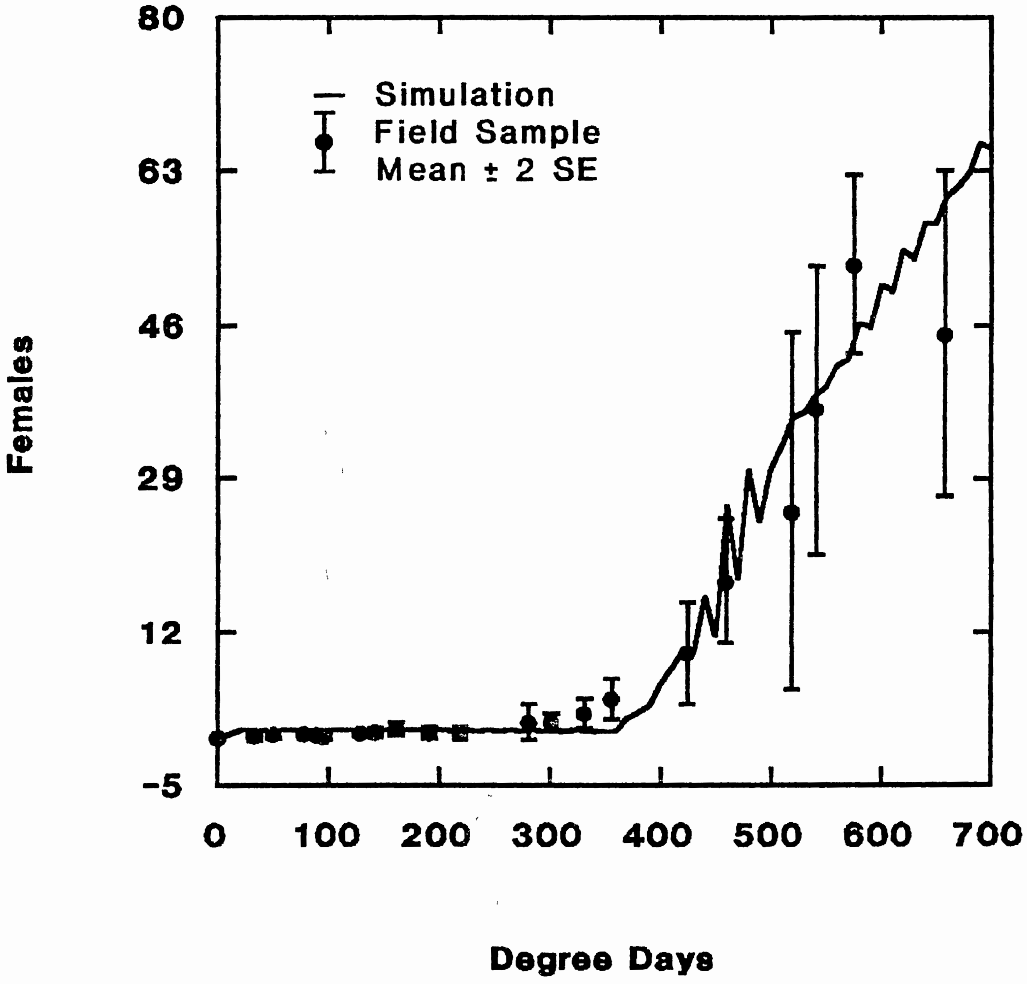

Figure 19. Comparison of simulated and field sampled squash bug female population for Perkins in 1985.

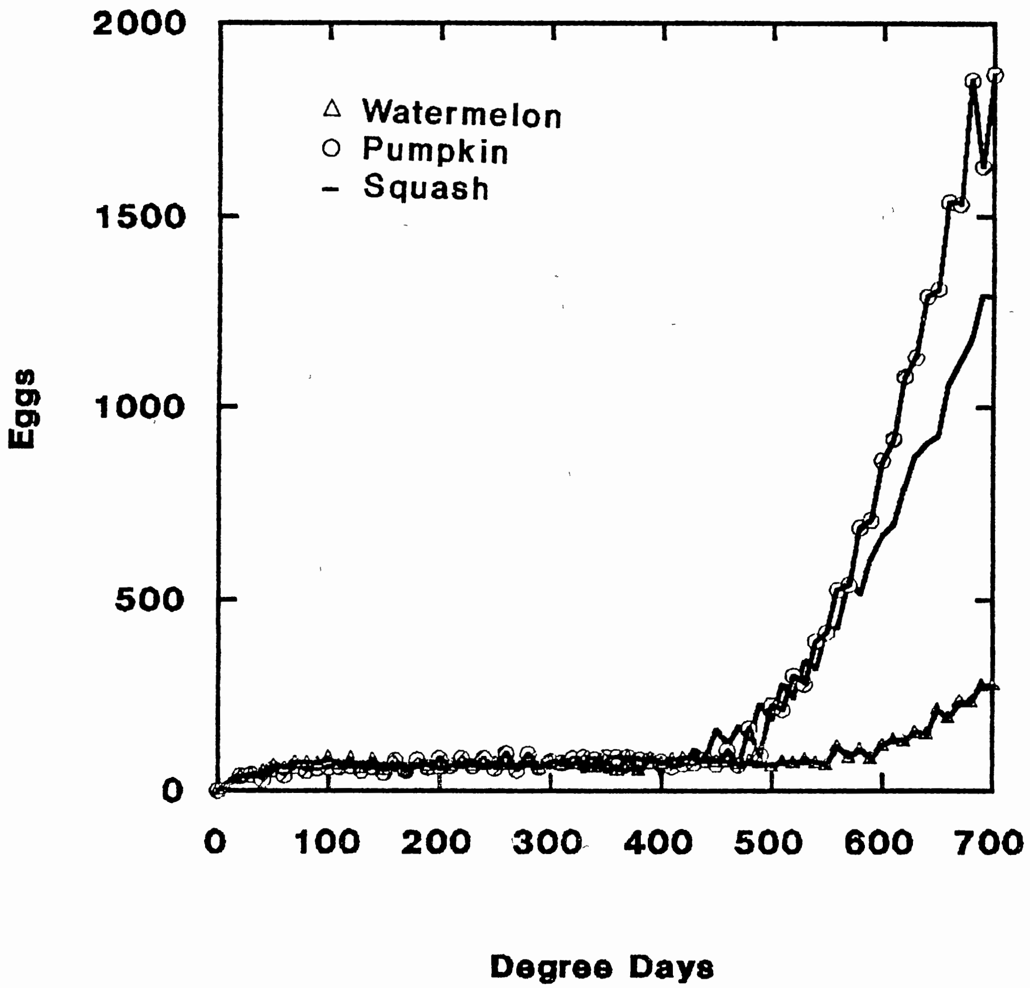

Figure 20. Comparison of simulated squash bug egg population for different host plants.

