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BIOLOGICAL STUDIES ON APHIDOLETES APHIDIMYZA (RONDANI) (DIPTERA:CECIDOMYIIDAE) AND ITS USE IN BIOLOGICAL CONTROL OF THE APPLE APHID APHIS POMI DEGEER (HOMOPTERA:APHIDIDAE)

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JOSEPH GRANT MORSE

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# BIOLOGICAL STUDIES ON *APHIDOLETES APHIDIMYZA* (RONDANI) (DIPTERA:CECIDOMYIIDAE) AND ITS USE IN BIOLOGICAL CONTROL OF THE APPLE APHID *APHIS POMI* DEGEER (HOMOPTERA:APHIDIDAE)

By

Joseph Grant Morse

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ABSTRACT

BIOLOGICAL STUDIES ON APHIDOLETES APHIDIMYZA (RONDANI) (DIPTERA:CECIDOMYIIDAE) AND ITS USE IN BIOLOGICAL CONTROL OF THE APPLE APHID APHIS POMI DEGEER (HOMOPTERA:APHIDIDAE)

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Aphidoletes aphidimyza is a larval predator which appears to show considerable promise in biological control of the apple aphid in Michigan commercial apple orchards. In addition, this cecidomyiid has potential as an aphid predator on a variety of agricultural crops, limited only by the susceptibility of the midge to dessication under conditions of low humidity.

A simulation model of apple aphid development and reproduction during summer months was first constructed from literature data using the heat unit concept with lower and upper developmental thresholds of 37 and 95°F. respectively. Model output was compared with field sleeve cage data.

Laboratory experiments on basic features of cecidomyiid biology were conducted to determine: (1) egg and larval developmental thresholds and developmental periods (larvae provided with excess aphids), (2) larval functional response to aphid density, (3) adult female longevity and fecundity under optimal conditions and (4) search and oviposition behavior of females. Field experiments in commercial orchards

were performed to investigate: (1) the timing and form of cecidomyiid pupal emergence from overwintering sites in the soil, (2) the use of aphid infested trap plants in monitoring adult occurance in both commercial and natural environments and (3) levels of cecidomyiid predation using terminal sleeve cages.

Data from the apple aphid model and field and laboratory experiments were combined to form a predation simulation model. Larvae appear to kill up to 45 apple aphids per cecidomyiid in commercial orchards.

Future research is needed on adult female search and oviposition behavior. Since larval mobility is limited, female behavior "regulates" the impact of cecidomyiid predation. Additional priorities in future research to further refine the predation simulation model are presented.

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# I. INTRODUCTION

The major insect and mite pests of Michigan commercial apple orchards may be classified into 3 categories: direct key pests, secondary (indirect) pests and sporadic pests (both direct and indirect) (Croft 1975a, Brunner and Howitt 1981, see Table 1). Direct pests cause direct damage to apple (i.e. to the fruit itself). The very low tolerance for fruit damage and infestation at harvest dictates that direct pests be held to very low levels in commercial apple orchards. Indirect pests of apple feed on leaves or woody portions of the tree and because of their indirect action may be tolerated at low to moderate levels. Because of this higher economic threshold for indirect pests, natural enemies of these species may often play important roles in commercial apple orchards. Sporadic pests are those species rarely found at economic levels in commercial apple orchards although they may occasionally appear and influence pest management decisions.

For the past 15 to 20 years, direct key pest control has relied heavily on the use of broadspectrum organophosphate (O-P) insecticides (Croft 1979). To date no direct key pest has developed resistance to O-Ps (Croft 1981). Although improved monitoring and prediction techniques for direct key pests (eg. Thompson et al. 1974, Riedl and Croft 1978, Welch et al. 1978) may assist in reducing unnecessary sprays, control of direct key pests of apple will most likely continue to depend on insecticide applications.

TABLE 1. Major Arthropod Pests Occurring in Apple Orchards of Michigan (adapted from Croft 1975a, Brunner and Howitt 1981)

---

DIRECT KEY PESTS
- codling moth - *Laspeyresia pomonella* L.
- plum curculio - *Conotrachelus nenuphar* Herbst
- apple maggot - *Rhagoletis pomonella* Walsh
- oriental fruit moth - *Grapholitha molesta* Busck
- red-banded leafroller - *Argyrotaenia velutinana* Walker

SECONDARY PESTS

APHIDS
- apple aphid - *Aphis pomi* DeGeer
- rosy apple aphid - *Dysaphis plantaginea* (Passerini)
- wooly apple aphid - *Erisoma lanigerum* (Hausmann)

MITES
- European red mite - *Panonychus ulmi* (Koch)
- two-spotted spider mite - *Tetranychus urticae* Koch
- apple rust mite - *Aculus schlechtendali* (Nalepa)

SCALES
- San Jose scale - *Quadraspidiotus perniciosus* (Comstock)
- oystershell scale - *Lepidosaphes ulmi* (L.)
- European fruit Lecanium scale - *Lecanium corni* (Bch.)

OTHERS
- oblique-banded leafroller - *Choristoneura rosaceana* Harris
- white apple leafhopper - *Typhlocyba pomaria* MacAtee
- tentiform leafminer - *Phyllonorycter blancardella* (F.)
- tarnished plant bug - *Lygus lineolaris* (P.de B.)

SPORADIC PESTS
- fruit tree leafroller - *Archips argyrospilus* Walker
- tufted apple budmoth - *Platynota idaeusalis* Walker
- variegated leafroller - *Platynota flavedana* Clemens
- green fruitworms - F. Noctuidae
- eyespotted bud moth - *Spilonota ocellana* Denis
- lesser appleworm - *Grapholitha prunivora* Walsh
- apple curculio - *Tachypterellus quadrigibbus* (Say)

The history of the response of secondary pests and their associated natural enemies to O-Ps applied for direct key pest control may be divided into 3 phases (Croft and Hoyt 1978, Croft 1979). Initially both secondary pests and natural enemies were controlled to very low levels by O-Ps (Phase I). Quite rapidly several secondary pests (especially mites and aphids, see Figure 1 in Croft 1980) developed resistance to O-Ps and caused severe problems in apple because of the absence of their natural enemies (Phase II). O-Ps continued to be used for control of direct key pests and after a period of years (Phase III), several natural enemies of secondary pests developed resistance (especially mite predators, Croft and Brown 1975, Croft 1977).

With the appearance of resistant natural enemies, the potential for integrated pest management (IPM) programs for secondary pest control has increased. Croft (1975b) has developed an IPM program for apple pest mites in Michigan utilizing the O-P resistant predatory mite Amblyseius fallacis. Suitable predator-prey ratios are maintained within the context of direct pest control through the conservation of mite predators with selective pesticides and proper cultural practices.

Within the past decade a cecidomyiid predator of aphids, Aphidoletes aphidimyza (Rondani), has become more common in commercial apple orchards (Adams 1977, Adams and Prokopy 1980). Warner (1981) has shown that O-P tolerant/resistant strains of this species are present in Michigan orchards

where they show considerable promise as biological control agents of the apple aphid, Aphis pomi.

This study was undertaken to investigate the possibility of utilizing this predator in an IPM program for aphid control similar to that already developed for phytophagous mites. The objectives of this project were threefold:

(1) To accumulate and organize existing biological data on the apple aphid (A. pomi) so that a simulation model of aphid development and reproduction could be developed (Section III),

(2) To gather basic biological data on the cecidomyiid predator A. aphidimyza through literature review and laboratory and field experiments (Section IV),

(3) To combine aphid and cecidomyiid biological data into a predation simulation model which could serve to (Section V):

(a) Evaluate the impact of cecidomyiid predation in apple aphid control and

(b) Orient future research on aphid-cecidomyiid population dynamics.

## II. GENERAL COMMENTS ON MATERIALS AND METHODS

### A. LABORATORY EXPERIMENTS

#### 1. Greenhouse Aphid Colonies

Greenhouse adapted pea aphids [Acyrthosiphon pisum (Harris)] and green peach aphids [Myzus persicae (Sulzer)] were used in many of the laboratory and field experiments as hosts for A. aphidimyza (both aphid colonies had been reared in MSU greenhouses for at least 3 years and were of unknown origin). Both species were reared in isolated 40x45x60 cm. screen covered cages in a greenhouse room attached to the Pesticide Research Center on the MSU campus. Pea aphids were chosen as the primary food source for the laboratory cecidomyiid colony because of their large size, rapid reproduction and ease of manipulation. They were reared on fava bean plants (Vicia fava L., purchased from W. Atlee Burpee Co., Clinton, IA, listed as long pod fava beans) grown in 14 cm. diameter clay pots with 5-15 bean plants per pot.

Green peach aphids were used in the larval functional response experiment because they were closer in size to apple aphids (see Section IV-C-3). These aphids were reared on turnip (Brassica rapa L., purple top, white globe - Northrop King seeds Minneapolis, MN) and jimsonweed (Datora stramoniom L., seeds collected from wild plants from the Lansing area courtesy of Lynn Oates) plants potted in 10.5 cm. diameter plastic pots.

## 2. Laboratory Cecidomyiid Colony

A laboratory A. aphidimyza colony was maintained in room B10 of the Pesticide Research Center at MSU for use in laboratory and field experiments. Room temperature and relative humidity averaged 25.15°C. (range 23.3-27.1) and 45% (25-100) as measured using a hygrothermograph. Two or four 60 Watt 2.4 m. flourescent lamps (suspended 10 cm. above each cage) provided an artificial light source with a 16:8 light/dark cycle (on 4am-8pm). A single 25 Watt light bulb (on 6pm-6am) was suspended 5-8 m. above the rearing cages to provide light for adult mating and oviposition (studies by Mansour 1976 indicate maximal oviposition at low light intensities with few eggs laid in unilluminated cages) and to allow for observation of adults after 8pm.

The initial laboratory cecidomyiid colony (1979-80 colony) was started with approximately 200 larvae (mostly $2^{nd}$ and $3^{rd}$ instars) collected on July 6, 1979 from apple aphid and rosy apple aphid colonies at the MSU Graham Horticulture Research Station near Grand Rapids, MI. In order to increase the colony size, approximately 300 eggs were collected from the Rose Lake Wildlife Station near Lansing, MI (using aphid infested trap plants to attract ovipositing females) on August 28, 1980 and were added to the eggs from the initial colony. This 1979-80 colony (made up of individuals collected from both sources) was carried through 18 distinct generations (from egg to first egg of the next generation) until the colony was discarded in May 1980 to make space available for the

1980-81 colony. Individuals from the 1979-80 colony were utilized in the (1) cecidomyiid egg development experiment (Section IV-C-1), (2) emergence cage testing experiment (Section IV-D-1) and (3) diapause seeding experiment (Section IV-D-1), with the remainder of the experiments utilizing the 1980-81 colony.

The 1980-81 colony was composed of eggs and larvae collected on four dates from the Graham Research Station. Approximately 85 larvae were collected on July 28, 1980 and another 300 on July 31. Approximately 600 and 250 eggs were collected on August 28-31 and September 1-4 respectively. The 1980-81 colony was carried through 15 distinct generations with 500-2500 adults produced per generation. Each generation consisted of 3-7 cages containing cecidomyiids reared from eggs laid over a 2-5 day period (see Table 2). Eggs for each cage were produced by adults from 2-4 cages of the previous generation (for example cage A eggs usually resulted from cages A and B of the previous generation; B from A,B,C; etc.).

Each cage held up to 12 clay pots (14 cm. in diameter), each pot containing 5-15 fava bean plants infested with pea aphids. Silica sand or vermiculite was spread on the base of each cage to provide pupation sites for mature larvae. The cages were placed in water filled trays to provide isolation.

As adult cecidomyiids appeared in a cage, 2-6 aphid infested pots (when possible young plants each 5 cm. tall were used so that a healthy aphid population would be supported for as long as possible; each pot was initially infested with approximately 100 pea aphids) were introduced into the cage for predator egg collection (if possible, colonies were worked with from 8am-noon

TABLE 2. 1980-81 Cecidomyiid Colony

| Generation | Cage | Date Eggs Laid | Generation | Cage | Date Eggs Laid |
|---|---|---|---|---|---|
| 1 | A | 8/12-8/14 | 9 | A | 1/12-1/13 |
| | B | 8/15-8/16 | | B | 1/14-1/17 |
| | C | 8/17-8/22 | | C | 1/18-1/19 |
| | | | | D | 1/20-1/21 |
| 2 | A | 8/27/8/29 | | E | 1/22-1/23 |
| | B | 8/30-9/2 | | F | 1/24-1/26 |
| | C | 9/3-9/4 | | | |
| | D | 9/5-9/7 | 10 | A | 1/27-1/29 |
| | | | | B | 1/30-2/1 |
| 3 | A | 9/12-9/17 | | C | 2/2-2/4 |
| | B | 9/18-9/21 | | D | 2/5-2/6 |
| | C | 9/22-9/23 | | E | 2/7-2/8 |
| | D | 9/24-9/26 | | F | 2/9-2/11 |
| 4 | A | 10/2-10/6 | 11 | A | 2/15-2/16 |
| | B | 10/7-10/9 | | B | 2/17-2/20 |
| | C | 10/10-10/12 | | C | 2/21-2/23 |
| | D | 10/13-10/15 | | D | 2/24-2/25 |
| | | | | E | 2/26-2/27 |
| 5 | A | 10/23-10/25 | | F | 2/28-3/1 |
| | B | 10/26-10/28 | | | |
| | C | 10/29-10/30 | 12 | A | 3/6-3/9 |
| | D | 10/31-11/2 | | B | 3/10-3/12 |
| | E | 11/3-11/5 | | C | 3/13-3/16 |
| | F | 11/6-11/9 | | D | 3/17-3/18 |
| | | | | E | 3/19-3/20 |
| 6 | A | 11/10-11/15 | | F | 3/21-3/22 |
| | B | 11/16-11/18 | | G | 3/23-3/24 |
| | C | 11/19-11/20 | | | |
| | D | 11/21-11/22 | 13 | A | 3/29-3/30 |
| | E | 11/23-11/26 | | B | 3/31-4/1 |
| | | | | C | 4/2-4/3 |
| 7 | A | 11/30-12/3 | | D | 4/4-4/5 |
| | B | 12/4-12/9 | | E | 4/6-4/7 |
| | C | 12/10-12/11 | | F | 4/8-4/11 |
| | D | 12/12-12/14 | | | |
| | E | 12/15-12/17 | 14 | A | 4/14-4/17 |
| | | | | B | 4/18-4/19 |
| 8 | A | 12/19-12/25 | | C | 4/20-4/22 |
| | B | 12/26-12/28 | | D | 4/23-4/25 |
| | C | 12/29-12/30 | | E | 4/26-4/27 |
| | D | 12/31-1/2 | | F | 4/28-5/1 |
| | E | 1/3-1/4 | | | |
| | F | 1/5-1/7 | 15 | A | 5/2-5/5 |
| | | | | B | 5/6-5/8 |

while adults were inactive; later in the afternoon adults became more active, and thus were more likely to escape from the cage). After several nights of oviposition, adults were removed from the plants (by tapping or blowing) and the pots were placed in a new cage. Aphid abundance was carefully monitored especially during periods of peak larval feeding and aphids were removed or added as necessary. After all larvae had dropped into the soil to pupate (about half pupated in the soil in the pots with the remainder in the sand on the cage floor) the bean stems were cut and removed and the pots stacked in the back of the cage to provide room for later introduction of plants for egg collection. The removal of the old stems insured that eggs would be laid on only the new plants.

Frequent watering (a minimum of every 2 days) was essential for maintenance of a healthy cecidomyiid colony in order to provide adequate plant growth for the aphids, high humidity conditions for the larvae and adequate soil moisture for the pupating cecidomyiids (sand on the cage floor and soil in the pots was watered after removal of the stems to maintain moisture levels for the pupae; the vermiculite and sand aided in water retention).

3. Hygrothermograph Records

Temperature and relative humidity records were maintained for several laboratory and field experiments. Hygrothermographs used were Bendix Model 549 and Weather Measure Corp. Model H311 using 1 week strip charts. Both models recorded degrees Fahrenheit and were calibrated weekly using a thermometer

(± 1°F.) and dial hygrometer (± 5%).

Estimates of constant temperature in laboratory experiments were calculated by averaging hourly hygrothermograph readings. Simulations of field conditions utilized daily maximum and minimum (from noon of the previous day to noon of the given day) temperatures (see Section VII-C for maximum and minimum temperatures for various field sites).

4. Adult Cecidomyiid Aspirator

Adult cecidomyiids are extremely fragile but are quite easy to collect if handled gently in morning hours (6am-2pm) when they are fairly inactive. An oversized aspirator was constructed using 1.5 cm. diameter plastic tubing which when combined with a very gentle aspiration pressure resulted in acceptable adult mortality (<10%).

5. Environmental Chambers

Several Sears Coldspot refrigerators which had been modified using the methods of Platner et al. (1973) were utilized in constant temperature laboratory experiments. Interior dimensions were 45x45x72 cm. with illumination provided by a single 15 Watt fluorescent lamp set on a 16:8 light-dark schedule (on 4am-8pm). Since plants were isolated (mainly from ants) by small water-filled trays, the humidity bath was discarded. A hygrothermograph was placed in the refrigerator to monitor temperature and relative humidity.

## B. FIELD EXPERIMENTS

### 1. Field Research Sites

#### a. Klein 1979,1980

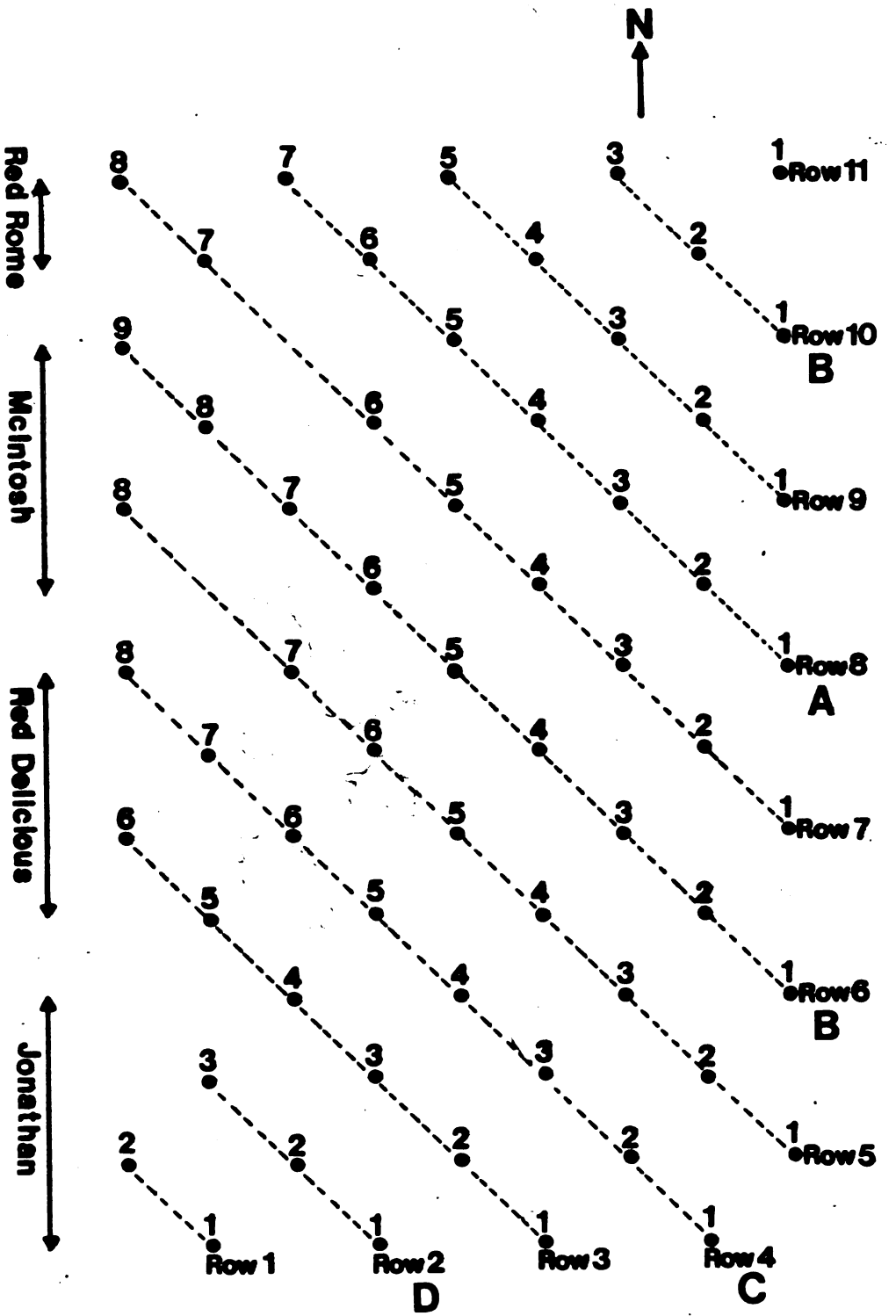
Two apple orchard blocks were used in several field experiments in 1979 and 1980. The first was a commercial block near Sparta, MI owned and operated by Joe Klein. The second block was part of the MSU Graham Horticulture Research Station located just west of Grand Rapids, MI.

The southeast block of Klein's orchard (12239 Fruit Ridge Rd., at the corner of Fruit Ridge and 13 Mile Rd.) was used in 1979 and 1980 to monitor cecidomyiid emergence from overwintering sites in the soil (Section IV-D-1). This block was chosen because large cecidomyiid populations were observed during July and early August of 1978 and 1979. The block consisted of approximately 415 standard sized trees of McIntosh, Jonathan, Spy and Banana varieties.

#### b. Graham 1980

Block 12 of the Graham Station was used in 1980 for a number of experiments. The Graham Station is a 3-3/4 acre research station containing apple, pear, cherry, plum and peach trees for horticultural research. Block 12 consists of 60 standard sized trees planted on seedling rootstock with Virginia Crab interstock. The block was planted in 1951 with a 8.5 m. tree spacing on the diagonal and contains 17 Jonathan, 18 Red Delicious, 16 McIntosh and 9 Red Rome trees (see Block 12 Map - Figure 1). The block is surrounded to the north by an open field, to the east by

FIGURE 1. Graham Station Block 12 (60 trees)



Block 10 and 11 (similar in structure to 12), to the south by a block of mixed variety apple trees and to the west by a block of young mixed variety trees (transplanted in 1978).

Pruning during the dormant season was performed to remove shoot growth in the inner portions and base of the tree. Weak and non-bearing limbs were also removed. Section VII-D contains the spray record for Block 12 and other apple trees on the Graham Station (see Figure 1 for fungicide treatment rows A-D).

2. Emergence Cages

Cone shaped emergence cages were used in 1979 and 1980 to trap cecidomyiid adults emerging from overwintering sites in the soil. The cages had a base diameter of 76 cm. and thus covered an area of .46 $m^2$. The cages were constructed of wire mesh screening with openings 1.6x1.6 mm. The cone was 66 cm. in height with an apex opening 11 cm. in diameter. A collection chamber was constructed from a jello mold 21 cm. in diameter and 6 cm. high. The inside lip of the mold was shortened to a height of 3 cm. The collection chamber was fit tightly over the emergence cone apex, filled with 2-5 cm. of a 1:2 ethylene glycol/water mixture and covered with a piece of plastic wrap (polyethylene) secured by a rubber band. Cecidomyiid larvae released into the cage in the laboratory were observed to fly upwards into the collection chamber where they eventually contacted the ethylene glycol and were captured (see results of laboratory tests on emergence cage trap efficiency, Section IV-D-1).

### 3. Sleeve Cages

Sleeve cages were constructed to enclose aphid and cecidomyiid infested apple terminals. The sleeves were built of white nylon parachute cloth (100% nylon, .88 oz./square yard, purchased from Army Surplus) and were approximately 50 cm. in length with a diameter of 20 cm. One end was sewn shut and the other end was slipped over the terminal and secured with a string.

The sleeve cages were tested using a Lamda Instruments Corp. LI-185 Quantum/Radiometer/Photometer (courtesy of Dr. Jim Flore) which showed light penetration reduced by the nylon cloth 21.08%. Temperatures and relative humidities inside the sleeve cages were estimated by enclosing a hygrothermograph with 3 apple terminals inside a specially constructed oversized sleeve cage (see Section VII-C).

# III. APPLE APHID SIMULATION

## A. INTRODUCTION

### 1. Prevalence and Host Plants

The apple aphid (Aphis pomi DeGeer) is of European origin and was first reported damaging young apple trees in the eastern United States in 1849 (Matheson 1919). It presently occurs throughout the apple growing areas of the United States and Canada as well as in Europe and Asia (Baker and Turner 1916, Brunner and Howitt 1981).

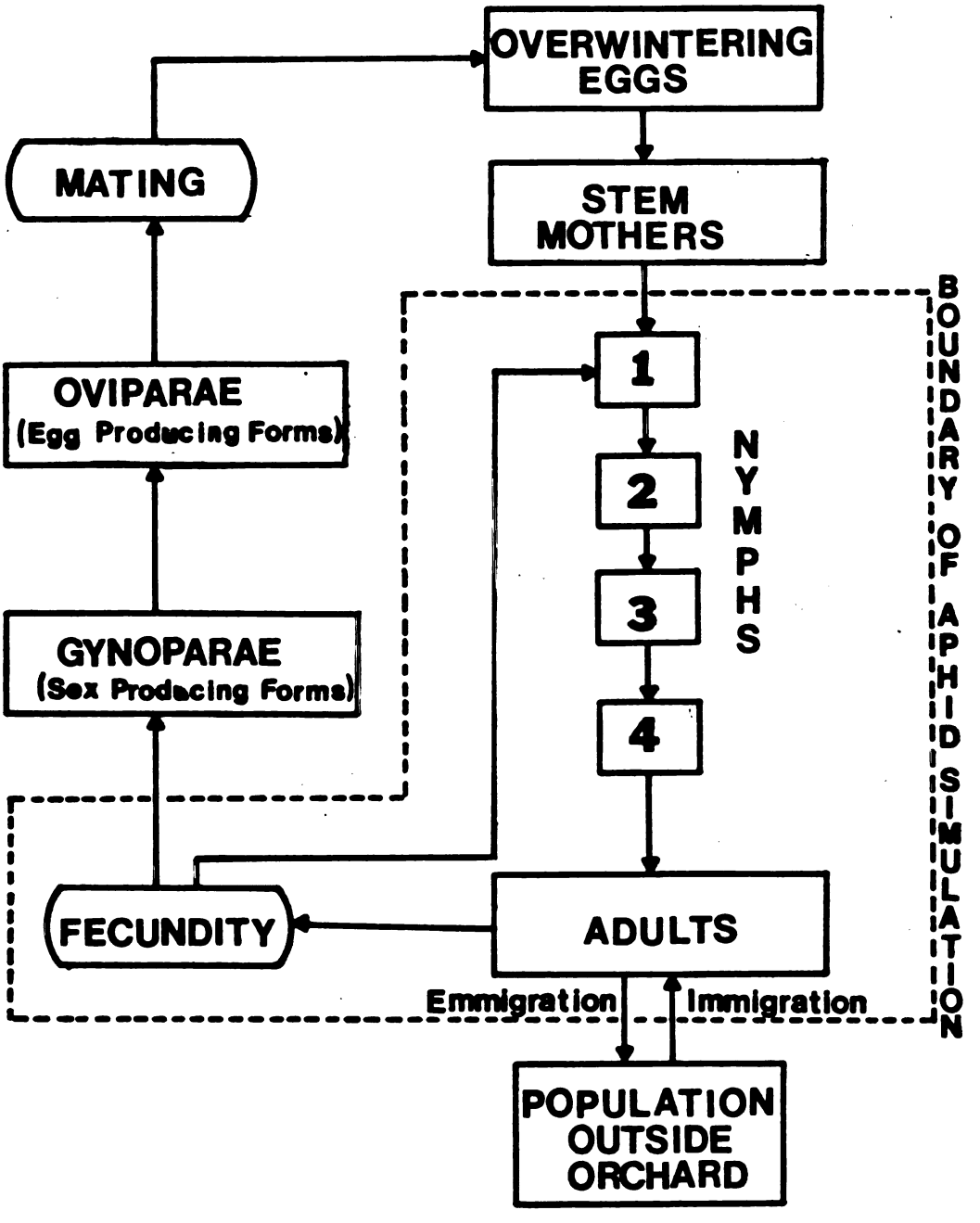
Patch (1923) lists 5 species of plants in the rose family (Rosaceae) upon which overwintering eggs are laid including apple (Malus sylvestris Mill.) and pear (Pyrus japonica Thunb.). Both Patch (1923) and Evenhuis (1963) indicate they believe the majority of overwintering eggs are laid on trees other than apple.

Patch (1923) also lists 49 species of plants in 24 different families upon which summer generations of the apple aphid have been observed. The majority of reports of large summer populations deal with apple and to a lesser extent pear although Fluckiger et al. (1978) have observed high levels on hawthorn (Crataegus monogyna).

### 2. Life Cycle on Apple

The life cycle of the apple aphid is depicted in Figure 2. The aphid overwinters as a diploid egg laid on the bark of water sprouts and terminals that have grown the previous season (Peterson 1918). Eggs hatch in mid-April to early May and give rise to the fundatrix or stem mother. The stem

FIGURE 2. Life Cycle of the Apple Aphid



mother is the first of a large number of summer parthenogenic generations. Three morphological forms of summer parthenogenic females are observed on apple. The majority of the 2nd generation (the offspring of the stem mothers) and lesser proportions of succeeding summer generations are composed of alate (winged) viviparous females which serve as the major means of population dispersal. Factors known to increase the ratio of alatae/apterae (wingless) aphids in other aphid species include high aphid density, poor host plant condition, ancestry and temperature/photoperiod (Lees 1966). The apterae (wingless viviparous females) are the most abundant form in the 3rd and following summer generations under uncrowded conditions. A relatively small number of aphids in each of the summer generations is observed to be of an intermediate form (Baker and Turner 1916, Matheson 1919). During August to September the sexual forms are produced which mate and lay the overwintering eggs.

3. Economic Importance on Apple

Table 3 lists the problems associated with large apple aphid populations on apple (adapted from Adams 1977). The greatest impact is on young trees where large populations may reduce growth and development. Apple aphids are rarely a severe problem on mature trees with standard rootstocks (Madsen et al. 1975, Brunner and Howitt 1981) although large continuous populations can cause economic damage due to deposition of honeydew on the fruit which provides an excellent medium for the growth of sooty mold fungus.

TABLE 3. Problems Associated with Large A. pomi Populations on Apple (adapted in part from Adams 1977)

1. Feeding on fruits.
2. Leaf curling.
3. Stunting of terminal growth, reduction of fruit size by large populations (Brunner and Howitt 1981).
4. Possible transmission of organism causing fireblight, Erwinia amylovora (Oatman and Legner 1961, Cutright 1963, Plurad et al. 1965). Later work by Plurad et al. 1967 have questioned A. pomi's role as a fireblight vector.
5. Honeydew may serve as primary food source for adult apple maggot, Rhagoletis pomonella (Neilson and Wood 1966, Boush et al. 1969).
6. Excretion of honeydew with subsequent growth of sooty mold fungus (Fumago vagans Fries) on fruits and foliage.
7. Overall effect on tree quality caused by nutrient withdrawal (poorly quantified).

## B. OBJECTIVE AND METHODOLOGY

### 1. Objectives

The objective of Section III was to develop a simulation model of apple aphid development and reproduction during summer months (June 1 - August 31) on a single apple terminal. This simulation was then coupled with the cecidomyiid development and predation simulation of Section V.

### 2. Use of the Heat Unit Concept

For a review of this concept see Davidson (1944), Andrewartha and Birch (1973) and Campbell et al. (1974). Since insects are poikilothermic animals, development would be expected to proceed as some function of accumulated heat units. A simple assumption proposed by Oettingen (1879) is a linear relationship between rate of development (inverse of developmental time if at constant temperature) and temperature. Several studies since have shown the actual relationship to be curvilinear (Janisch 1925, Davidson 1944), the departure from linearity being most pronounced at the extremes of temperature. The types of errors introduced by assuming the linear relationship are discussed in Arnold (1959), Campbell et al. (1974) and Gutierrez and Wang (1977).

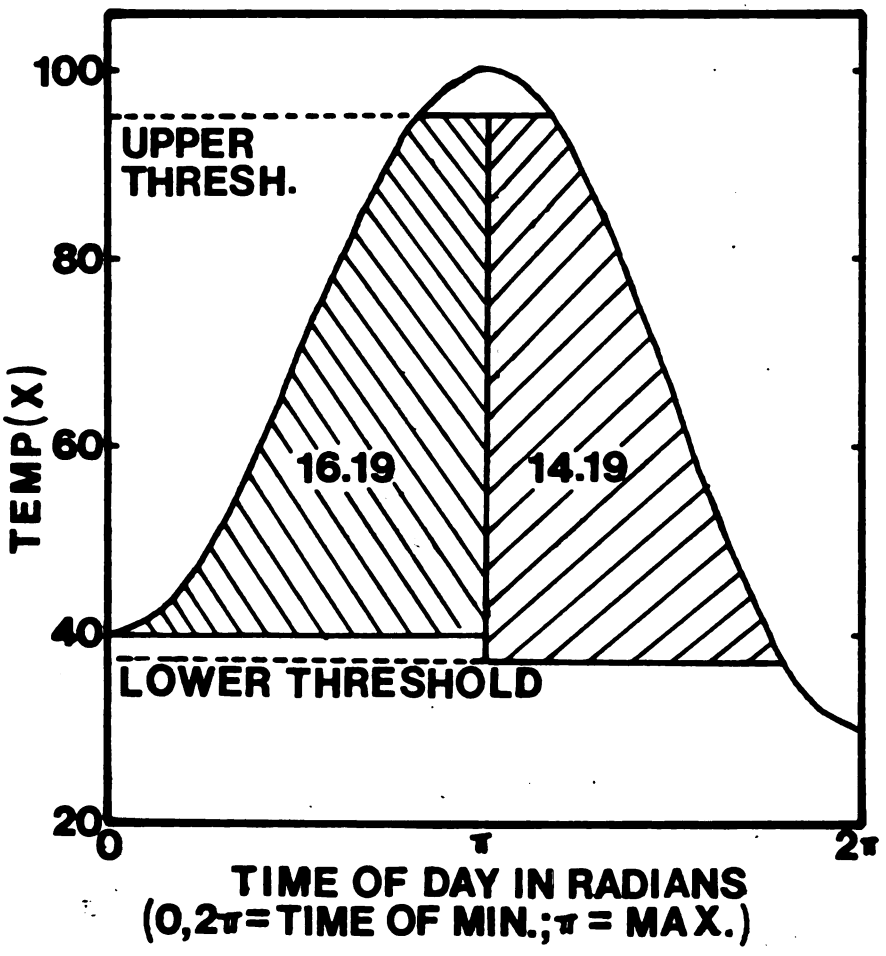
The majority of biological data accumulated in this thesis is expressed using heat unit accumulations above a theoretical developmental threshold (with the linear relationship assumption) as the independent variable. Daily field temperature fluctuations are assumed to approximate a modified 3-point sine wave (Baskerville and Emin 1969,

Allen 1976, see Subroutine DEGD in Section VII-B-2) fit to daily maximum and minimum temperatures. Figure 3 depicts an example of a heat unit calculation using the 3-point sine wave on a hypothetical day with a maximum temperature of 100°F. and minimums of 40° and 30°F. (minimum that morning and the night following, respectively). Heat units are calculated by integrating under the sine wave below an upper developmental threshold of 95°F. and above a lower threshold of 37°F. (note that the Fahreheit scale is used because both climatological records and hygrothermograph charts are scaled in °F.).

3. Methodology

The majority of model parameters for the aphid section were estimated from analysis of literature data (Section III-C). The output of the simulation model constructed using these parameters was then compared with data obtained from 34 sleeve cages placed on aphid infested terminals at Graham Station during the summer of 1980. Additional model parameters (which were unavailable from literature sources) were then estimated by "tuning" the simulation model with the aphid sleeve cage data. Model structure, estimated model parameters and simulation results are presented in Section III-D.

FIGURE 3. Sine Wave Simulation of Diurnal Temperatures




EQUATIONS: AMP= (MAX-MIN)/2
TBAR= (MAX+MIN)/2
TEMP(X)= AMP*SIN(X-PI/2)+TBAR

PARAMETERS:

| | First Half Day | Second Half |
|---|---|---|
| Maximum Temperature (°F.) | 100 | 100 |
| Minimum Temperature (°F.) | 40 | 30 |
| AMP | 30 | 35 |
| TBAR | 70 | 65 |
| Calculated Heat Units | 16.19 | 14.19 |

Lower Threshold= 37°F.
Upper Threshold= 95°F.

## C. LITERATURE REVIEW AND ANALYSIS

### 1. Determination of Thermal Developmental Thresholds

#### a. Lower Threshold

Lathrop (1923) measured development times (from date of birth to date first young produced) for 20 aphids held in sleeve cages on apple terminals at Corvallis, OR during the summer of 1920. He also calculated the mean temperature over the developmental period of each aphid (the average of 1/2 hour temperature readings on a recording thermometer). He plotted average temperature versus days to develop (Figure 8 in his paper) and estimated the lower developmental threshold to be 41°F. (5°C.) using a hyperbolic relationship between average temperature and days.

Lathrop's original data (as they appear in Table 5 of his paper, see Table 5 of this paper) are reanalyzed using linear regression (Figure 4). In Figure 4, the inverse of days to develop is plotted versus mean temperature, resulting in a $r^2$ value of .70 and a theoretical developmental threshold of 37.2°F. (using the x-intercept method of Arnold 1959). Note that this linear regression method is more accurate but mathematically equivalent to Lathrop's hyperbolic curve method.[1]

---

[1]Equivalence may be seen as follows:

Linear Regression: $1/D = mT + c$ D = days to develop, T = average temperature, c = x-intercept

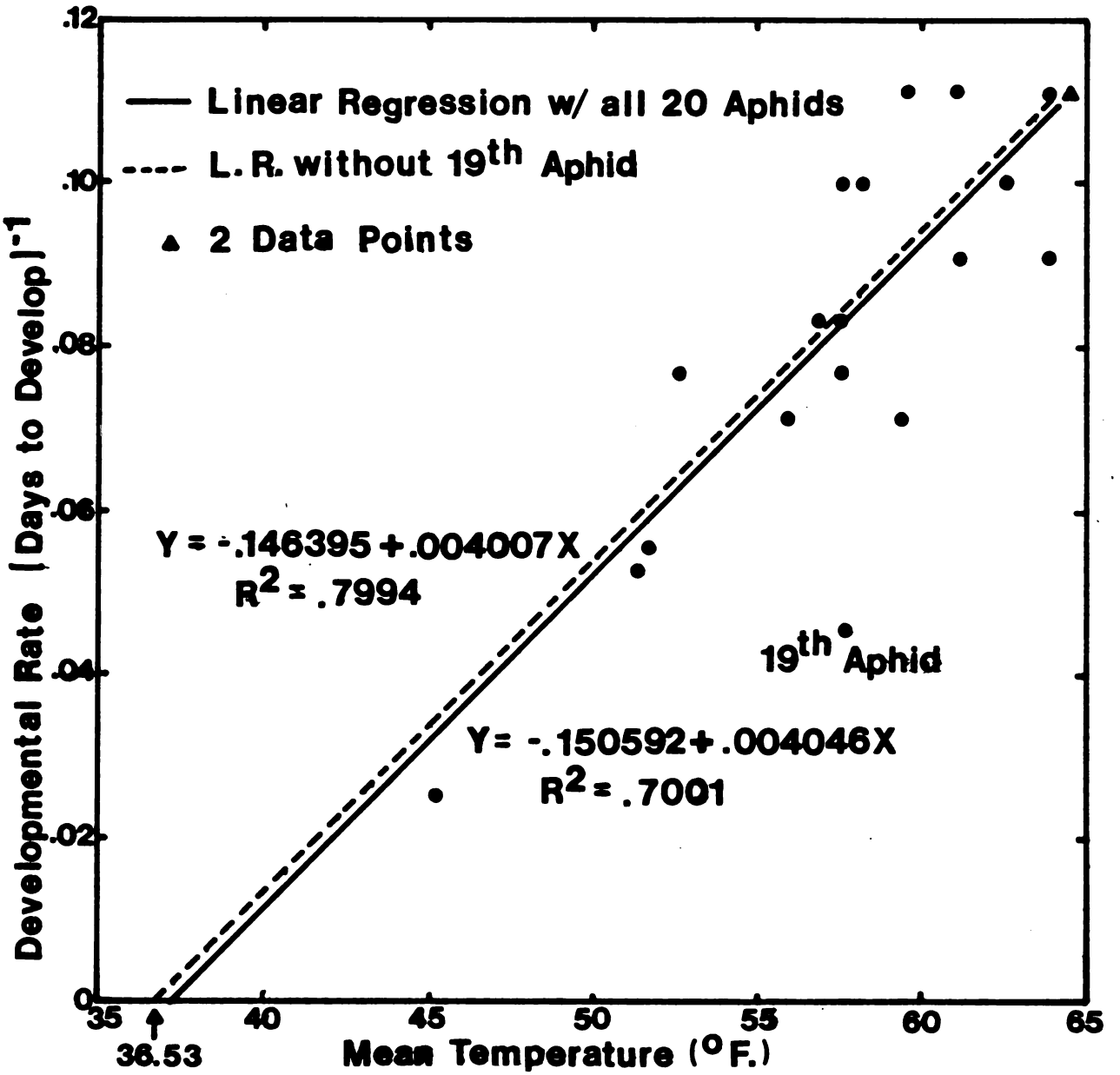
$1/Dm = T + c/m$

$D = (1/m)/(T + c/m)$

Lathrop's Hyperbolic Equation: $x = a/(y-b)$; x = days to develop, y = average temperature, b = his threshold

These are equivalent with $1/m = a, b = -c/m$

FIGURE 4. Aphid Developmental Rate Versus Mean Temperature (Data from Lathrop 1923)



Lathrop noted that aphid no. 19 was reared on mature foliage which retarded its development (see $19^{th}$ aphid in Figure 4). This data point was deleted from the data set and a new linear regression performed resulting in an $r^2$ value of .80 and a theoretical developmental threshold of $36.5^{o}F$.

A second method of calculating the base temperature is the lowest coefficient of variation method (Arnold 1959). Heat unit summations are calculated for a data set using various base temperatures and the one giving the least variation is chosen as the lower theoretical developmental threshold. These two methods are equivalent when using the same temperature profile (Arnold 1959), although the x-intercept method is quicker and has the advantage of indicating any departures from the assumed linear relationship between temperature and developmental rate.

The lowest coefficient of variation method was also used in analysis of Lathrop's (1923) 19 aphids. Daily maximum and minimum temperatures (from Table 2 of his paper) were used with Subroutine DEGD (see Section VII-B-2, daily temperature fluctuations were assumed to be in the form of a sine wave fit to daily maximum and minimums) to calculate heat unit sums over the developmental period for each aphid. Sums are listed in Table 4 and include 1/2 of the heat units on the day the aphid was born and none of the heat units on the day first young were produced. As can be seen from Table 4, this method indicates $42^{o}F$. as the best lower developmental threshold versus $37^{o}F$. using the x-intercept method.

TABLE 4. Coefficient of Variation Determination of Base Temperature

| Lower Threshold (°F.) | Upper Threshold (°F.) | Mean Heat Units for 19 aphids ($\bar{x}$) | Standard Deviation (Sx) | Coefficient of Variation (Sx/$\bar{x}$) |
|---|---|---|---|---|
| 36 | 95 | 260.458 | 46.468 | .178 |
| 37 | 95 | 248.684 | 42.396 | .170 |
| 38 | 95 | 237.416 | 39.477 | .166 |
| 39 | 95 | 226.184 | 36.528 | .162 |
| 40 | 95 | 215.153 | 33.949 | .158 |
| 41 | 95 | 204.353 | 31.725 | .155 |
| 42 | 95 | 193.784 | 29.893 | .154 |
| 43 | 95 | 183.447 | 28.470 | .155 |
| 44 | 95 | 123.353 | 27.373 | .158 |

Most studies to date using a heat unit calculation for the apple aphid (Lathrop 1923, 1928, Westigard and Madsen 1965, Specht 1970, 1972, Jokinen 1980) have used Lathrop's (1923) 41°F. (5°C.) threshold. Since more accurate temperature data was used in the x-intercept method (1/2 hour temperature readings versus daily maximum and minimums) I have chosen to use the 37°F. lower theoretical developmental threshold. Certainly more data (calculations are based on 19 aphids reared at a single site) is needed to resolve this question. Note that the accuracy of the lower threshold is of importance only when the range of temperature fluctuations frequently crosses the threshold (during early and late season).

b. Upper Threshold

LeRoux (1959) noted 48 and 95% reductions in two apple aphid populations sampled after a 3-day exposure to temperatures averaging 90°F. in Rougemont, Quebec. Madsen et al. (1975) observed that prolonged high temperatures (up to 110°F.) caused considerable apple aphid mortality in a California orchard. Based on observations over a 3-year period at Watsonville, CA, Westigard and Madsen (1965) stated that temperatures below 90°F. had no appreciable effect on apple aphid populations but that prolonged exposure to temperatures above 95°F. caused aphid mortality. Based on these reports an upper developmental threshold of 95°F. with a horizontal cutoff was used (Baskerville and Emin 1968, see Figure 3). Since daily summer temperatures in Michigan rarely average 95°F. or greater (based on climatological records) aphid mortality from high temperatures was assumed to be negligible.

## 2. Nymph Developmental Period

Many factors influence the rate of nymph development including temperature, humidity, tree nutrient status and aphid density. For the purposes of the aphid simulation, nymph development was modeled on the basis of heat unit accumulations for the months of June-August. The effects of poor tree nutrient status and high aphid density were modeled by reducing aphid fecundity using scalar functions (see Section III-D-4).

Data for estimation of nymph developmental parameters comes from aphid cage studies from Ithaca, NY (Matheson 1919) and Corvallis, OR (Lathrop 1923). Table 5 contains heat unit totals (over the nymph developmental period) for this data calculated using Subroutine DEGD (Section VII-B-1). Table 6 summarizes the data organized by the month of birth. For the 119 aphids born June 1 - August 31 the mean developmental period was 272.19 $\pm$ 63.98 HU (Heat Units $\pm$ standard deviation with thresholds 37,95; see Figure 8 for a comparison of literature data from Table 6 and the results of the simulation model).

## 3. Adult Fecundity and Survival

Model parameters for adult fecundity and survival were obtained through analysis of the life histories of 39 aphids (generations 2-8 in Reproduction Chart 1 of his paper, apterous females only) reared by Matheson (1919) at Ithaca, NY during the summer of 1915. Adult longevity (in terms of heat units) was first calculated and is displayed in Table 7. Adults lived an average of 655.79 $\pm$ 154.35 heat units (see

TABLE 5. HEAT UNITS CALCULATED FOR NYMPH DEVELOPMENTAL PERIOD

A. Data for 60 aphids reared at Ithaca, NY in 1915 by Matheson (1919). Temperature data from U.S. Weather Service, Climatological Data 1915 for Ithaca, NY.

| Generation | Date Born | Heat Units[1] | Generation | Date Born | Heat Units |
|---|---|---|---|---|---|
| 1 | 4/25 | 3* (331.7) | 7 | 7/14 | 3* (306.8) |
| | 4/26 | 319.1 | | 7/14 | 344.3 |
| | 4/28 | 227.1 | | 7/16 | 268.8 |
| 2 | 5/14 | 445.8 | 8 | 7/21 | 396.3 |
| | 5/14 | 310.3 | | 7/24 | 265.0 |
| | 5/17 | 419.5 | 9 | 7/29 | 591.6 |
| | 5/17 | 441.5 | | 8/1 | 438.0 |
| 3 | 6/1 | 455.5 | | 8/2 | 2* (397.8) |
| | 6/3 | 6* (408.8) | | 8/3 | 368.0 |
| | 6/3 | 311.1 | 10 | 8/15 | 3* (255.0) |
| 4 | 6/11 | 358.0 | | 8/15 | 288.6 |
| | 6/12 | 350.3 | | 8/17 | 287.5 |
| | 6/12 | 294.1 | 11 | 8/23 | 319.3 |
| | 6/13 | 263.8 | | 8/23 | 250.8 |
| | 6/14 | 265.5 | | 8/24 | 3* (317.0) |
| | 6/14 | 229.0 | | 8/24 | 283.7 |
| 5 | 6/24 | 2* (303.0) | 12 | 8/29 | 348.0 |
| | 6/24 | 329.8 | 13 | 9/4 | 464.0 |
| | 6/25 | 282.2 | | 9/5 | 389.8 |
| | 6/25 | 309.0 | | 9/5 | 460.8 |
| 6 | 7/4 | 313.2 | | 9/6 | 357.5 |
| | 7/4 | 276.6 | | 9/6 | 397.5 |
| | 7/4 | 351.6 | | | |

B. Data for 72 aphids reared at Corvallis, OR in 1919 by Lathrop (1923). Temperature data from U.S. Weather Service, Climatological Data 1919 for Albany, OR (near Corvallis).

| Aphid Number | Date Born | Heat Units | Aphid Number | Date Born | Heat Units |
|---|---|---|---|---|---|
| 1 | 3/31 | 383.6 | 10 | 6/10 | 275.8 |
| 2 | 4/29 | 301.6 | 11 | 6/12 | 270.2 |
| 3 | 5/17 | 292.9 | 12 | 6/13 | 229.0 |
| 4 | 6/2 | 277.7 | 13 | 6/17 | 274.0 |
| 5 | 6/3 | 276.5 | 14 | 6/18 | 250.2 |
| 6 | 6/4 | 250.0 | 15 | 6/20 | 239.0 |
| 7 | 6/5 | 250.3 | 16 | 6/21 | 239.3 |
| 8 | 6/6 | 256.3 | 17 | 6/22 | 240.3 |
| 9 | 6/9 | 268.0 | 18 | 6/23 | 219.3 |

[1]Heat units totals (37,95)calculated using Subroutine DEGD include ½ of the day of birth and none on the day first young were produced. Multiple data points indicated as n*(H) (n aphids, with H heat units over the developmental period).

TABLE 5 (cont.)

B. Corvallis, OR 1919 (cont.)

| Aphid Number | Date Born | Heat Units | Aphid Number | Date Born | Heat Units |
|---|---|---|---|---|---|
| 19 | 6/24 | 253.0 | 46 | 8/11 | 231.0 |
| 20 | 6/25 | 272.8 | 47 | 8/12 | 240.8 |
| 21 | 6/26 | 275.5 | 48 | 8/13 | 214.8 |
| 22 | 6/27 | 255.7 | 49 | 8/14 | 287.0 |
| 23 | 6/28 | 268.0 | 50 | 8/16 | 244.3 |
| 24 | 6/29 | 217.2 | 51 | 8/19 | 268.0 |
| 25 | 6/30 | 267.7 | 52 | 8/20 | 293.6 |
| 26 | 7/1 | 275.6 | 53 | 8/21 | 257.8 |
| 27 | 7/2 | 270.9 | 54 | 8/23 | 253.5 |
| 28 | 7/3 | 242.6 | 55 | 8/24 | 283.1 |
| 29 | 7/4 | 269.7 | 56 | 8/25 | 293.0 |
| 30 | 7/6 | 257.7 | 57 | 8/26 | 266.5 |
| 31 | 7/7 | 306.3 | 58 | 8/27 | 278.0 |
| 32 | 7/8 | 331.5 | 59 | 8/28 | 317.3 |
| 33 | 7/9 | 268.8 | 60 | 8/29 | 306.3 |
| 34 | 7/11 | 268.8 | 61 | 8/30 | 516.2 |
| 35 | 7/12 | 322.1 | 62 | 8/31 | 284.0 |
| 36 | 7/13 | 296.1 | 63 | 9/1 | 300.0 |
| 37 | 7/14 | 219.1 | 64 | 9/2 | 280.0 |
| 38 | 7/16 | 252.2 | 65 | 9/3 | 332.8 |
| 39 | 7/29 | 269.8 | 66 | 9/5 | 315.5 |
| 40 | 7/30 | 272.3 | 67 | 9/6 | 294.5 |
| 41 | 7/31 | 278.5 | 68 | 9/8 | 308.2 |
| 42 | 8/3 | 214.1 | 69 | 9/10 | 265.8 |
| 43 | 8/4 | 379.0 | 70 | 9/11 | 298.5 |
| 44 | 8/7 | 293.7 | 71 | 9/13 | 368.1 |
| 45 | 8/8 | 292.0 | 72 | 9/16 | 314.3 |

C. Data for 20 aphids reared at Corvallis, OR in 1920 by Lathrop (1923). Temperature data from Lathrop (1923, see Section III-C-1-a).

| Aphid Number | Date Born | Heat Units | Aphid Number | Date Born | Heat Units |
|---|---|---|---|---|---|
| 1 | 3/28 | 351.2 | 11 | 6/27 | 230.5 |
| 2 | 5/3 | 195.6 | 12 | 6/30 | 231.8 |
| 3 | 5/13 | 273.1 | 13 | 7/7 | 274.0 |
| 4 | 5/16 | 262.8 | 14 | 7/9 | 223.5 |
| 5 | 5/31 | 243.5 | 15 | 7/18 | 250.8 |
| 6 | 6/2 | 279.8 | 16 | 7/28 | 228.3 |
| 7 | 6/9 | 243.1 | 17 | 8/12 | 305.0 |
| 8 | 6/14 | 250.8 | 18 | 8/20 | 299.3 |
| 9 | 6/17 | 194.3 | 19 | 8/20 | 482.4[2] |
| 10 | 6/21 | 184.5 | 20 | 8/23 | 203.1 |

[2] 19th aphid reared on mature foliage was deleted in average developmental period calculation (see Section III-C-1-a).

TABLE 6. Nymph Developmental Period Arranged by Month of Birth

| Month Born | Site & Year[1] | Number | Developmental Period (Heat Units) Mean | Standard Deviation |
|---|---|---|---|---|
| March-April | Itha 1915 | 5 | 322.2 | 45.3 |
| | Alba 1919 | 2 | | |
| | Corv 1920 | 1 | | |
| May | Itha 1915 | 4 | 320.6 | 92.3 |
| | Alba 1919 | 1 | | |
| | Corv 1920 | 4 | | |
| June | Itha 1915 | 19 | 286.4 | 63.9 |
| | Alba 1919 | 22 | | |
| | Corv 1920 | 7 | | |
| July | Itha 1915 | 11 | 293.8 | 67.5 |
| | Alba 1919 | 16 | | |
| | Corv 1920 | 4 | | |
| August | Itha 1915 | 16 | 297.9 | 62.3 |
| | Alba 1919 | 21 | | |
| | Corv 1920 | 3 | | |
| September | Itha 1915 | 5 | 343.2 | 61.8 |
| | Alba 1919 | 10 | | |
| | Corv 1920 | 0 | | |

[1]Sites and data sources were:
Ithaca, NY, 1915 - Matheson (1919)
Albany, OR, 1919 - Lathrop (1923)
Corvallis, OR, 1920 - Lathrop (1923)

TABLE 7. Adult Aphid Longevity

Heat units over the adult life are calculated for the 39 aphids in generations 2-8 (apterous females only) from the data of Matheson (1919)

| Generation | Day 1st Young | Day Died | Heat Units (37,95)[1] |
|---|---|---|---|
| 2 | 6/9 | 7/9 | 845.5 |
| | 6/9 | 7/12 | 936.0 |
| | 6/10 | 7/2 | 626.1 |
| | 6/4 | 6/19 | 452.1 |
| | 6/4 | 6/20 | 479.0 |
| 3 | 6/15 | 7/5 | 578.7 |
| | 6/18 | 7/6 | 503.8 |
| | 6/18 | 7/2 | 383.6 |
| | 6/18 | 7/13 | 706.8 |
| | 6/18 | 7/16 | 818.1 |
| | 6/18 | 7/17 | 854.8 |
| | 6/18 | 7/17 | 854.8 |
| | 6/18 | 7/4 | 448.3 |
| 4 | 6/25 | 7/20 | 783.3 |
| | 6/24 | 7/18 | 738.0 |
| | 6/22 | 7/19 | 810.0 |
| | 6/22 | 7/18 | 774.5 |
| | 6/24 | 7/14 | 591.3 |
| | 6/22 | 7/22 | 889.5 |
| | 6/22 | 7/9 | 466.2 |
| 5 | 7/5 | 7/21 | 515.0 |
| | 7/5 | 7/22 | 539.8 |
| | 7/5 | 7/26 | 675.8 |
| | 7/6 | 7/19 | 433.5 |
| | 7/6 | 7/29 | 746.0 |
| 6 | 7/15 | 8/6 | 755.8 |
| | 7/14 | 8/1 | 630.5 |
| | 7/16 | 8/1 | 555.5 |
| | 7/19 | 8/10 | 734.8 |
| | 7/15 | 7/27 | 410.0 |
| 7 | 7/24 | 8/14 | 726.7 |
| | 7/24 | 8/7 | 497.5 |
| | 7/24 | 8/9 | 561.5 |
| | 7/25 | 8/16 | 761.0 |
| | 7/25 | 8/8 | 492.3 |
| 8 | 8/1 | 8/22 | 675.8 |
| | 8/2 | 8/25 | 737.3 |
| | 8/8 | 9/6 | 852.2 |
| | 8/7 | 9/1 | 734.5 |
| | | | 655.8 ± 154.4 |
| | | | Range 383.6 - 436.0 |

[1]Heat units include ½ of the amount on the day of death and all of the heat on the first day young were produced.

Figure 10 for a comparison of simulation model output and literature data from Table 7).

Adult fecundity was estimated by calculating cumulative fecundity of the 39 aphids based on a heat unit scale (Table 8). Average fecundity for Matheson's (1919) 39 aphids was 60.72 offspring per female (see Figure 11 for comparison of simulation model output and literature data from Table 8).

TABLE 8. Adult Aphid Fecundity[1]

| Heat Units (37,95) | Cumulative Aphids Born to 39 Females | Cumulative Young Per Female |
|---|---|---|
| 0- 20 | 137 | 3.51 |
| 20- 40 | 184 | 4.72 |
| 40- 60 | 313 | 8.03 |
| 60- 80 | 417 | 10.69 |
| 80-100 | 513 | 13.15 |
| 100-120 | 623 | 15.97 |
| 120-140 | 722 | 18.51 |
| 140-160 | 840 | 21.54 |
| 160-180 | 943 | 24.18 |
| 180-200 | 1035 | 26.54 |
| 200-220 | 1129 | 28.95 |
| 220-240 | 1217 | 31.21 |
| 240-260 | 1307 | 33.51 |
| 260-280 | 1410 | 36.15 |
| 280-300 | 1503 | 38.54 |
| 300-320 | 1624 | 41.64 |
| 320-340 | 1713 | 43.92 |
| 340-360 | 1822 | 46.72 |
| 360-380 | 1904 | 48.82 |
| 380-400 | 1974 | 50.62 |
| 400-420 | 2056 | 52.72 |
| 420-440 | 2093 | 53.67 |
| 440-460 | 2133 | 54.69 |
| 460-480 | 2194 | 56.26 |
| 480-500 | 2236 | 57.33 |
| 500-520 | 2248 | 57.64 |
| 520-540 | 2275 | 58.33 |
| 540-560 | 2304 | 59.08 |
| 560-580 | 2313 | 59.31 |
| 580-600 | 2326 | 59.64 |
| 600-620 | 2343 | 60.08 |
| 620-640 | 2346 | 60.15 |
| 640-660 | 2352 | 60.31 |
| 660-680 | 2357 | 60.44 |
| 680-700 | 2361 | 60.54 |
| 700-720 | 2366 | 60.67 |
| 720-740 | 2366 | 60.67 |
| 740-760 | 2367 | 60.69 |
| 760-780 | 2367 | 60.69 |
| 780-800 | 2367 | 60.69 |
| 800-820 | 2368 | 60.72 |

[1]Data based on cumulative fecundity of 39 females (Matheson 1919) calculated on a heat unit scale.

## D. APPLE APHID SIMULATION

### 1. Simulation Structure

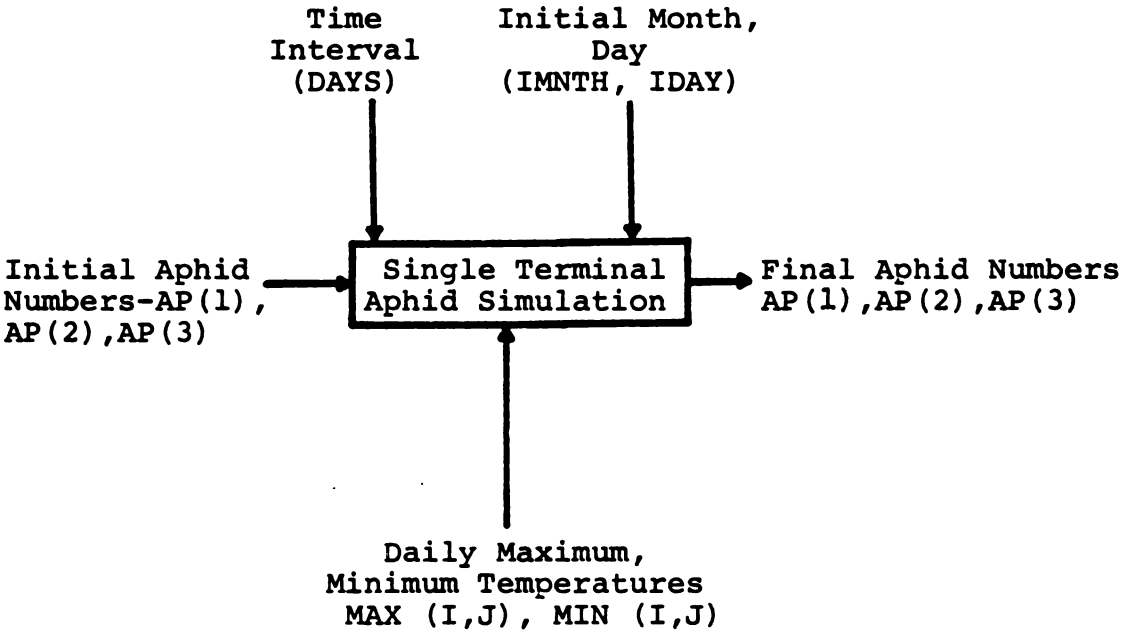
Figure 5 presents a black box model of the single-terminal aphid simulation. Aphids were classified into 3 categories: (1) the number of $1^{st}$ + $2^{nd}$ instar nymphs = AP(1), (2) the number of $3^{rd}$ + $4^{th}$ instars = AP(2) and the number of adults = AP(3) (both apterae and alatae). Future aphid numbers were predicted on the basis of heat units accumulated.

Figure 6 depicts a flowchart of the simulation. Nymphs and adults were aged and fecundity computed using a time step of 5 heat units with output printed every ½ day. The following 2 sections describe the nymph and adult developmental models respectively.

### 2. Nymph Developmental Model

Nymph development was modeled using a distributed delay developmental model (Manetsch 1976, see conceptual diagram in Figure 7). The advantage of using the distributed delay over a discrete delay (such as the one used for adult development - see Figure 9) is that variability in nymph maturation times was introduced. The distributed delay is characterized by two parameters: (1) DEL - the mean delay time in heat units (set to 272.19, see Section III-C-2) and (2) K - the number of substages in the delay process. The variability in nymph maturation times is related to K and DEL by the equation $Sx^2 = DEL^2/K$ (where $Sx^2$ is the

FIGURE 5. Black Box Model of Aphid Simulation




Explanation of Variables:

AP(1) - Number of $1^{st}$, $2^{nd}$ instar apple aphids

AP(2) - Number of $3^{rd}$, $4^{th}$ instar apple aphids

AP(3) - Number of adult aphids

DAYS - Time interval in half day units

IMNTH - Month simulation starts on (6-8 i.e. June-August)

IDAY - Day simulation starts on (1-31)

MAX (I,J) - Maximum temperature on month = I, day = J

MIN (I,J) - Minimum temperature on month = I, day = J

FIGURE 6. Flowchart of Aphid Simulation

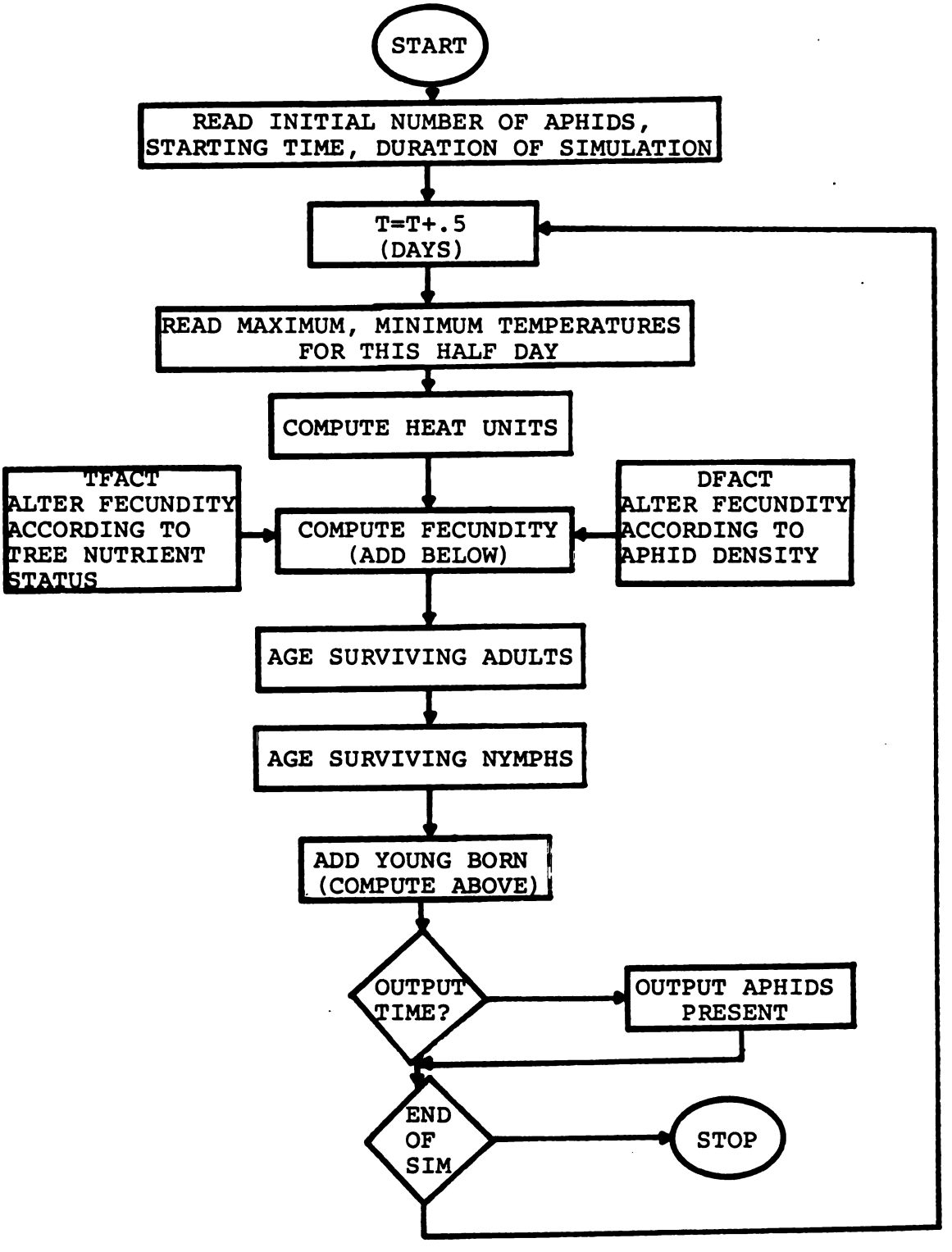
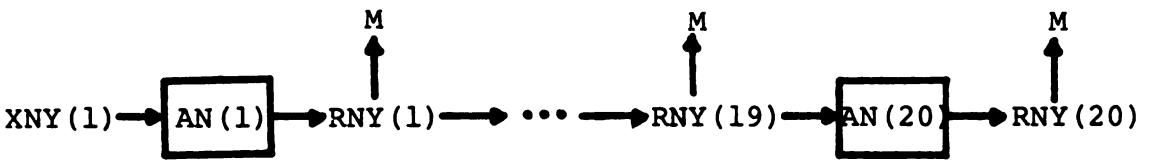


FIGURE 7. Conceptual Diagram of Nymph Distributed Delay Developmental Model (After Manetsch 1976)




$$DEL = 272.19$$

$$K = 20$$

$$PLR = .00038$$

$$DT = 5$$

$$RNY(i,T+DT) = RNY(i,T) + A*(R(i-1,T) - B*R(i,T))$$

$$A = K*DT/DEL$$

$$B = 1 + PLR*DEL/K$$

$$AN(i) = RNY(i)*DEL/K$$

$$AP(1) = \sum_{i=1}^{6} AN(i)$$

$$AP(2) = \sum_{i=7}^{20} AN(i)$$

Explanation of Variables and Parameters:

XNY(1) - input rate variable into nymph stage
XNY(2) - output rate variable out of nymph stage = RNY(20)
RNY(i) - array of K intermediate rates, the outputs of the K substages of the delay process
AN(i) - storage in the $i^{th}$ substage
M - mortality (set by PLR)
DEL - mean delay for nymph development (in heat units)
K - number of substages in the delay process
PLR - proportional loss rate (PLR = .00038 results in average mortality of 10% over the nymph stage)
T - time expressed in heat units
DT - time increment in heat units
AP(1) - total first and second instar aphids
AP(2) - total third and fourth instar aphids

square of the standard deviation). Using the data of Section III-C-2, K was set to 20 ($K = 272.19^2/63.98^2 = 18.10$; each instar was initially assumed to be of equal duration; K was set to 20 so that each instar was represented by 5 substages). Figure 8 compares developmental times for the literature data from Table 5 with the output of the distributed delay model using the above parameters.

No literature data was found on nymph mortality rates. Nymph mortality in the present simulation was set to 10% distributed evenly over the nymph developmental period.

A time step of heat units was chosen for the aphid simulation (nymph and adult development and fecundity were updated every 5 heat units). This time step was large enough to prevent excessive computer costs while small enough to avoid numerical instability (the distributed delay fails to conserve flow if DT<DEL/(2*K).

3. Adult Survivorship and Fecundity Model

Adult survivorship was simulated using a discrete delay developmental model (Manetsch and Park 1977, Ch. 12). A distributed delay model was initially attempted but was abandoned due to an inability to accurately simulate adult fecundity while maintaining biological realism.

Figure 9 presents a conceptual diagram of the adult discrete delay model in which the adult stage is divided into 18 equally spaced substages. The contents of each substage were moved into the next substage (minus mortality) every 50 heat units (10 time steps). Input into the first

FIGURE 8. Aphid Nymph Development

Developmental times of the 119 nymphs born June 1 - August 31 (Table 5) are compared with the output of the nymph distributed delay simulation model with parameters DEL= 272.19, K=20.

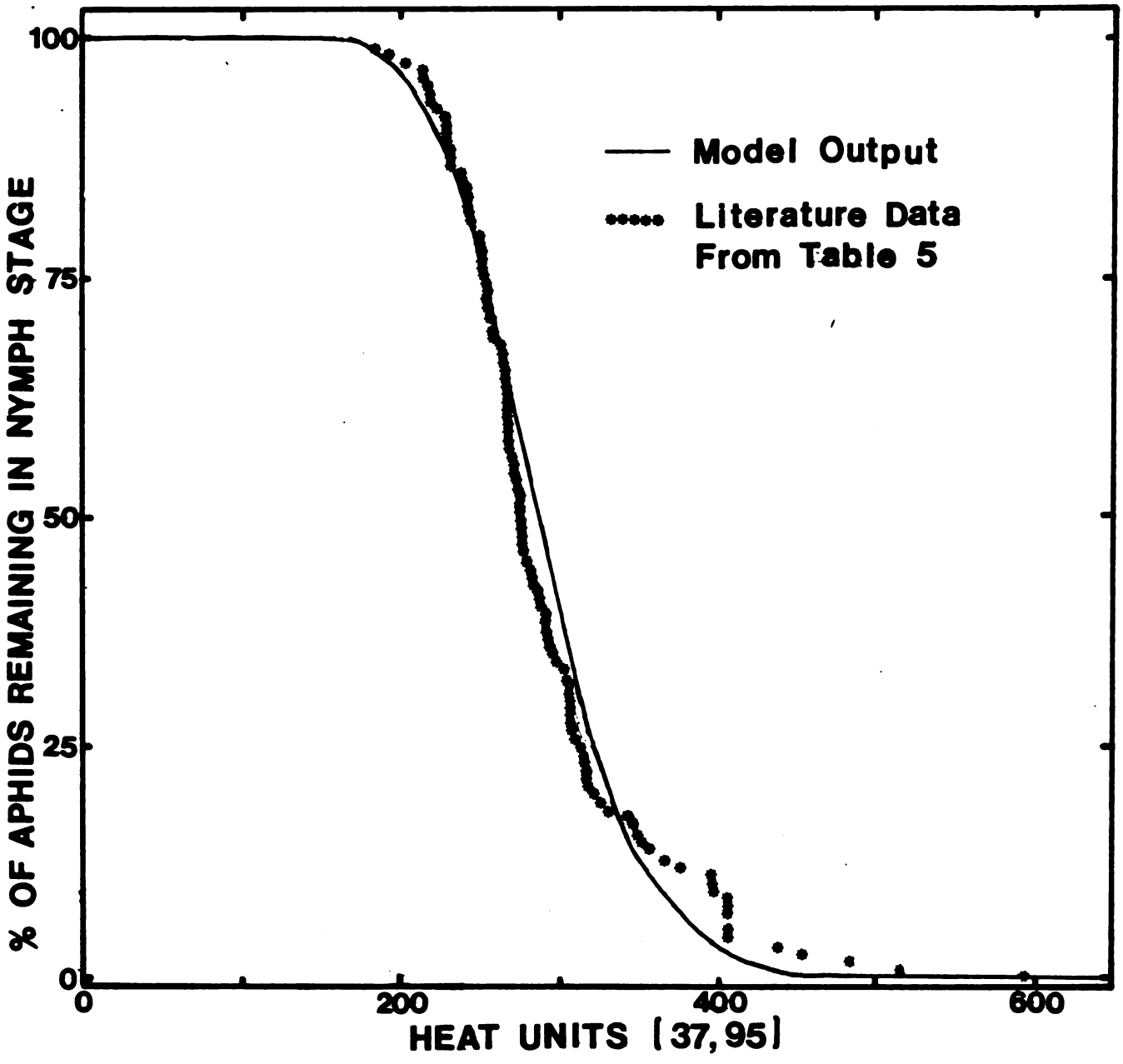
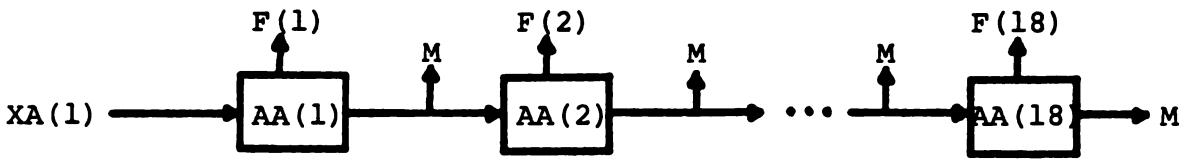


FIGURE 9. Conceptual Diagram of Adult Discrete Delay Developmental Model (After Manetsch and Park 1977)




DDEL = 900

K2 = 18

DT = 50

XA(1) = XNY(2) * DEL/K

AA(i,T+DT) = AA(i,T) * SURV (i)

F(i) = AA(i) * FEC(i)

$$BORN = \sum_{i=1}^{18} F(i); \quad AP(3) = \sum_{i=1}^{18} AA(i); \quad APTOT = \sum_{i=1}^{3} AP(i)$$

Explanation of Variables and Parameters Not Defined in Figure 7:

XA(1) - input amount variable into adult stage

AA(i) - number of aphids in $i^{th}$ adult substage

F(i) - fecundity from $i^{th}$ substage

M - mortality

DDEL - total delay of adult stage

K2 - number of substages in adult stage

SURV(i) - survivorship from $i^{th}$ to $(i+1)^{st}$ stage (see Table 9)

FEC(i) - fecundity array (see Table 9)

BORN - total fecundity

AP(3) - total number of adults

APTOT - total number of aphids

adult substage (XA(1)) was obtained from the output of the nymph developmental model (the rate XNY(2) was first converted to an amount/time step). Fecundity was assumed constant over each substage with total fecundity the sum of contributions from the 18 substages.