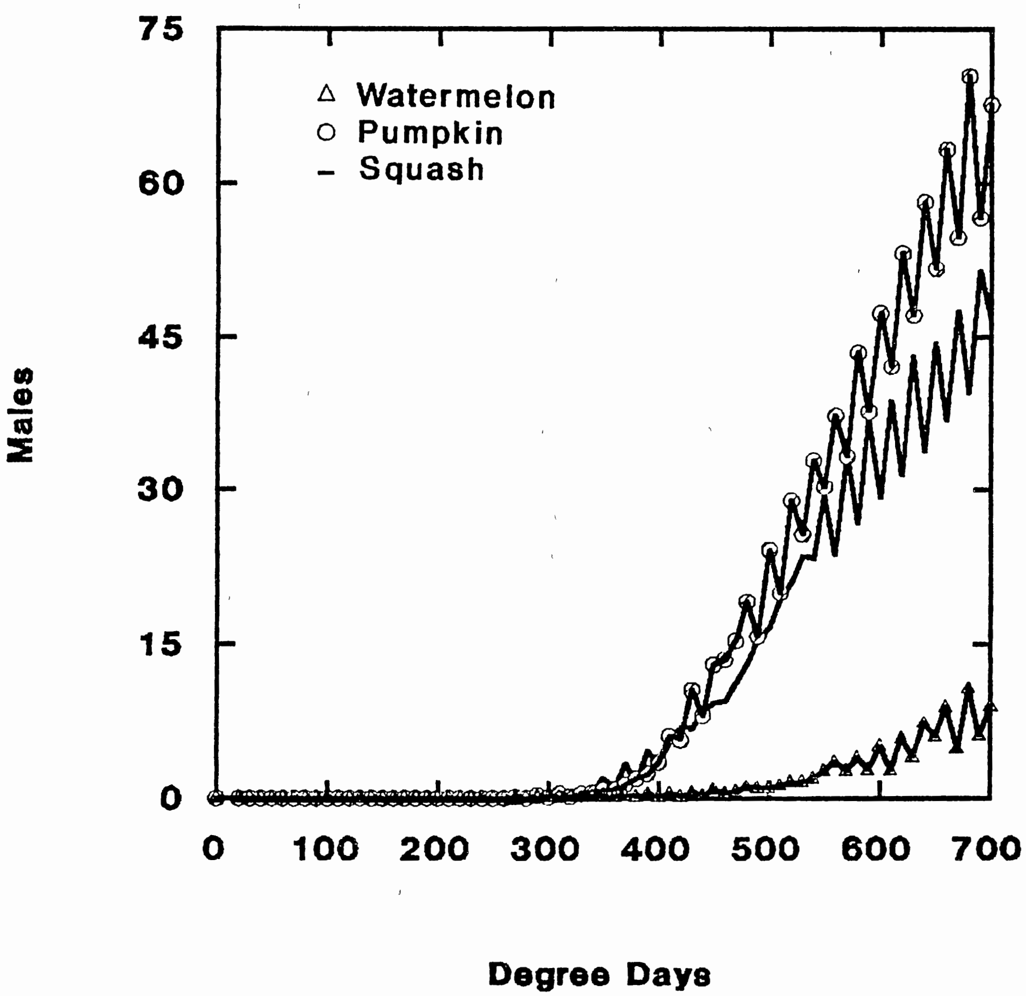

Figure 21. Comparison of simulated squash bug male population for different host plants.

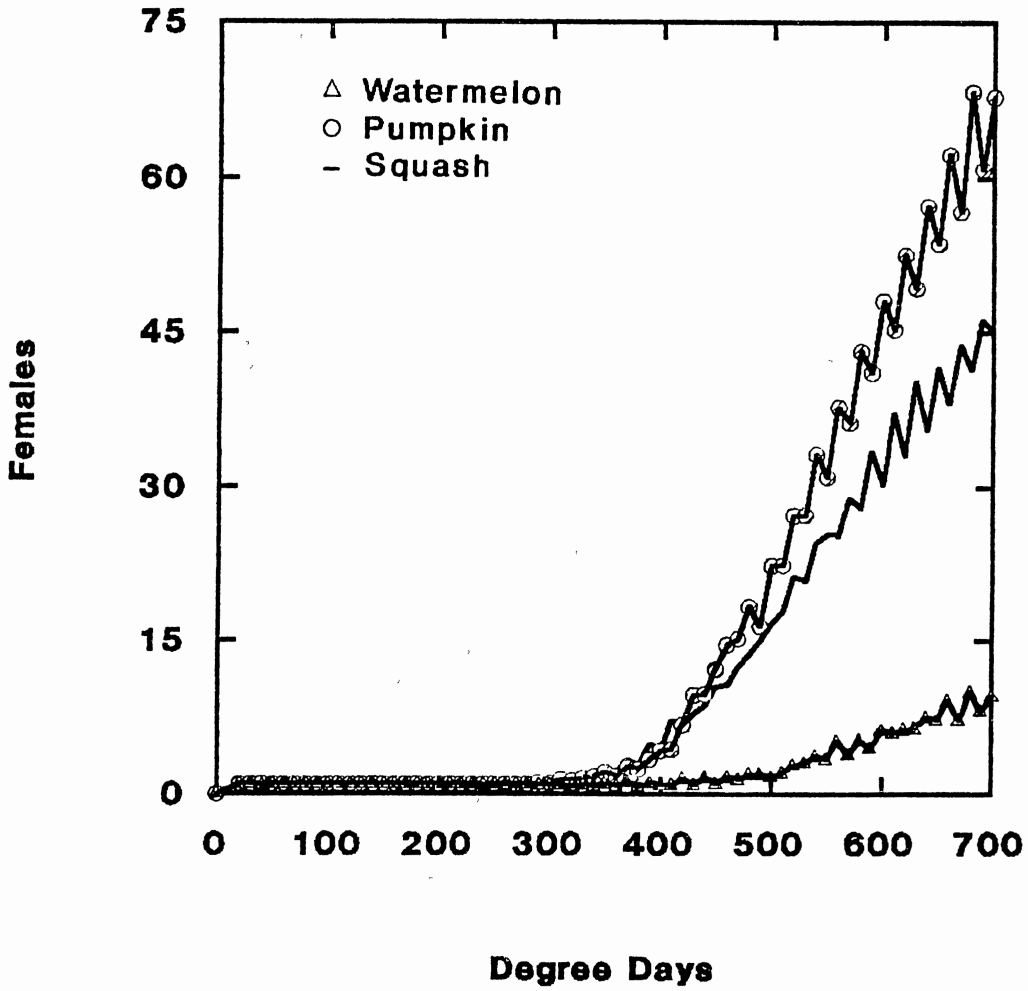

Figure 22. Comparison of simulated squash bug female population for different host plants.

CHAPTER 6

AN ANALYSIS OF GROWTH IN AREA OF LEAVES AND LEAF SURFACE OF <u>CUCURBITA</u> <u>PEPO</u>

ABSTRACT A bush variety of squash (Cucurbita pepo L. var. melopepo, 'Hyrific') was grown under seven constant temperatures (21.1, 24.0, 27.0, 29.4, 32.2, 35.0, and 37.8°C) with the growth of the plants estimated ca. every 48 hr. This paper describes aspects of leaf emergence, expansion, and total leaf area development in these plants.

A positive linear relationship was found between the number of visible leaves and time over all temperatures. The application of nonlinear curve fitting techniques showed that the expansion of each leaf studied could be accurately described by the Gompertz growth function. Furthermore, in all leaves, the trend in expansion time was similar, despite possible 10-fold differences in the final area of the leaves due to position on the stem.

Total plant leaf surface area was also accurately described by the Gompertz equation over the entire range of temperatures used in the study. Temperature was found to influence the final size of the plant and the time taken to achieve it.

KEY WORDS: Cucurbita pepo, plant growth, Gompertz equation

IN COMPARING plant growth under different conditions, it is convenient to fit the growth curves by some mathematical expression defined by a small number of parameters. Gregory (1921) showed that the logistic (autocatalytic, Verhulst-Pearl) curve serves well for Cucumis leaves. However, several studies of leaf expansion have found the logistic function unsuitable for leaves that are strongly asymmetrical (Hackett & Rawson (1974), Rees & Chapas (1963), and Amer & Williams (1957)).

The growth rate of squash, Cucurbita pepo L. var. melopepo, 'Hyrific', reaches a maximum after ca 3 weeks, and continues more slowly for another 6-9 weeks under normal conditions. The rate curve is strongly asymmetrical, and cannot be even approximately fitted by the logistic curve. Generalized 'skew logistic' curves may be devised, but are difficult to fit. However, similar analyses to this one have been performed (Amer & Williams 1957, Hackett & Rawson 1974) and found that the Gompertz function fitted the expansion of leaves.

Amer & Williams (1957) also remarked that this type of leaf expansion analysis could be useful in defining environmental effects on leaf expansion. If the effects of environment on leaf expansion could be related to growth functions, it might be possible to define these effects in a form which is predictively useful. Monteith (1972) stated that one of the major stumbling blocks in the simulation of crop growth is the inability to predict leaf expansion. The purpose of this paper is to characterize the effects of temperature on the rate of emergence of leaves, the rate of leaf expansion, and the rate of total leaf area growth over time.

Materials and Methods

The cultivar used was a straight-necked yellow squash, <u>Cucurbita</u> <u>pepo</u> L. var. <u>melopepo</u>, 'Hyrific'. Plants were grown in 25.4 cm^2 plastic pots containing a mix of 1/3 peat and 2/3 soil. Pots were seeded with 2 seeds per pot and thinned to 1 plant per pot following cotyledon expansion. Plants were grown in a walk-in bio-chamber at 21.1, 24.0, 27.0, 29.4, 32.2, 35.0, and 37.8°C at 50-70% RH with a photoperiod of 16:8 (L:D). Twenty replications were made at 21.1, 24.0, 27.0, and 29.4°C, while twelve replications were made at 32.2, 35.0, and 37.8°C. Plants were watered as needed and received a complete nutrient solution weekly.

The data collected were number of leaves per plant, leaf area per leaf, and total plant leaf area. Leaf area was estimated nondestructively by the method of Fargo et al. (1986) using leaf length and width. Plants were measured every 48 hours for ca 32 days post emergence.

Results

A linear relationship was found between the number of visible leaves and age. The number of visible leaves against age for 21.1°C is shown in Fig. 1. This linear relationship with age was found at all temperatures and demonstrates a constant rate of leaf emergence (Table 1) over time. The rate of leaf emergence (slope) initially increased with temperature, reaching a maximum at 32.2°C and decreasing thereafter.

The information sought from the data on the expansion of individual leaves was the final size of each leaf (A_{max}), the relationship between expansion and time, and the relationship between A_{max} and leaf position. The natural logarithm of individual leaf area was plotted against age. Values of A_{max} were then estimated using those leaves whose expansion had ceased or was 95% complete 48 hrs prior to the final measurement. Then a growth function was sought which would apply to all leaves. The Gompertz function (Richards 1969, Hunt 1982) proved suitable. The form used was:

$$\text{Log}_e \text{ Area} = a * \exp(-b * \exp(-c * t))$$

where Area is the individual leaf area at age t, and *a*, *b*, and *c* are parameters to be estimated. The parameter *a* is an estimate of A_{max}, *b* has little physiological significance, but *c* is related, inversely, to the time span of the expansion process.

Nonlinear regression analysis was used to determine the coefficients for those leaves for which expansion had been completed. The growth curves derived for nine individual leaves at 21.1°C are shown in Fig. 2 along with the means of the data. The Gompertz function provided an acceptable fit to the means. Parameter estimates of the function at different temperatures appear in Tables 2 - 8. Estimates of A_{max}, *a*, *b*, and *c* are listed plus data derived from the growth functions: t_i, the age of the plant in days at which each leaf attained maximum absolute growth rate and dArea/dt, the absolute relative growth rate at t_i in cm^2 day^{-1}. The day t_i was determined from $\log_e b/c$. Negative values for leaf number 1 at 27.0 and 29.4°C indicate that t_i occurred before observation began. Examination of *c* values shows that at all temperatures, more time is required for expansion for each succeeding leaf (Tables 2 - 8). Time required for expansion in leaves 1 - 6 initially decreased with increasing temperature, reaching a maximum at 32.2°C and then increasing. Maximum size, *a*, attained by each leaf decreased with temperature.