Survivorship and fecundity parameters (SURV(i) and FEC(i)) are calculated from the literature data in Tables 7 and 8 respectively and are listed in Table 9. In Figures 10 and 11 literature data are compared with the output of the simulation model.

4. Model Improvement Using Field Sleeve Cage Data

Output of the aphid simulation model was compared with population growth on aphid infested terminals enclosed in sleeve cages at Graham Station during the summer of 1980 (see Sections II-B-1-b and II-B-3 for description of the Graham Station and sleeve cages respectively). Initial colony size was determined by counting the number of $1^{st}$ and $2^{nd}$ instar nymphs = AP(1), $3^{rd}$ and $4^{th}$ instar = AP(2) and adults = AP(3). Insecticides (primarily azinphosmethyl) were applied approximately every 14 days at Graham Station during the summer of 1980 (see spray records of Section VIII-D). In order to minimize the effect of insecticides on population growth measurements, sleeve cage counts were started a minimum of 5-7 days after insecticide applications and completed before the next application.

The sleeve cage simulations were driven by heat units calculated using maximum and minimum temperatures recorded

TABLE 9. Adult Survivorship and Fecundity Parameters (Estimated from Tables 7,8 respectively)

| Adult Substage (i) | SURV(i) | Model Output: Adults Present At T = 50i[1] | FEC(i) | Model Output: Cumulative Young Per Female Born at T = 50i[2] |
|---|---|---|---|---|
| 1 | 1.0000000 | 100 | .6250000 | 6.25 |
| 2 | 1.0000000 | 100 | .6250000 | 12.50 |
| 3 | 1.0000000 | 100 | .6250000 | 18.75 |
| 4 | 1.0000000 | 100 | .6250000 | 25.00 |
| 5 | 1.0000000 | 100 | .6250000 | 31.25 |
| 6 | 1.0000000 | 100 | .6250000 | 37.50 |
| 7 | 1.0000000 | 100 | .6250000 | 43.75 |
| 8 | 1.0000000 | 95 | .6250000 | 50.00 |
| 9 | .9500000 | 85 | .3863158 | 53.67 |
| 10 | .8947368 | 75 | .4305882 | 57.33 |
| 11 | .8823529 | 65 | .1746667 | 58.64 |
| 12 | .8666667 | 55 | .1538462 | 59.64 |
| 13 | .8461538 | 45 | .0818182 | 60.09 |
| 14 | .8181818 | 35 | .1000000 | 60.54 |
| 15 | .7777778 | 25 | .0257143 | 60.63 |
| 16 | .7142857 | 15 | .0360000 | 60.72 |
| 17 | .6000000 | 5 | .0000000 | 60.72 |
| 18 | .3333333 | 0 | .0000000 | 60.72 |

[1]Adults alive at 50 heat unit intervals assuming 100 adults placed in first substage of the adult stage at T = 0.

[2]Cumulative young per female at 50 heat unit intervals assuming 1 adult placed in the first aubstage of the adult stage at T = 0.

FIGURE 10. Aphid Adult Survivorship

Longevity of the 39 females from Table 6 are compared with the output of the adult discrete delay simulation model with parameters DDEL = 900, K2 = 18.

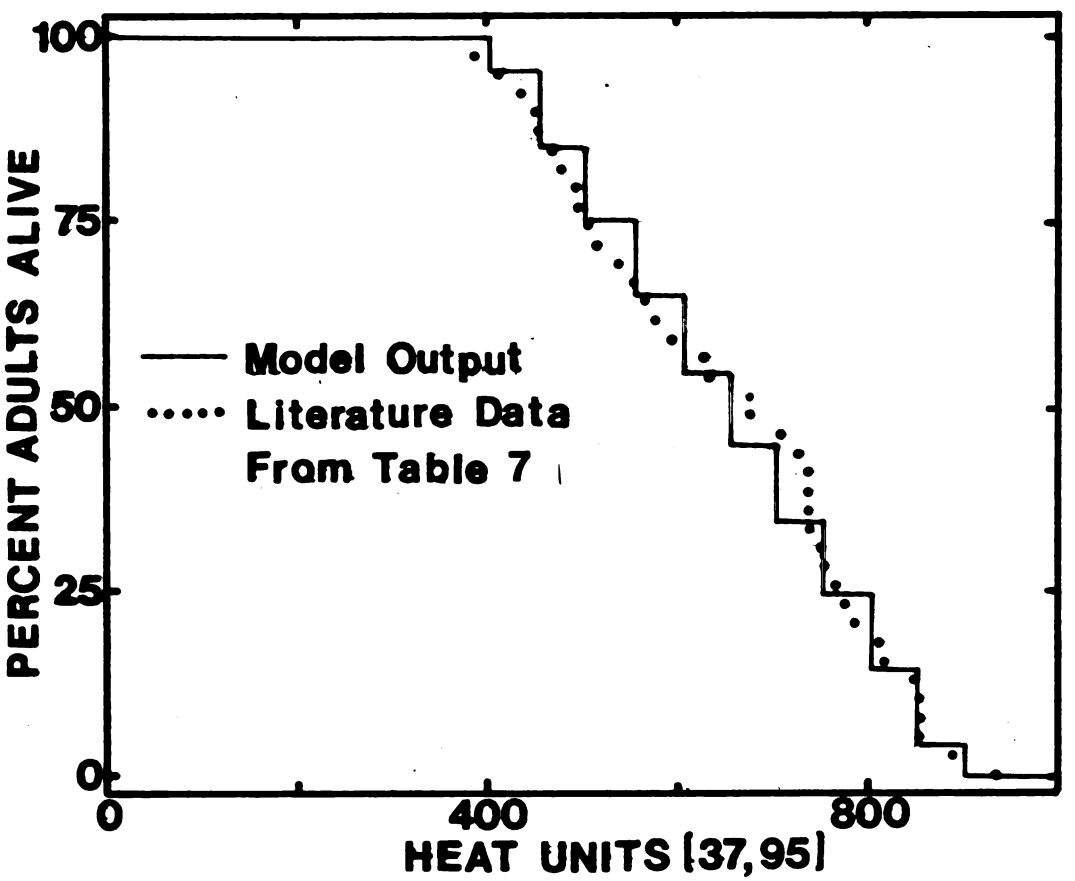
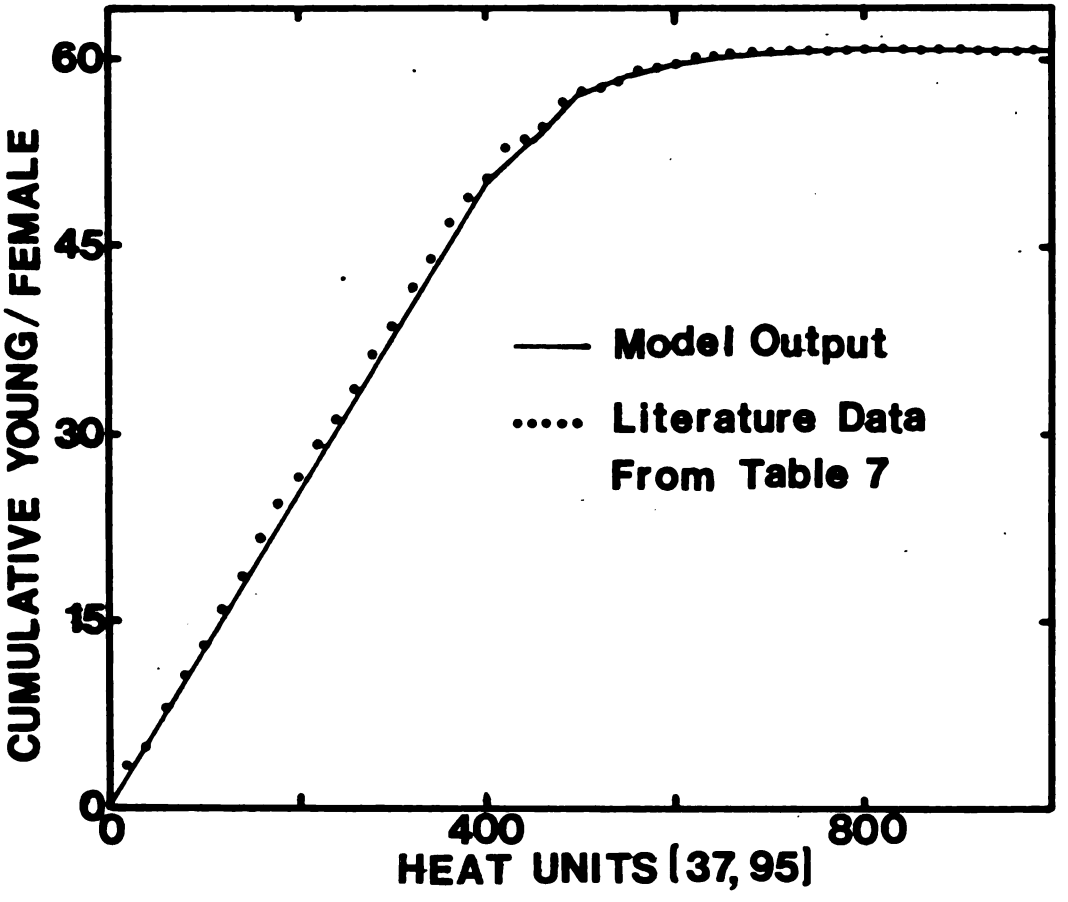


FIGURE 11. Aphid Fecundity

Cumulative fecundity per female for 39 females from Table 7 is compared with output of the discrete delay simulation model with FEC(i) as given in Table 8.



inside an oversized sleeve cage (see Section VII-D-2) for the dates of 7/14 to 9/03. A comparison of temperatures for these dates inside the sleeve cage versus the normal hygrothermograph records indicated that daily maximum and minimum temperatures inside the sleeves were elevated by an average of 2.56 and .29$^{o}$F. respectively (see Section VII-C-2). Thus sleeve cage simulations for dates on which sleeve cage temperature records were not available (6/01 to 7/13) were driven by the normal Graham Station temperature records with 3 and 0 degrees added to maximum and minimum daily temperatures respectively.

The output of the simulation model as described to present agreed only fairly well with sleeve cage data. Three main areas of disagreement were as follows:

(1) Although the total number of aphids predicted was fairly accurate, the numbers of 1$^{st}$ and 2$^{nd}$ instar nymphs (AP(1)) was too high while the number of 3$^{rd}$ and 4$^{th}$ instar nymphs (AP(2)) was too low.

(2) While the number of aphids predicted at low densities was fairly accurate, the number predicted at high aphid densities was too high.

(3) Prediction early in the season was somewhat low. As the season progressed prediction was increasingly high.

The disagreement of simulation output with sleeve cage data was not surprising in view of the many simplistic assumptions made in model construction. The following 3

sections describe modifications to the basic model made in order to more accurately simulate factors influencing aphid population dynamics. A major objective of this simulation (and modifications) was to maintain biological realism.

a. Relative Duration of Nymphal Instars

To this point, nymph development was modeled as consisting of 20 equally spaced substages (K = 20) with each of the four instars represented by 5 successive substages (see Section III-D-2). This assumption was based on Baker and Turner's (1916) statement that for summer generations of apterous forms of the apple aphid (reared at Vienna, VA) the average duration of the nymphal instar was 7-8 days, the time being equally divided between the four stages. Development of alates was observed to be similar except that two extra days were spent in the fourth instar.

In order to mimic sleeve cage data, instars were reassigned as follows: $1^{st}$ and $2^{nd}$ instars - substages 1-6; $3^{rd}$ and $4^{th}$ instars - substages 7-20. Note that as far as aphid development is concerned assignment of instars is unimportant.

b. Effect of Aphid Density

Evidence exists (Way 1973) for an optimum colony size in aphid populations. Small aggregations presumably benefit because group feeding may improve the nutritional status of the plant at the feeding site. As colony size increases beyond a relatively small optimum level, the multiplication rate of the colony dramatically decreases.

Aphid caging studies from which model parameters were derived (see Section III-C-2,3) were performed under low aphid density conditions (individual aphids were confined on separate apple terminals). Thus developmental and fecundity parameters were assumed to be close to optimal levels. Table 10 lists the adjustment for aphid density made in the aphid simulation. Aphid fecundity was reduced by the parameter DFACT (Density FACTor) as the aphid density rose above 100 aphids/terminal. No adjustment in aphid developmental times or mortality rates was made in relation to density.

### c. Effect of Tree Nutrient Status

Very little usable data exists on the relationship between tree nutrient status and aphid population dynamics. In arriving at a submodel of the effect of tree nutrient status, several literature data sets were utilized qualitatively to derive the form of the effect. Baker and Turner (1916) measured apterae fecundity at Vienna, VA of aphids reproducing before July 6 (2617 HU using a tree developmental threshold of 41$^{o}$F. - Ashcroft et al. 1977) at 55.4 young/female and for aphids reproducing July 6 - Sept. 10 (2617-4647 HU) at 30.9 young/female (a reduction of 56%).

Jokinen (1980) measured the pattern of apple leaf primordia decline over the season at Graham Station for 1977 (for trees in similar condition as those used for sleeve cages in the present study). He noted a very rapid decline starting at approximately 1100 HU and continuing to approx-

TABLE 10. Simulated Effect of Aphid Density and Tree Nutrient Status on Aphid Fecundity

FECUNDITY EQUATION:

APHIDS BORN = BORN * DFACT * TFACT
where BORN = # aphids born in absence of density and nutritional factors

| APHID DENSITY = APTOT[1] | DFACT |
|---|---|
| 0 - 100 | 1.0 |
| 100 - 1000 | $1.0 - .75 * (\log_{10}(APTOT) - 2.0)$ |
| > 1000 | .25 |

| Date | Heat Units (41)[2] | TFACT |
|---|---|---|
| 6/1 - 7/4 | 748.8 - 1500 | 1.3[3] |
| 7/5 - 7/20 | 1500 - 2000 | .9 |
| 7/21 - 8/6 | 2000 - 2500 | .6 |
| 8/7 - 8/24 | 2500 - 3000 | .5 |
| 8/25 - 8/31 | 3000 - 3209.7 | .4 |

[1]Total number of aphids on the terminal.

[2]Tree heat units above a threshold of 41°F. calculated for Graham Station 1980 using Subroutine DEGD.

[3]Fecundity data calculated from Table 7 was for females fecund 6/4-8/30. Thus fecundity factor during period of optimal tree nutrient status (6/1-7/4) was elevated above unity.

imately 2200 HU (Figure 2C in his paper). He also noted that aphids are observed to distribute themselves in close association with active plant growing sites (Kennedy et al. 1950, Kennedy 1958).

Table 10 lists the adjustment made to aphid fecundity in response to changing tree nutrient status through the season (parameter TFACT-Tree FACTor; again no adjustments were made to developmental or survivorship parameters). Heat units listed for various dates are for Graham Station 1980 (using a tree developmental threshold of 41$^{o}$F.). Early in the season (6/1-7/4), nutrient availability was assumed to be at optimum levels and TFACT was set to 1.3 (greater than unity since model fecundity data was derived from aphids reared June 1 - August 31, see Section III-C). TFACT was reduced as shown in Table 10 as the season progressed.

5. Simulation Results

Table 11 lists sleeve cage data and the results of sleeve cage simulations. Simulation output was classified as accurate if predicted population levels were within $\pm$ 1/3 of actual counts (see Table 12 footnote for the equation used). Table 12 summarizes the accuracy of the simulation. Total aphid population levels were classified as accurate in 19 of the simulations, high in 10 and low in the remaining 5. Figure 12 graphically presents the data of Tables 11 and 12.

TABLE 11. Sleeve Cage and Simulation Data for Graham Station 1980

| Sleeve Cage Number | Dates | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | Total Aphids APTOT[2] |
|---|---|---|---|---|---|
| 1 | 6/16 2:00 | 131 | 34 | 31 | 196 |
| | 6/24 4:30 | 399 | 384 | 81 | 864 |
| | Simulation[3] | 328.3A | 441.2A | 89.0A | 858.5A |
| 2 | 6/16 2:00 | 6 | 4 | 15 | 25 |
| | 6/24 5:00 | 135 | 147 | 9 | 291 |
| | Simulation | 105.2A | 179.2A | 15.7H | 300.1A |
| 3 | 6/16 2:00 | 2 | 0 | 1 | 3 |
| | 6/24 5:00 | 8 | 16 | 8 | 32 |
| | Simulation | 10.0A | 11.6A | 12.6H | 22.9A |
| 4 | 6/16 2:00 | 3 | 1 | 1 | 5 |
| | 6/24 5:00 | 25 | 35 | 3 | 63 |
| | Simulation | 24.4A | 21.8L | 2.5A | 48.6A |
| 5 | 6/16 2:00 | 0 | 0 | 3 | 3 |
| | 6/24 5:30 | 18 | 19 | 3 | 40 |
| | Simulation | 17.1A | 31.0H | 2.0L | 50.2A |
| 6 | 7/2 1:00 | 175 | 148 | 26 | 349 |
| | 7/6 2:15 | 306 | 327 | 102 | 735 |
| | Simulation | 372.9H | 347.2A | 102.4A | 822.4A |
| 7 | 7/2 1:00 | 33 | 29 | 6 | 68 |
| | 7/6 2:30 | 80 | 61 | 19 | 160 |
| | Simulation | 150.0H | 92.3H | 20.7A | 263.0H |
| 8 | 7/2 1:00 | 67 | 84 | 13 | 164 |
| | 7/6 3:00 | 124 | 247 | 35 | 406 |
| | Simulation | 289.2H | 195.2A | 56.8H | 541.3H |
| 9 | 7/2 2:00 | 147 | 197 | 17 | 361 |
| | 7/6 3:30 | 208 | 324 | 66 | 598 |
| | Simulation | 426.7H | 351.2A | 123.9H | 901.7H |

[1]Sleeve cages were placed around aphid infested terminals on the first date after removing all natural enemies. On the second date, sleeve cages were removed and aphid population counted.

[2]Simulation output rounded to one decimal place. Thus AP(1) + AP(2) + AP(3) may not add up to APTOT.

[3]Results of aphid simulation initialized with aphid numbers from first date. Model results were compared with observed population levels and classified as high (H), accurate (A) or low (L) - see Table 12.

TABLE 11. (cont.)

| Sleeve Cage Number | Dates | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | Total Aphids APTOT |
|---|---|---|---|---|---|
| 10 | 7/2 2:30 | 1 | 0 | 1 | 2 |
| | 7/6 3:30 | 4 | 10 | 0 | 14 |
| | Simulation | 5.7H | 4.2L | 0.7H | 10.6A |
| 11 | 7/2 2:30 | 175 | 295 | 47 | 517 |
| | 7/6 3:30 | 231 | 617 | 160 | 1008 |
| | Simulation | 523.9H | 465.4L | 200.5H | 1189.8H |
| 12 | 7/2 3:00 | 51 | 71 | 12 | 134 |
| | 7/6 4:00 | 354 | 159 | 38 | 551 |
| | Simulation | 265.9H | 169.2A | 48.7H | 483.8A |
| 13 | 7/2 4:00 | 86 | 119 | 21 | 226 |
| | 7/6 5:30 | 263 | 267 | 72 | 602 |
| | Simulation | 354.0H | 254.4A | 82.3A | 690.7A |
| 14 | 7/2 4:30 | 80 | 48 | 13 | 141 |
| | 7/6 5:30 | 152 | 173 | 13 | 338 |
| | Simulation | 209.6H | 168.1A | 36.4H | 414.1H |
| 15 | 7/14 1:00 | 93 | 80 | 13 | 186 |
| | 7/19 4:00 | 630 | 343 | 80 | 1053 |
| | Simulation | 319.7L | 382.6A | 96.4A | 798.7A |
| 16 | 7/16 3:00 | 25 | 31 | 2 | 58 |
| | 7/21 4:00 | 142 | 126 | 22 | 290 |
| | Simulation | 162.3A | 142.7A | 28.8H | 333.9A |
| 17 | 7/16 3:00 | 55 | 60 | 21 | 136 |
| | 7/21 4:00 | 253 | 301 | 48 | 602 |
| | Simulation | 251.6A | 292.1A | 66.9H | 610.6A |
| 18 | 7/16 3:00 | 67 | 30 | 6 | 103 |
| | 7/21 4:00 | 61 | 123 | 40 | 224 |
| | Simulation | 162.0H | 180.7H | 34.3A | 377.0H |
| 19 | 7/16 4:00 | 39 | 57 | 3 | 99 |
| | 7/21 4:30 | 297 | 308 | 39 | 644 |
| | Simulation | 235.3A | 223.1L | 51.9H | 510.0A |
| 20 | 7/16 4:00 | 27 | 15 | 4 | 46 |
| | 7/21 4:30 | 139 | 117 | 21 | 277 |
| | Simulation | 105.1A | 100.9A | 17.2A | 223.1A |
| 21 | 7/16 4:00 | 59 | 39 | 25 | 123 |
| | 7/21 4:30 | 229 | 342 | 46 | 617 |
| | Simulation | 205.5A | 263.6A | 52.5A | 521.6A |

TABLE 11. (cont.)

| Sleeve Cage Number | Dates | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | Total Aphids APTOT |
|---|---|---|---|---|---|
| 22 | 7/16 4:30 | 121 | 67 | 15 | 203 |
| | 7/21 5:00 | 250 | 508 | 93 | 851 |
| | Simulation | 258.3A | 318.3L | 74.9A | 651.5A |
| 23 | 7/28 3:00 | 19 | 37 | 8 | 64 |
| | 7/31 1:00 | 104 | 56 | 16 | 176 |
| | Simulation | 106.3A | 46.5L | 23.3H | 176.2A |
| 24 | 7/28 3:30 | 7 | 5 | 4 | 16 |
| | 7/31 1:30 | 15 | 9 | 5 | 29 |
| | Simulation | 25.0H | 12.1H | 5.5H | 42.6H |
| 25 | 7/28 3:30 | 13 | 23 | 8 | 44 |
| | 7/31 1:30 | 52 | 35 | 9 | 96 |
| | Simulation | 79.7H | 32.1A | 17.0H | 128.7H |
| 26 | 7/28 3:45 | 21 | 16 | 5 | 42 |
| | 7/31 1:30 | 37 | 25 | 6 | 68 |
| | Simulation | 54.9H | 32.0H | 11.3H | 98.2H |
| 27 | 7/28 4:00 | 18 | 31 | 2 | 51 |
| | 7/31 1:30 | 52 | 47 | 7 | 106 |
| | Simulation | 79.2H | 37.4L | 15.7H | 132.3H |
| 28 | 7/28 4:00 | 84 | 93 | 16 | 193 |
| | 7/31 2:00 | 180 | 177 | 45 | 402 |
| | Simulation | 185.9A | 137.9L | 55.3H | 379.1A |
| 29 | 8/11 11:30 | 5 | 9 | 4 | 18 |
| | 8/14 2:00 | 31 | 24 | 6 | 61 |
| | Simulation | 26.9A | 11.7L | 7.1H | 45.8L |
| 30 | 8/11 11:15 | 9 | 9 | 1 | 19 |
| | 8/14 2:00 | 12 | 16 | 5 | 33 |
| | Simulation | 19.4 | 13.5 | 4.7 | 37.7 |
| | 8/18 11:30 | 43 | 20 | 5 | 68 |
| | Simulation | 46.1A | 36.0H | 9.9H | 92.0H |
| 31 | 8/11 1:30 | 20 | 54 | 7 | 81 |
| | 8/14 2:00 | 60 | 86 | 22 | 168 |
| | Simulation | 106.2 | 53.7 | 29.0 | 188.9 |
| | 8/18 11:30 | 285 | 182 | 40 | 507 |
| | Simulation | 170.3L | 170.0A | 54.1H | 394.4A |
| 32 | 8/11 11:30 | 0 | 7 | 0 | 7 |
| | 8/14 2:00 | 2 | 5 | 2 | 9 |
| | Simulation | 12.3 | 4.4 | 3.0 | 19.7 |
| | 8/18 11:30 | 18 | 16 | 6 | 40 |
| | Simulation | 31.0H | 20.4H | 6.1A | 57.5H |

TABLE 11. (cont.)

| Sleeve Cage Number | Dates | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | Total Aphids APTOT |
|---|---|---|---|---|---|
| 33 | 8/11 11:30 | 14 | 34 | 8 | 56 |
| | 8/14 2:30 | 59 | 60 | 17 | 136 |
| | Simulation | 81.2 | 36.7 | 21.2 | 139.2 |
| | 8/18 11:30 | 172 | 114 | 45 | 331 |
| | Simulation | 129.5A | 128.9A | 36.3A | 294.6A |
| 34 | 8/11 12:00 | 4 | 4 | 2 | 10 |
| | 8/14 3:00 | 14 | 9 | 2 | 25 |
| | Simulation | 12.7 | 6.8 | 3.4 | 22.9 |
| | 8/18 11:30 | 39 | 26 | 5 | 70 |
| | Simulation | 23.8L | 21.6A | 5.3A | 50.6A |

TABLE 12. Comparison of Simulation Model Output and Sleeve Cage Data[1]

| Accuracy[2] Category | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | Total Aphids |
|---|---|---|---|---|
| H | 15 | 7 | 20 | 12 |
| L | 3 | 9 | 1 | 1 |
| A | 16 | 18 | 13 | 21 |

[1] 34 sleeve cages were simulated. Results list the number of sleeve cage simulations falling into each accuracy category.

[2] H (High) - $(P_F-A_F)/(A_F-A_I) > 1/3$

A (Accurate) - $|A_F-P_F|/(A_F-A_I) < 1/3$

L (Low) - $(A_F-P_F)/(A_F-A_I) > 1/3$

where $A_F$ = final sleeve cage populations
$P_F$ = final simulation prediction
$A_I$ = initial sleeve cage population

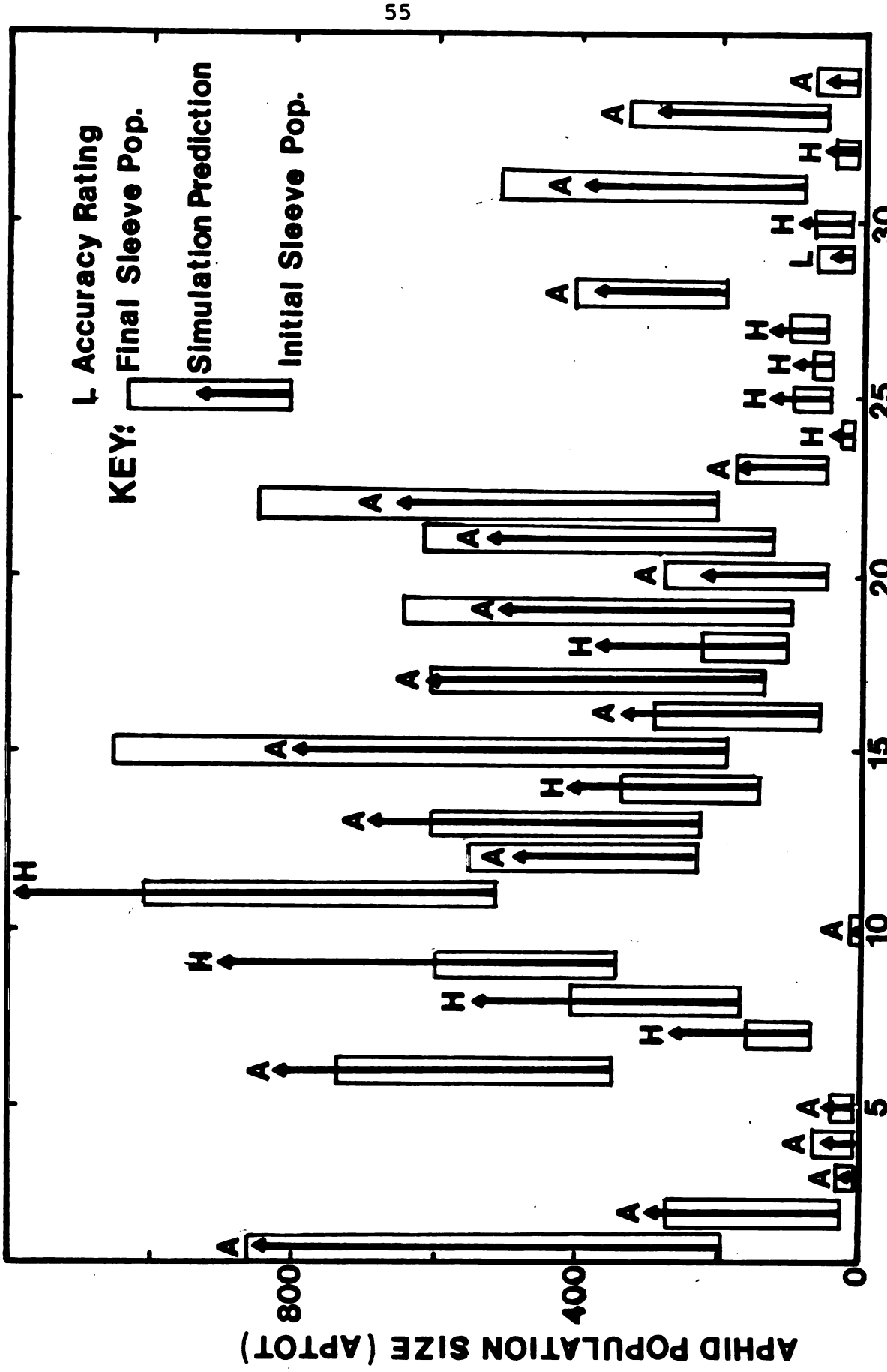



FIGURE 12. Sleeve Cage Data Compared with Simulation Model Output

## IV. CECIDOMYIID EXPERIMENTS

### A. INTRODUCTION

#### 1. Taxonomy and Worldwide Use in Biological Control

Several recent taxonomic studies (Harris 1966, 1973, Nijveldt 1969, Gagne 1971, 1973) have helped to clarify classification of aphidophagous Cecidomyiidae. Harris (1973) reports that there are 5 species which feed exclusively on aphids and are the only Cecidomyiidae definitely known to do so. Aphidoletes aphidimyza (Rondani) is by far the most common and widespead of these species with a host range of at least 61 aphid species. A. urticariae (Kieffer) is behaviorally and morphologically quite similar to A. aphidimyza but appears to be less common with perhaps a more northerly distribution. Both A. abietis (Kieffer) and A. thompsoni Möhn are fairly uncommon and are reported feeding only on adelgids. Monobremia subterranea (Kieffer) is a rare species reported to feed on root aphids.

Within the past decade, a great deal of interest has been shown worldwide in the use of A. aphidimyza. Table 13 presents a partial list (only one reference is included for each country or state) of research reports dealing with the possible use of this species in biological control programs for aphids in glasshouses and on field crops and fruit trees. Within Finland, this species has been used commercially since 1978 for glasshouse control of aphids on vegetables and ornamental plants (Markkula and Tiittanen 1980).

TABLE 13. Worldwide Reports of the Use of A. aphidimyza in Biological Control

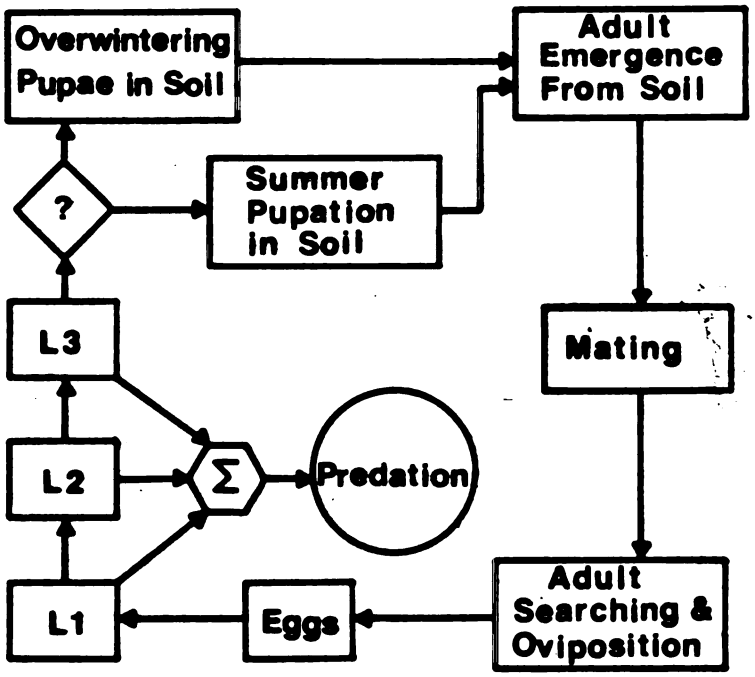
| Aphid Control in Glasshouses | Reference |
|---|---|
| USSR | Asyakin 1973 |
| West Germany | El Titi 1974a |
| Finland | Markkula and Tiittanen 1977 |
| Denmark | Hansen 1980 |
| Czechoslovakia | Havelka 1980b |
| **Aphid Control on Field Crops** | |
| Italy | Roberti 1946 |
| England | Dunn 1949 |
| Egypt | Azab et al. 1965a |
| Netherlands | Nijveldt 1969 |
| Rumania | Constantinescu 1972 |
| Chile | Apablaza and Tiska 1973 |
| USSR | Narjikulov and Umarov 1975 |
| **Aphid Control on Fruit Trees** | |
| Israel | Nijveldt 1957 |
| France | Coutin 1974 |
| Bulgaria | Pelov 1977 |
| Lebanon | Talhouk 1977 |
| U.S. | Adams and Prokopy 1980(Mass.), Jokinen 1980(MI). |
| Poland | Olszak 1979 |

## 2. Life Cycle

The biology of A. aphidimyza has been reviewed by several authors (Azab et al. 1965b, Harris 1973, Markkula et al. 1979, Adams and Prokopy 1980). The following account includes observations from laboratory rearing cages as described in Section II-A-2 (entrained to artificial light on 4am-8pm). Figure 13 presents a diagram of the cecidomyiid life cycle. Adult midges emerge from pupal sites in the soil with peak emergence occurring in late afternoon hours (4-8pm). Adults are nocturnal and hide during daylight hours in dim protected areas. During the first night of adult life mating occurs and very few eggs are laid. Females live up to 16 days in captivity and lay ca. 150 eggs (see Section IV-C-4). Males do not live as long as females (a maximum of 9 nights was observed at 23.33°C.). Adults appear to feed on aphid honeydew and its presence increases both longevity and fertility (Wilbert 1977, Kuo 1977). The species is monogenic (Sell 1976) with males apparently having no effect on the sex of their progeny. The ratio of arrhenogenic to thelygenic females as well as the ratio of females to males appears to be close to 1:1 (Sell 1976, Linskii 1977).

The majority of oviposition occurs at late evening hours (6-12pm) under laboratory conditions. Eggs are laid singly or in clusters of up to 40 and are sometimes laid directly on the aphids. Females are able to locate aphid colonies even at quite low aphid densities (El Titi 1974b, see Section IV-C-5) and appear to lay eggs only in close

FIGURE 13. Cecidomyiid Life Cycle



proximity to aphids (El Titi 1973). Increasing levels of aphids and honeydew serve as "releasing mechanisms" which promote increased oviposition (El Titi 1974b).

Eggs are .3 mm. long, orange, and are barely visible with the naked eye. Hatching occurs in 2-3 days (see Section IV-C-1) and it is generally agreed that there are 3 larval instars although some reports have indicated 4 (Azab et al. 1965b, El-Gayer 1976). First instar larvae locate aphid prey from short distances, probably using a sense of smell (Wilbert 1973,1974). In addition females appear to orient their eggs toward nearby aphids (Wilbert 1972). Recently hatched larvae lived an average of 5.3 hours without food and traveled an average of 49 mm. before dying (Wilbert 1972).

Larvae usually attack their prey by piercing a leg joint with their mandibles (Solinas 1968) and paralyze the aphid through the injection of a salivary enzyme (Mayr 1975). The enzyme also serves to liquify the gut contents which are withdrawn after a period of time. Handling times vary from 30-60 minutes, decreasing with increasing aphid density (Azab et al. 1965b). The shrivelled bodies of the aphids generally remain attached to the plant, indicating that the aphids were overcome before their stylets were retracted from the plant tissues (Harris 1973).