Fig. 3 shows estimated A_{max} plotted against leaf position for plants grown at 21.1°C. The existence of a correlation between A_{max} for one leaf and that for the next is obvious. The curves for the other temperatures are similar in form, the main difference being that the curves for 35.0 and 37.8°C were set 2 - 4 leaf positions to the right of curves from the lower temperatures.

The information sought from the data on the growth of total leaf surface was the final size (A_{tla}), the relationship between growth and age, and the relationship between A_{tla} and temperature. The data used for this analysis included leaf area estimates of all leaves, not just the fully expanded leaves. Although it has been shown that the early growth of many plant species in constant temperature conditions is approximately exponential, squash in this experiment were increasing in leaf area at a higher rate than the exponential case. For these plants, the Gompertz function provided a better fit to the data. The form used was the same as that for leaf expansion:

$$\mathrm{Log}_e \text{ Area} = a * \exp(-b * \exp(-c * t))$$

here Area is the total plant leaf area at time t, and a, b, and c are as above.

Nonlinear regression analysis was again used to estimate the parameters. The $\log_e$ growth curve of total leaf surface area derived for 21.1°C is shown in Fig. 4 along with the data. An acceptable fit was given by the Gompertz function. Table 9 contains estimates of A_{tla}, *b*, and *c*. Examination of the values for *c* shows no clear trend over temperature. There were no significant differences found in *c* between plants grown at 21.1, 24.0, 27.0, and 29.4°C. The maximum size, A_{tla}, attained by the plants increased with temperature, reaching a maximum at 29.4°C and decreasing thereafter.

Discussion

The linear increase in the number of leaves over time was an unexpected finding. Hackett & Rawson (1974) found a curvilinear relationship between the emergence of leaves and time using Nicotiana tabacum L. as did Gregory (1921) using Cucumis sativus L. My results may be due to the conditions in which the plants were grown or that these data cover only a small portion of the time required for the plant's total growth. Squash is typically in the field for 9 - 12 weeks from emergence.

A striking outcome of the analysis of leaf expansion was the finding that the leaves had similar growth characteristics across temperatures. The Gompertz growth function described leaf expansion very well and the trend in time span was similar at all temperatures for each leaf. An analysis comparable to this one was performed by Amer & Williams (1957), who found that the Gompertz function fit the expansion of Pelargonium zonale L. leaves. They measured leaves grown under different water regimes and claimed that parameter *c* was almost constant and hence could be considered characteristic of the species. Hackett & Rawson (1974), in a study involving long day and short day growth of Nicotiana tabacum, found that *c* could take a somewhat wider range of values. This study confirms Hackett & Rawson's (1974) conclusion; their data and my data demonstrate that a fairly wide range of values is possible for any one species. Furthermore, since the value obtained for *c* depends to some extent on the starting point of measurement (e.g. whether at the initiation or emergence of the leaves), there will be difficulty in making direct comparisons between species or between independent investigations of the same species.

The increase in area of the total leaf surface closely follows a Gompertz growth function. Temperature has an overriding influence on the ultimate size of a plant and how soon it achieves that final size. This is hardly surprising as the increase in total leaf area depends upon two underlying factors: the rate of production of successive leaves, and the rate of expansion of individual leaves. Both of which are strongly influenced by temperature. While the data for individual leaf expansion showed a wide range of possible values for *c*, the data for total leaf surface was more stable. Only at 32.2 and 37.8°C did *c* depart significantly from the other temperatures. Gregory (1921) found that high temperature increased plant respiration, resulting in a reduction in plant growth. The conclusion reached from these data is that temperature had a greater effect on the magnitude of A_{tla} and the time needed to reach A_{tla} than on the basic form of the growth curve.

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Table 1. Parameters of the fitted linear regression models to the number of leaves vs age by temperature.

Temperature	Constant	Slope	n	r^2
21.1	-1.318	0.630	412	0.965
24.0	-2.022	0.725	412	0.962
27.0	-1.991	0.993	516	0.987
29.4	-1.798	1.104	502	0.984
32.2	-2.208	1.204	255	0.987
35.0	-2.140	1.056	296	0.983
37.8	-0.519	0.710	279	0.977

Table 2. Characterization of the expansion of squash leaves at 21.1°C.

Leaf Position	Estimated A_{max} (cm^2)	c	S.E. of c	b	t_I	dA/dt at t_I (cm^2 day^{-1})
1	6.280	0.308	0.021	1.728	1.776	2.037
2	7.169	0.281	0.018	4.613	5.441	2.098
3	7.510	0.271	0.014	9.487	8.302	2.114
4	7.886	0.236	0.013	11.018	10.168	1.983
5	8.146	0.222	0.016	14.663	12.096	1.945
6	8.438	0.199	0.016	15.759	13.856	1.855
7	8.581	0.178	0.015	15.326	15.335	1.754
8	8.699	0.161	0.015	15.019	16.828	1.674
9	8.861	0.147	0.017	16.092	18.900	1.615

Table 3. Characterization of the expansion of squash leaves at 24.0°C.

Leaf Position	Estimated A_{max} (cm^2)	c	S.E. of c	b	t_i	dA/dt at t_i (cm^2 day^{-1})
1	6.387	0.382	0.006	1.607	1.242	2.454
2	7.089	0.349	0.013	5.882	5.077	2.485
3	7.582	0.309	0.018	10.587	7.636	2.368
4	8.010	0.267	0.020	11.400	9.115	2.196
5	8.029	0.304	0.013	30.364	11.228	2.455
6	8.353	0.230	0.018	17.364	12.410	2.027

Table 4. Characterization of the expansion of squash leaves at 27.0°C.

Leaf Position	Estimated A_{max} (cm^2)	c	S.E. of c	b	t_1	dA/dt at t_1 (cm^2 day^{-1})
1	6.251	0.450	0.006	0.833	-0.406	2.815
2	6.702	0.492	0.004	3.223	2.379	3.364
3	7.199	0.427	0.016	6.207	4.276	3.098
4	7.618	0.438	0.015	13.277	5.904	3.413
5	7.848	0.414	0.015	20.245	7.265	3.304
6	7.980	0.375	0.013	23.296	8.395	3.007
7	8.031	0.350	0.013	26.773	9.393	2.812
8	8.059	0.317	0.009	27.032	10.401	2.560
9	8.047	0.275	0.008	22.680	11.351	2.257
10	7.988	0.257	0.006	24.870	12.505	2.128
11	8.017	0.231	0.010	22.517	13.482	1.976
12	8.080	0.206	0.011	19.664	14.460	1.845
13	8.033	0.196	0.014	22.190	15.814	1.785
14	8.218	0.179	0.017	21.176	17.055	1.718
15	8.431	0.180	0.019	28.444	18.600	1.748
16	8.614	0.176	0.025	31.662	19.631	1.747

Table 5. Characterization of the expansion of squash leaves at 29.4°C.

Leaf Position	Estimated A_{max} (cm^2)	c	S.E. of c	b	t_I	dA/dt at t_I (cm^2 day^{-1})
1	5.805	0.518	0.021	0.659	-0.805	3.023
2	6.252	0.463	0.024	1.982	1.478	2.901
3	6.762	0.561	0.012	9.128	3.942	4.037
4	7.202	0.442	0.017	8.849	4.933	3.225
5	7.531	0.407	0.017	12.991	6.300	3.088
6	7.758	0.395	0.015	19.973	7.581	3.087
7	7.899	0.369	0.017	24.629	8.683	2.922
8	8.018	0.353	0.017	30.681	9.699	2.833
9	8.071	0.346	0.021	41.674	10.780	2.794
10	8.149	0.339	0.021	53.369	11.732	2.763
11	8.225	0.332	0.022	65.993	12.619	2.731
12	8.206	0.328	0.020	84.194	13.516	2.692
13	8.184	0.320	0.019	100.713	14.413	2.621
14	8.259	0.303	0.018	102.291	15.273	2.511
15	8.467	0.253	0.018	58.662	16.094	2.199
16	8.733	0.222	0.017	44.134	17.060	2.041
17	9.360	0.190	0.018	32.708	18.356	1.924
18	10.281	0.169	0.025	29.881	20.102	1.895

Table 6. Characterization of the expansion of squash leaves at 32.2°C.

Leaf Position	Estimated A_{max} (cm^2)	c	S.E. of c	b	t_1	dA/dt at t_1 (cm^2 day^{-1})
1	6.101	0.630	0.009	1.512	0.656	4.112
2	6.584	0.547	0.017	4.452	2.730	3.762
3	7.023	0.533	0.015	10.535	4.418	3.963
4	7.354	0.505	0.017	16.914	5.600	3.921
5	7.613	0.455	0.012	22.553	6.848	3.576
6	7.761	0.423	0.011	27.795	7.860	3.346
7	7.881	0.399	0.012	33.907	8.831	3.180
8	8.040	0.353	0.014	30.878	9.717	2.841
9	8.138	0.360	0.012	49.454	10.836	2.938
10	8.259	0.321	0.018	41.433	11.601	2.652
11	8.407	0.294	0.018	40.421	12.583	2.483

Table 7. Characterization of the expansion of squash leaves at 35.0°C.

Leaf Position	Estimated A_{max} (cm^2)	c	S.E. of c	b	t_1	dA/dt at t_1 (cm^2 day^{-1})
1	5.510	0.622	0.033	1.288	0.407	3.528
2	5.780	0.599	0.015	3.886	2.266	3.574
3	6.159	0.459	0.018	5.599	3.753	2.829
4	6.577	0.402	0.013	7.444	4.994	2.645
5	6.817	0.361	0.014	11.563	6.781	2.473
6	7.124	0.356	0.023	19.824	8.390	2.542
7	7.209	0.371	0.018	35.988	9.658	2.675
8	7.315	0.401	0.016	75.985	10.799	2.942
9	7.433	0.384	0.015	92.924	11.802	2.858
10	7.420	0.365	0.011	109.702	12.871	2.708
11	7.610	0.320	0.013	79.224	13.663	2.449
12	7.674	0.296	0.014	77.179	14.683	2.306
13	7.769	0.282	0.014	77.728	15.437	2.239

Table 8. Characterization of the expansion of squash leaves at 37.8°C.

Leaf Position	Estimated A_{max} (cm^2)	c	S.E. of c	b	t_1	dA/dt at t_1 (cm^2 day^{-1})
1	4.846	0.576	0.029	1.296	0.450	2.792
2	5.090	0.480	0.012	3.353	2.521	2.457
3	5.305	0.539	0.012	14.626	4.977	2.863
4	5.674	0.482	0.013	22.674	6.476	2.735
5	5.796	0.426	0.014	28.963	7.901	2.480
6	5.873	0.388	0.013	37.263	9.325	2.312
7	5.995	0.361	0.011	46.312	10.624	2.217

Table 9. Characterization of the growth of squash plant leaf area at 21.1 to 37.8°C.

Temp	Estimated A_{tla} (cm^2)	c	S.E. of c	95% CI on c Upper	Lower	b
21.1	10.066	0.141	0.004	0.133	0.149	1.680
24.0	10.309	0.135	0.005	0.125	0.145	1.606
27.0	10.820	0.139	0.003	0.132	0.146	1.233
29.4	11.070	0.124	0.003	0.119	0.129	1.137
32.2	10.612	0.165	0.005	0.155	0.174	1.353
35.0	10.537	0.117	0.004	0.109	0.125	1.215
37.8	8.288	0.157	0.005	0.148	0.166	1.262