Reports of the number of aphids killed by cecidomyiid larvae vary greatly with the aphid species and experimental conditions. Uygun (1971) reports a minimum requirement of

7 Myzus persicae (Sulzer) for larval development. The number of aphids killed during larval development greatly influences fecundity levels of adult females (Uygun 1971). Mature larvae drop into the soil to construct small silk coccoons within the top 3 cm. (Roberti 1946). Occasionally coccoons may be spun on plant leaves within a cluster of dead aphids. Cecidomyiids overwinter as pupae in the soil with emergence occurring during late May and early June (see Section IV-D-1).

## B. OBJECTIVES AND METHODOLOGY

The objectives of this section were to gather basic experimental data on several diverse features of cecidomyiid biology as they affect aphid predation. Section C presents laboratory experiments on egg and larval developmental periods, larval functional response and adult female search and oviposition. Section D lists field experiments on adult emergence from overwintering sites, the use of aphid infested trap plants in monitoring adult cecidomyiids and a comparison of direct terminal samples with trap plant samples in a commercial apple orchard. Section V presents the cecidomyiid computer simulation which was constructed utilizing much of the biological data gathered in Section IV.

## C. LABORATORY EXPERIMENTS

### 1. Cecidomyiid Egg Development

Uygun (1971) calculated mean egg hatch for a laboratory colony from Göttingen, West Germany to be 2.5 days at 21°C. Havelka (1980a) measured constant temperature egg development in a laboratory population of A. aphidimyza collected originally form Leningrad, USSR (see Table 14). This data is analyzed and compared to experimental data in Table 17.

In order to compare egg development for a Michigan cecidomyiid colony with the above data, jimsonweed plants (these plants were chosen because they were easier to observe under a microscope without disturbing the eggs) infested with green peach aphids were left for 2 hours in a laboratory cecidomyiid colony containing a large adult population. The plants were removed, checked for the absence of adults and a map was made of all eggs deposited. The plants were held at constant temperatures and were checked at approximately 2 hour intervals over the duration of egg hatch (preliminary experiments had indicated the interval for expected first hatch). During observations each plant was removed from the environmental chamber for approximately 5 minutes (with room temperature 23.3-25.1°C.). Cumulative percent hatch versus time (for both experimental and literature data) was fit to a cumulative normal distribution using the MSU Entomology department computer program BNPGPROBIT which estimated time and standard deviation to 50% hatch.

Table 15 lists experimental data for egg hatch at 5

TABLE 14. Literature Data on Cecidomyiid Egg Hatch[1]

| Mean Laboratory Temperature (°C.) | Days Post Oviposition | Percent Hatch | Probit Equation y = percent hatch in probits x = days | Days to 50% Hatch | Standard Deviation |
|---|---|---|---|---|---|
| 15 | 4.75 | 23.1 | y=3.2940x -11.3886 | 4.9753 | .3036 |
| | 5.00 | 53.5 | | | |
| | 5.13 | 68.1 | | | |
| | 5.25 | 82.4 | | | |
| 20 | 2.37 | 6.2 | y=7.9581x -15.3726 | 2.5600 | .1257 |
| | 2.50 | 33.1 | | | |
| | 2.75 | 93.3 | | | |
| 25 | 1.58 | 28.2 | y=7.9027x -8.0731 | 1.6543 | .1265 |
| | 1.83 | 90.7 | | | |
| | 1.87 | 96.1 | | | |
| | 1.92 | 100.0[2] | | | |

[1]Data from Havelka (1980a) analyzed by this author using BNPGPROBIT.

[2]This data point deleted in analysis.

TABLE 15. Experimental Cecidomyiid Egg Hatch Data

(see Table 16 for experimental conditions of experiments A-D)

| | Hours Post Oviposition | Percent Hatch | | Hours Post Oviposition | Percent Hatch |
|---|---|---|---|---|---|
| EXP.A | 208.50 | 1.5 | EXP.C | 48.25 | 27.17 |
| | 225.75 | 16.7 | | 50.50 | 62.60 |
| | 227.25 | 22.7 | | 52.25 | 84.25 |
| | 229.75 | 29.5 | | | |
| | 231.25 | 36.4 | | | |
| | 232.75 | 43.9 | EXP.D | 34.25 | 48.80 |
| | 234.25 | 47.0 | | 35.75 | 60.24 |
| | 257.00 | 90.9 | | 37.75 | 81.33 |
| | 258.50 | 91.7 | | 40.50 | 90.36 |
| | 260.00 | 92.4 | | 43.75 | 96.39 |
| | 274.00 | 94.7 | | 49.00 | 96.99 |
| | 276.00 | 97.7 | | | |
| | 279.00 | 99.2 | | | |
| EXP.B | 73.75 | 18.18 | | | |
| | 76.25 | 36.36 | | | |
| | 77.75 | 57.95 | | | |
| | 79.00 | 64.77 | | | |
| | 80.50 | 73.86 | | | |
| | 82.00 | 77.27 | | | |
| | 83.50 | 80.68 | | | |

constant temperatures with the experimental conditions and probit analysis listed in Table 16. The inverse of estimated days to 50% hatch versus temperature is plotted in Figure 14 for both literature and experimental data (using the x-intercept method of Arnold 1959). Linear regression was performed on the data giving a theoretical developmental threshold (x-intercept) of 10.48°C. (51°F.) and a developmental period (inverse of the slope) of 25.49 heat units (45.88 °F.-HU). Table 17 lists heat units and standard deviations above the 10.48°C. base ($HU_{10.48}$) calculated for each data point.

More data is needed to accurately determine egg mortality rates. Mortality at intermediate temperatures appears to be in the range of 10-15% with higher levels indicated at either of the two extremes (Table 16).

2. Larval Development With Excess Food

Some disagreement has existed over the number of larval instars of A. aphidimyza. Azab et al. (1965b) reported that "larval stages...are very difficult to separate" and that "it seems...there are" four instars. El-Gayer (1976) and Adams (1977) also assume 4 larval instars.

Roberti (1946) states that there are 3 larval instars and Harris (1973) and Markkula and Tiittanen (1977) agree that this is most likely the case. My own observations and those of Warner (unpublished) indicate that there are 3 larval instars.

Several authors have measured larval developmental

TABLE 16. Experimental Conditions and Probit Analysis for the Cecidomyiid Egg Hatch Experiment

| Experiment | Experimental Conditions | Temp. (°C.) Mean | Temp. (°C.) Range | Relative Humidity (%) Mean | Relative Humidity (%) Range | Number of Eggs Observed | Percent Hatch | Probit Equation y=percent hatch in probits; x=hours | Days to 50% Hatch | Standard Deviation (Days) |
|---|---|---|---|---|---|---|---|---|---|---|
| A | Environmental Chamber | 13.89 | 12.9-15.1 | 81 | 70-100 | 210 | 62.86 | y=.0585x-9.0323 | 9.9966 | .7124 |
| B | Environmental Chamber | 17.78 | 16.8-18.7 | 86 | 76-95 | 95 | 89.90 | y=.1839x-9.3025 | 3.2404 | .2266 |
| C | Cage in Room B10 | 24.17 | 23.3-25.1 | 75 | 66-86 | 283 | 89.75 | y=.4036x-15.0733 | 2.0725 | .1033 |
| D | Environmental Chamber | 29.17 | 28.4-29.7 | 80 | 63-98 | 198 | 83.84 | y=.1343x+.6215 | 1.3584 | .3103 |
| E | Environmental Chamber | 31.17 | 30.6-31.7 | 47 | 40-54 | 94 | 6.38 | - | - | - |

FIGURE 14. Cecidomyiid Egg Developmental Rate

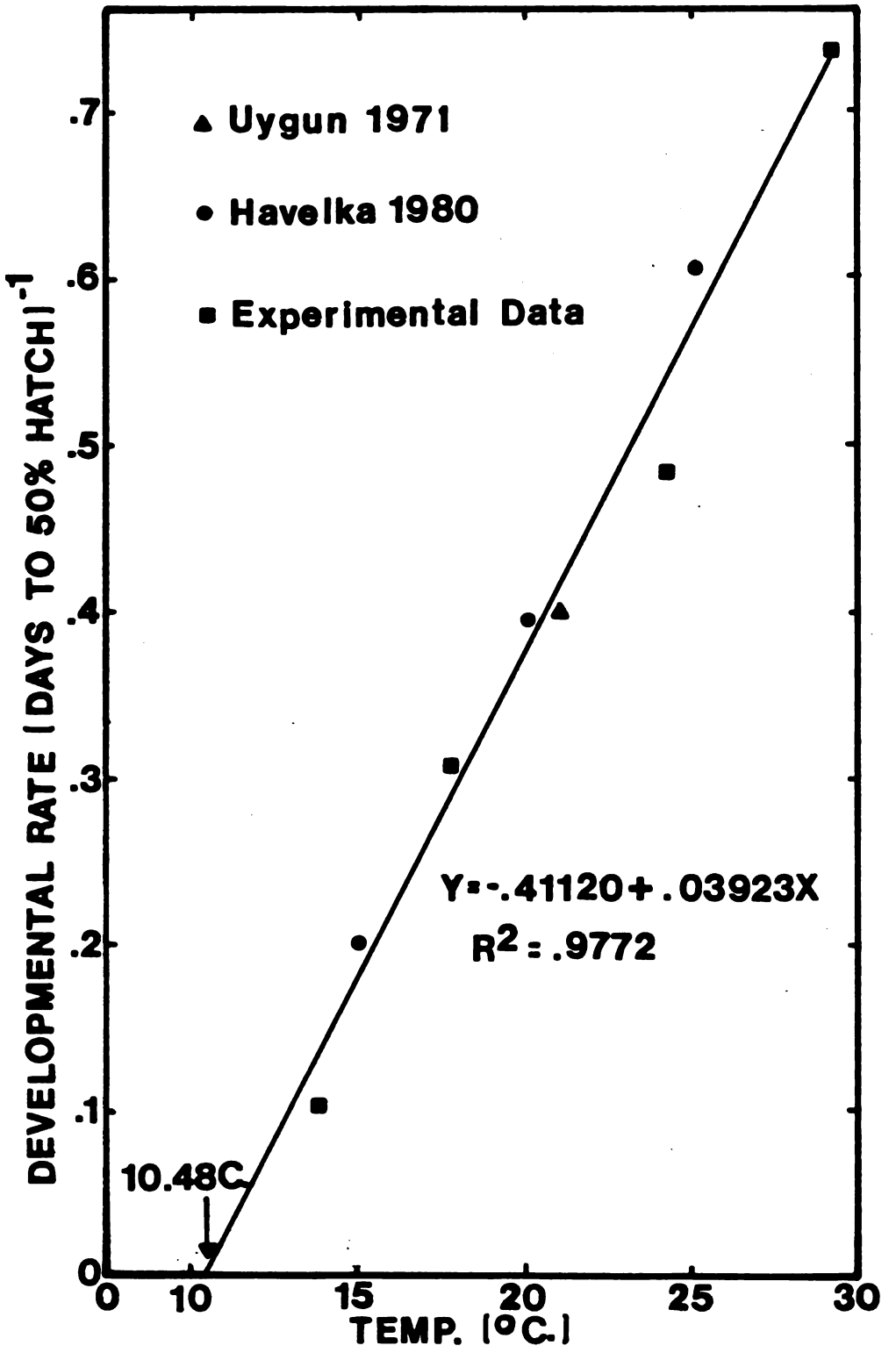


TABLE 17. Heat Units and Standard Deviations for Literature and Experimental Data on Cecidomyiid Egg Hatch

| Source | Mean Temp. (°C.) | Estimated 50% Hatch (Days) | Standard Deviation (Days) | HU 10.48°C. (degree-days)[1] | Standard Deviation[2] (Heat Units) |
|---|---|---|---|---|---|
| Uygun 1971 | 21 | 2.5 | - | 26.2988 | - |
| Havelka 1980a | 15 | 4.9753 | .3036 | 22.4860 | 1.3720 |
| | 20 | 2.5600 | .1257 | 24.3699 | 1.1961 |
| | 25 | 1.6543 | .1265 | 24.0189 | 1.8373 |
| Experimental Data | 13.89 | 9.9966 | .7124 | 34.0736 | 2.4282 |
| | 17.78 | 3.2404 | .2266 | 23.6472 | 1.6533 |
| | 24.17 | 2.0725 | .1033 | 28.3653 | 1.4131 |
| | 29.17 | 1.3584 | .3103 | 25.3838 | 5.7125 |
| | | | Means | 26.0805 | 2.2304 |

[1] $HU_{10.48}$ = (Mean Temp. - 10.48) x (days to estimated 50% hatch).

[2] Standard Deviation (Heat Units) = (Mean Temp. - 10.48) x (Standard Deviation in days).

rates of cecidomyiids provided with excess food (see Table 18) and their data are compared with experimental data in Figure 15.

The objectives of this section were to compare larval developmental rates (with excess food) of a Michigan cecidomyiid population with the above data. Cecidomyiid eggs which had been collected over a 4 hour interval were held at room temperature (approx. 25°C.) and were checked once per hour during the duration of egg hatch. Newly hatched larvae (which had not yet fed on any aphids) were transferred to a pea aphid infested fava bean stem using a camel hair brush. Plants were held in environmental chambers (or at room temperature) and were checked every 2-4 hours for completion of larval development (this involved removal from the environmental chamber to room temperature for approximately 5 minutes; the larval stage was "completed" when larvae dropped from the aphid infested leaf onto a petri dish containing moist sand for pupation).

The data for these experiments are presented in Tables 19 and 20. Results are compared with literature data in Figure 15. Linear regression was fit to the 3 main data sets (Uygun 1971, Havelka 1980a, Experimental Data) with theoretical developmental threshold of 4.80, 5.27, and 8.10°C indicated respectively.

The data displayed in Figure 15 is for cecidomyiid populations collected from widely separated geographical regions reared using different experimental techniques and

TABLE 18. Literature Data on Larval Development With Excess Food Supplied

| Data Source | Origin of Cecidomyiid Strain | Aphid Prey Species | Average Temp. (°C.) | Probit Equation y=% Dev. in probits, x=days | Estimated 50% Dev. (days) | Standard Deviation (days) |
|---|---|---|---|---|---|---|
| Azab et al. 1965 | Giza, Egypt | *Aphis punicae* Pass. | 27.8 | - | 5.85 | - |
| Uygun 1971 | Göttingen, West Germany | *Myzus persicae* (Sulzer) | 15 | - | 6.7 | - |
| | | | 21 | - | 3.8 | - |
| | | | 27 | - | 3.0 | - |
| Havelka[1] 1980 | Leningrad, USSR | *Aphis fabae* Scop., | 15 | y=.6605x-1.8448 | 10.3637 | 1.5141 |
| | | *Megoura viciae* Buckt. | 20 | y=.7698x-.2973 | 6.8815 | 1.2991 |
| | | | 25 | y=2.0074x-5.2717 | 5.1170 | .4892 |

[1]The data of Havelka (1980a) was analyzed independantly by this author using BNPGPROBIT.

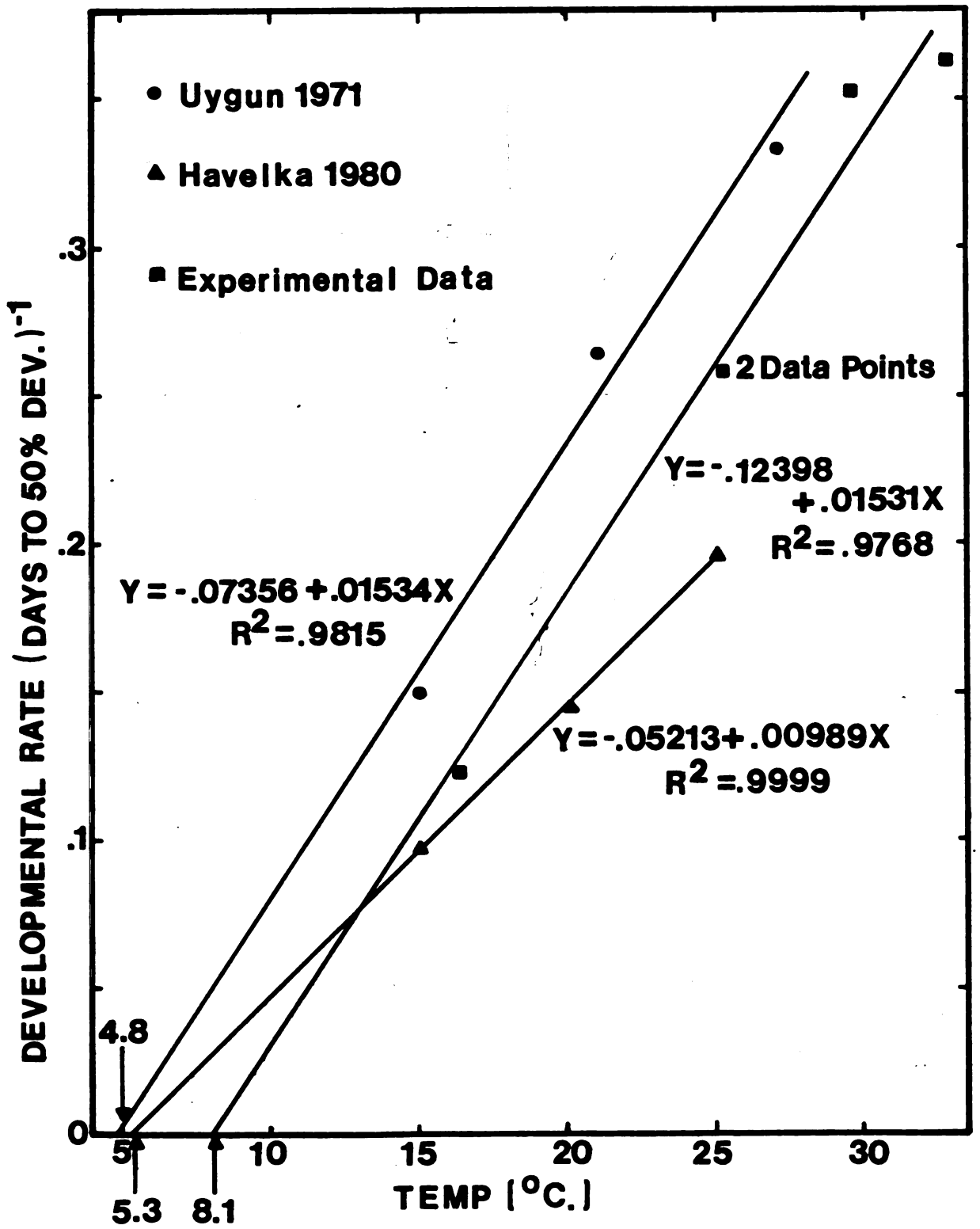
TABLE 19. Experimental Larval Developmental Data (Excess Food)

| | Hours Post Hatch | Percent Develop. |
|---|---|---|
| Experiment A | 82.50 | 3.77 |
| | 90.50 | 54.72 |
| | 94.25 | 73.58 |
| | 98.75 | 77.36 |
| | 102.50 | 81.13 |
| | 113.50 | 96.23 |
| Experiment B | 56.00 | 4.17 |
| | 63.00 | 50.00 |
| | 66.00 | 62.50 |
| | 70.00 | 70.83 |
| | 75.75 | 83.33 |
| Experiment C | 175.75 | 11.76 |
| | 186.00 | 29.41 |
| | 198.00 | 62.75 |
| | 209.75 | 72.55 |
| | 221.50 | 96.08 |
| Experiment D | 81.00 | 6.98 |
| | 85.00 | 18.60 |
| | 89.00 | 46.51 |
| | 94.25 | 65.12 |
| | 100.75 | 72.09 |
| | 114.00 | 97.67 |
| Experiment E | 56.00 | 2.20 |
| | 60.00 | 13.19 |
| | 64.00 | 39.56 |
| | 67.50 | 63.74 |
| | 71.75 | 78.02 |
| | 76.00 | 85.71 |
| | 91.25 | 98.90 |

TABLE 20. Experimental Conditions and Probit Analysis for Larval Development

| Experiment | Experimental Environment | Temp. (°C.) Mean | Range | Number of Larvae | Probit Equation y= % dev. in probits, x=hours | Estimated Days to 50% dev. | Standard Deviation (Days) | $HU_{8.10^{\circ}C}$ (degree-days) | Standard Deviation (HU) |
|---|---|---|---|---|---|---|---|---|---|
| A | Cage in Room B10 | 25.15 | 23.3-27.1 | 53 | y=.0990x-4.1955 | 3.8688 | .4207 | 65.9637 | 7.1734 |
| B | Environmental Chamber | 32.87 | 30.0-34.6 | 24 | y=.1273x-3.4115 | 2.7523 | .3272 | 68.1751 | 8.1050 |
| C | Environmental Chamber | 16.26 | 15.0-17.8 | 51 | y=.0610x-6.9063 | 8.1282 | .6827 | 66.3258 | 5.5706 |
| D | Cage in Room B10 | 25.21 | 23.3-26.5 | 43 | y=.0992x-4.2439 | 3.8813 | .4189 | 66.4092 | 7.1841 |
| E | Environmental Chamber | 29.51 | 26.7-36.3 | 91 | y=.1172x-2.9926 | 2.8405 | .3554 | 60.8152 | 7.6089 |
| | | | | | | | Average | 65.5378 | 7.1284 |

FIGURE 15. Maximal Larval Developmental Rate
(Excess Food Supplied)



aphid prey species. Thus the disagreement in larval development rates is not surprising. Probably the most important variable in this type of experiment (given differences in the cecidomyiid populations collected from different areas) is the availability of the prey species to the cecidomyiids. In this author's experiment an excess number of pea aphids (which are a comparatively large species of aphid) were provided, thus allowing for a maximal rate of development (the cecidomyiids appeared to have no problem attacking the large pea aphids; this assumes no significant nutritional differences between the aphid species).

For the Michigan cecidomyiid population, a developmental threshold of 8.10°C. (46.58°F.) and developmental period of 65.54 (117.57 °F.-HU) heat units was indicated.

3. Larval Functional Response

Reports of the number of aphids killed by cecidomyiid larvae over their developmental period have ranged from 5.2 Myzus persicae reported by Nijveldt (1966) to 60-80 Aphis gossypii reported by Roberti (1946). The objective of this section was to estimate the number of A. pomi that would be killed under different aphid densities and temperature conditions.

Green peach aphids (M. persicae) reared on jimsonweed (see Section II-A-1) were used as apple aphid substitutes for the following laboratory experiments. The data in Table 35 in Section VII-A indicate that these two species are quite similar in size although green peach aphids have 5 immature

instars whereas the apple aphid has 4.

Young jimsonweed plants having trifoliet leaves with an average area of 9.9 $cm.^2$ (measured using a Lambda Instruments Corp. LI-300 Portable Area Meter) were used in the experiments. Two of the leaves were trimmed from the plant shortly before the start of the experiment so that the experimental arena was confined to the 9.9 $cm.^2$ area (aphids normally stayed on the underside of the leaf, cecidomyiids were not observed to search on the other side of the leaf or the stem). Shortly after hatch, a single cecidomyiid was transferred to the leaf arena. Since aphid levels did fluctuate somewhat (due to reproduction), the number of aphids was counted once - at a time which the larval developmental experiments (previous section) had indicated was 2/3 of the normal larval period. Previous experiments had indicated that the majority of aphids were killed by the $3^{rd}$ larval stage (which was assumed to begin at approximately this time) and thus the number of aphids were counted at the 2/3 time interval instead of at the beginning of the experiment. Post experimental analysis indicated that 24.28% of the aphids were killed prior to the 2/3 time interval and that the number of aphids killed by the young instars showed little correlation with aphid density (see Figure 16).

In order to include any dead aphids which fell off the leaf, a large petri dish rimmed with tanglefoot was placed below the leaf (a hole was cut for the stem and then taped up). Very few dead aphids were found in the petri dish - confirming the observation that most aphids are killed before they can

remove their stylets from the leaf. However, dead aphids were observed to stick to the mature larvae and as many as 29 aphids were carried off the leaf as the cecidomyiids dropped to the petri dish to pupate.

The total number of aphids killed (of each aphid life stage) was recorded at 3 overall mean temperatures of 16.79, 24.61 and 29.87$^{o}$C. and is listed in Table 21. The total number of aphids killed by both the 2$^{nd}$ and 3$^{rd}$ instar larvae was first plotted separately for the 3 experimental temperatures. Since the data for the 3 temperatures appeared similar (for 3$^{rd}$ instar larvae, data for the 3 temperatures fit the curve shown in Figure 17 with mean square relative errors of .101, .083 and .081 respectively), it was pooled in the following account. Uygun (1971) has reported that 1$^{st}$ instar larvae kill only one aphid. Thus the number of aphids killed up to the 2/3 time interval (minus 1) was attributed to the 2$^{nd}$ instar larvae. This 2$^{nd}$ instar functional response (aphids killed at the 2/3 time interval minus 1, versus aphids assumed to be present midway through the interval = alive at the 2/3 time interval plus 1/2 of those killed over that interval) is displayed in Figure 16. The line drawn is the relation used in the simulation model of Section V. As mentioned earlier, the number of aphids killed by the 2$^{nd}$ instars did not seem to be greatly affected by aphid density.

The remaining number of aphids killed was attributed to the 3$^{rd}$ instars. Figure 17 presents this functional response data (aphids killed after the 2/3 time interval versus aphids assumed to be present midway through the

TABLE 21. Functional Response Data

A. Overall Mean of 16.79°C. (Exp.1-3)

Experiment 1: Mean Temperature 16.78°C. (Range 15.6-17.9); N = 7: Aphids Counted After 131.75 hours

| Cecid. | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Number | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 68 | 18 | 86 | 10 | 24 | 12 | 3 | - | 2 | - | 51 |
| 2 | 24 | 11 | 35 | 3 | 10 | 7 | 3 | 1 | 1 | - | 25 |
| 3 | 23 | 9 | 32 | 1 | 14 | 6 | 4 | - | - | 1 | 26 |
| 4 | 9 | 11 | 20 | 1 | 5 | 3 | 1 | 1 | - | - | 11 |
| 5 | 36 | 7 | 43 | 2 | 6 | 6 | 4 | 4 | 1 | - | 23 |
| 6 | 18 | 9 | 27 | 1 | 12 | 9 | 2 | 2 | - | - | 26 |
| 7 | 18 | 15 | 33 | 2 | 10 | 8 | 5 | 4 | 2 | - | 31 |

Experiment 2: Mean Temperature 16.74°C. (Range 15.7-18.7); N = 6; Aphids Counted After 126.5 hours

| Cecid. | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Number | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 138 | 14 | 152 | 2 | 30 | 6 | 5 | 3 | 1 | 1 | 48 |
| 2 | 111 | 7 | 118 | 1 | 29 | 12 | 2 | 2 | - | - | 46 |
| 3 | 22 | 7 | 29 | 2 | 7 | 1 | - | - | 1 | - | 11 |
| 4 | 28 | 7 | 35 | - | 6 | 3 | 3 | 3 | 1 | - | 16 |
| 5 | 23 | 4 | 27 | 1 | 1 | 7 | 1 | 1 | - | 1 | 12 |
| 6 | 70 | 12 | 82 | - | 18 | 13 | 2 | 1 | - | 2 | 36 |

Experiment 3: Mean Temperature 16.82°C. (Range 15.6-18.1); N = 10; Aphids Counted After 136.5 hours

| Cecid. | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Number | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 62 | 13 | 75 | - | 18 | 9 | 5 | 3 | 2 | - | 37 |

TABLE 21. (cont.)

Experiment 3. (cont.)

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 2 | 12 | 11 | 23 | - | 11 | 4 | 2 | 1 | 1 | - | 19 |
| 3 | 182 | 4 | 186 | - | 15 | 11 | - | 1 | 1 | 1 | 29 |
| 4 | 103 | 11 | 114 | 2 | 14 | 9 | 2 | 1 | 1 | - | 29 |
| 5 | 28 | 12 | 40 | - | 17 | 8 | 1 | 1 | - | 1 | 28 |
| 6 | 140 | 9 | 149 | - | 13 | 20 | 6 | 2 | - | - | 41 |
| 7 | 73 | 14 | 87 | 1 | 11 | 14 | 9 | 3 | 1 | - | 39 |
| 8 | 93 | 7 | 100 | - | 18 | 9 | 5 | 1 | 1 | 1 | 35 |
| 9 | 35 | 7 | 42 | - | 12 | 11 | 6 | 1 | 2 | 2 | 34 |
| 10 | 74 | 5 | 79 | 2 | 18 | 10 | 2 | 1 | 1 | - | 34 |

B. Overall Mean of 24.61°C. (Exp. 4-5)

Experiment 4: Mean Temperature 24.33°C. (Range 21.7-26.7)
N = 26; Aphids Counted After 62.00 hours

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 52 | 8 | 60 | 14 | 20 | 4 | 4 | 2 | 3 | - | 47 |
| 2 | 84 | 7 | 91 | 5 | 22 | 14 | 4 | 5 | 1 | - | 51 |
| 3 | 27 | 4 | 31 | 2 | 9 | 3 | 4 | 6 | 2 | - | 26 |
| 4 | 40 | 8 | 48 | 9 | 8 | 5 | 6 | 6 | 2 | - | 36 |
| 5 | 92 | 4 | 96 | - | 10 | 11 | 8 | 6 | 1 | - | 36 |
| 6 | 73 | 6 | 79 | 10 | 15 | 8 | 1 | 1 | 3 | - | 38 |
| 7 | 61 | 5 | 66 | 1 | 10 | 6 | 4 | 4 | 1 | - | 26 |
| 8 | 95 | 7 | 102 | 12 | 18 | 8 | 6 | 4 | 2 | - | 50 |
| 9 | 56 | 6 | 62 | 2 | 7 | 3 | 7 | 4 | 1 | - | 24 |

TABLE 21. (cont.)

Experiment 4.(cont.)

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 10 | 115 | 9 | 124 | 3 | 12 | 15 | 10 | 1 | 1 | - | 42 |
| 11 | 31 | 7 | 38 | 2 | 13 | 8 | 3 | - | 1 | - | 27 |
| 12 | 152 | 8 | 160 | 3 | 14 | 13 | 7 | 7 | 1 | - | 45 |
| 13 | 49 | 7 | 56 | 3 | 9 | 10 | 8 | 4 | 2 | - | 36 |
| 14 | 125 | 8 | 133 | 8 | 21 | 10 | 4 | 3 | 1 | - | 47 |
| 15 | 46 | 6 | 52 | 6 | 7 | 4 | 5 | 3 | - | - | 25 |
| 16 | 75 | 13 | 88 | 10 | 8 | 10 | 8 | 9 | 2 | - | 47 |
| 17 | 26 | 7 | 33 | 4 | 10 | 10 | 2 | 3 | 3 | - | 32 |
| 18 | 66 | 6 | 72 | 3 | 21 | 8 | 5 | 1 | 1 | - | 39 |
| 19 | 19 | 6 | 25 | 2 | 3 | 6 | 5 | 4 | - | - | 20 |
| 20 | 33 | 7 | 40 | 3 | 9 | 7 | 9 | 5 | - | - | 33 |
| 21 | 61 | 7 | 68 | 4 | 8 | 6 | 3 | 2 | 1 | - | 24 |
| 22 | 219 | 7 | 226 | - | 19 | 13 | 2 | 1 | 1 | - | 36 |
| 23 | 85 | 4 | 89 | - | 18 | 10 | 6 | 4 | 3 | - | 41 |
| 24 | 42 | 8 | 50 | 5 | 8 | 9 | 4 | 2 | 1 | - | 29 |
| 25 | 109 | 6 | 115 | 2 | 21 | 8 | 4 | 3 | 1 | - | 39 |
| 26 | 14 | 6 | 20 | 2 | 5 | 5 | 4 | 3 | - | - | 19 |

Experiment 5: Mean Temperature 25.12°C. (Range 23.3-26.4)
N = 14; Aphids Counted After 66.5 hours

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 94 | 9 | 103 | 15 | 13 | 16 | 5 | 4 | 4 | - | 57 |
| 2 | 35 | 6 | 41 | 4 | 3 | 4 | 3 | 3 | 1 | 1 | 19 |
| 3 | 109 | 7 | 116 | 16 | 24 | 5 | 1 | - | - | - | 46 |

TABLE 21. (cont.)

Experiment 5.(cont.)

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 4 | 96 | 12 | 108 | 20 | 25 | 9 | 1 | 2 | - | - | 57 |
| 5 | 171 | 2 | 173 | 18 | 18 | 4 | 3 | 8 | 2 | - | 53 |
| 6 | 51 | 5 | 56 | 9 | 4 | 4 | 1 | 1 | 3 | - | 22 |
| 7 | 52 | 4 | 56 | 2 | 9 | 11 | 2 | 2 | 2 | - | 28 |
| 8 | 55 | 5 | 60 | 7 | 12 | 11 | 3 | 2 | 6 | - | 41 |
| 9 | 12 | 3 | 15 | 2 | 5 | 6 | - | 1 | - | - | 14 |
| 10 | 61 | 5 | 66 | 9 | 20 | 7 | 5 | 3 | 6 | - | 50 |
| 11 | 360 | 4 | 364 | 1 | 15 | 19 | 3 | 2 | - | - | 40 |
| 12 | 88 | 5 | 93 | 4 | 27 | 12 | 4 | 1 | - | - | 48 |
| 13 | 185 | 8 | 193 | 2 | 29 | 16 | 4 | 2 | 2 | 1 | 56 |
| 14 | 282 | 10 | 292 | 2 | 19 | 15 | 6 | 5 | 1 | - | 48 |

C. Overall Mean of 29.87°C.(Exp.6-9)

Experiment 6: Mean Temperature 29.62°C.(Range 26.9-30.8)
N = 9; Aphids Counted After 47.00 hours

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 56 | 14 | 70 | - | 12 | 13 | 4 | 2 | 1 | - | 32 |
| 2 | 103 | 15 | 118 | - | 11 | 19 | 4 | 2 | 1 | - | 37 |
| 3 | 69 | 10 | 79 | 1 | 9 | 12 | 4 | 4 | - | - | 30 |
| 4 | 128 | 10 | 138 | 2 | 18 | 11 | 5 | 3 | 2 | - | 41 |
| 5 | 178 | 10 | 188 | - | 16 | 16 | 3 | 4 | 2 | - | 41 |
| 6 | 336 | 5 | 341 | 2 | 11 | 19 | 4 | 1 | 1 | 1 | 39 |
| 7 | 58 | 15 | 73 | - | 14 | 16 | 5 | 4 | 2 | - | 41 |

TABLE 21. (cont.)

Experiment 6.(cont.)