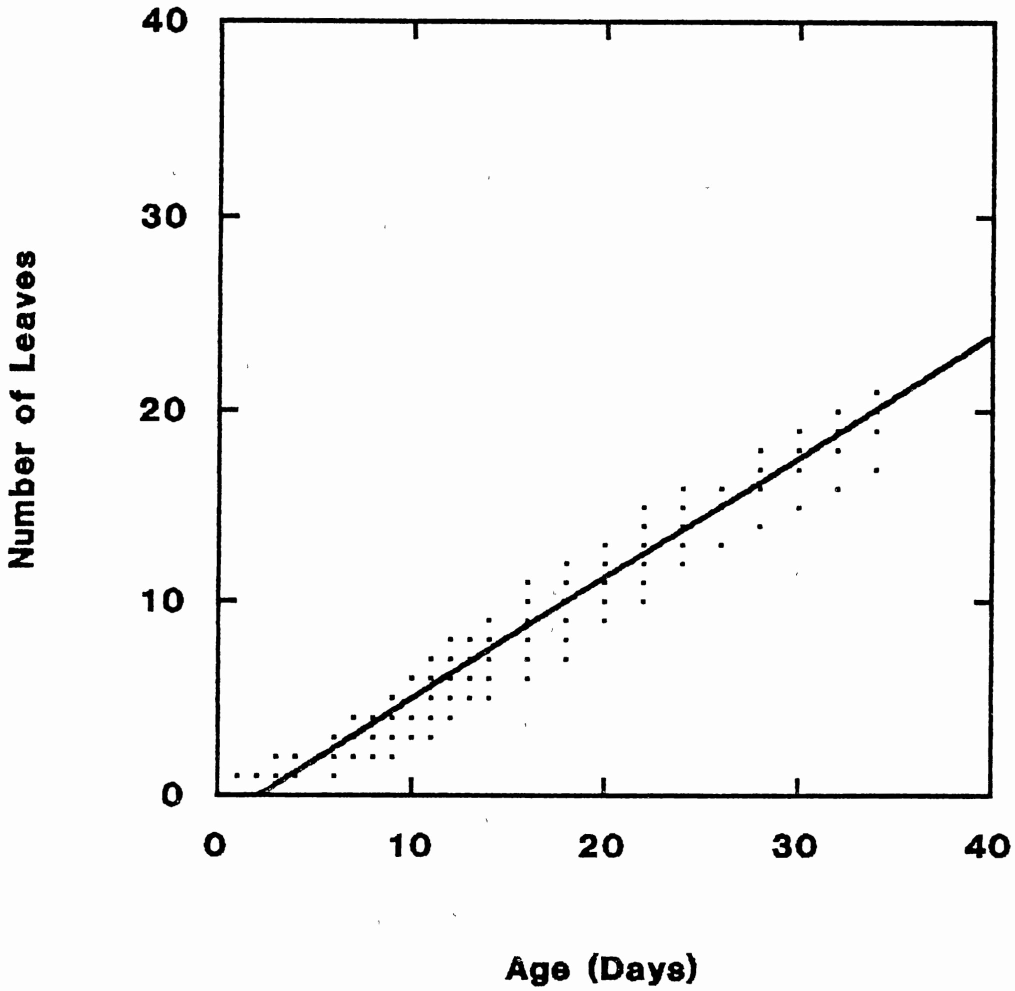

Figure 1. Number of visible leaves vs age at 21.1°C with curve fitted by linear regression analysis.

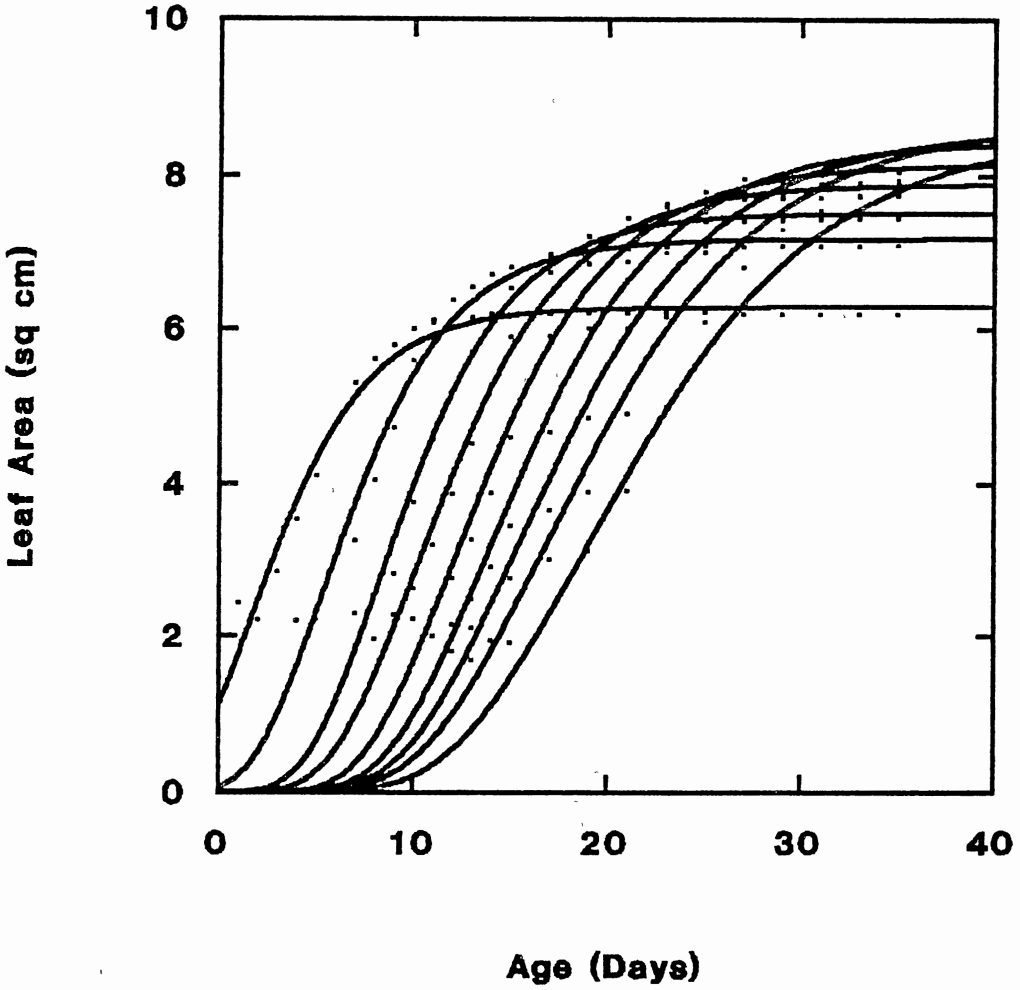

Figure 2. Log_e plot for the expansion of leaves 1-9 on squash grown at 21.1°C. The curve is a Gompertz growth function fitted as described in the text.