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 8 | 41 | 15 | 56 | 1 | 18 | 14 | 5 | 1 | - | - | 39 |
| 9 | 68 | 9 | 77 | - | 10 | 5 | 5 | 5 | 4 | - | 29 |

Experiment 7: Mean Temperature 29.42°C.(Range 28.4-32.1)
N = 5; Aphids Counted After 47.00 hours

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 193 | 7 | 200 | 1 | 18 | 17 | 4 | 1 | 1 | - | 42 |
| 2 | 71 | 14 | 85 | 3 | 18 | 15 | 4 | 1 | - | - | 41 |
| 3 | 102 | 8 | 110 | - | 5 | 13 | 8 | 3 | 1 | - | 30 |
| 4 | 59 | 7 | 66 | - | 12 | 2 | 5 | 10 | 5 | - | 34 |
| 5 | 5 | 10 | 15 | - | 3 | 8 | 1 | 2 | - | - | 14 |

Experiment 8: Mean Temperature 29.61°C.(Range 27.4-30.7)
N = 2: Aphids Counted After 46.25 hours

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 82 | 3 | 85 | - | 11 | 8 | 8 | 1 | 2 | - | 30 |
| 2 | 278 | 14 | 292 | - | 38 | 12 | 8 | 4 | 1 | - | 63 |

Experiment 9: Mean Temperature 30.86°C.(Range 30.2-31.9)
N = 5; Aphids Counted After 46.25 hours

| Cecid. Number | Aphids Counted | | | Aphids Killed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Alive | Dead | Total | I | II | III | IV | V | Ad | Al | Total |
| 1 | 29 | 16 | 45 | 3 | 4 | 9 | 4 | 5 | 2 | - | 27 |
| 2 | 226 | 15 | 241 | - | 18 | 16 | 5 | 2 | 1 | 1 | 43 |
| 3 | 380 | 11 | 391 | - | 22 | 14 | 4 | 9 | 4 | - | 53 |
| 4 | 163 | 13 | 176 | 1 | 12 | 18 | 9 | 4 | 2 | - | 46 |
| 5 | 21 | 14 | 35 | 1 | 12 | 11 | 1 | 2 | 2 | - | 29 |

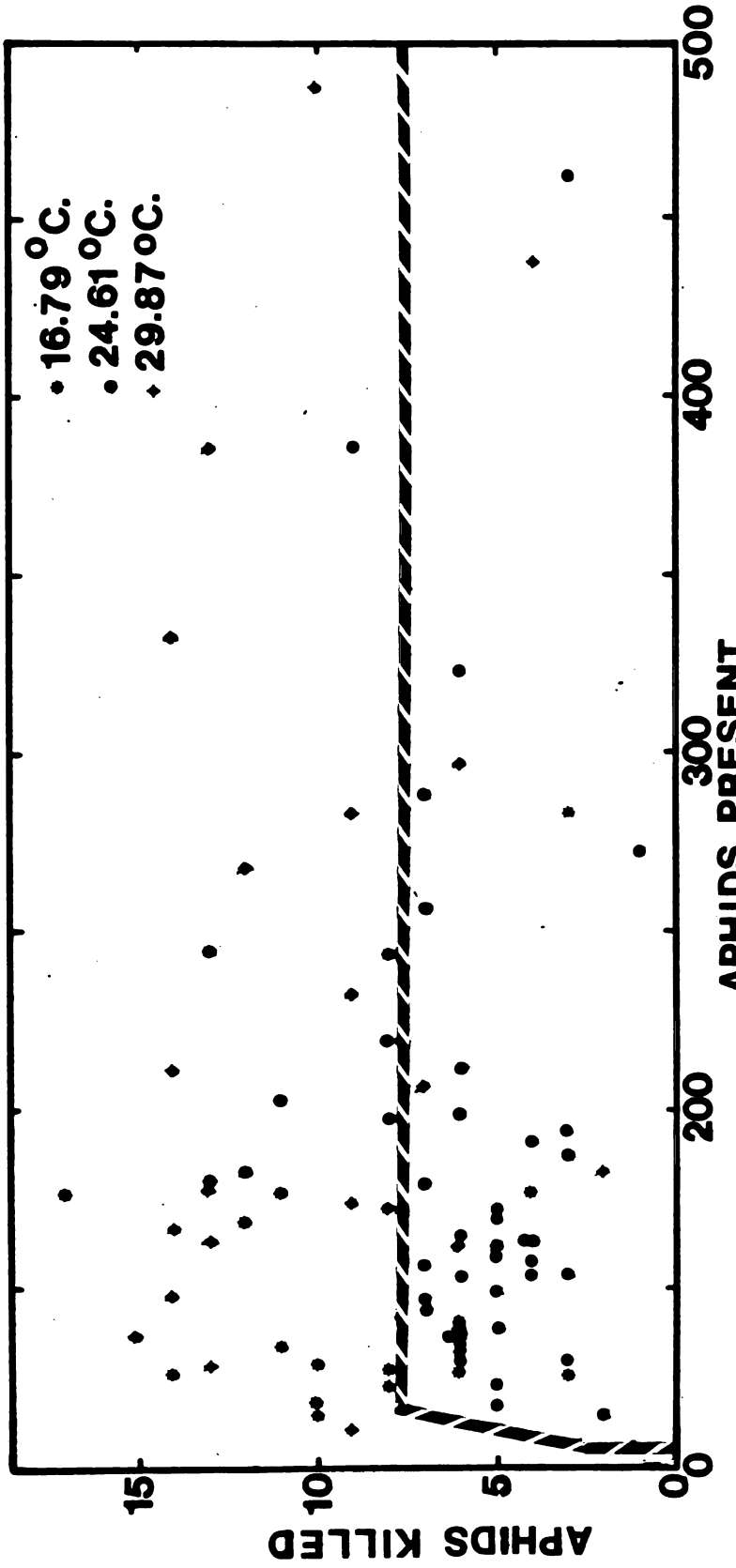



FIGURE 16. Second Instar Functional Response

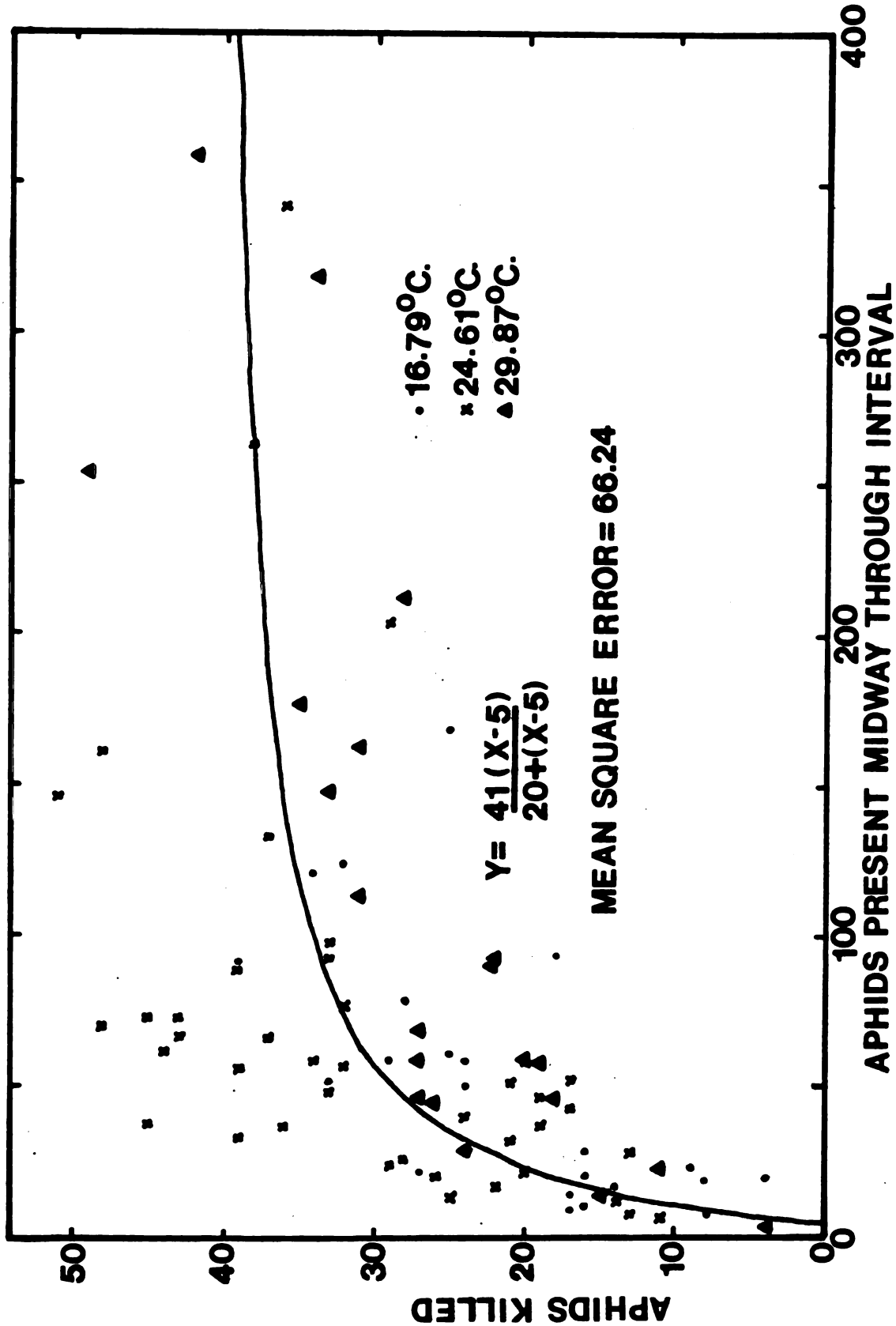



FIGURE 17. Third Instar Functional Response

interval = alive at the 2/3 time interval minus 1/2 killed over the last interval) for the 3rd instars which was fit to a Michaelis-Menton saturation curve (Lehninger 1970, using a computer program courtesy of Dr. Erik Goodman, Dept. of Electrical Engineering and Systems Science, MSU). The curve has a y-asymptote of 41 aphids killed per cecidomyiid.

4. Adult Female Fecundity and Longevity

The objective of this section was to measure fecundity and longevity of cecidomyiid females under assumed optimal conditions. El Titi (1973) has demonstrated that females respond to aphid aggregations, laying more eggs when presented with higher aphid densities. In this study, recently emerged females which had been provided with excess food as larvae were confined with 2 males on single fava bean plants (grown in plastic pots) infested with a minimum of 300 (300-400, average 350) pea aphids (see Section II-A-1 for description of materials, this number of aphids resulted in fairly dense colonies which were assumed to be optimal in "releasing" oviposition - see El Titi 1974b). Adults were confined to each plant using plastic cylinders 9 cm. in diameter and 21 cm. tall. One end of the chamber was capped with a plastic petri dish while the other end was pushed into the dirt surrounding the plant. Four to five 2 cm. diameter holes were cut in the cylinders and covered with screening to allow air circulation.

Plants were changed daily at midday with the adults transferred to new plants. Since adults were inactive during

the day this was accomplished with little disturbance of the females. The number of eggs deposited on each plant was counted using a microscope. The experiment was performed at room temperature (23.33°C.) and in an environmental chamber set at 16.39°C. (see Section II-A-5).

Tables 22 and 23 list daily fecundity and longevity of 22 and 31 females for the two temperatures. Figure 18 shows daily fecundity (per female alive at the start) for the two data sets. Total fecundity per female was slightly higher (163.41 to 150.55 eggs per female) at the higher temperature while longevity was somewhat less (7.41 versus 10.68 days).

5. Female Search and Oviposition

El Titi (1973) has shown that cecidomyiid females respond to aphid aggregation, laying more eggs with increasing density. In addition he showed qualitatively (El Titi 1974a) that females could find aphid colonies under low density conditions (one plant in 75 infested). In this section, the quantitative effect of low aphid density on female oviposition was studied.

Cecidomyiid females which were provided with excess food as larvae were confined their first night of adult life with excess males and several fava bean plants heavily infested with pea aphids. At 6:00pm (lab colonies were entrained to light on 4am-8pm, these experiments were performed during winter months) on the second night of adult life, 10-30 females were released into a 4.1x3.4x2.9 m.

TABLE 22. Fecundity and Longevity of 22 Cecidomyiid Females at 23.33°C. (Range 21.1-25.6)

| Cecid. Number | Night of Adult Life 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 61 | 20 | 12 | 4 | 0 | 2 | 0 | 0 | 14 | 0D[1] | - | - | - | 113 |
| 2 | 0 | 56 | 62 | 39 | 37 | 27 | 16 | 17 | 0D | - | - | - | - | - | 270 |
| 3 | 0 | 53 | 17 | 31 | 4D | - | - | - | - | - | - | - | - | - | 105 |
| 4 | 0 | 48 | 46 | 21 | 18 | 12D | - | - | - | - | - | - | - | - | 145 |
| 5 | 0 | 70 | 37 | 26 | 29 | 36 | 26 | 7D | - | - | - | - | - | - | 231 |
| 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 114 | 43 | 28 | 20 | 14 | 6D | - | 225 |
| 7 | 0 | 49 | 55 | 42 | 38 | 35 | 23 | 19D | - | - | - | - | - | - | 261 |
| 8 | 0 | 33 | 23 | 25 | 27 | 13D | - | - | - | - | - | - | - | - | 121 |
| 9 | 0 | 0 | 43 | 40 | 33 | 18 | 11 | 0D | - | - | - | - | - | - | 145 |
| 10 | 0 | 25 | 18 | 0D | - | - | - | - | - | - | - | - | - | - | 43 |
| 11 | 0 | 27 | 30 | 33 | 6D | - | - | - | - | - | - | - | - | - | 96 |
| 12 | 0 | 35 | 42 | 34 | 33 | 30 | 9 | 15 | 7 | 7 | 0 | 0D | - | - | 212 |
| 13 | 0 | 38 | 40 | 27 | 10D | - | - | - | - | - | - | - | - | - | 115 |
| 14 | 0 | 43 | 40 | 45 | 40 | 0D | - | - | - | - | - | - | - | - | 168 |
| 15 | 4 | 44 | 57 | 46 | 8 | 7 | 0D | - | - | - | - | - | - | - | 166 |
| 16 | 0 | 52 | 50 | 31 | 49 | 38 | 19 | 18 | 10 | 11D | - | - | - | - | 278 |
| 17 | 0 | 0D | - | - | - | - | - | - | - | - | - | - | - | - | 0 |
| 18 | 0 | 83 | 57 | 55 | 36 | 17 | 10 | 0D | - | - | - | - | - | - | 258 |
| 19 | 0 | 21 | 18 | 41 | 42 | 35 | 9 | 14 | 0D | - | - | - | - | - | 180 |
| 20 | 0 | 8 | 0D | - | - | - | - | - | - | - | - | - | - | - | 8 |
| 21 | 0 | 46 | 24 | 41 | 30 | 29 | 19 | 0D | - | - | - | - | - | - | 266 |
| 22 | 0 | 66 | 49 | 40 | 46 | 39 | 17 | 9 | 0D | - | - | - | - | - | 189 |
| Sum | 4 | 858 | 728 | 629 | 490 | 336 | 161 | 213 | 76 | 60 | 20 | 14 | 6 | 0 | 3595 |
| # Alive | 22 | 22 | 21 | 20 | 19 | 16 | 13 | 12 | 7 | 5 | 3 | 2 | 1 | 0 | |
| Sum/22 | 0.18 | 39.00 | 33.09 | 28.59 | 22.27 | 15.26 | 7.32 | 9.68 | 3.45 | 2.73 | 0.91 | 0.64 | 0.27 | 0.0 | 163.41 |

[1]D indicates that the female was found dead the following morning.

TABLE 23. Fecundity and Longevity of 31 Female Cecidomyiids at 16.39°C. (Range 15.0-17.8)

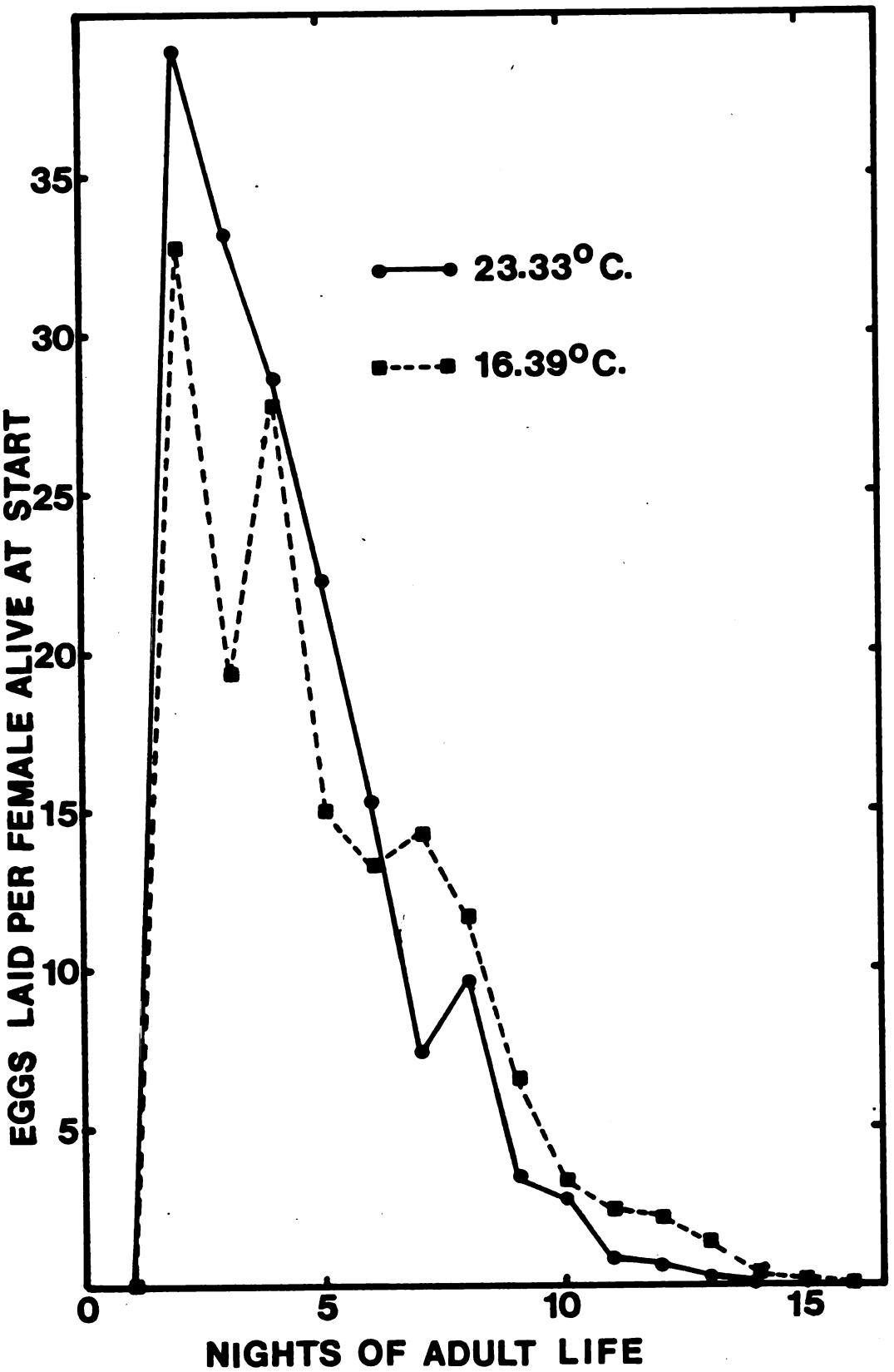
| Cecid. Number | Night of Adult Life | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | Total |
| 1 | 0 | 0 | 58 | 20 | 7 | 20 | 16 | 0 | 0 | 0D[1] | - | - | - | - | - | 121 |
| 2 | 0 | 23 | 0 | 34 | 14 | 17 | 10 | 16 | 0 | 10 | 4 | 5 | 4 | 0D | - | 137 |
| 3 | 0 | 36 | 6 | 24 | 10 | 20 | 23 | 20 | 14 | 1 | 12 | 7 | 6 | 2D | - | 181 |
| 4 | 0 | 0 | 0 | 33 | 0 | 0 | 46 | 7 | 4 | 6 | 0 | 0 | 0D | - | - | 96 |
| 5 | 0 | 34 | 8 | 18 | 31 | 4 | 22 | 37 | 14 | 0 | 0 | 6 | 0D | - | - | 174 |
| 6 | 0 | 0 | 46 | 19 | 14 | 19 | 9 | 47 | 4 | 6 | 5 | 2 | 0D | - | - | 171 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0D | - | - | - | - | - | 10 |
| 8 | 0 | 34 | 39 | 36 | 25 | 18 | 12 | 13 | 4D | - | - | - | - | - | - | 181 |
| 9 | 0 | 0 | 0 | 15 | 7 | 15 | 3 | 28 | 2 | 0 | 0 | 0 | 0D | - | - | 70 |
| 10 | 0 | 97 | 40 | 0D | - | - | - | - | - | - | - | - | - | - | - | 137 |
| 11 | 0 | 21 | 24 | 27 | 19 | 27 | 7 | 21 | 23 | 13 | 10D | - | - | - | - | 192 |
| 12 | 0 | 91 | 32 | 0 | 16 | 12 | 10 | 14 | 5 | 10 | 0 | 11 | 7 | 0D | - | 208 |
| 13 | 0 | 28 | 15 | 53 | 15 | 17 | 43 | 5 | 9 | 0 | 0D | - | - | - | - | 185 |
| 14 | 0 | 44 | 20 | 44 | 24 | 36 | 15 | 18 | 12 | 22 | 0 | 0 | 0D | - | - | 235 |
| 15 | 0 | 36 | 22 | 44 | 17 | 32 | 21 | 1 | 13 | 0 | 16 | 0D | - | - | - | 202 |
| 16 | 0 | 47 | 8 | 37 | 14 | 9 | 16 | 12 | 19 | 12 | 0 | 11 | 0D | - | - | 185 |
| 17 | 0 | 34 | 16 | 38 | 15 | 26D | - | - | - | - | - | - | - | - | - | 129 |
| 18 | 0 | 41 | 9 | 28 | 16 | 4 | 0D | - | - | - | - | - | - | - | - | 98 |
| 19 | 0 | 33 | 24 | 22 | 29 | 8 | 22 | 2 | 0D | - | - | - | - | - | - | 140 |
| 20 | 0 | 34 | 0 | 48 | 16 | 10 | 47 | 28 | 4 | 5 | 5 | 2 | 6 | 0 | 0D | 205 |
| 21 | 0 | 54 | 13 | 28 | 43 | 23 | 34 | 20 | 35 | 9 | 18 | 11 | 11 | 6 | 1D | 306 |
| 22 | 0 | 35 | 20 | 22 | 9 | 2 | 0 | 0 | 0D | - | - | - | - | - | - | 88 |
| 23 | 0 | 0 | 0 | 77 | 15 | 4 | 0 | 13 | 10 | 1 | 0D | - | - | - | - | 120 |

[1]D indicates that the female was found dead the following morning.

TABLE 23.(cont.)

| Cecid. Number | Night of Adult Life 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 24 | 0 | 19 | 26 | 0 | 1 | 0D | - | - | - | - | - | - | - | - | - | 46 |
| 25 | 0 | 12 | 53 | 23 | 12 | 14 | 18 | 0 | 4 | 0D | - | - | - | - | - | 136 |
| 26 | 0 | 44 | 9 | 29 | 7 | 20 | 4 | 5 | 2D | - | - | - | - | - | - | 120 |
| 27 | 0 | 50 | 12 | 24 | 23 | 6 | 11 | 6 | 0D | - | - | - | - | - | - | 132 |
| 28 | 0 | 37 | 43 | 34 | 29 | 21 | 24 | 21 | 14 | 12 | 5 | 10 | 9 | 4D | - | 263 |
| 29 | 0 | 51 | 3 | 29 | 10 | 5 | 0D | - | - | - | - | - | - | - | - | 98 |
| 30 | 0 | 30 | 34 | 34 | 25 | 6 | 29 | 26D | - | - | - | - | - | - | - | 184 |
| 31 | 0 | 57 | 17 | 23 | 2 | 15 | 3 | 0D | - | - | - | - | - | - | - | 117 |
| Sum | 0 | 1022 | 597 | 863 | 465 | 410 | 445 | 360 | 202 | 107 | 75 | 65 | 43 | 12 | 1 | 4667 |
| #Alive | 31 | 31 | 31 | 31 | 30 | 30 | 28 | 26 | 24 | 19 | 16 | 13 | 12 | 6 | 2 | |
| Sum/31 | 0 | 32.97 | 19.26 | 27.84 | 15.00 | 13.23 | 14.35 | 11.61 | 6.52 | 3.45 | 2.42 | 2.10 | 1.39 | 0.39 | 0.03 | 150.55 |

FIGURE 18. Cecidomyiid Fecundity at Two Temperatures



greenhouse room containing 1-100 fava bean plants with plants infested with pea aphids as shown in Table 24. The number of eggs deposited on infested plants was determined the following morning.

In addition to the females released into the room, 10 females were confined to single fava bean plants identical to those used in Section IV-C-4. These controls were used to monitor variability in the laboratory colony and greenhouse room environment since individual experiments were performed at approximately 10 day intervals to insure that females released for the previous experiment had died. Temperature within the room fluctuated within the range of 15.6 and 23.9°C. over the duration of the experiment (6pm-8am) for all 6 experiments.

The results of the experiments shown in Table 24 indicate that:

(1) Control fecundity (range 30.3-34.9 at temperatures fluctuating between 15.6-23.9°C.) was similar to that observed in the lab fecundity experiments (previous section) at 16.39 and 23.33°C. (32.97 and 39.00 respectively for the 2nd night of adult life).

(2) With 10 infested plants alone in the room, fecundity was reduced somewhat over that of the controls although this effect was less at the higher aphid density (21.7 at a density of 150-250 aphids/plant, 31.7 at 500-700/plant and an average of

TABLE 24. Cecidomyiid Search and Oviposition Data

| Experiment Number | Number of Infested Plants | Number of Uninfested Plants | Infestation Level[1] | Number of Females Released | Eggs Per Female | | Percent Reduction from Experiment A |
|---|---|---|---|---|---|---|---|
| | | | | | Controls | Infested Plants[2] | |
| 1A | 10 | 0 | M | 30 | 31.1 | 21.7 | - |
| 1B | 10 | 90 | M | 30 | 34.2 | 14.7 | 67.7 |
| 1C | 1 | 99 | M | 10[3] | 32.6 | 11.6 | 53.5 |
| 2A | 10 | 0 | H | 30 | 34.9 | 31.7 | - |
| 2B | 10 | 90 | H | 30 | 34.6 | 26.3 | 83.0 |
| 2C | 1 | 99 | H | 10 | 30.3 | 20.1 | 63.4 |
| | | | | | 32.95 | | |

[1]M (Moderate) 150-250 aphids/plant
H (High) 500-700 aphids/plant

[2]All infested at the level of the previous section = 300-400 aphids/plant. Average for 10 females confined individually on single fava bean plants.

[3]Number of females released was reduced to insure that competition between females did not reduce fecundity levels.

32.95 with controls at 300-400/plant). This reduction might be caused by the escape of some females from the room (every effort was made to insure against this) or more likely by a reduction caused by searching (10 plants in a $4.04 \times 10^7$ cm.$^3$ room versus 1 plant in the $1.34 \times 10^3$ cm.$^3$ confinement cylinder).

(3) The presence of additional uninfested plants also reduced fecundity levels with the effect less noticeable at the higher aphid density (at 10 and 1% of the plants infested, reductions were 67.7 and 53.6% at the moderate aphid density and 83.0 and 63.4% at high density repectively).

## D. FIELD EXPERIMENTS

### 1. Adult Emergence From Overwintering Sites

Adams (1977), working in a Massachussettes orchard, placed 10 emergence cages beneath apple terminals which had harbored A. aphidimyza colonies the previous fall and caught 4 adults on June 11, 1976. This "late" appearance of A. aphidimyza agreed with his egg sampling data and he concluded that "owing to a lack of biological synchrony between predator and prey", (the apple aphid appears and builds up somewhat earlier), "Aphidoletes is unable to prevent early season aphid damage."

Jokinen (1980) placed 10 emergence cages at the base of apple trees at the Graham Station in 1977. His trap catch was quite high (eg. 110 A. aphidimyza caught 5/18-5/25) and this author questions whether all of the specimens were A. aphidimyza. In the author's emergence cages at Graham Station, a great number of other Cecidomyiidae of similar appearance were captured.

The objective of this section was to characterize the season-long pattern of cecidomyiid emergence from overwintering sites in the soil.

#### a. Klein's Orchard 1979

Forty emergence cages (see Section II-B-2 for a description of cage design) were placed in Klein's orchard (field research sites are described in Section II-B-1) on April 1 and monitored weekly until August 13. Nine trees were chosen randomly with 4 emergence cages placed beneath

each tree. Four cages were placed outside the canopy of one tree. All cages were covered with a single layer of cheesecloth to prevent escape of adults from the cages. Terminals above the cages containing aphids or cecidomyiids were pruned so that emergence records represented adults emerging from overwintering sites.

All specimens resembling A. aphidimyza were placed in alcohol, removed to the laboratory and examined under a microscope for positive identification. Genitalia off all male specimens believed to be A. aphidimyza were examined and compared with the drawings of Harris (1966).

Table 25 presents the data for the 1979 Klein emergence cages. A total of 31 A. aphidimyza adults were captured (8 males, 23 females). No adults were caught in the 4 cages outside the canopy of the one tree. This data is compared with following emergence cage data from 1980 in Figure 19. The data is plotted using a lower heat unit threshold of 41°F. since pupal developmental data by Havelka (1980), analyzed independently by this author, indicated a lower pupal developmental threshold of 41.2°F.

b. Testing Emergence Cage Design

The low trap catch observed during the summer of 1979 prompted laboratory testing of emergence cage trap efficiency during the following winter. Adult cecidomyiids were aspirated from laboratory colonies (recently emerged adults were used) and released into an emergence cage set up in a greenhouse room (time of release was 11 am - 7 pm since peak

TABLE 25. Klein 1979 Emergence Cage Data

| Date | Heat Units$_{(41,95)}$ | ♂ | ♀ | Cumulative Total | Cumulative % of Total |
|---|---|---|---|---|---|
| 4/1 | 158.6 | 0 | 0 | 0 | 0.0 |
| 6/7 | 1459.1 | 0 | 0 | 0 | 0.0 |
| 6/15 | 1719.9 | 4 | 2 | 6 | 19.4 |
| 6/22 | 1909.9 | 1 | 7 | 14 | 45.2 |
| 6/29 | 2100.1 | 2 | 8 | 25 | 80.6 |
| 7/6 | 2290.9 | 1 | 2 | 28 | 90.3 |
| 7/16 | 2592.6 | 0 | 1 | 29 | 93.5 |
| 7/23 | 2780.1 | 0 | 1 | 30 | 96.8 |
| 7/30 | 2995.1 | 0 | 0 | 30 | 96.8 |
| 8/13 | 3390.1 | 0 | 1 | 31 | 100.0 |
| | Totals | 8 | 23 | | |

eclosion observed in laboratory colonies was over this time period). The number of adults killed in the aspiration process (measured as the number of dead cecidomyiids still in the aspirator) and numbers caught were counted after 48 hours. Two cage designs were tested - with and without a single layer of cheesecloth covering the exterior of the cage.

Table 26 presents the data for the laboratory testing of the emergence cage design. The results indicate a recapture rate of approximately 75% with little difference observed when the cheesecloth was removed.

c. Fall Seeding of Field Emergence Cages

An attempt was made to artificially increase the number of cecidomyiids overwintering in the soil beneath 3 emergence cages at the two trap sites for 1979-80. Laboratory colonies were taken to the field sites and placed in emergence cages on August 25, September 27 and October 4, 1979. The colonies were checked and new aphid infested plants introduced approximately every 2 weeks. Cecidomyiid larvae were observed as late as November 2. Emergence cages were left in place throughout the winter to mark the position of the pupae for monitoring during the spring and summer of 1980.

d. 1980 Emergence Cages

Twenty emergence cages were monitored every 3 to 7 days at both field sites (Klein 1980, Graham 1980) from May 4 to September 8. Methods were similar to 1979 except that the cheesecloth covering the exterior of the cages

TABLE 26. Testing Emergence Cage Design

| Time of Release | Time of Observation | Number Released | Number[1] Dead | Number Caught | % Capture[2] Efficiency |
|---|---|---|---|---|---|
| **A. Cage without cheesecloth** | | | | | |
| 1/16/80 1:00pm | 1/18/80 | 45 | 2 | 35 | 81.40 |
| 1/18/80 3:30pm | 1/20/80 | 34 | 4 | 21 | 70.00 |
| 1/28/80 11:00am | 1/30/80 | 45 | 4 | 35 | 80.49 |
| 1/30/80 11:00am | 2/1/80 | 50 | 8 | 30 | 71.43 |
| 2/14/80 5:45pm | 2/16/80 | 87 | 5 | 57 | 69.51 |
| | Totals | 261 | 23 | 176 | 73.95 |
| **B. Exterior of cage covered with cheesecloth** | | | | | |
| 2/17/80 2:30pm | 2/19/80 | 70 | 15 | 45 | 81.82 |
| 2/25/80 7:00pm | 2/27/80 | 55 | 5 | 33 | 66.00 |
| 3/5/80 12 noon | 3/7/80 | 44 | 5 | 35 | 89.74 |
| 3/7/80 4:00pm | 3/9/80 | 42 | 6 | 27 | 75.00 |
| 3/24/80 1:00pm | 3/26/80 | 40 | 7 | 21 | 63.64 |
| | Totals | 251 | 38 | 161 | 75.59 |

[1]Number dead in aspirator after 48 hours

[2]Number caught/(Number released - Number dead)

was removed. Emergence from seeded cages represents the sum of natural and seeded populations.

Data for 1980 emergence cages are presented in Tables 27 and 28. In 1980, 288 adults were captured, 30.6% of which were male and 48.3% were from the 6 seeded cages. Cumulative percent emergence for 1979 and 1980 is plotted in Figure 19 on a heat unit scale using a 41°F. lower threshold. 1979 and 1980 data are in some disagreement when compared on a heat unit scale (Figure 19), although data for the two sites in 1980 do seem to agree quite well. It is quite possible that some unexplained phenomenon (perhaps soil moisture) triggers spring cecidomyiid emergence. It is also likely that air temperatures don't accurately mimic the pattern of soil temperature fluctuations to which the diapausing pupae are exposed.

Of interest is the bimodal form of emergence observed in 1980 with very little emergence from 1400-2300 heat units. It is possible that 1979 monitoring was discontinued prematurely (Aug. 13 versus Sept. 8 in 1980) which resulted in a failure to observe a late season peak in 1979.

2. Trap Plants Placed in a Non-Commercial Setting

During the summers of 1978 and 1979, field observations and scout reports had indicated that cecidomyiid larvae seemed to appear in many different crops whenever appreciable aphid populations appeared. Earlier work by Jokinen (1980) had indicated that fairly large populations overwinter in some commercial apple orchards. In addition,

TABLE 27. Klein 1980 Emergence Cage Data

| Date | Heat Units (41,95) | Seeded Cages Males | Seeded Cages Females | Natural Cages Males | Natural Cages Females | Cumulative Percent of Total(95) |
|---|---|---|---|---|---|---|
| 5/4 | 261.0 | 0 | 0 | 0 | 0 | 0.0 |
| 6/2 | 766.0 | 0 | 0 | 0 | 0 | 0.0 |
| 6/5 | 828.0 | 0 | 0 | 0 | 2 | 2.1 |
| 6/8 | 896.2 | 0 | 0 | 0 | 0 | 2.1 |
| 6/13 | 962.0 | 0 | 0 | 1 | 3 | 6.3 |
| 6/16 | 1033.2 | 0 | 0 | 0 | 3 | 9.5 |
| 6/20 | 1108.0 | 0 | 0 | 0 | 1 | 10.5 |
| 6/24 | 1214.7 | 1 | 3 | 0 | 9 | 24.2 |
| 6/28 | 1343.7 | 0 | 2 | 1 | 2 | 29.5 |
| 7/2 | 1445.2 | 0 | 0 | 0 | 7 | 36.8 |
| 7/6 | 1553.5 | 0 | 0 | 0 | 1 | 37.9 |
| 7/11 | 1704.5 | 0 | 0 | 0 | 1 | 39.0 |
| 7/19 | 1968.2 | 0 | 0 | 0 | 1 | 40.0 |
| 7/25 | 2151.7 | 0 | 0 | 1 | 0 | 41.1 |
| 7/31 | 2323.7 | 1 | 1 | 1 | 1 | 45.2 |
| 8/7 | 2537.5 | 1 | 2 | 0 | 4 | 52.6 |
| 8/14 | 2735.0 | 1 | 1 | 3 | 10 | 68.4 |
| 8/21 | 2935.7 | 0 | 1 | 4 | 4 | 77.9 |
| 8/28 | 3147.0 | 1 | 2 | 0 | 5 | 86.3 |
| 9/4 | 3353.0 | 4 | 4 | 0 | 3 | 97.9 |
| 9/8 | 3462.7 | 0 | 1 | 0 | 1 | 100.0 |
| Totals | | 9 | 17 | 11 | 58 | |

TABLE 28. Graham 1980 Emergence Cage Data

| Date | Heat Units (41,95) | Seeded Cages Males | Seeded Cages Females | Natural Cages Males | Natural Cages Females | Cumulative Percent of Total(193) |
|---|---|---|---|---|---|---|
| 5/4 | 256.6 | 0 | 0 | 0 | 0 | 0.0 |
| 5/26 | 600.3 | 0 | 0 | 0 | 0 | 0.0 |
| 6/2 | 766.8 | 2 | 3 | 0 | 0 | 2.6 |
| 6/5 | 830.3 | 7 | 3 | 0 | 0 | 7.8 |
| 6/8 | 896.8 | 3 | 2 | 1 | 0 | 10.9 |
| 6/13 | 961.3 | 4 | 7 | 0 | 0 | 16.6 |
| 6/16 | 1033.8 | 0 | 1 | 1 | 1 | 18.1 |
| 6/20 | 1096.7 | 3 | 2 | 0 | 1 | 21.2 |
| 6/24 | 1187.7 | 4 | 9 | 0 | 1 | 28.5 |
| 6/28 | 1317.4 | 0 | 7 | 0 | 0 | 32.1 |
| 7/2 | 1415.4 | 0 | 0 | 0 | 0 | 32.1 |
| 7/6 | 1517.9 | 0 | 1 | 0 | 0 | 32.6 |
| 7/11 | 1665.4 | 0 | 0 | 0 | 0 | 32.6 |
| 7/19 | 1923.2 | 1 | 1 | 0 | 1 | 34.2 |
| 7/25 | 2109.7 | 0 | 0 | 0 | 1 | 34.7 |
| 7/31 | 2275.4 | 2 | 3 | 5 | 2 | 40.9 |
| 8/7 | 2493.4 | 3 | 2 | 4 | 14 | 52.9 |
| 8/14 | 2688.4 | 1 | 1 | 4 | 14 | 63.2 |
| 8/21 | 2875.9 | 3 | 11 | 4 | 8 | 76.7 |
| 8/28 | 3079.2 | 6 | 11 | 2 | 6 | 89.6 |
| 9/4 | 3292.7 | 1 | 5 | 4 | 4 | 96.9 |
| 9/8 | 3399.2 | 2 | 2 | 0 | 2 | 100.0 |
| Totals | | 43 | 70 | 25 | 55 | |

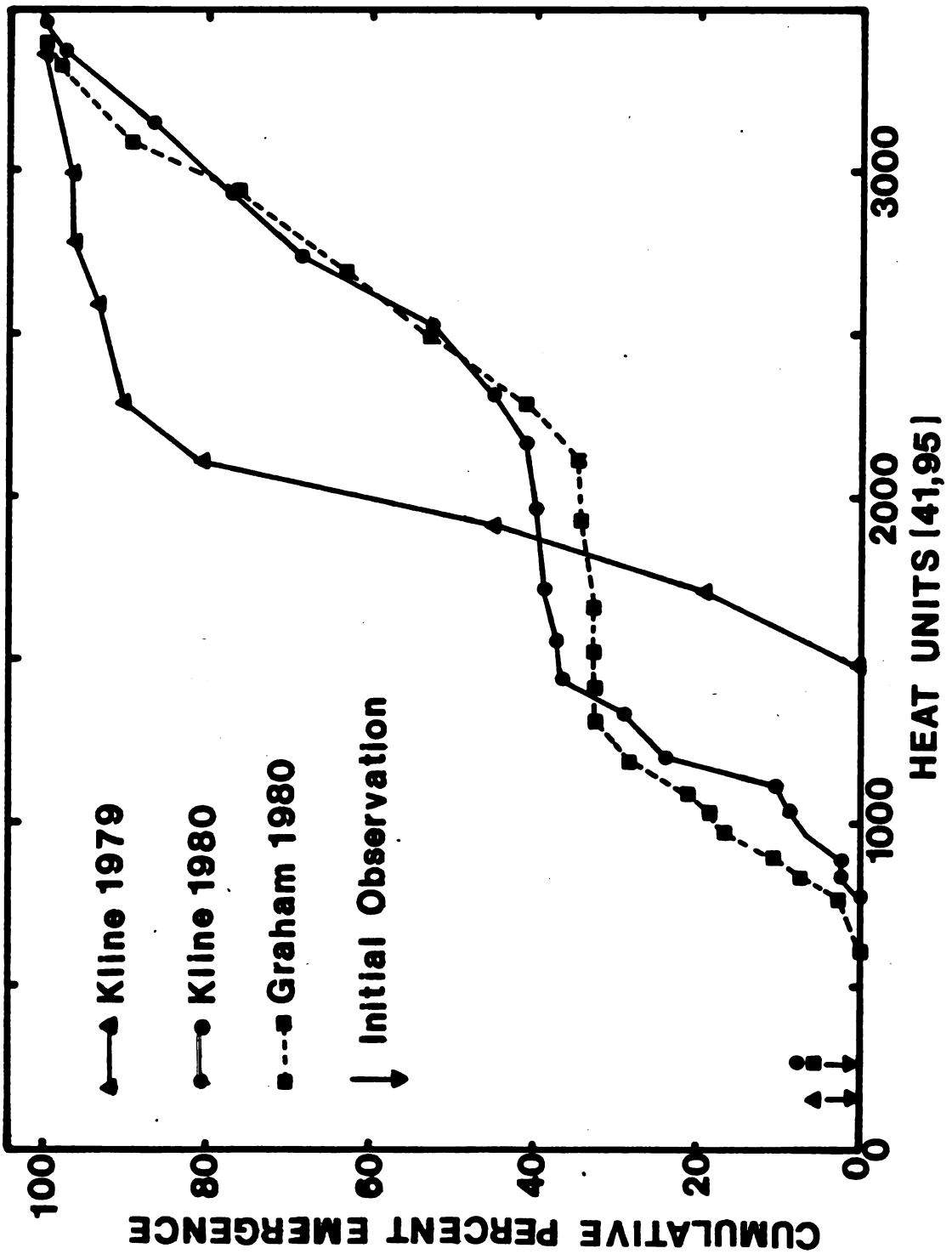



FIGURE 19. Cumulative Adult Emergence from Orchard Overwintering Sites

aphid infested plants left at several abandoned orchard sites had indicated that cecidomyiid females could be attracted to the plants and would deposit eggs close to the aphid colonies. The objective of this section was to investigate the qualitative abundance of cecidomyiids in a natural setting, remote from any commercial apple orchards.

The Rose Lake Wildlife Research and Game Area, located northeast of Lansing, MI was chosen for this experiment. No known commercial apple orchards were present within a distance of 10 miles. Four clay pots, each containing 3 fava bean plants infested with approximately 650 (range ± 200) pea aphids, were placed in locations separated by approximately 300 m. Plants were placed in water filled trays (to eliminate ants) on the ground and were replaced with fresh plants every 2-7 days. The plants were cut into sections and examined under a microscope for the presence of cecidomyiid and syrphid eggs (several different species of syrphids were observed).

Results are listed in Table 29 and plotted in Figure 20. An astounding number of eggs were captured in late June, July and early August. Data from Section IV-C-4 have indicated that laboratory fecundity under optimal conditions for 2 nights was 72.09 eggs/female (nights 2 and 3, Table 22). Thus eggs trapped 8/18-8/19 represent a minimum of 21.6 females (and probably a good deal more). This data indicate that cecidomyiid levels in this natural setting

TABLE 29. 1980 Rose Lake Trap Plants Data[1]

| Dates Plants Left in Field | Cecidomyiid Eggs | Syrphid Eggs |
|---|---|---|
| 5/5-5/8 | 0 | 10 |
| 5/13-5/15 | 0 | 0 |
| 5/19-5/22 | 0 | 216 |
| 5/27-5/30 | 12 | 160 |
| 5/30-6/3 | 44 | 89 |
| 6/3-6/6 | 160 | 63 |
| 6/6-6/8 | 13 | 455 |
| 6/8-6/15 | 602 | 138 |
| 6/15-6/17 | 16 | 33 |
| 6/17-6/21 | 6 | 29 |
| 6/21-6/25 | 92 | 48 |
| 6/25-6/29 | 466 | 28 |
| 6/29-7/1 | 75 | 111 |
| 7/1-7/4 | 217 | 51 |
| 7/4-7/9 | 116 | 41 |
| 7/9-7/12 | 520 | 34 |
| 7/12-7/15 | 766 | 10 |
| 7/15-7/18 | 916 | 26 |
| 7/18-7/21 | 419 | 6 |
| 7/21-7/24 | 562 | 6 |
| 7/24-7/29 | 849 | 15 |
| 7/29-8/1 | 981 | 46 |
| 8/1-8/5 | 1185 | 3 |
| 8/5-8/8 | 728 | 3 |
| 8/8-8/12 | 1798 | 54 |
| 8/12-8/15 | 913 | 25 |
| 8/18-8/19 | 1560 | 39 |
| 8/19-8/23 | 501 | 13 |
| 8/23-8/26 | 2631 | 1 |
| 8/26-8/30 | 1708 | 6 |
| 8/30-9/2 | 1381 | 0 |
| 9/2-9/5 | 324 | 10 |
| 9/5-9/8 | 124 | 42 |
| 9/8-9/11 | 131 | 16 |

[1]Eggs are the total deposited on 4 pots each containing 3 fava bean plants. Each pot was infested with approximately 650 pea aphids.

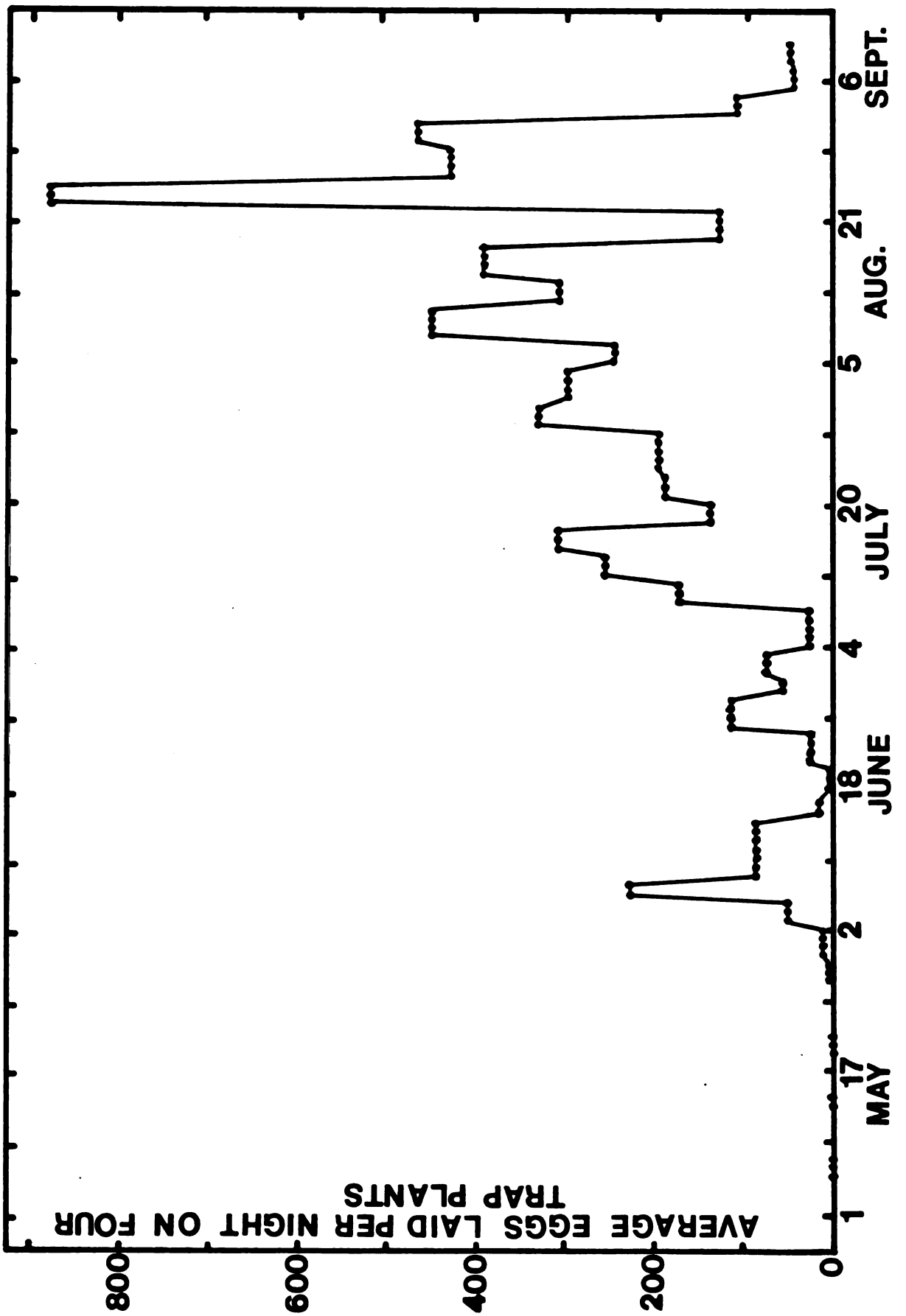



FIGURE 20. 1980 Rose Lake Trap Plants

are quite high and/or cecidomyiid females are extremely good at locating aphid colonies (see Section IV-C-5).

3. Summary of Early Season Cecidomyiid Appearance

Data on early season cecidomyiid appearance was obtained from several sources: (1) Emergence cages were placed in favorable orchard sites (Section IV-D-1), (2) Aphid infested trap plants were placed in a remote wildlife area (Section IV-D-2) and (3) Michigan field scouts were asked to report any cecidomyiids spotted during the spring of 1979 and 1980.

Data on early season appearance and heat units since Jan. 1 (using a 41°F. lower threshold) are listed in Table 30. Several factors complicate prediction of first appearance of cecidomyiids based on a heat unit concept. Cecidomyiid larvae construct a cocoon at a depth of about 2 cm. (Markkula and Tiittanen 1977) and thus air temperature may not accurately represent soil temperature to which the pupae are exposed. Secondly, relatively few cecidomyiids overwinter in the orchard and thus data using emergence cages is based on a small smaple size. In addition, other factors such as soil moisture levels may influence overwinter emergence.

4. Commercial Orchard Trap Plants Compared With Direct Larval Sampling

Trap plants were also placed in Block 12 of the Graham Station during the summer of 1980. Direct terminal samples of aphid and cecidomyiid populations were performed for correlation with trap plant catch. The objective was to

TABLE 30. First Appearance of Cecidomyiids in the Spring

| Data Source | Date | Location | Heat Units (41,95) | Comments[1] |
|---|---|---|---|---|
| Adams 1977 | 6/11/76 | Belchertown, MA | 1350.5 | 10 emergence cages 4 °C caught on 6/11 |
| Jokinen 1980 | 5/7/77 | Graham Station Grand Rapids,MI | 510.1 | 10 emergence cages |
| This Report | 6/7/79 | Klein Orchard Sparta,MI | 1719.9 | 40 emergence cages |
| | 6/5/80 | Klein Orchard Sparta,MI | 828.0 | 20 emergence cages with 3 "seeded" cages |
| | 6/2/80 | Graham Station Grand Rapids,MI | 766.8 | 20 emergence cages with 3 "seeded" cages |
| | 5/28/80 | Rose Lake,near Lansing,MI | 630.2 | 4 aphid infested trap plants[2] |
| | 5/22/80 | Washtenaw Co., MI | 539.6 | observation of larvae in rosy apple aphid colony[3] |

[1]All observations are adults caught in emergence cages except where noted.

[2]Twelve eggs were collected from trap plants left in the field 5/27-5/29. Night of oviposition was assumed to be 5/29 because of the stage of egg development. Latest date of emergence was set as 5/28 (first eggs are usually laid the 2nd night of adult life).

[3]Late instar larvae were reported from a commercial orchard by field scout Robert Kriegel on 5/30. Assuming a late 2nd instar larvae, date of emergence was calculated to be at least as early as 5/22.

determine whether trap plants could be used to monitor early season cecidomyiid populations before high apple aphid populations outcompeted the trap plants.

Four trap pots (identical to those used in Section IV-D-2) were suspended at head height in trees chosen at random from Block 12. New plants were placed in the orchard every 3-5 days and predators collected were counted using a lab microscope.

Terminal samples were taken by choosing 10 trees randomly from Block 12 (see block map in Section II-B-1-b) and counting the number of aphids and predators on each of 10 watersprouts located within the inner 1/2 diameter of each tree. Predator eggs were included in the totals when observed. Syrphid, chrysopid and hemerobiid eggs were fairly easy to see but cecidomyiid eggs were rarely observed although lab inspection (using a microscope) of leaves indicated they were present.

Table 31 lists the data for both trap plant and terminal sample observations for each date. Figure 21 compares the pattern of cecidomyiid eggs trapped and the number of aphids sampled from the terminals with the emergence cage data of Section IV-D-1. It was hoped that the cecidomyiid trap plants would indicate early season appearance of cecidomyiid females. Data from the Graham 1980 emergence cages showed initial overwinter emergence during 5/26-6/2 with 28.5% of the cecidomyiids emerged by 6/24. In view of the low number of aphids present during this time, it is

TABLE 31. Trap Plant and Terminal Sampling Data from Graham Station 1980

| Trap Plants[1] | | | | Samples on First Data[2] | | | | |
|---|---|---|---|---|---|---|---|---|
| Dates Plants Left | Cec. Eggs | Syrphid[3] Eggs | Other[4] | Aphids | Cec. | Syrphids | Others | Sprays[5] |
| 6/2-6/5 | 0 | 58 | 1CH | 0(0) | 0(0) | 0(0) | 1(1)CH | |
| 6/5-6/8 | 0 | 85 | | 0(0) | 0(0) | 0(0) | | |
| 6/8-6/13 | 0 | 7 | | 19(4) | 0(0) | 0(0) | | 6/11 Guthion |
| 6/13-6/16 | 0 | 13 | 6CH | 16(7) | 0(0) | 0(0) | 6(1)CH | ½#/100 gal. |
| 6/16-6/20 | 0 | 38 | | 90(9) | 0(0) | 0(0) | | |
| 6/20-6/24 | 0 | 14 | | 197(8) | 0(0) | 1(1) | | |
| 6/24-6/28 | 0 | 36 | | 515(28) | 0(0) | 8(5) | | 6/25 Guthion |
| 6/28-7/2 | 19 | 111 | | 362(25) | 0(0) | 5(3) | | ½#/100 gal. |
| 7/2-7/6 | 11 | 155 | | 1050(39) | 8(1) | 9(4) | | |
| 7/6-7/11 | 59 | 98 | | 4930(68) | 0(0) | 59(27) | | 7/9 Guthion |
| 7/11-7/14 | 122 | 64 | | 4317(78) | 7(3) | 68(28) | | ½#/100 gal. |
| 7/14-7/19 | 119 | 65 | | 7922(86) | 55(17) | 41(21) | | |
| 7/19-7/22 | 48 | 24 | | 15225(94) | 71(23) | 79(32) | | 7/21 Guthion |
| 7/22-7/25 | 39 | 0 | | 2415(63) | 4(2) | 4(3) | | ½#/100 gal. |
| 7/25-7/28 | 0 | 68 | | 4748(80) | 17(9) | 16(7) | 2(2)CH | |
| 7/28-7/31 | 55 | 32 | | 6730(90) | 34(12) | 10(6) | | |
| 7/31-8/4 | 121 | 67 | | 7848(92) | 72(20) | 4(2) | | |

[1]Numbers are total number of eggs deposited on 4 trap plants hung in the orchard.

[2]Samples are total number of insects (% of terminals infested) on 10 trees with 10 terminals inspected per tree. Samples are for the first date given - i.e. 6/2-6/5 means samples taken on 6/2.

[3]Of the syrphids encountered during the summer of 1980 at Graham Station the major species were Syrphus luniger Meigen (roughly 85%) and S. balteatus (DeGeer) as determined by the keys of Scott(1939) and Dixon(1960).

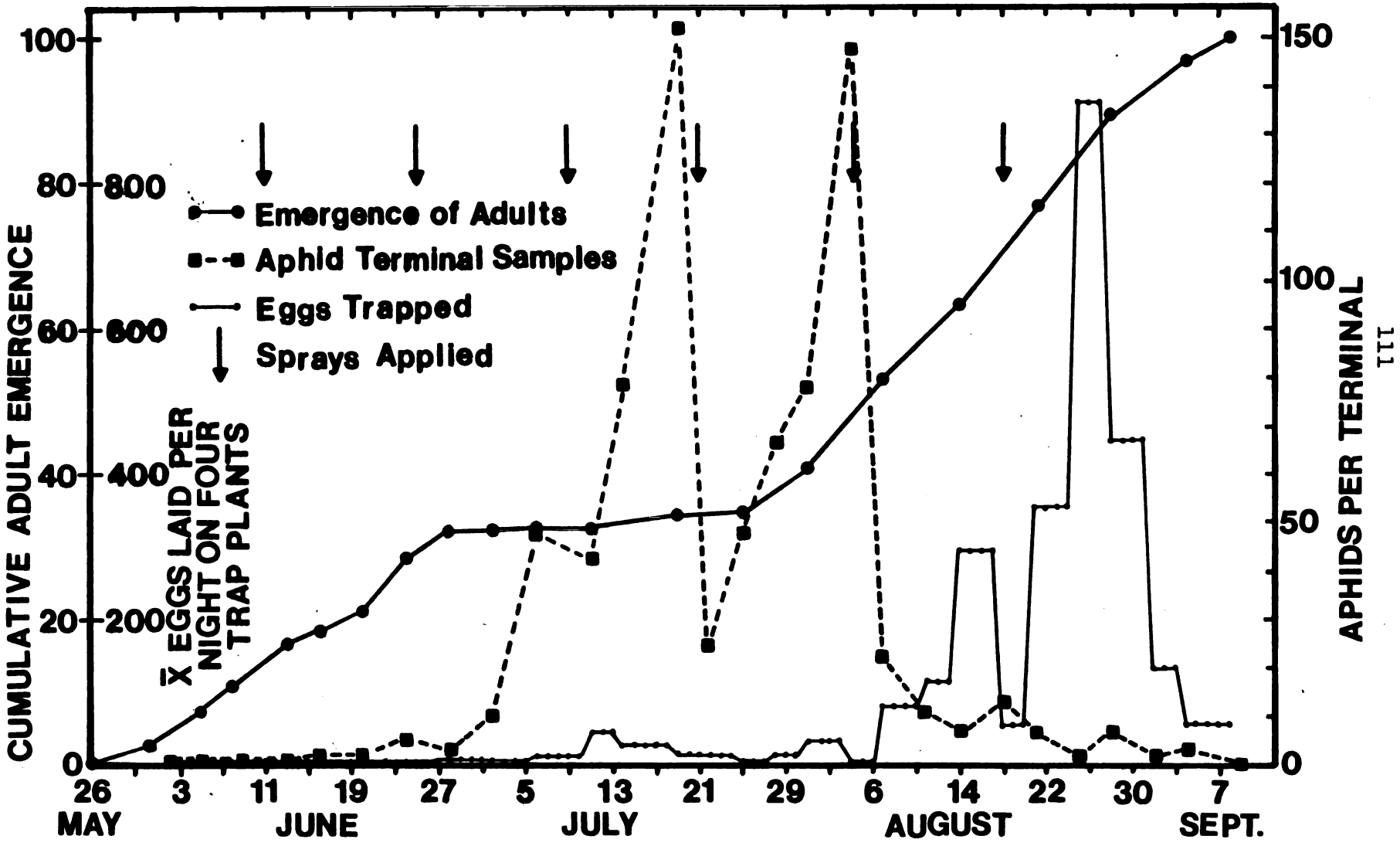
[4]Other predators observed were Chrysopidae (CH), Hemerobiidae (HE) and Orius insidiosus Say (Anthocoridae) which was not counted.

[5]See Section VIII-D for full list of sprays applied to Block 12.

TABLE 31. (cont.)

| Trap Plants | | | | Samples on First Data | | | | |
|---|---|---|---|---|---|---|---|---|
| Dates Plants Left | Cec. Eggs | Syrphid Eggs | Other | Aphids | Cec. | Syrphids | Others | Sprays |
| 8/4-8/7 | 10 | 21 | | 14865(97) | 212(27) | 62(28) | | 8/4 Guthion |
| 8/7-8/11 | 320 | 26 | 3CH | 2260(78) | 17(9) | 12(9) | 4(3)CH | ½#/100 gal. |
| 8/11-8/14 | 296 | 74 | 5HE | 1173(40) | 12(6) | 4(3) | | |
| 8/14-8/18 | 1191 | 57 | 3CH,1HE | 796(39) | 3(3) | 1(1) | 1(1)CH,4(4)HE | |
| 8/18-8/21 | 176 | 8 | | 1331(49) | 48(12) | 1(1) | | 8/18 Guthion |
| 8/21-8/25 | 1413 | 23 | | 612(36) | 24(8) | 1(1) | 1(1)CH, 1(1)HE | ½#/100 gal. |
| 8/25-8/28 | 2728 | 28 | | 191(7) | 3(2) | 0(0) | | |
| 8/28-9/1 | 1772 | 14 | | 635(11) | 108(8) | 3(1) | | |
| 9/1-9/4 | 400 | 6 | | 166(6) | 4(2) | 0(0) | | |
| 9/4-9/9 | 290 | 0 | 1CH | 324(1) | 8(1) | 6(1) | 1(1)HE | |
| 9/9 | | | | 0(0) | 0(0) | 0(0) | | |

FIGURE 21. Trap Plant and Terminal Sampling Data from Graham Station 1980



surprising that so few eggs were collected on the trap plants. It is possible that the sprays applied on 6/11 and 6/25 reduced trap plant egg deposition.

As aphid levels increased (after July 1), trap plant catch remained low although larvae became prevalent as demonstrated by the terminal samples. It was expected that competition from apple aphids would reduce trap plant catch during this period. Also as expected, large trap plant catch began once the orchard apple aphid population had "crashed" in late season (after Aug. 10).

# V. CECIDOMYIID PREDATION SIMULATION

## A. OBJECTIVES AND METHODOLOGY

The objective of this section was to combine the aphid development and reproduction simulation of Section III with the biological data on cecidomyiid development and predation in Section IV into a simulation of cecidomyiid predation on a single apple terminal. The components of the predation simulation are listed in Section V-B and the output of the simulation is compared with aphid/cecidomyiid sleeve cage data in Section V-C.

B. SIMULATION STRUCTURE

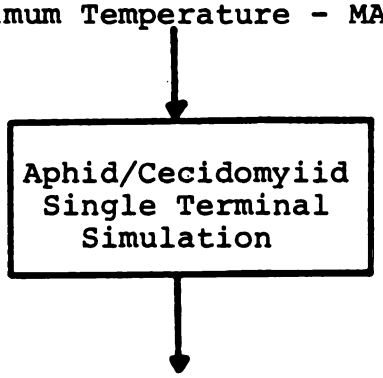
Figure 22 presents a black box model of the aphid/cecidomyiid single terminal simulation (see Figure 5 for further description of the aphid portion of the simulation). Input to the simulation included the initial number of aphids and cecidomyiids present on the terminal, the duration of the simulation and the temperature profile (daily maximum and minimums) over the period of the simulation. Output included the final number of aphids and cecidomyiids (cecidomyiid larvae which have completed their development on the terminal are converted to pupae) on the terminal and the number of aphids killed by the cecidomyiids. Lines 4560-6520 of the computer program listing in Section VII-B contain the cecidomyiid portion of the simulation.

1. Egg Stage

Linear regression performed on literature and experimental data (see Figure 14, Section IV-C-1) indicated an egg developmental threshold of 51°F. and a developmental period (inverse of the slope x 9/5) of 45.88 heat units (°F.-HU). Since the variability in the egg developmental period was fairly small (see standard deviation in Table 17) the egg stage was modeled using a discrete delay (Manetsch and Park 1977) developmental model as shown in Figure 23. The egg stage was divided into 9 equal substages, each of 5 heat units (above the 51°F. developmental threshold) in duration. For the purposes of the sleeve cage simulations, egg mortality (failure to hatch = EMORT) was set to zero since sleeve cage

FIGURE 22. Black Box Model of Aphid/Cecidomyiid Simulation

Initial Month, Day, Time - IMNTH, IDAY, ITIMIN
Inital Number of Aphids - AP(i), i=1,3
Initial Number of Cecidomyiids - CEGG(i),i=1,9;CLARV(i),i=1,33
Duration of Simulation - DAYS
Daily Maximum, Minimum Temperature - MAX(I,J),MIN(I,J)




Final Aphid Numbers - AP(i),i=1,3
Final Cecidomyiid Numbers - CLARV(i),i=1,33;CTPUP
Aphids Killed - APKILD

Explanation of Variables Not Defined in Figure 5:

ITIMIN - Time of day simulation starts on (1=early morning, 2=noon)

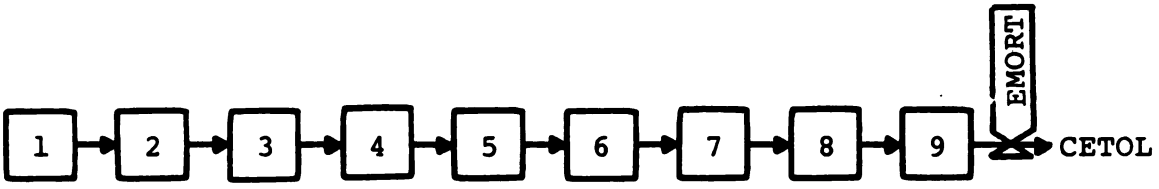
CEGG(i) - Number of cecidomyiid eggs in each substage

CLARV(i) - Number of cecidomyiid larvae in each substage

CTPUP - Total number of cecidomyiid pupae

APKILD - Total aphids killed by the cecidomyiids

FIGURE 23. Cecidomyiid Egg Discrete Delay Developmental Model




CEGG(i):i=1,2,...9

EQUATIONS:

CEGG(i+1,T+DT) = CEGG(i,T)  i=1,2,...8

CETOL(T+DT) = CEGG(9,T)*(1 - EMORT)

DT = 5

EMORT = 0

Definition of Variables:

CEGG(i) - Number of cecidomyiid eggs in the $i^{th}$ substage.

CETOL - Number of recently hatched eggs which are transferred to the larval stage.

DT - Time step (5 heat units above a developmental threshold of $51^{o}$F.).

EMORT - Egg mortality (failure to hatch); Since only surviving cecidomyiids were counted in the sleeve cages, this was set to 0 for this simulation.

data is reported in terms of the number of 2nd instar larvae present in each sleeve.

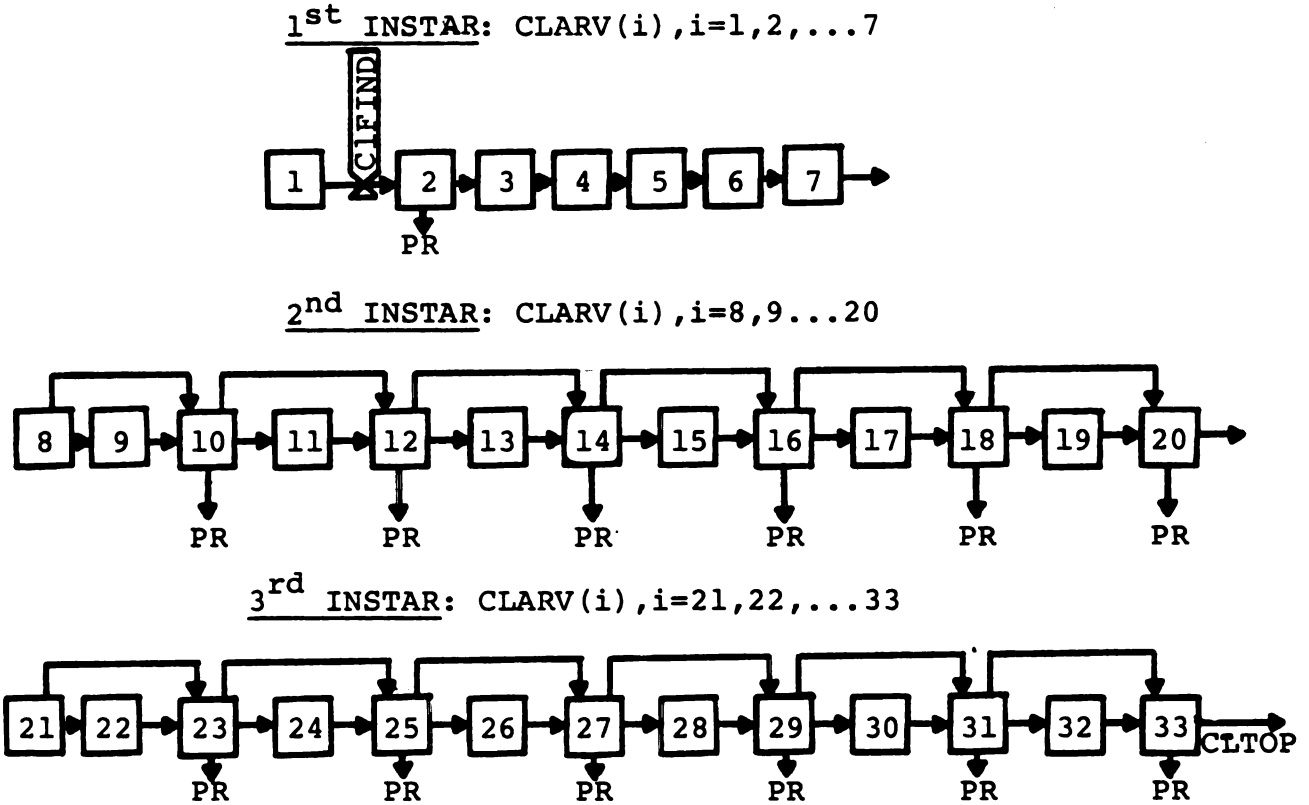
2. Larval Stage

Linear regression on experimental data (see Figure 15, Section IV-C-2) indicated a larval developmental threshold of 46.58°F. and a developmental period of 117.57 heat units. Since data for the 2 literature data sets (Uygun 1971 - 40.64°F., Havelka 1980 - 41.54°F.) indicated lower developmental thresholds, the experimental threshold was rounded downwards and a 46°F. threshold was used. The larval stage was also simulated using a discrete delay developmental model as shown in Figure 24. The 3 larval instars were divided into 7, 13 and 13 substages respectively.

The number of aphids present on the terminal was assumed to affect the speed of larval development as shown in Table 32 (also see equations in Figure 24). First instar larvae molt to the second instar after killing and feeding on a single aphid (Uygun 1971). The proportion of 1st substage cecidomyiids which successfully attacked their first aphid was represented by the variable ClFIND. In the sleeve cage simulations ClFIND was set to unity since only surviving cecidomyiids were counted. The duration of the 1st instar was 35 heat units (above the 46°F. threshold) regardless of aphid density.

The durations of both the 2nd and 3rd larval stages varied from 35 to 65 heat units, increasing with decreasing aphid density as controlled by the variable FRFIND. Under

FIGURE 24. Cecidomyiid Larval Discrete Delay Developmental Model




EQUATIONS:

CLARV(1,T) = CETOL(T)

CLARV(2,T+DT) = CLARV(1,T)*C1FIND

CLARV(i+1,T+DT) = CLARV(i,T) for i = 2,3,...7

CLARV(i+1,T+DT) = CLARV(i,T)*(1-FRFIND) i=8,10,...18; 21,23,...31

CLARV(i+2,T+DT) = CLARV(i,T)*FRFIND+CLARV(i+1,T)

CLARV(21,T+DT) = CLARV(20,T)

CLTOP(T+DT) = CLARV(33,T)

C1FIND = 1 (only surviving cecidomyiids were counted in sleeve cages)
DT = 5 Heat units above a 46°F. threshold
PR - Predation (see Table 33)
FRFIND - see Table 32

TABLE 32. Simulated Effect of Aphid Density on the Speed of Larval Development

| APTOT | FRFIND |
|---|---|
| 0- 10 | 0.00 |
| 10- 20 | 0.10 |
| 20- 30 | 0.35 |
| 30- 50 | 0.65 |
| 50-100 | 0.90 |
| > 100 | 1.00 |

APTOT - Total number of aphids present on the terminal.

FRFIND - Fraction of 2nd and 3rd instar cecidomyiids which are advanced "quickly" due to adequate availability of prey.

Duration of Stage in Heat Units

| Life Stage | Quick Development (FRFIND=1.00) | Slow Development (FRFIND=0.00) |
|---|---|---|
| 1st Instar | 35 | 35 |
| 2nd Instar | 35 | 65 |
| 3rd Instar | 35 | 65 |
| Total | 105 | 165 |

high aphid density conditions, cecidomyiids passed directly from one feeding stage to the next (feeding stages denoted by PR; eg. from stage 10 to 12). If fewer aphids were present, larvae spent time in an intermediate substage (eg.11) searching for prey. Mature larvae from substage 33 were transferred to the pupal stage (CLTOP).

Predation was simulated as shown in Table 33 (also see Figure 24). First instar larvae killed a single aphid while in the $2^{nd}$ substage. As mentioned, predation by $2^{nd}$ and $3^{rd}$ instar larvae was attributed to 6 feeding substages in each stage (denoted by PR in Figure 24). The relative proportion of aphids killed by each feeding substage was set by the array CSUBKL(i) (see Table 33, e.g. $2^{nd}$ instar larvae in the final feeding substage killed six times as many aphids as those in the initial feeding substage).

The number of aphids which would be killed by each larval stage (APK2 for $2^{nd}$ instar larvae, APK3 for $3^{rd}$) was first computed as a function of the number of aphids present, using the functional response data of Figures 16 and 17 (Section IV-C-3). This level was then multiplied by the proportion of aphids killed by each substage (CSUBKL(i)) in order to obtain the number of aphids killed by the substage. Note that the total number of aphids killed over a given stage (the sum of aphids killed by each of the 6 feeding substages) would not necessarily equal the level given by the functional response curves since aphid levels would vary over the duration of the stage.

TABLE 33. Simulated Cecidomyiid Predation

A. Aphids Killed by Each Feeding Substage

| Instar | Feeding Substage | Aphids Killed Per Cecidomyiid |
|---|---|---|
| 1 | 2 | 1 |
| 2 | 10 | APK2 * CSUBKL(1) |
| | 12 | APK2 * CSUBKL(2) |
| | 14 | APK2 * CSUBKL(3) |
| | 16 | APK2 * CSUBKL(4) |
| | 18 | APK2 * CSUBKL(5) |
| | 20 | APK2 * CSUBKL(6) |
| 3 | 23 | APK3 * CSUBKL(1) |
| | 25 | APK3 * CSUBKL(2) |
| | 27 | APK3 * CSUBKL(3) |
| | 29 | APK3 * CSUBKL(4) |
| | 31 | APK3 * CSUBKL(5) |
| | 33 | APK3 * CSUBKL(6) |

B. Relative Proportion of Aphids Killed by Each Feeding Substage

| i | CSUBKL(i) | CSUBKL(i)/.05 |
|---|---|---|
| 1 | .05 | 1 |
| 2 | .1 | 2 |
| 3 | .15 | 3 |
| 4 | .2 | 4 |
| 5 | .2 | 4 |
| 6 | .3 | 6 |

C. Functional Response Equations Derived from Figures 16 and 17

| APTOT | APK2 (see Figure 16) |
|---|---|
| 0- 5 | 0 |
| 5-15 | APTOT/15.*7.56[1] |
| 15 | 7.56 |

APK3 = (41.*(APTOT-5))/(20+APTOT-5) (see Figure 17)
APK3 = 0 if APTOT 5

[1]The number of aphids killed by 2nd instar larvae showed little correlation with aphid density above 15 aphids/terminal (see Figure 16). The average number of aphids killed by 2nd instar larvae in the laboratory functional response experiment (Table 21) was 7.56 aphids.

Functional response data was calculated for a single cecidomyiid confined on an aphid infested leaf (Section IV-C-3). The effect of competition between cecidomyiids was simulated using the variable CFACT as shown in Figure 25. The ratio (RAT) of the number of aphids that would be killed in the absence of competition (i.e. the number of cecidomyiids on the terminal multiplied by the number that would be killed by a single cecidomyiid) divided by the number of aphids present (APTOT) was first computed. CFACT represents the proportional reduction in the number of aphids killed (as a function of this ratio) due to competition.

The number of aphids killed during each model iteration was computed as a function of the total number of aphids present on the terminal regardless of life stage. Aphids were then removed (i.e. killed) in proportion to the numbers present on the terminal in each life stage (i.e. if 10% of the aphids were killed, 10% of each life stage was removed). Thus cecidomyiids were not assumed to preferentially attack one life stage over another.