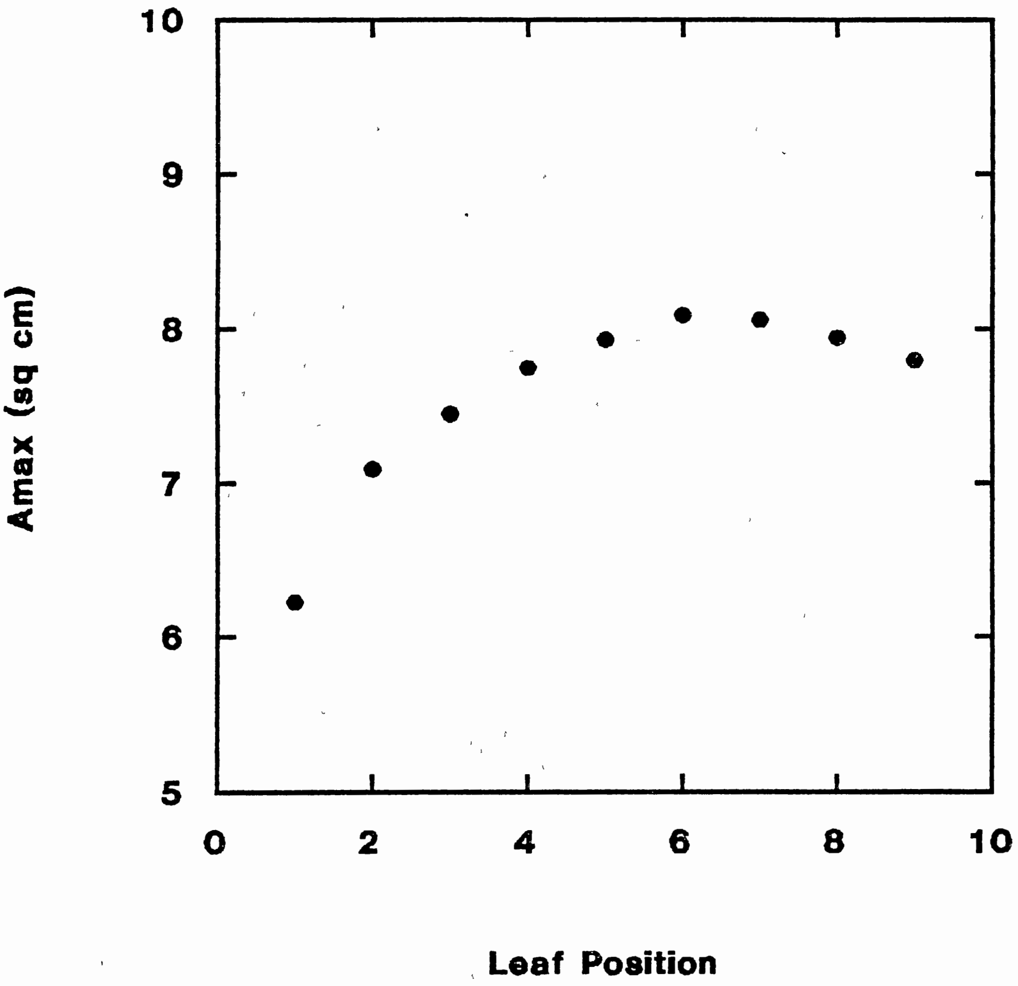

Figure 3. Log_e plot for mean final area, A_{max}, of leaves 1-9 of squash grown at 21.1°C.

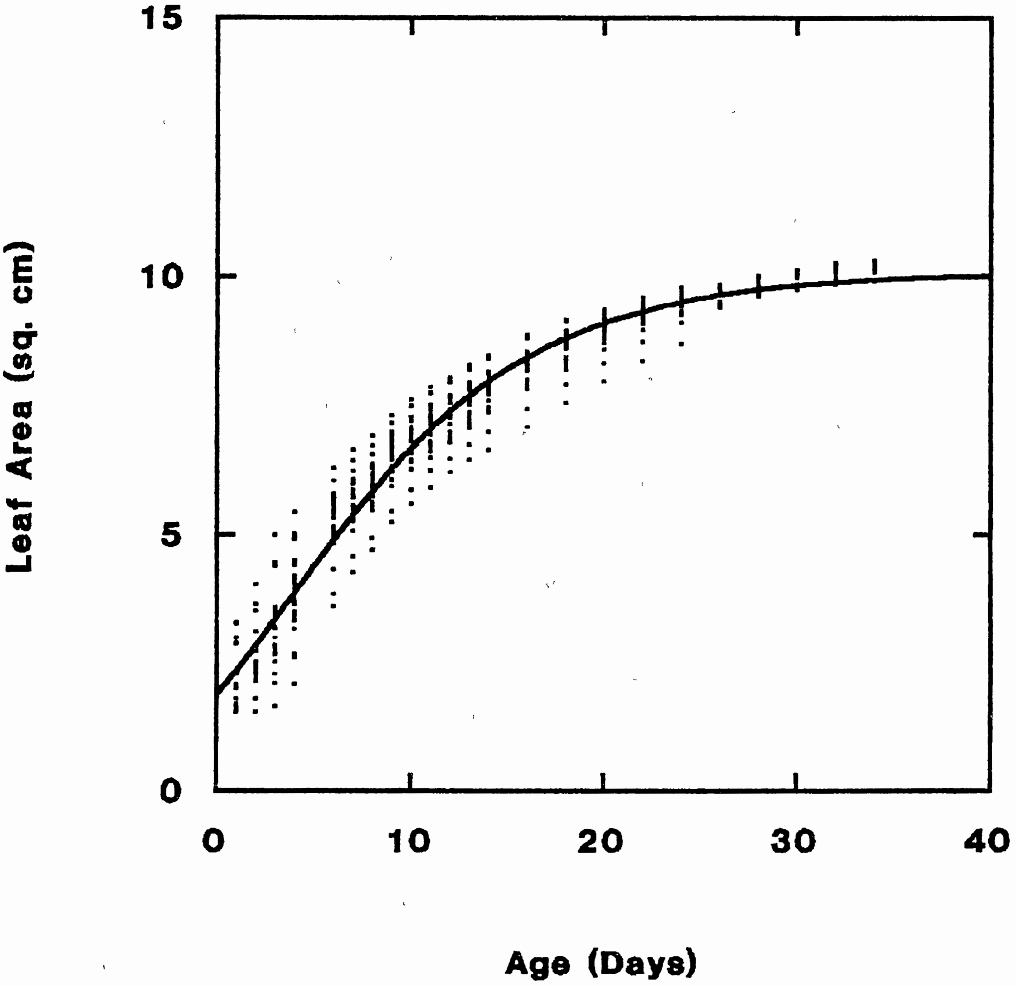

Figure 4. Log_e plot for growth in total leaf surface area of squash grown at 21.1°C. The curve is a Gompertz growth function fitted as described in the text.