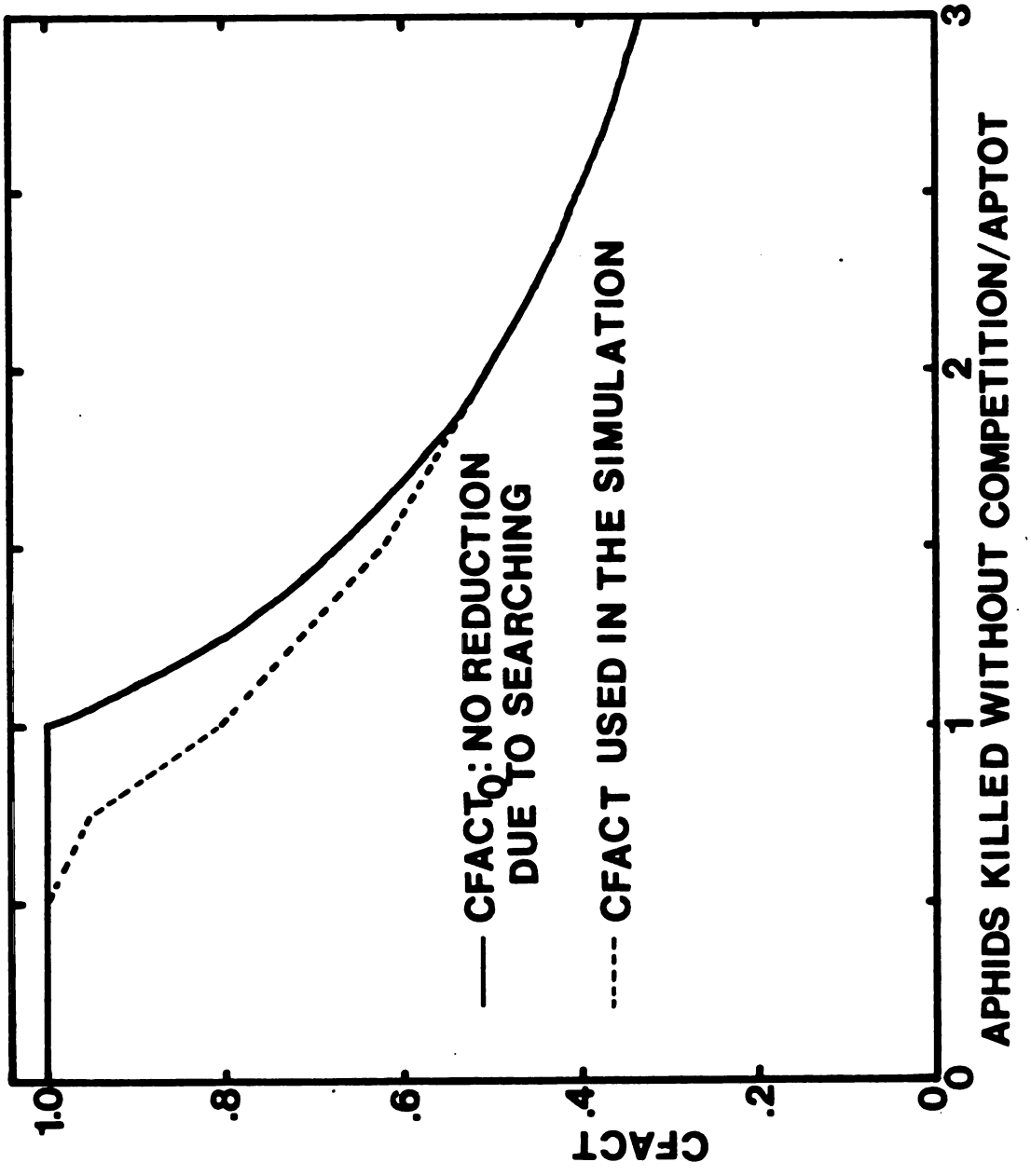



FIGURE 25. Reduction in Predation Due to Competition: CFACT

C. SIMULATION RESULTS

Table 34 presents sleeve cage data for Graham Station 1980 compared with simulation model output. Cecidomyiids were placed on the terminals as recently hatched (unfed) larvae and were simulated as first substage larvae. The number of surviving larvae (late $2^{nd}$ or early $3^{rd}$ instar) inside the sleeve cage was checked 3 to 4 days after the start of the experiment (listed as initial cecidomyiids). The number of surviving aphids and the number killed by the cecidomyiids was counted at the end of the experiment. Comparisons of the number of aphids present in the sleeve cages with the number predicted by the simulation was rated using the accuracy criterion listed in Table 34 (modified slightly from the equation used in the aphid sleeve cage simulations since aphid numbers could decrease due to predation). The results of the 22 simulations were rated high in 4 cases, accurate in 13 and low in the remaining 5. This data is displayed graphically in Figure 26.

The number of aphids killed per cecidomyiid versus the ratio of aphids to cecidomyiids present at the start of the experiment is presented in Figure 27. The solid line shows the same relationship for the simulation model output with one cecidomyiid present per terminal at the beginning of the experiment. Also included is the data of Adams (1977) for similar sleeve cage studies.

TABLE 34. Predation Data for Sleeve Cages Compared with Simulation Model Output

| Sleeve Cage Number | Dates | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | APTOT | Initial Cecids. | Initial Ratio[1] | APKPC[2] |
|---|---|---|---|---|---|---|---|---|
| 1 | 6/28 5:30 | 23 | 27 | 2 | 52 | 1 | 52.0 | |
| | 7/6 5:30 | 208 | 136 | 46 | 390 | | | 39.0 |
| | Simulation | 128.4 | 98.4 | 16.1 | 242.8L[3] | | | 44.7 |
| 2 | 6/28 5:45 | 11 | 18 | 1 | 30 | 2 | 15.0 | |
| | 7/6 5:30 | 18 | 22 | 5 | 45 | | | 36.5 |
| | Simulation | 39.2 | 24.0 | 3.8 | 66.9H | | | 39.1 |
| 3 | 6/28 5:45 | 5 | 22 | 2 | 29 | 4 | 7.3 | |
| | 7/6 5:30 | 11 | 2 | 1 | 14 | | | 18.5 |
| | Simulation | 4.4 | 2.5 | .4 | 7.3L | | | 28.2 |
| 4 | 6/28 6:00 | 31 | 5 | 2 | 38 | 1 | 38.0 | |
| | 7/6 5:30 | 44 | 22 | 4 | 68 | | | 43.0 |
| | Simulation | 25.3 | 28.9 | 2.9 | 57.1A | | | 37.4 |
| 5 | 6/28 6:00 | 51 | 34 | 3 | 88 | 1 | 88.0 | |
| | 7/6 6:00 | 129 | 73 | 11 | 213 | | | 53.0 |
| | Simulation | 157.0 | 141.7 | 22.9 | 321.6H | | | 45.9 |

[1]Initial ratio of numbers of aphids/number of cecidomyiids.

[2]Aphids killed per cecidomyiid.

[3]Accuracy rating was as follows:

H (High) - $(P_F-A_F)/MAX(A_F,A_F-A_I) > 1/3$

A (Accurate) - $|A_F-P_F|/MAX(A_F,A_F-A_I) < 1/3$

L (Low) - $(A_F-P_F)/MAX(A_F,A_F-A_I) > 1/3$

where $A_F$ = final sleeve cage population

$P_F$ = final simulation prediction

$A_I$ = initial sleeve cage population

TABLE 34. (cont.)

| Sleeve Cage Number | Dates | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | APTOT | Initial Cecids. | Initial Ratio | APKPC |
|---|---|---|---|---|---|---|---|---|
| 6 | 6/28 6:00 | 21 | 6 | 1 | 28 | 1 | 28.0 | |
| | 7/6 6:00 | 33 | 10 | 0 | 43 | | | 35.0 |
| | Simulation | 23.5 | 21.1 | 2.5 | 47.1A | | | 35.9 |
| 7 | 6/28 6:30 | 98 | 32 | 8 | 138 | 3 | 46.0 | |
| | 7/6 6:00 | 108 | 163 | 28 | 299 | | | 51.3 |
| | Simulation | 114.6 | 115.4 | 16.1 | 246.1A | | | 45.9 |
| 8 | 7/14 1:00 | 15 | 13 | 3 | 31 | 1 | 31.0 | |
| | 7/19 4:00 | 87 | 25 | 7 | 119 | | | 44.0 |
| | Simulation | 50.9 | 31.4 | 6.1 | 88.4A | | | 39.3 |
| 9 | 7/14 1:30 | 50 | 84 | 8 | 142 | 6 | 23.7 | |
| | 7/19 4:00 | 104 | 34 | 14 | 152 | | | 40.7 |
| | Simulation | 103.0 | 49.9 | 13.0 | 165.9A | | | 45.5 |
| 10 | 7/14 2:30 | 24 | 28 | 6 | 58 | 3 | 19.3 | |
| | 7/19 4:00 | 69 | 23 | 7 | 99 | | | 41.3 |
| | Simulation | 45.7 | 26.3 | 5.2 | 77.2A | | | 41.4 |
| 11 | 7/14 2:30 | 212 | 178 | 12 | 402 | 6 | 67.0 | |
| | 7/19 4:00 | 286 | 201 | 76 | 563 | | | 45.5 |
| | Simulation | 310.7 | 253.7 | 79.5 | 644.0A | | | 48.0 |
| 12 | 7/14 2:45 | 131 | 78 | 41 | 250 | 8 | 31.3 | |
| | 7/19 4:30 | 122 | 97 | 29 | 248 | | | 32.4 |
| | Simulation | 126.6 | 87.2 | 20.1 | 233.8A | | | 46.8 |
| 13 | 7/14 3:30 | 61 | 48 | 4 | 113 | 6 | 18.8 | |
| | 7/19 4:30 | 5 | 5 | 0 | 10 | | | 35.2 |
| | Simulation | 8.2 | 4.3 | .8 | 13.3A | | | 39.1 |

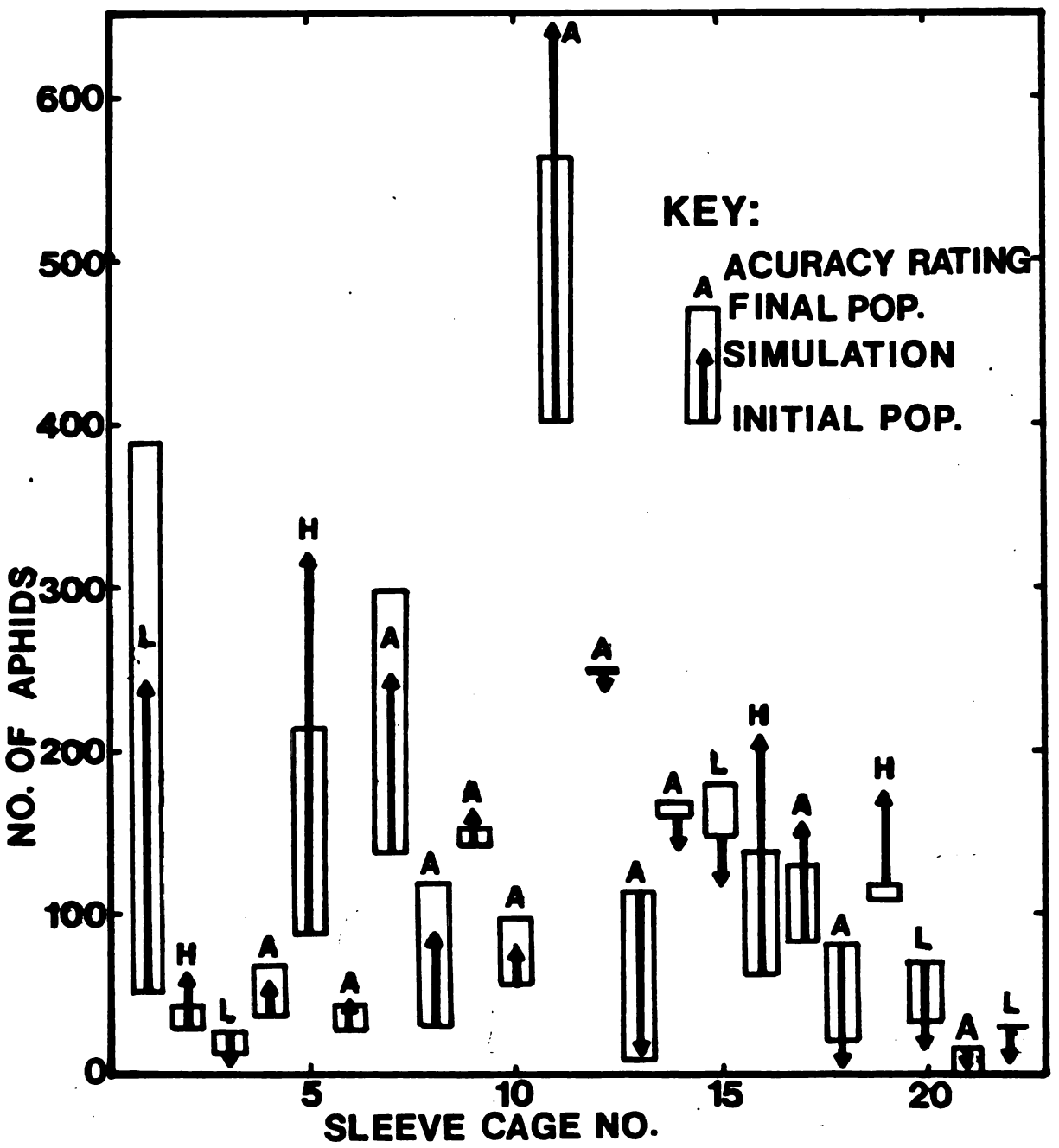
TABLE 34. (cont.)

| Sleeve Cage Number | Dates | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | APTOT | Initial Cecids. | Initial Ratio | APKPC |
|---|---|---|---|---|---|---|---|---|
| 14 | 7/14 4:00 | 83 | 64 | 13 | 160 | 6 | 26.7 | |
| | 7/19 5:00 | 103 | 42 | 24 | 169 | | | 48.2 |
| | Simulation | 82.4 | 46.7 | 10.2 | 139.3A | | | 45.3 |
| 15 | 7/14 4:30 | 92 | 50 | 6 | 148 | 5 | 29.6 | |
| | 7/19 5:15 | 84 | 83 | 11 | 178 | | | 46.6 |
| | Simulation | 67.1 | 41.2 | 8.0 | 116.3L | | | 44.6 |
| 16 | 7/14 4:30 | 31 | 30 | 1 | 62 | 1 | 62.0 | |
| | 7/19 5:15 | 81 | 48 | 10 | 139 | | | 47.0 |
| | Simulation | 118.4 | 74.8 | 16.2 | 209.4H | | | 43.9 |
| 17 | 7/14 5:00 | 39 | 41 | 4 | 84 | 3 | 28.0 | |
| | 7/19 5:15 | 65 | 55 | 10 | 130 | | | 32.3 |
| | Simulation | 90.1 | 51.6 | 11.1 | 152.8A | | | 43.9 |
| 18 | 7/14 5:00 | 56 | 21 | 4 | 81 | 5 | 16.2 | |
| | 7/19 5:15 | 11 | 8 | 3 | 22 | | | 33.4 |
| | Simulation | 3.6 | 2.6 | .4 | 6.6A | | | 29.5 |
| 19 | 7/14 5:00 | 75 | 36 | 6 | 117 | 3 | 39.0 | |
| | 7/19 6:00 | 54 | 40 | 13 | 107 | | | 49.3 |
| | Simulation | 92.5 | 67.9 | 12.5 | 173.0H | | | 44.7 |
| 20 | 8/11 12:00 | 16 | 47 | 7 | 70 | 4 | 17.5 | |
| | 8/18 11:30 | 19 | 10 | 5 | 34 | | | 40.3 |
| | Simulation | 10.9 | 4.7 | 2.0 | 17.6L | | | 37.3 |

TABLE 34. (cont.)

| Sleeve Cage Number | Dates | I & II Instars AP(1) | III & IV Instars AP(2) | Adults AP(3) | APTOT | Initial Cecids. | Initial Ratio | APKPC |
|---|---|---|---|---|---|---|---|---|
| 21 | 8/11 12:00 | 8 | 19 | 1 | 28 | 3 | 9.3 | |
| | 8/18 11:30 | 0 | 1 | 0 | 1 | | | 20.3 |
| | Simulation | 3.5 | 1.5 | .6 | 5.7H | | | 18.0 |
| 22 | 8/11 1:15 | 16 | 13 | 1 | 30 | 2 | 15.0 | |
| | 8/18 11:45 | 14 | 11 | 5 | 30 | | | 21.5 |
| | Simulation | 4.9 | 3.1 | .9 | 9.0L | | | 24.2 |

FIGURE 26. Sleeve Cage Data Compared with Simulation Model Output (with Predation)



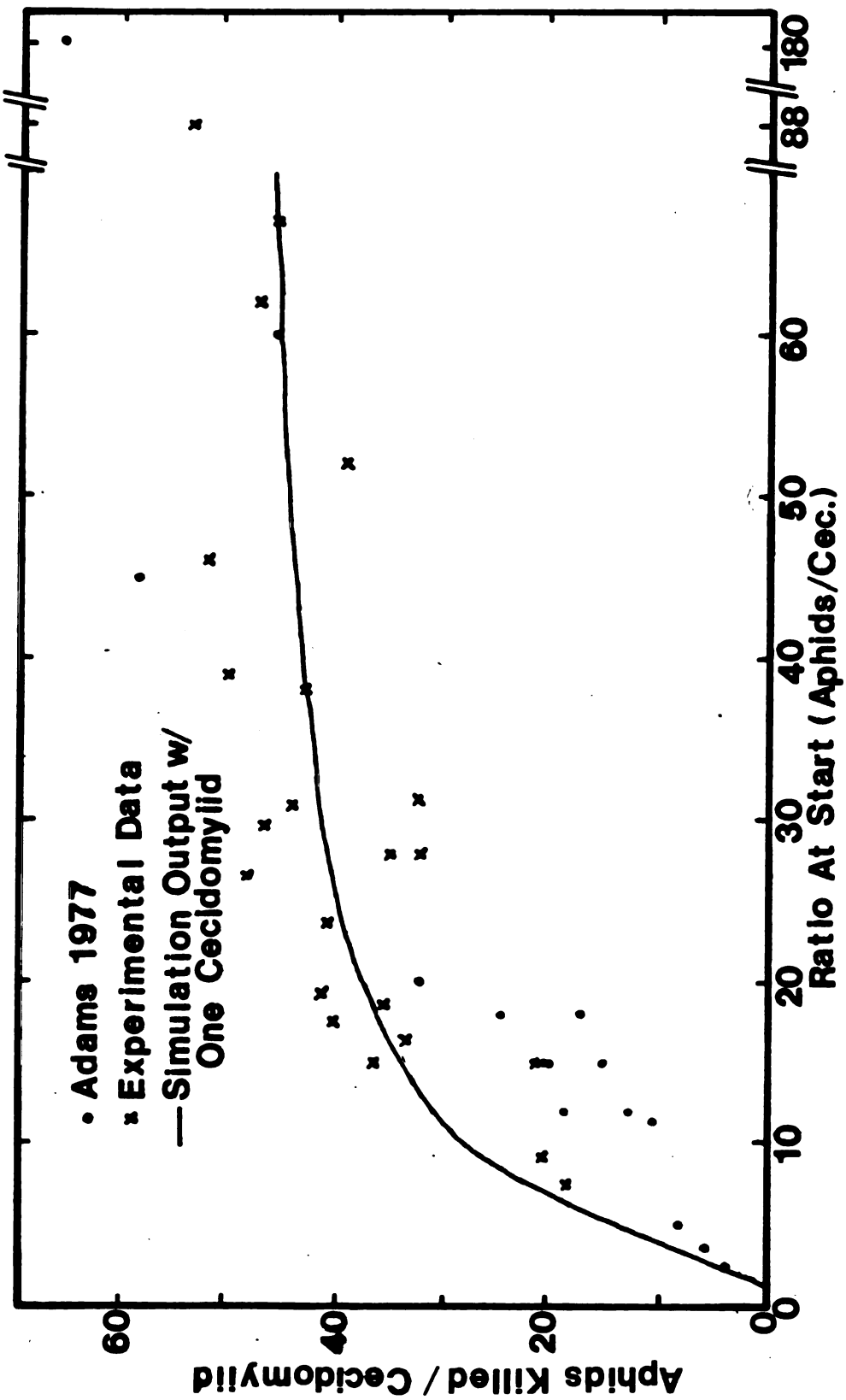



FIGURE 27. Comparison of Observed and Simulated Predation

# VI. DISCUSSION AND CONCLUSIONS

## A. APHID SIMULATION

Reanalysis of Lathrop's (1923) aphid developmental data indicated a 37°F. developmental threshold in contrast to the 41°F. threshold used commonly by other authors (Lathrop 1923, 1928, Westigard and Madsen 1965, Specht 1970, 1972, Jokinen 1980). In addition, the upper developmental threshold was tentatively set at 95°F. Additional data to support or refute these thresholds (particularly the upper threshold) would be useful.

Grouping data on nymph developmental periods by the month of birth revealed an interesting relationship. Mean developmental periods of aphids born early in the season (March-April 322.2, May - 320.6) were somewhat higher than periods during mid-season (June - 286.4, July - 293.8, August - 297.9). The September mean (343.2) was more in the range of the early season means. This relationship may have been due to the use of a lower developmental threshold which was too low (use of a low lower threshold results in heat summations which decrease as the mean temperature increases - Arnold 1959). Use of a higher developmental threshold (41°F.) resulted in better agreement between early and mid-season developmental periods but resulted in a late season (September) period that was still high in comparison. A second factor which may have caused slower development in early and late season is the influence of tree nutrient status. Especially in late

season, reduced nutrient availability may have slowed aphid development.

The aphid simulation presented in Section III was fairly successful in predicting short-term (3-7 days) population trends of aphids confined to a single apple terminal. The effects of tree nutrient status and aphid density on population dynamics were crudely mimicked using the equations presented in Table 10. More accurate simulation of population trends over longer time periods will depend on more accurate data on the effect of these factors.

The effects of pesticides applied for control of other apple pest species is an additional factor which limits the feasibility of long-term aphid simulations. Data on the effect of sub-lethal pesticide doses on aphid development and reproduction would be especially useful.

B. EXPERIMENTS ON CECIDOMYIID BIOLOGY

Laboratory experiments on basic features of cecidomyiid biology provided useful data for the simulation model of Section V. Additional data on female search and oviposition behavior would be quite useful in extending the simulation beyond its present scope. This aspect of cecidomyiid behavior appears especially significant in view of the limited dispersal abilities of cecidomyiid larvae (Wilbert 1972). Cecidomyiid females appear functionally equivalent to many insect parasitoids. Females search for aphid colonies and the number of eggs laid increases with increasing aphid density (El Titi 1974b). Larvae are essentially at the mercy of the environment in which they were placed as eggs. Thus female search and oviposition behavior "regulates" subsequent predation by the larvae.

Field experimental data indicated some rather useful and surprising features of cecidomyiid biology. Emergence from overwintering sites appears to start in early June and continues throughout the season. This "late" appearance of cecidomyiids (aphids appear somewhat earlier), necessitates early season aphid control by alternative means. Emergence distributed over the summer is most likely a survival mechanism evolved in response to the ephemeral nature of most aphid populations (of which the apple aphid is an exception) and to the possibility of exploitation of a number of aphid species. In general, aphids are an r-adapted species, well suited to capitalize on a flush of growth on a host plant, and then disperse to a new

host. Continuous emergence of cecidomyiids over the season insures that at least some of the predators will survive to perpetuate the species.

Aphid infested trap plants appear to be a good qualitative tool to sample for the presence of adult cecidomyiids. Trap plant catch from the Rose Lake area and other non-commercial sites indicated that large populations are present outside of commercial apple orchards. Trap plants were not shown to be useful in predicting early season appearance of cecidomyiids at Graham Station during 1980. Perhaps insecticide sprays applied during this period reduced trap plant egg deposition. Additional research is needed to develop an efficient sampling method for cecidomyiids present at low densities (direct larval samples are laborious and useful only at moderate cecidomyiid densities).

C. PREDATION SIMULATION

The objectives of this section were only partially met. The predation simulation of Section V was fairly successful in predicting the number of aphids killed by cecidomyiid larvae at different aphid densities. Evaluation of the impact of cecidomyiid predation on orchard aphid control, however, requires additional data on long-term aphid population dynamics, the sub-lethal effects of pesticides on aphid development and reproduction and extension of the cecidomyiid portion of the simulation model to include between-generation phenomena. Adequate data are available on cecidomyiid pupal developmental rates (Havelka 1980) and the effect of pesticides on cecidomyiid life stages (Warner 1981). Thus the major limitation to extending the cecidomyiid simulation is the need for additional data on female search and oviposition behavior.

It is this aspect of cecidomyiid biology - aphid host location and egg deposition by the female, which determines the impact of cecidomyiid predation. Further research in this area would greatly improve our understanding of this species which shows so much promise as a biological control agent of aphids on a wide variety of agricultural crops.

# VII. APPENDIX

## A. SIZE AND WEIGHT COMPARISONS FOR A. PISUM, M. PERSICAE AND A. POMI

Aphid length (excluding cornicles) and width were measured using a microscope eyepiece micrometer (100 divisions/cm.). Weight was estimated by weighing 50-100 aphids (recently killed using ethyl acetate) using a Mettler H31AR balance ($\pm$ .0001 g.; courtesy Dr. Jim Miller). Pea aphids [Acyrthosiphon pisum (Harris)] were collected from a colony reared on fava beans (Vicia fava L.). Apple aphids (A. pomi) were collected from apple terminals on July 28, 1980 from an abandoned orchard on the MSU campus. Green peach aphids [Myzus persicae (Sulzer)] were collected from a laboratory colony reared on jimsonweed (Datura stramonium L.).

Table 35 lists size and weight measurements for each species. Pea aphids are much larger than the other two species. Green peach aphids are very similar in size and weight to apple aphids and thus were assumed equivalent in the cecidomyiid larvae functional response experiment of Section IV-C-3.

TABLE 35. Size and Weight Measurement for 3 Aphid Species

| Species | Instar | Length[1] (cm.) | Width[1] (cm.) | Average Weight (mg.) |
|---|---|---|---|---|
| A. pisum | 1 | .11±.01 | .05±.01 | .13 |
| | 2 | .14±.02 | .06±.01 | .26 |
| | 3 | .19±.02 | .09±.01 | .71 |
| | 4 | .25±.01 | .12±.01 | 1.42 |
| | Apterae | .33±.01 | .15±.01 | 2.64 |
| | Alatae | .25±.01 | .09±.01 | 2.85 |
| M. persicae | 1 | .05±.01 | .03±.01 | .02 |
| | 2 | .07±.01 | .04±.01 | .03 |
| | 3 | .09±.01 | .05±.01 | .07 |
| | 4 | .12±.01 | .06±.01 | .12 |
| | 5 | .14±.01 | .07±.01 | .18 |
| | Apterae | .15±.01 | .10±.01 | .32 |
| | Alatae | .13±.01 | .06±.01 | .21 |
| A. pomi | 1 | .05±.01 | .03±.01 | .03 |
| | 2 | .09±.01 | .05±.01 | .04 |
| | 3 | .11±.01 | .06±.01 | .14 |
| | 4 | .13±.01 | .07±.01 | .25 |
| | Apterae | .16±.01 | .10±.01 | .34 |
| | Alatae | .15±.01 | .07±.01 | .22 |

[1]Length and width measurements are average ± 1/2 range; i.e. .33±.01 corresponds to an observed range of .32-.34

B. COMPUTER PROGRAM LISTING

Section VII-B contains a listing of the computer program used for the aphid simulation of Section III and the cecidomyiid predation simulation of Section V. The program is written in FORTRAN IV for the MSU Cyber 750.

1. Program Term

This is the main program which interfaces with subroutines DEGD, DELAY, INITIAL, CONVERT and OUTPT. Daily maximum and minimum temperatures are read from an input file attached locally as TAPE1 (Section VII-C contains some of the weather data contained in TAPE1).

```
100=C*************************************************************
120=      PROGRAM TERM(INPUT=65,OUTPUT=65,TAPE1)
140=C*************************************************************
160=C
180=C     THIS PROGRAM SIMULATES A SINGLE APPLE TERMINAL
200=C     ATTACH WEATHER DATA AS TAPE1
220=C     CATALOGED AS EWPGJMTERM
240=C
260=      COMMON /ALL/RNY(20),K,DEL,XNY(2),AP(3),
280=     +APTOT,ISTART,TOTHU(4),ITIMIN,AA(18),CSTART,APDIE,
300=     +CEGG(9),CLARV(33),CTEGG,CTLARV(3),CTPUP,TCEC,
320=     +TAPKLD,TBORN
340=C
360=      DIMENSION MAX(5,31),MIN(5,31),IDPM(12),ITHRLO(4),
380=     +ITHRHI(3),DD(3),FEC(18),SURV(17),THEAT(3),NITT(3),
390=     +CSUBKL(6)
400=C
420=      DATA DEL/292.19/
440=      DATA K/20/
460=      DATA SURV/7*1.0,.95,.8947368,.8823529,.8666667,
480=     +.8461538,.8181818,.7777778,.7142857,.6,.3333333/
500=      DATA FEC/1.39,7*.625,.3863158,.4305882,.1746667,
520=     +.1538462,.0818182,.1,.0257143,.036,2*0.0/
540=C     FEC(1)=1.39(NOT .625) COMPENSATES FOR 1ST STAGE
560=C     ADULTS NOT LEFT THERE FOR FULL 50 HU
580=      DATA PLR/.00038/
600=C     PLR=.00038 GIVES 10 PERCENT MORTALITY OVER NYMPH STAGE
620=      DATA ITHRLO,ITHRHI/37,51,46,3*95/
640=      DATA IDPM/31,28,31,30,31,30,31,31,30,31,30,31/
700=      DATA CSUBKL/.05,.1,.15,.2,.2,.3/
```

```
720=C
740=C***** CONTROL SECTION
760=       IREP=0
780=2      ISTART=1
920=       IF(ISTART.NE.1)GO TO 8
940=C      ITIMIN=1 MEANS SIMULATION STARTS IN THE MORNING
960=       PRINT *," ENTER MONTH,DAY,TIME (10R2) SIM STARTS ON..."
980=       READ *,IMNTH,IDAY,ITIMIN
1000=8      CONTINUE
1020=C
1060=       ITIM=ITIMIN
1260=       IF(IREP.EQ.1)GO TO 40
1280=C
1300=C***** READ WEATHER DATA FROM TAPE1
1320=C
1360=       REWIND 1
1380=       PRINT *," ENTER SITE,YEAR TO RUN SIMULATION FOR..."
1400=       READ 4,SRUN,IYRRUN
1420=4      FORMAT(A4,1X,I4)
1440=C
1460=5      READ(1,10) IYR,SITE
1480-10     FORMAT(1X,I4,1X,A4)
1500=       IF(IYR.EQ.IYRRUN.AND.SITE.EQ.SRUN) GO TO 20
1520=       READ(1,15)
1540=15     FORMAT(23(/))
1560=       IF(EOF(1).NE.0)PRINT *," END WEATHER FILE ENCOUNTERED"
1580=       GO TO 5
1600=C
1620=20     READ(1,25)
1640=25     FORMAT(7(/))
1660=       DO 30 I=5,9
1680=         READ(1,35) (MAX(I,J),J=1,31)
1700=30       READ(1,35) (MIN(I,J),J=1,31)
1720=35     FORMAT(4X,31I3)
1780=C
1800=C***** INITIALIZATIONS
1820=C
1840=40     CONTINUE
1880=       PRINT *," ENTER DAYS,OUTFR..."
1900=       READ *,DAYS,OUTFR
2580=C
2600=       CESURV=1.0
2700=       IF(ISTART.EQ.0)GO TO 50
2720=       CALL INITIAL
2730=       CTPUP=0.
2735=       APDIE=0.
2740=       CALL CONVERT
2750=       CSTART=TCEC
2760=       IF(ITIMIN.EQ.1)ITIM=0
2780=       IF(ITIMIN.EQ.2)ITIM=1
2820=       DO 52 I=1,4
2830=52     TOTHU(I)=0.
2831=       TAPKLD=0.
```

```
2840=       TBORN=0.
2860=       CALL OUTPT(IMNTH,IDAY,ITIM)
2880=C
2900=       OUT=.0001
2920=       CETOL=CLTOP=0.
2940=       APKILD=0.
2980=       BORN=0.
3020=       APDIE=0.
3040=       NTHR=3
3060=       DO 44 I=1,4
3080=44     THEAT(I)=0.
3100=       IADAP=0
3120=       DT=5.
3140=       CELAID=0.
3160=50     CONTINUE
3180=C
3200=       NIT=DAYS/.5+.0001
3220=C**********
3240=       DO 200 IDUM=1,NIT
3260=C**********
3280=C
3300=C      OVERALL TIME STEP IS 1/2 DAY; WITHIN EACH HALF DAY
3320=C      EACH STAGE IS UPDATED SEPARATELY DUE TO DIFFERENT
3340=C      DEVELOPMENTAL THRESHOLDS
3360=C
3380=       ITIM=ITIM+1
3400=       IF(ITIM.EQ.3)ITIM=1
3420=C
3440=60     IF(ITIM.EQ.2)GO TO 65
3460=       IF(ISTART.EQ.1)GO TO 65
3480=       IDAY=IDAY+1
3500=       IF(IDAY.LE.IDPM(IMNTH)) GO TO 65
3520=       IDAY=1
3540=       IMNTH=IMNTH+1
3560=65     CONTINUE
3580=C
3600=       ISTART=0
3640=       IMN=IMNTH
3660=       IDY=IDAY
3680=       IF(ITIM.EQ.1)GO TO 70
3700=       IDY=IDAY+1
3720=       IF(IDAY.NE.IDPM(IMNTH))GO TO 70
3740=       IMN=IMNTH+1
3760=       IDY=1
3780=70     CONTINUE
3800=C
3980=       MX=MAX(IMNTH,IDAY)
4000=       MN=MIN(IMN,IDY)
4060=89     CONTINUE
4080=C
4180=       DO 90 JTHR=1,NTHR
4200=          CALL DEGD(MX,MN,ITHRLO(JTHR),0,ITHRHI(JTHR),
4210=      +DD(JTHR))
4220=          THEAT(JTHR)=THEAT(JTHR)+DD(JTHR)*.5
```

```
4240=          TOTHU(JTHR)=TOTHU(JTHR)+DD(JTHR)*.5
4260=          NITT(JTHR)=THEAT(JTHR)/DT
4280=          THEAT(JTHR)=THEAT(JTHR)-(NITT(JTHR)*DT)
4300=90        CONTINUE
4320=91     CONTINUE
4340=C
4360=       ITCEG=ITCLA=ITAP=0
4380=       NITMAX=NITT(1)
4400=       IF(NITMAX.LT.NITT(2))NITMAX=NITT(2)
4420=       IF(NITMAX.LT.NITT(3))NITMAX=NITT(3)
4440=       IF(NITMAX.LT.1)GO TO 161
4460=C***
4480=       DO 160 ITERA=1,NITMAX
4500=       CALL CONVERT
4520=C***
4540=C
4560=C*****CECIDOMYIID SECTION
4580=C
4940=C*     UPDATE LARVAE
4960=       ITCLA=ITCLA+1
4980=       IF(ITCLA.GT.NITT(3))GO TO 84
5020=C
5040=C*     DETERMINE DELAY IN DEVELOPMENT DUE TO SEARCHING
5050=C      FOR APHIDS
5060=       FRFIND=1.
5080=       IF(APTOT.GE.100.)GO TO 79
5100=       FRFIND=.9
5120=       IF(APTOT.GE.50.)GO TO 79
5140=       FRFIND=.65
5160=       IF(APTOT.GE.30.)GO TO 79
5180=       FRFIND=.35
5200=       IF(APTOT.GE.20.)GO TO 79
5220=       FRFIND=.1
5240=       IF(APTOT.GE.10.)GO TO 79
5260=       FRFIND=0.
5280=79     CONTINUE
5300=C
5320=C*     3RD INSTARS (CLARV(21-33))
5360=       CTPUP=CTPUP+CLARV(33)
5380=       DO 80 I=1,6
5390=       ISUB=35-I*2
5400=       CLARV(ISUB)=CLARV(ISUB-2)*FRFIND+CLARV(ISUB-1)
5410=80     CLARV(ISUB-1)=CLARV(ISUB-2)*(1.-FRFIND)
5420=       CLARV(21)=CLARV(20)
5500=C
5520=C*     2D INSTARS (CLARV(8-20))
5550=       DO 81 I=1,6
5560=       ISUB=22-I*2
5570=       CLARV(ISUB=CLARV(ISUB-2)*FRFIND+CLARV(ISUB-1)
5580-81     CLARV(ISUB-1)=CLARV(ISUB-2)*(1.-FRFIND)
5590=       CLARV(8)=CLARV(7)
5620=C
5640=C*     1ST INSTAR (CLARV(1-7))
```

```
5680=       CLARV(1)=CLARV(1)+CETOL
5700=       CETOL=0.
5720=       DO 86 I=1,5
5740=       ISUB=8-I
5760=86     CLARV(ISUB)=CLARV(ISUB-1)
5800=       C1FIND=1.
5820=       CLARV(2)=CLARV(1)*C1FIND
5840=       CLARV(1)=0.
5860=C
5880=C*     COMPUTE NUMBER OF APHIDS KILLED
5890=       CPR2EQ=CPR3EQ=0.
5895=       DO 82 I=1,6
5900=       ISUB1=2*I+8
5905=       CPR2EQ=CPR2EQ+CLARV(ISUB1)*CSUBKL(I)
5910=       ISUB2=2*I+21
5915=82     CPR3EQ=CPR3EQ+CLARV(ISUB2)*CSUBKL(I)
5920=       APK2=7.56
5925=       IF(APTOT.LT.15.)APK2=APTOT/15.*7.56
5926=       AI(APTOT.LT.5.)APK2=0.
5935=       APK3=(41.*(APTOT-5.))/(20.+APTOT-5.)
5940=       IF(APTOT.LT.5.)APK3=0.
5945=       TKILD=CLARV(2)+CPR2EQ*APK2+CPR3EQ*APK3
5950=       RAT=TKILD/APTOT
5955=C
5960=C      REDUCE APHIDS KILLED DUE TO COMPETITION BETWEEN
5970=C      CECIDS
5975=       CFACT=1.
5976=       IF(TCEC.LE.1.)GO TO 802
5977=       IF(RAT.LE..5)GO TO 802
5978=       CFACT=1.-.05*(RAT-.5)/.25
5979=       IF(RAT.LE..75)GO TO 802
5980=       CFACT=.95-.15*(RAT-.75)/.25
5981=       IF(RAT.LE.1.)GO TO 802
5982=       CFACT=.8-.18*(RAT-1.)/.5
5983=       IF(RAT.LE.1.5)GO TO 802
5984=       CFACT=.62-.12*(RAT-1.5)/.5
5985=       IF(RAT.LE.2.)GO TO 802
5986=       CFACT=1./RAT
6025=802    CONTINUE
6030=       APKILD=CFACT*TKILD
6035=84     CONTINUE
6320=C
6340=C*     UPDATE EGGS
6380=       ITCEG=ITCEG+1
6400=       IF(ITCEG.GT.NITT(2))GO TO 94
6420=       CETOL=CETOL+CEGG(9)*CESURV
6440=       DO 93 I=1,4
6460=         ISUB=10-I
6480=93       CEGG(ISUB)=CEGG(ISUB-1)
6500=       CEGG(1)=0.
6520=94     CONTINUE
6540=C
6560=C*****APHID SECTION - ALL ON SAME THRESHOLD (37)
```

```
6580=C
6600=       ITAP=ITAP+1
6620=       IF(ITAP.GT.NITT(3))GO TO 118
6640=C
6760=C      REDUCE FECUNDITY BY DFACT; 0-100 DFACT=1.;
6770=C      100-1000 DFACT= 1.-.25; GT.1000 DFACT=.25
6820=       DFACT=1.
6860=       IF(APTOT.LE.100.)GO TO 100
6880=       DFACT=.25
6900=       IF(APTOT.GT.1000.)GO TO 100
6920=       DFACT=1.-.75*(ALOG10(APTOT)-2.)
6940=100    CONTINUE
6960=C
6980=C      REDUCE FECUNDITY BY TFACT BY DATE
7000=       IF(ITAP.GT.1)GO TO 101
7020=       TFACT=1.3
7060=       IF(IMNTH.LE.6)GO TO 101
7080=       IF(IMNTH.EQ.7.AND.IDAY.LE.4)GO TO 101
7100=       TFACT=.9
7120=       IF(IMNTH.EQ.7.AND.IDAY.LE.20)GO TO 101
7140=       TFACT=.6
7160=       IF(IMNTH.EQ.7)GO TO 101
7180=       IF(IMNTH.EQ.8.AND.IDAY.LE.6)GO TO 101
7200=       TFACT=.5
7220=       IF(IMNTH.EQ.8.AND.IDAY.LE.24)GO TO 101
7240=       TFACT=.4
7260=101    CONTINUE
7280=C
7300=C*     APHID FECUNDITY (ADD LATER)
7340=       DO 102 ISUB=1,18
7360=102    BORN=BORN+AA(ISUB)*FEC(ISUB)
7380=       BORN=BORN*DFACT*TFACT
7400=106    CONTINUE
7420=C
7440=C*     APHIDS KILLED BY CECIDS HERE
7470=       IF(APKILD.LT..0001)GO TO 808
7500=       DO 800 I=1,18
7520=800    AA(I)=AA(I)*(1.-APKILD/APTOT)
7540=       DO 801 I=1,20
7560=801    RNY(I)=RNY(I)*(1.-APKILD/APTOT)
7580=808    TAPKLD=TAPKLD+APKILD
7620=       APKILD=0.
7640=C
7660=C*     UPDATE ADULT APHIDS WITH MORTALITY (DISCRETE
7670=C      EVERY 50 HU)
7760=       IADAP=IADAP+1
7780=       IF(IADAP.NE.10)GO TO 110
7800=       IADAP=0
7820=       APDIE=APDIE+AA(18)
7840=       DO 108 I=1,17
7860=       ISUB=18-I
7880=108    AA(ISUB+1)=AA(ISUB)*SURV(ISUB)
7900=       AA(1)=0.
```

```
7920=110    CONTINUE
7940=C
7960=C*     UPDATE APHID NYMPHS
8020=       CALL DELAY(XNY(1),XNY(2),RNY(1),PLR,DEL,DT,K)
8030=C      NOTE XNY(2) CHANGED TO AMOUNT IN DELAY
8031=       AA(1)=AA(1)+XNY(2)
8040=117    CONTINUE
8080=       RNY(1)=RNY(1)+BORN*K/DEL
8100=       TBORN=TBORN+BORN
8120=       BORN=0.
8140=118    CONTINUE
8160=C
8200=C***
8220=160    CONTINUE
8240=C***
8260=161    CONTINUE
8280=C
8300=C*     DETERMINE IF TIME FOR OUTPUT
8340=       OUT=OUT+.5
8360=       IF(OUT.LT.OUTFR)GO TO 200
8380=       CALL CONVERT
8400=       OUT=.0001
8420=       CALL OUTPT(IMNTH,IDAY,ITIM)
8440=C
8620=C**********
8640=200    CONTINUE
8660=C**********
8680=C
8700=C*     RERUNS
8720=       PRINT 240
8740=240    FORMAT(/,"WISH TO CONTINUE THIS RUN (YORN)...")
8760=260    FORMAT(A1)
8800=       IF(ANS.EQ.1HY)GO TO 40
8820=C
8840=       PRINT*,"WISH TO START A NEW RUN FROM SAME SITE?..."
8860=       READ 260,ANS
8880=       IF(ANS.EQ.1HN)GO TO 270
8900=       IREP=1
8920=       GO TO 2
8940=270    CONTINUE
8960=C
8980=       END
```