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APPENDIX

COMPUTER PROGRAM FOR SIMULATION OF SQUASH BUG POPULATIONS

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GEN,DAVID WOODSON,SB MODEL,7/12/89,20;
LIM,1,3,45000;
NETWORK;
;***
;*** TIME => 1 UNIT = 10 DEGREE DAYS ***
;*** ATR(1)=BIRTHDAY
;*** ATR(2)=OVIPOSITIONAL TIME FOR NEW ADULTS
;*** ATR(3)=DAILY FECUNDITY
;***
BEG    CREATE,,0,1,1,1;
       ACT/1,,,OVWN;FEM ARRIVES
OVWN   ASSIGN,ATR(2)=RNORM(39.48,9.4,1)+TNOW,1;
       ACT/2,,,G1;
G1     GOON,1;
;***
;*** DECIDE TO LAY EGG MASS OR NOT
;*** ASSIGN NUMBER OF EGGS PER MASS
;***
       ACT/3,,0.63,FEC;EGGS
       ACT/4,,0.37,G2;NO EGGS
FEC    ASSIGN,ATR(3)=TRIANG(1,13,37,2),2;
;***
;*** CHECK IF FEMALES HAVE REACHED ADULT LONGEVITY
;***
       ACT/5,,,G2;
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      ACT/6,,,MASS;EGG MASS
G2    GOON,1;
      ACT/7,,ATR(2).LE.TNOW,FDTH;
;***
;*** DELAY BETWEEN EGG MASSES
;***
      ACT/9,RNORM(1.41,1.36,3),,G1;
MASS  UNBATCH,3,1;
      ACT/10,,,EGGS;
;***
;*** ASSIGN BIRTHDAY TO EGGS,ATR(1)
;*** NON-OVIPOSITING FEMALES=XX(1)
;***
EGGS  ASSIGN,ATR(1)=TNOW,1;
      ASSIGN,XX(1)=NNACT(13),1; 1 IN
      ASSIGN,XX(2)=NNACT(15),1; 2 IN
      ASSIGN,XX(3)=NNACT(17),1; 3 IN
      ASSIGN,XX(4)=NNACT(19),1; 4 IN
      ASSIGN,XX(5)=NNACT(21),1; 5 IN
      ASSIGN,XX(6)=NNACT(26),1; MALES
      ASSIGN,XX(7)=NNACT(27)+NNACT(28),1; NONOVIP FEMALES
      ASSIGN,XX(8)=NNACT(9),1; OVIP FRMALES
;***
;*** ASSIGN DEVELOPMENTAL PARAMETERS
;*** ASSIGN SURVIVAL PARAMETERS
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;***
        ACT/11,,0.0272,EDTH;DEAD EGGS
        ACT/12,RNORM(9.74,0.35,4),0.9728,N1;VIABLE EGGS
N1      GOON,1;
        ACT/13,RNORM(2.94,0.11,5),0.9486,N2;N1 DEV TIME
        ACT/14,,0.0514,N1D;
N2      GOON,1;
        ACT/15,RNORM(6.26,0.31,6),0.8857,N3;N2 DEV TIME
        ACT/16,,0.1143,N2D;
N3      GOON,1;
        ACT/17,RNORM(4.20,0.24,7),0.9343,N4;N3 DEV TIME
        ACT/18,,0.0657,N3D;
N4      GOON,1;
        ACT/19,RNORM(5.29,0.27,8),0.9514,N5;N4 DEV TIME
        ACT/20,,0.0486,N4D;
N5      GOON,1;
        ACT/21,RNORM(9.23,0.99,9),0.8414,NTM;N5 DEV TIME
        ACT/22,,0.1586,N5D;
NTM     COLCT,INT(1),NYMPH DEV. TIME,,1;
        ACT/23,,,SEX;
;***
;*** ASSIGN SEX RATIO
;***
SEX     GOON,1;
        ACT/24,,.50,MALE;50% MALE
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      ACT/25,,.50,FEMS;50% FEMALE
MALE  COLCT,INT(1),MALE DEV. TIME,,1;
      ACT/26,RNORM(180.3,78.3,1),,MDTH;MALE LIFE
FEMS  COLCT,INT(1),FEMS DEV. TIME,,1;
;***
;*** ASSIGN REPRODUCTIVE CYCLE
;***
      ACT/27,RNORM(7.58,1.89,2),,PREM;PREM SPAN
PREM  GOON,1;
      ACT/28,RNORM(4.16,2.19,3),,OVIP;PREOVIP SPAN
OVIP  ASSIGN,ATR(2)=RNORM(90.23,31.81,4)+TNOW,1;REST OF LIFE
      ACT/29,,,G1;
;***
;*** DEATH AND TERMINATE NODES ***
;***
EDTH  COLCT,ALL,DUD EGGS,,1;
      TERM;
N1D   COLCT,ALL,DEAD N1,,1;
      TERM;
N2D   COLCT,ALL,DEAD N2,,1;
      TERM;
N3D   COLCT,ALL,DEAD N3,,1;
      TERM;
N4D   COLCT,ALL,DEAD N4,,1;
      TERM;
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N5D   COLCT,ALL,DEAD N5,,1;
      TERM;
FDTH  COLCT,INT(1),DEAD FEMALES,,1;
      TERM;
MDTH  COLCT,INT(1),DEAD MALE,,1;
      TERM;
      END NETWORK;
RECORD,TNOW,DEGREE DAYS X 10,0,B,2.5,;
      VAR,NNACT(12),E,VIABLE EGGS;
      VAR,XX(1),1,1ST INSTARS;
      VAR,XX(2),2,2ND INSTARS;
      VAR,XX(3),3,3RD INSTARS;
      VAR,XX(4),4,4TH INSTARS;
      VAR,XX(5),5,5TH INSTARS;
      VAR,XX(6),M,MALES;
      VAR,XX(7),N,NONOVIP FEMALES;
      VAR,XX(8),O,OVIP FEMALES;
INIT,0,70;
FIN;
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VITA

William David Woodson

Candidate for the Degree of

Doctor of Philosophy

Thesis: MODELING SEASONAL DEVELOPMENT OF SQUASH BUGS (HETEROPTERA: COREIDAE) AND SQUASH

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Minor Field: Statistics

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Personal Data: Born in Seminole, Texas, August, 25 1956, the son of Sidney B. and Nancy L. Woodson.

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