2. Subroutine DEGD

This subroutine calculates heat units in a day using a sine wave temperature profile based on daily maximum and minimum temperatures (adapted from Baskerville and Emin 1968, Allen 1976). When used with a 3 point sine wave (in which the two minimums may be different, see Figure 3), the subroutine was called twice a day with DD (degree-days) halved (see lines 4180-4300 in Program TERM).

```
11120=C     ************************************************
11140=      SUBROUTINE DEGD (MAX,MIN,K1,K2,K3,DD)
11160=C     ************************************************
11300=C
11320=      DATA PI/3.14159/
11360=C**** NO UPPER THRESHOLD CUTS MADE
11380=C
11400=C*    NO HEAT, MAX BELOW K1
11420=      TBAR=(MAX+MIN)/2.
11440=      AMP=(MAX-MIN)/2.
11460=      DD=0.
11480=      IF(MAX.LE.K1)RETURN
11500=C
11520=C*    CASE A, NO CUTS, UPPER.GT.MAX AND MIN.GT.K1
11540=      DD=TBAR-K1
11560=      IF(K3.GE.MAX.AND.MIN.GE.K1)RETURN
11580=      IF(K2.GE.MAX.AND.MIN.GE.K1)RETURN
11600=C
11620=C*    CASE B, CUT AT BOTTOM, UPPER.GE.MAX AND K1.GT.MIN
11640=      IF(K3.EQ.0.AND.MAX.GT.K2) GO TO 100
11660=      IF(K2.EQ.0.AND.MAX.GT.K3)GO TO 10
11680=      TH1=ASIN((FLOAT(K1)-TBAR)/AMP)
11700=      DD=(AMP*COS(TH1)+(TBAR-K1)*(PI/2.-TH1))/PI
11720=      RETURN
11740=C
11760=C**** HORIZONTAL CUTOFF (K3)
11780=C
11800=C*    CASE C1, CUT TOP, MAX.GT.K3 AND MIN.GT.K1
11820=10    TH2=ASIN((FLOAT(K3)-TBAR)/AMP)
11840=      IF(K1.GT.MIN)GO TO 20
11860=      DD=((K3-K1)*(PI/2.-TH2)+(TBAR-K1)*
11870=     +(TH2+PI/2.)-AMP*COS(TH2))/PI
11900=      RETURN
11920=C
11940=C*    CASE C2, CUT AT TOP AND BOTTOM, MAX.GT.K3, K1.GT.MIN
```

```
11960=20     TH1=ASIN((FLOAT(K1)-TBAR)/AMP)
11980=       DD=(AMP*(COS(TH1)-COS(TH2))+(K3-K1)*(PI/2.-TH2)-
12000=      +(K1-TBAR)*(TH2-TH1))/PI
12020=       RETURN
12040=C
12060=C****VERTICAL CUTOFF (K2)
12080=C
12100=C*     CASE D1, CUT TOP, MAX.GT.K2 AND MIN. GT.K1
12120=100    TH2+ASIN((FLOAT(K2)-TBAR)/AMP)
12140=       IF(K1.GT.MIN)GO TO 110
12160=       DD=((TH2+PI/2.)*(TBAR-K1)-AMP*COS(TH2)))/PI
12180=       RETURN
12200=C
12220=C*     CASE D2, CUT AT TOP AND BOTTOM, MAX.GT.K2, K1.GT.MIN
12240=110    TH1+ASIN((FLOAT(K1)-TBAR)/AMP)
12260=       DD=((TH2-TH1)*(TBAR-K1)+AMP*(COS(TH1)-COS(TH2)))/PI
12280=       RETURN
12300=       END
12320=C
```

## 3. Subroutine DELAY

This subroutine implements the distributed delay model of aphid nymph development (modified from Manetsch 1976).

```
10630=C*******************************************************
10640=      SUBROUTINE DELAY(VIN,VOUT,R,PLR,DEL,DT,K)
10650=C*******************************************************
10660=C
10690=      DIMENSION R(1)
10700=      FK=FLOAT(K)
10740=C
10760=      B=1.+PLR*DEL/FK
10780=      IDT=1.+2.*DT*FK/DEL*AMAX1(B,0.)
10800=      A=FK*DT/(DEL*FLOAT(IDT))
10820=C
10840=      KM1=K-1
10860=C
10880=      VOUT=R(K)*A*B*DEL/K
10900=C
10920=      DO 20 J=1,IDT
10940=        DO 10 IC=1,KM1
10960=           I=K-IC+1
10980=10         R(I)=R(I)+A*(R(I-1)-B*R(I))
11000=20      R(1)=R(1)+A*(VIN-B*R(1))
11020=C
11040=      RETURN
11060=      END
11080=C
11100=C
```

4. Other Subroutines

These 3 subroutines interface with Program TERM. Subroutine INITIAL initializes aphids and cecidomyiids at the beginning of each simulation. The aphid simulation of Section III is run with 0 cecidomyiids. Subroutine CONVERT converts the number of aphids and cecidomyiids in each sub-stage into their respective stage totals. Subroutine OUTPT prints the output data (output time, heat units and numbers in each life stage for the two species) for each simulation.

```
12340=C     ************************************************
12360=      SUBROUTINE INITIAL
12380=C     ************************************************
12400=C
12420=      COMMON /ALL/RNY(20),K,DEL,XNY(2),AP(3),
12440=     +APTOT,ISTART,TOTHU(4),ITIMIN,AA(18),CSTART,APDIE
12460=     +CEGG(9),CLARV(33),CTEGG,CTLARV(3),CTPUP,TCEC,
12470=     +TAPKLD,TBORN
12480=C
12500=      DIMENSION APHIN(3)
12520=C
12580=C*****APHID SECTION
12600=C
12620=      ISUB12=6
12660=      PRINT *," ENTER INITIAL APHIDS(1-2,3-4,AD-AL)..."
12680=      READ*,(APHIN(I),I=1,3)
12700=C
12720=201   INYDIS=2
12740=      IADDIS=3
12840=C
12860=C     FIRST SET ALL TO ZERO
12880=      DO 2 I=1,20
12900=2     RNY(I)=0.
12920=      DO 3 I=1,18
12940=3     AA(I)=0.
12960=      XNY(1)=XNY(2)=0.
12980=C
13000=C***  NYMPHS
13020=C     PUT IN BEGINNING OF NYMPH STAGE
13040=      IF(INYDIS.NE.1)GO TO 20
13060=      RNY(1)=APHIN(1)*K/DEL
13080=      RNY(ISUB12+1)=APHIN(2)*K/DEL
13100=      GO TO 50
13120=20    CONTINUE
13140=C
```

```
13160=C      DISTRIBUTE EVENLY
13180=       APHIN(1)=APHIN(1)/ISUB12*K/DEL
13200=       APHIN(2)=APHIN(2)/(20.-ISUB12)*K/DEL
13220=       DO 30 ISUB=1,ISUB12
13240=30     RNY(ISUB)=APHIN(1)
13260=       IIN=ISUB12+1
13280=       DO 31 ISUB=IIN,20
13300=31     RNY(ISUB)=APHIN(2)
13320=C
13340=C***   ADULTS
13360=C      PUT IN BEGINNING OF ADULT STAGE
13380=50     CONTINUE
13400=       IF(IADDIS.NE.1)GO TO 25
13420=       AA(1)=APHIN(3)
13440=       GO TO 70
13460=25     CONTINUE
13480=C
13500=C      PUT IN FRONT END OF ADULT STAGE
13520=       IF(IADDIS.NE.2)GO TO 40
13540=       APHIN(3)=APHIN(3)/5.
13560=       DO 41 ISUB=1,5
13580=41     AA(ISUB)=APHIN(3)
13600=       GO TO 70
13620=40     CONTINUE
13640=C
13660=C      DISTRIBUTE EVENLY
13680=       APHIN(3)=APHIN(3)/18.
13700=       DO 60 ISUB=1,18
13720=60     AA(ISUB)=APHIN(3)
13740=70     CONTINUE
13760=C
13780=C*****CECID SECTION
13800=C
13820=C      FIRST SET ALL TO ZERO
13840=       DO 90 I=1,9
13860=90     CEGG(I)=0.
13880=       DO 91 I=1,33
13900=01     CLARV(I)=0.
13920=C
13940=100    PRINT*," ENTER CEC- IMORE,ISTAGE,ISUB,IAMT-"
13950=       READ*,IMORE,IST,ISUB,AMT
13955=       IF(IMORE.EQ.2)GO TO 120
13960=       IF(IST.EQ.2)GO TO 105
14020=       CEGG(ISUB)=AMT
14030=       IF(IMORE.EQ.0)GO TO 120
14040=       GO TO 100
14060=105    CLARV(ISUB)=AMT
14080=       IF(IMORE.EQ.1) GO TO 100
14090=120    CONTINUE
14120=C
14180=       RETURN
14200=       END
OK-
```

```
9020=C*************************************************************
9040=       SUBROUTINE CONVERT
9060=C*************************************************************
9080=C
9100=       COMMON /ALL/RNY(20),K,DEL,XNY(2),AP(3),
9120=      +APTOT,ISTART,TOTHU(4),ITIMIN,AA(18),CSTART,APDIE
9140=      +CEGG(9),CLARV(33),CTEGG,CTLARV(3),CTPUP,TCEC,
9150=      +TAPKLD,TBORN
9160=C
9220=C*****APHID SECTION
9240=       AP(1)=AP(2)=0.
9260=       DO 10 ISUB=1,6
9280=10     AP(1)=AP(1)+RNY(ISUB)
9300=       AP(1)=AP(1)*DEL/K
9320=C
9340=       DO 20 ISUB=7,20
9360=20     AP(2)=AP(2)+RNY(ISUB)
9380=       AP(2)=AP(2)*DEL/K
9400=C
9420=       AP(3)=0.
9440=       DO 30 ISUB=1,18
9460=30     AP(3)=AP(3)+AA(ISUB)
9480=C
9500=       APTOT=AP(1)+AP(2)+AP(3)
9520=C
9540=C*****CECID SECTION
9560=       CTEGG=0.
9580=       DO 40 I=1,9
9600=40     CTEGG=CTEGG+CEGG(I)
9620=C
9640=       DO 45 I=1,3
9660=45       CTLARV(I)=0.
9680=       DO 46 I=1,7
9700=46       CTLARV(1)=CTLARV(1)+CLARV(I)
9720=       DO 57 I=8,20
9740=47       CTLARV(2)=CTLARV(2)+CLARV(I)
9760=       DO 48 I=21,33
9780=48       CTLARV(3)=CTLARV(3)+CLARV(I)
9800=C
9810=       TCEC=CTEGG+CTLARV(1)+CTLARV(2)+CTLARV(3)+CTPUP
9811=C
9860=       RETURN
9880=       END
9900=C
```

```
9920=C*************************************************************
9940=       SUBROUTINE OUTPT(IMNTH,IDAY,ITIM)
9960=C*************************************************************
9980=C
10000=       COMMON /ALL/RNY(20),K,DEL,XNY(2),AP(3),
10020=      +APTOT,ISTART,TOTHU(4),ITIMIN,AA(18),CSTART,APDIE,
10040=      +CEGG(9),CLARV(33),CTEGG,CTLARV(3),CTPUP,TCEC,
10050=      +TAPKLD,TBORN
10060=C
10090=       TIMDY="E"
10095=       IF(ITIM.EQ.0)TIMDY="M"
10100=       IF(ITIM.EQ.1)TIMDY="N"
10105=C
10120=       IF(ISTART.NE.1)GO TO 4
10125=       PRINT 1
10130=1      FORMAT(/,7X,"TOTHU(1)",4X,"1-2",9X,"3-4",
10135=      +7X,"ADULTS",6X,"TOTAL",7X,"TOT CEC")
10140=       PRINT 2
10145=2      FORMAT(7X,"TOTHU(3)",4X,"EGGS",7X,"LARV1",
10150=      +6X,"LARV2",7X,"LARV3",7X,"PUPAE",/)
10155=4      CONTINUE
10160=5      PRINT 10,IMNTH,IDAY,TIMDY,TOTHU(1),
10161=      +(AP(I),I=1,3),APTOT,TCEC
10165=10     FORMAT(1X,I2,"/",I2,A1,F6.1,5E12.5)
10170=C
10195=       PRINT 20,TOTHU(3),CTEGG,(CTLARV(I),I=1,3),CTPUP
10200=20     FORMAT(7X,F6.1,5E12.5)
10250=C
10500=       RETURN
10520=       END
10540=C
```

C. FIELD TEMPERATURE DATA

Hygrothermograph temperature records (daily maximum and minimums) taken by this author are reported in this section for field research sites at the Klein Orchard and the MSU Graham Horticultural Research Station (see Section II-B-1 for description of sites, Section II-A-3 for hygrothermograph methods). Hygrothermographs (except for the sleeve cage hygrothermograph) were enclosed in white painted shelters (the bases were built with metal screening to expose the hygrothermographs to the air) placed on posts approximately 1.5 m. above the ground.

The hygrothermograph used to monitor conditions inside the sleeve cages was placed (without the shelter) on a post 1.5 m. above the ground midway between the trunk and drip line of an apple tree. Three apple terminals together with the hygrothermograph were enclosed inside a specially constructed oversized sleeve cage secured at the base of the terminals with a string (see Section II-B-3 for description of sleeve cages).

A comparison of temperatures for the sheltered hygrothermograph vs. the sleeve cage enclosed hygrothermograph showed that daily maximums and minimums were elevated inside the sleeves by $2.56 \pm 1.56$ (mean $\pm$ standard deviation, range -1 to 9, n=51) and $.29 \pm .94^{o}F.$ (range -2 to 2, n=51) respectively.

TABLE 36. Field Temperature Data

A. Temperature Data for Klein's Orchard 1979[1]

Temperature Record (°F.)[2]

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 1 | 36 | 38 | 48 | 40 | 46 | 28 | 36 | 32 | 44 | 48 | 40 | 72 | 52 | 48 | 49 |
| | | 53 | 59 | 62 | 64 | 70 | 56 | 64 | 71 | 62 | 62 | 50 | 56 | 42 | 50 | 42 |
| 3 | 2 | 33 | 33 | 27 | 33 | 31 | 18 | 17 | 31 | 28 | 23 | 32 | 36 | 47 | 35 | 38 |
| | | 38 | 30 | 32 | 33 | 40 | 53 | 34 | 36 | 47 | 56 | 42 | 35 | 34 | 24 | 36 |
| 4 | 1 | 55 | 69 | 53 | 54 | 52 | 66 | 75 | 81 | 78 | 78 | 72 | 53 | 62 | 63 | 62 |
| | | 65 | 68 | 78 | 70 | 69 | 62 | 65 | 65 | 56 | 66 | 62 | 60 | 63 | 75 | 62 76 |
| 4 | 2 | 31 | 44 | 48 | 34 | 27 | 48 | 46 | 60 | 65 | 62 | 62 | 39 | 32 | 46 | 41 |
| | | 33 | 43 | 55 | 57 | 39 | 42 | 36 | 50 | 44 | 41 | 42 | 44 | 46 | 36 | 48 53 |
| 5 | 1 | 71 | 75 | 80 | 80 | 77 | 80 | 76 | 80 | 71 | 72 | 68 | 67 | 71 | 78 | 83 |
| | | 84 | 71 | 71 | 79 | 80 | 80 | 72 | 62 | 67 | 56 | 72 | 74 | 76 | 73 | 76 |
| 5 | 2 | 60 | 42 | 54 | 58 | 56 | 55 | 68 | 66 | 64 | 66 | 44 | 37 | 40 | 49 | 64 |
| | | 65 | 68 | 56 | 50 | 66 | 69 | 60 | 40 | 40 | 39 | 42 | 59 | 50 | 57 | 60 |
| 6 | 1 | 66 | 82 | 78 | 74 | 75 | 76 | 81 | 81 | 86 | 84 | 85 | 90 | 89 | 83 | 88 |
| | | 84 | 77 | 81 | 81 | 82 | 84 | 85 | 86 | 73 | 70 | 75 | 79 | 77 | 78 | 76 75 |
| 6 | 2 | 58 | 54 | 52 | 58 | 43 | 45 | 47 | 55 | 62 | 58 | 64 | 65 | 66 | 71 | 68 |
| | | 60 | 56 | 48 | 48 | 49 | 54 | 56 | 62 | 64 | 66 | 53 | 51 | 61 | 49 | 52 64 |
| 7 | 1 | 67 | 72 | 74 | 76 | 76 | 74 | 80 | 71 | 75 | 81 | 83 | 88 | 86 | 82 | 86 |
| | | 83 | 77 | 78 | 80 | 83 | 83 | 84 | 86 | 78 | 76 | 79 | 83 | 81 | 83 | 83 83 |
| 7 | 2 | 57 | 54 | 54 | 56 | 56 | 52 | 58 | 61 | 52 | 63 | 64 | 65 | 66 | 67 | 66 |
| | | 59 | 52 | 47 | 52 | 53 | 55 | 61 | 63 | 69 | 70 | 57 | 58 | 65 | 55 | 65 65 |
| 8 | 1 | 73 | 78 | 79 | 83 | 82 | 79 | 86 | 79 | 80 | 80 | 74 | 73 | 69 | | |
| 8 | 2 | 62 | 58 | 62 | 61 | 62 | 52 | 64 | 65 | 60 | 65 | 45 | 45 | 55 | | |

[1]Data for 7/11-8/13 and the maximum for 7/10 were obtained from the Peach Ridge recording station (near Sparta,MI).

[2]The first two numbers in each row are the month (eg. 3=March) and the maximum (=1) or minimum (=2).

TABLE 36. (cont.)

B. Temperature Data for Klein's Orchard 1980[3]

Temperature Record (°F.)

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 1 | 36 | 37 | 37 | 37 | 38 | 38 | 38 | 39 | 39 | 39 | 40 | 40 | 41 | 41 | 42 |
| | | 42 | 43 | 43 | 43 | 44 | 44 | 45 | 46 | 46 | 47 | 47 | 48 | 48 | 49 | 49 | 44 |
| 3 | 2 | 19 | 19 | 20 | 20 | 20 | 21 | 21 | 21 | 22 | 22 | 22 | 23 | 23 | 23 | 24 |
| | | 24 | 24 | 25 | 25 | 26 | 26 | 26 | 27 | 27 | 27 | 28 | 28 | 29 | 29 | 29 | 30 |
| 4 | 1 | 50 | 62 | 44 | 48 | 58 | 65 | 60 | 58 | 40 | 36 | 41 | 41 | 44 | 34 | 40 |
| | | 46 | 50 | 64 | 65 | 75 | 69 | 79 | 56 | 40 | 50 | 54 | 52 | 52 | 53 | 56 |
| 4 | 2 | 33 | 42 | 38 | 36 | 36 | 38 | 48 | 50 | 36 | 33 | 35 | 34 | 27 | 32 | 30 |
| | | 24 | 23 | 38 | 47 | 40 | 44 | 54 | 40 | 28 | 30 | 36 | 42 | 42 | 43 | 44 |
| 5 | 1 | 63 | 70 | 79 | 80 | 78 | 66 | 50 | 48 | 55 | 64 | 62 | 68 | 57 | 57 | 61 |
| | | 65 | 58 | 64 | 72 | 73 | 80 | 82 | 80 | 79 | 77 | 75 | 76 | 78 | 75 | 76 | 72 |
| 5 | 2 | 47 | 41 | 47 | 47 | 55 | 43 | 36 | 36 | 35 | 42 | 50 | 45 | 49 | 37 | 40 |
| | | 39 | 53 | 50 | 50 | 49 | 43 | 45 | 50 | 62 | 58 | 44 | 46 | 52 | 60 | 61 | 59 |
| 6 | 1 | 62 | 72 | 72 | 73 | 69 | 74 | 75 | 60 | 63 | 58 | 68 | 74 | 77 | 78 | 62 |
| | | 70 | 70 | 76 | 60 | 73 | 75 | 80 | 85 | 85 | 84 | 84 | 77 | 81 | 73 | 71 |
| 6 | 2 | 49 | 52 | 55 | 47 | 50 | 59 | 59 | 43 | 51 | 37 | 34 | 42 | 57 | 62 | 59 |
| | | 44 | 42 | 57 | 57 | 47 | 52 | 60 | 61 | 64 | 66 | 69 | 61 | 56 | 63 | 55 |
| 7 | 1 | 79 | 80 | 82 | 77 | 80 | 76 | 85 | 84 | 80 | 84 | 88 | 80 | 83 | 89 | 83 |
| | | 82 | 80 | 79 | 85 | 90 | 73 | 78 | 78 | 78 | 81 | 68 | 72 | 80 | 80 | 75 | 82 |
| 7 | 2 | 52 | 58 | 48 | 58 | 64 | 53 | 58 | 70 | 60 | 57 | 63 | 68 | 60 | 64 | 72 |
| | | 66 | 64 | 59 | 70 | 70 | 68 | 64 | 56 | 52 | 64 | 66 | 65 | 66 | 63 | 55 | 66 |
| 8 | 1 | 82 | 77 | 82 | 82 | 77 | 81 | 82 | 80 | 83 | 71 | 72 | 79 | 69 | 81 | 78 |
| | | 72 | 67 | 79 | 84 | 86 | 79 | 81 | 83 | 81 | 74 | 83 | 84 | 82 | 84 | 78 | 70 |
| 8 | 2 | 66 | 62 | 59 | 54 | 66 | 65 | 67 | 67 | 67 | 64 | 60 | 56 | 52 | 67 | 57 |
| | | 51 | 63 | 64 | 56 | 68 | 72 | 62 | 54 | 54 | 63 | 65 | 64 | 67 | 65 | 66 | 66 |
| 9 | 1 | 74 | 75 | 79 | 83 | 78 | 79 | 78 | 88 | | | | | | | | |
| 9 | 2 | 67 | 64 | 52 | 61 | 55 | 59 | 56 | 58 | | | | | | | | |

[3]Data for March are Normals from the Peach Ridge recording station (near Sparta, MI). Data from 8/09 to 8/13 and 8/14 minimum are also from this station.

TABLE 36. (cont.)

C. Temperature Data for Graham Station 1980[4]

Temperature Record (°F.)

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 1 | 36 | 37 | 37 | 37 | 38 | 38 | 38 | 39 | 39 | 39 | 40 | 40 | 41 | 41 | 42 |
| | | 42 | 43 | 43 | 43 | 44 | 44 | 45 | 46 | 46 | 47 | 47 | 48 | 48 | 49 | 49 | 40 |
| 3 | 2 | 19 | 19 | 20 | 20 | 20 | 21 | 21 | 21 | 22 | 22 | 22 | 23 | 23 | 23 | 24 |
| | | 24 | 24 | 25 | 25 | 26 | 26 | 26 | 27 | 27 | 27 | 28 | 28 | 29 | 29 | 29 | 30 |
| 4 | 1 | 43 | 56 | 41 | 44 | 52 | 62 | 60 | 60 | 39 | 35 | 41 | 41 | 44 | 36 | 39 |
| | | 43 | 51 | 63 | 76 | 79 | 71 | 83 | 58 | 38 | 49 | 53 | 56 | 56 | 54 | 57 |
| 4 | 2 | 26 | 38 | 35 | 32 | 30 | 38 | 47 | 52 | 36 | 32 | 34 | 33 | 26 | 31 | 30 |
| | | 21 | 20 | 34 | 38 | 38 | 43 | 56 | 41 | 28 | 30 | 31 | 42 | 40 | 44 | 45 |
| 5 | 1 | 63 | 71 | 89 | 84 | 89 | 67 | 51 | 51 | 51 | 55 | 67 | 69 | 59 | 58 | 63 |
| | | 66 | 58 | 73 | 72 | 75 | 80 | 82 | 80 | 78 | 75 | 77 | 76 | 82 | 78 | 88 | 72 |
| 5 | 2 | 43 | 41 | 42 | 43 | 51 | 39 | 36 | 37 | 37 | 32 | 40 | 46 | 50 | 36 | 36 |
| | | 41 | 52 | 50 | 49 | 50 | 42 | 42 | 48 | 62 | 54 | 42 | 44 | 50 | 60 | 58 | 59 |
| 6 | 1 | 68 | 75 | 70 | 71 | 70 | 78 | 75 | 64 | 64 | 58 | 67 | 77 | 80 | 79 | 62 |
| | | 65 | 68 | 73 | 62 | 71 | 76 | 80 | 85 | 85 | 85 | 85 | 78 | 80 | 75 | 71 |
| 6 | 2 | 48 | 52 | 59 | 47 | 50 | 60 | 50 | 42 | 48 | 32 | 31 | 40 | 55 | 62 | 60 |
| | | 41 | 37 | 50 | 56 | 42 | 46 | 43 | 58 | 60 | 63 | 63 | 60 | 57 | 59 | 52 |
| 7 | 1 | 79 | 80 | 82 | 74 | 79 | 75 | 86 | 84 | 80 | 84 | 86 | 78 | 83 | 89 | 85 |
| | | 83 | 80 | 79 | 87 | 92 | 76 | 79 | 79 | 79 | 82 | 69 | 73 | 79 | 80 | 75 | 85 |
| 7 | 2 | 50 | 59 | 45 | 54 | 64 | 51 | 56 | 70 | 59 | 55 | 61 | 65 | 59 | 63 | 72 |
| | | 67 | 62 | 57 | 66 | 72 | 68 | 65 | 55 | 52 | 56 | 66 | 64 | 65 | 58 | 52 | 65 |
| 8 | 1 | 84 | 78 | 80 | 85 | 78 | 83 | 83 | 82 | 80 | 72 | 71 | 75 | 68 | 82 | 75 |
| | | 70 | 65 | 77 | 84 | 87 | 80 | 79 | 81 | 80 | 76 | 84 | 85 | 87 | 87 | 80 | 71 |
| 8 | 2 | 66 | 62 | 60 | 54 | 67 | 62 | 67 | 67 | 63 | 66 | 64 | 58 | 50 | 63 | 54 |
| | | 48 | 59 | 62 | 53 | 66 | 71 | 59 | 51 | 52 | 60 | 61 | 63 | 68 | 67 | 66 | 64 |
| 9 | 1 | 76 | 75 | 80 | 84 | 79 | 78 | 78 | 85 | | | | | | | | |
| 9 | 2 | 66 | 65 | 52 | 62 | 52 | 56 | 55 | 56 | | | | | | | | |

[4]Data for March are Graham Station Normals.

TABLE 36. (cont.)

D. Temperature Data for Graham Station Sleeve Cages 1980[5]

Temperature Record (°F.)

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 88 | |
| | | 86 | 83 | 80 | 89 | 93 | 75 | 82 | 86 | 88 | 87 | 71 | 73 | 81 | 83 | 77 | 87 |
| 7 | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 71 | |
| | | 66 | 62 | 57 | 66 | 72 | 67 | 65 | 55 | 52 | 58 | 66 | 65 | 65 | 58 | 53 | 65 |
| 8 | 1 | 87 | 77 | 84 | 89 | 79 | 85 | 84 | 85 | 86 | 74 | 74 | 80 | 70 | 82 | 79 | |
| | | 74 | 66 | 82 | 86 | 87 | 82 | 82 | 83 | 85 | 77 | 87 | 88 | 90 | 90 | 84 | 73 |
| 8 | 2 | 65 | 63 | 60 | 53 | 65 | 61 | 66 | 67 | 64 | 67 | 64 | 58 | 52 | 64 | 56 | |
| | | 49 | 60 | 62 | 54 | 66 | 71 | 59 | 51 | 52 | 61 | 62 | 63 | 67 | 68 | 68 | 66 |
| 9 | 1 | 78 | 77 | 82 | | | | | | | | | | | | | |
| 9 | 2 | 68 | 66 | 52 | | | | | | | | | | | | | |

[5]Readings for July start on 7/15.

D. SPRAY RECORDS FOR GRAHAM STATION 1980

Sprays were applied using a Bean 447 air-blast sprayer. Amounts are lbs./100 gallons (dilute) with approximately 350 gallons applied per acre. A - D are four fungicide treatments for Block 12 (see orchard map in Section II-B-1-b.) with applications applied on both sides of a treatment row and outside of both guard rows (see diagram below).

Table 37 lists spray applications and dates. CGA 64251 is an experimental fungicide similar to BAYCOR. The C treatment on August 4 was accidently made at a double rate of 1 lb./100 gal. guthion (azinphosmethyl).

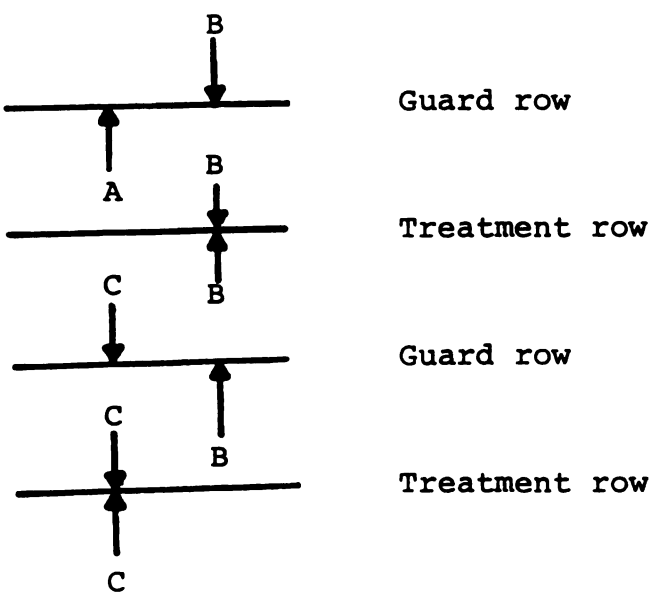


TABLE 37. Spray Records for Graham Station 1980

| Date | Block(s) | Treatment Row(s)[1] | Compound | Rate (/100 gal. dilute) |
|---|---|---|---|---|
| 4/22 | All | All | Cyprex | ½# |
| | All | All | Oil | 2 gal. |
| 4/29 | 10-12 | A | Dikar | 2# |
| | 10-12 | B | CGA64251 | 2.5 oz. |
| | 10-12 | C | Captan | 2# |
| | 10-12 | D | Baycor | 6 oz. |
| | Rest | All | Cyprex | ½# |
| 5/6 | All | All | Thiodan 50WP | 1# |
| | All | All | Fungicides | as 4/29 |
| 5/14 | 10-12 | A-C | Fungicides | as 4/29 |
| | 10-12 | D | Baycor | 4 oz. |
| | Rest | All | Fungicides | as 4/29 |
| 6/4 | All | All | Fungicides | as 5/14 |
| 6/11 | All | All | Guthion 50WP | ½# |
| | 10-12 | A | Dikar | 1½# |
| | 10-12 | B | CGA64251 | 2.5 oz. |
| | 10-12 | C | Captan | 1½# |
| | 10-12 | D | Baycor | 2.5 oz. |
| | Rest | All | Cyprex | 3/8# |
| 6/25 | All | All | Guthion 50WP | ½# |
| | 10-12 | A-C | Fungicides | as 6/11 |
| | 10-12 | D | Baycor | 4 oz. |
| | Rest | All | Cyprex | 3/8# |
| 7/9 | All | All | Guthion 50WP | as 6/25 |
| | All | All | Fungicides | as 6/25 |
| 7/21 | All | All | Guthion 50WP | as 6/25 |
| | All | All | Fungicides | as 6/25 |
| 8/4 | 10-12 | A,B,D | Guthion 50WP | ½# |
| | 10-12 | C | Guthion 50WP | 1# |
| | All | All | Fungicides | as 6/25 |
| 8/7 | 10-12 | All | $CaCl_2$ | - |
| 8/18 | All | All | Guthion 50WP | ½# |
| | All | All | Fungicides | as6/25 |

[1]See Figure 1 for a map of Block 12 showing treatment rows A-D.

# LIST OF REFERENCES

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